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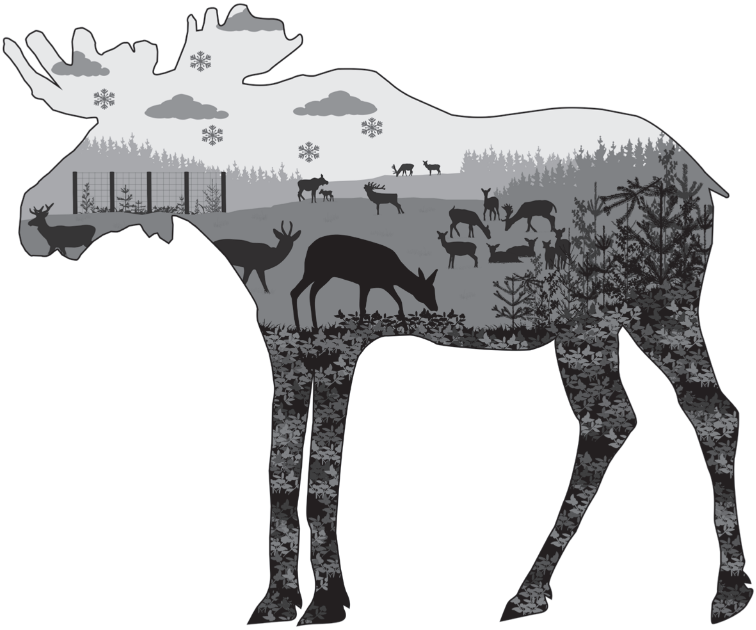
SABINE E. PFEFFER



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Abstract

During the past decades, the population density and distribution of deer (*Cervidae*) has increased across Europe. Particularly in Sweden, this led to an increased co-occurrence of several deer species in landscapes highly dominated by humans. In this novel setting, a deep understanding on the impacts of multi-species deer communities on boreal forests is needed across a variety of spatial and temporal scales. In this comprehensive thesis, I used national to local scale, observational and experimental data to investigate the drivers and effects of deer damage on economically important tree species in young forests by collating and linking diverse public and ecological datasets on multiple deer species. At the current wildlife management scale, which is centred on moose (*Alces alces*), I found that the whole deer community should be considered for regulating deer damage on Scots pine (*Pinus sylvestris*), especially in areas with high densities of the smaller deer species. Regulating only moose densities does not appear to control deer damage effectively. Forage availability, on the other hand, seems to affect damage levels on Scots pine across space and time and predicted deer damage equally or better than deer densities. This suggests a co-management between deer and forests. I also found that the spatial variation, influenced likely via landscape characteristics such as forage availability, seems to introduce a higher variation in damage levels than the temporal variation, influenced via e.g. climatic factors such as snow. At the plant community and individual plant scale, the whole plant-community should be considered to regulate deer damage. Associational effects and competition from neighbouring plant species might increase damage levels and limit conifer growth. Therefore, a full exclusion of deer might not promote conifer growth during the initial years of conifer regeneration. In conclusion, this thesis shows that the relationship between deer densities, forage availability, and deer damage in young forests requires a management approach beyond moose. Furthermore, it is highly scale-dependent and management actions should not be generalized across spatial and temporal scales.

Keywords: *Cervidae*, deer damage, even-aged forest management, mammalian herbivory, multi-species management, *Pinus sylvestris*, species interactions.

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Betydelsen av hjortdjurssamhällen och fodertillgång för viltskador på skog

Sammanfattning

Under de senaste decennierna har hjortdjurens (*Cervidae*) antal och utbredning ökat i hela Europa. Särskilt i Sverige samexisterar nu fler hjortarter i produktionslandskap än tidigare. Det saknas dock idag kunskap om vilka effekter de nya hjortdjurssamhällena har på boreala skogar och på risken för viltskador. I min avhandling använde jag data från inventeringar och experiment för att undersöka vilka faktorer som påverkar risken för viltskador på ekonomiskt värdefulla trädarter i ungskog över olika geografiska och tidsmässiga skalor från ett flerartsperspektiv. Jag sammanställde och analyserade offentliga data från olika källor och ekologiska databaser. När jag analyserade data per älgförvaltningsområde fann jag att det är viktigt att ta hänsyn till hela hjortdjurssamhället för att reglera viltskador på tall (*Pinus sylvestris*). Detta gällde särskilt i områden där tätheten av de mindre hjortarterna var hög. Generellt sett verkar en minskning av endast antalet älgar (*Alces alces*) inte reglera skadorna på ett effektivt sätt. Tillgång till föda hade lika stor eller större betydelse än antalet hjortdjur för regleringen av viltskador på tall, såväl geografiskt som tidsmässigt. Detta understryker vikten av en gemensam förvaltning av hjortdjur och skogar. Jag fann även att den geografiska variationen i skadenivåer, sannolikt orsakad av landskapsegenskaper som t.ex. fodertillgång, var större än den tidsmässiga variationen i skador, som sannolikt orsakas av variationer i väderlek mellan år som t.ex. snö. Vidare bör hela växtsamhället tas i åtanke för att reglera viltskador på en lokal nivå. Experimentella undersökningar visade att konkurrerande lövträd kan begränsa barrträdens tillväxt. En fullständig uteslutning av hjortdjur främjar förmodligen inte tillväxten av barrträd under de första åren efter plantering. Sammanfattningsvis visar min avhandling att sambanden mellan hjortdjur, föda och viltskador i ungskog kräver en förvaltningsstrategi som inte bara fokuserar på antalet älgar. Vidare är mekanismerna beroende av vilken skala man använder; förvaltningsåtgärder bör inte generaliseras över geografiska och tidsmässiga skalor.

Nyckelord: artinteraktioner, skogsskador, flerartsförvaltning, hjortvilt, trakthyggesbruk, tall, växtätare, älgbetesinventering.

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Auswirkungen von Gemeinschaften mit mehreren Hirscharten auf boreale Waldbestände

Zusammenfassung

In den letzten Jahrzehnten hat die Populationsdichte und Verbreitung von Hirschen (*Cervidae*) in ganz Europa zugenommen. Insbesondere in Schweden führte dies zu einem vermehrten, gleichzeitigen Vorkommen mehrerer Hirscharten in stark vom Menschen dominierten Landschaften. In dieser neuen ökologischen Situation ist ein systematisches Verständnis der Auswirkungen von Gemeinschaften mit mehreren Hirscharten auf boreale Waldbestände über verschiedene räumliche und zeitliche Ebenen erforderlich. Um das Vorkommen von Verbissschäden und deren Effekte auf wirtschaftlich wichtige Baumarten in jungen schwedischen Waldbeständen zu untersuchen, habe ich Daten von nationaler bis lokaler Ebene analysiert. Bezüglich der zentralen Verwaltungsebene von Elchen (*Alces alces*), zeigen meine Resultate, dass die gesamte Hirschgemeinschaft für die Regulierung der Verbissschäden an Waldkiefern (*Pinus sylvestris*) in Betracht gezogen werden sollte. Dies gilt insbesondere in Gebieten, in denen die Dichte der kleineren Hirscharten hoch ist. Eine alleinige Regulierung der Elchdichte scheint das Schadensniveau nicht zu kontrollieren. Andererseits scheint die Nahrungsverfügbarkeit die Verbissschäden räumlich und zeitlich zu beeinflussen und ist von gleicher oder höherer Bedeutung als die Hirschdichte. Dies legt nahe, dass Hirsche und Wälder gemeinsam verwaltet werden sollten. Des Weiteren scheint die räumliche Variation – beeinflusst durch z.B. Landschaftsmerkmale, die den Nahrungszugang charakterisieren – eine höhere Variation der Schadensniveaus zu erklären als die zeitliche Variation – beeinflusst durch z.B. Klima wie Schnee. Auf der Ebene der einzelnen Pflanzen sollte die gesamte Pflanzengemeinschaft berücksichtigt werden, um Verbissschäden zu regulieren. Die Konkurrenz benachbarter Pflanzen kann das Schadensniveau erhöhen und das Nadelbaumwachstum begrenzen. Daher begünstigt ein völliger Ausschluss von Hirschen das Nadelbaumwachstum in den ersten Jahren der Regeneration nicht. Zusammenfassend zeigt diese Arbeit, dass die Beziehung zwischen Hirschen, Nahrung und Verbissschäden in jungen Waldbeständen über die alleinige Regulierung der Elchdichte hinausgeht. Darüber hinaus sollten Verwaltungsmaßnahmen an verschiedene räumliche und zeitliche Ebenen angepasst werden.

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Dedication

To my parents – Marianne & Thomas

I took a walk in the woods and came out taller than the trees.
Henry David Thoreau (1817-1862)

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. Pfeffer, S.E.*, Singh, N.J., Cromsigt, J.P.G.M., Kalén, C., Widemo, F. (2021). Predictors of browsing damage on commercial forests – A study linking nationwide management data. *Journal of Forest Ecology and Management*, Volume 479, 118597.

II. Pfeffer, S.E.*, Cromsigt, J.P.G.M., Neumann, W., Widemo, F., Singh, N.J. Tree density and associational effects rather than deer density determine forest damage by deer in a multi-species landscape. (manuscript)

III. Pfeffer. S.E.*, Singh, N.J., Cromsigt, J.P.G.M., Widemo, F. Summer and winter browsing affect conifer growth differently: an experimental study in a multi-species ungulate community. (submitted manuscript)

IV. Pfeffer, S.E.*, Kalén, C., Cromsigt, J.P.G.M., Widemo, F., Neumann, W., Singh, N.J. Evaluating the spatial vs. temporal variation in monitoring deer damage in forests: the case of the Swedish deer damage inventory. (manuscript)

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* Corresponding author

The contribution of Sabine E. Pfeffer to the papers included in this thesis was as follows:

I. Designed the study together with FW, NS, and JC. Extracted and arranged the data with contributions from CK. Carried-out all analyses and visualization. Wrote the manuscript with contributions by the co-authors.

II. Conducted parts of the field work. Arranged the data set. Carried-out main analyses and visualization. Had main responsibility for writing the manuscript.

III. Formulated part of the idea. Was fully responsible for planning and conducting field work during the years 2017-2019. Carried out all analyses and visualization. Had main responsibility for writing the manuscript.

IV. Designed the study together with NS, JC, FW, and CK. Arranged data with contributions from CK. Carried-out all analyses and visualization. Wrote the manuscript with contributions by the co-authors.

Abbreviations

DDI	Deer damage inventory (*sv: Älgbetesinventering*, *Äbin*)
GLMM	Generalized linear mixed model
MMA	Moose management area (*sv: Älgförvaltningsområde*, *Äfo*)
PCT	Pre-commercial thinning
SCB	Statistics Sweden (*sv: Statistiska centralbyrån*)
SFA	Swedish Forest Agency (*sv: Skogsstyrelsen*)
SFIF	Swedish Forest Industries Federation
SMHI	Swedish Meteorological and Hydrological Institute

1. Introduction

1.1 Boreal forests and their management

Since several millennia, human impacts on nature are reshaping landscape structures, where anthropogenic landscape modifications are influencing the distribution of plant and animal communities considerably (Boivin *et al.*, 2016). Today, one dominant example for such large-scale landscape modifications in the northern hemisphere is represented by the effects of forestry on boreal forests. Boreal forests are intensively managed, where clear-cutting and reforestation through mainly planted production trees form a common management practice (Kuuluvainen *et al.*, 2012; Gauthier *et al.*, 2015). These management practices lead to patches of stands with even tree age structures and are known as *even-aged forest management*. During the first regeneration phase after reforestation, these stands are also referred to as *young forest stands*. In Sweden, even-aged forest management intensified since the mid-20th century leading to an increasing availability of young forest stands across the landscape (Esseen *et al.*, 1997; Kuuluvainen *et al.*, 2012; Edenius *et al.*, 2015).

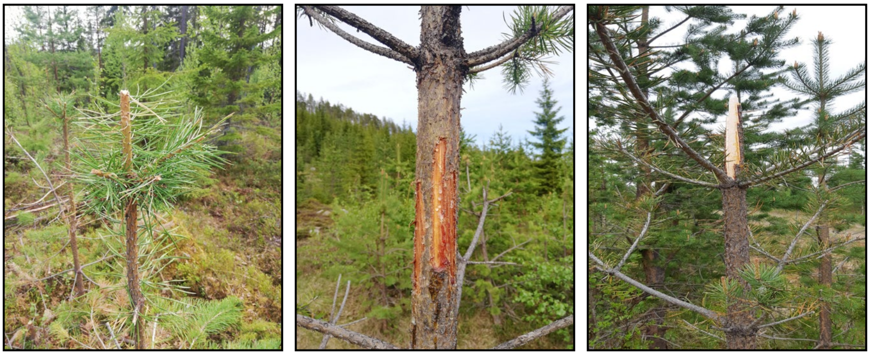
The intensification of forestry together with an increased availability of young forest stands after clear-cutting is affecting a variety of species across all scales (Esseen *et al.*, 1997). For example, negative consequences are detected in animal species, which are dependent on dead wood and older trees with large diameters (e.g., forest birds; Roberge *et al.*, 2008; Virkkala, 2016), whereas positive consequences are reported in species, which are favouring clear-cuts as habitat (e.g., field voles, *Microtus agrestis*; Essen *et al.*, 1997; Magnusson *et al.*, 2015). Besides the consequences for many other species groups, young forest stands also influence the population growth and distribution of deer species (*Cervidae*) by increasing the availability and distribution of forage (Kuijper *et al.*, 2009; Edenius *et al.*, 2015).

1.2 Impacts of increasing deer populations

In many parts of Europe, including boreal forests, the number of deer species and their population sizes increased during the past decades partly as a consequence of anthropogenic impacts via active management actions (Apollonio *et al.*, 2010; Deinet *et al.*, 2013). Such management actions include the above described intensification of forest management (i.e., increasing forage availability), but also changes in deer management such as species introductions and translocations, regulated hunting, and supplementary feeding (Lavsund *et al.*, 2003; Liberg *et al.*, 2010; Linnell & Zachos, 2010).

Increasing deer population sizes influence their environment in a human-dominated and -modified landscape (Liberg *et al.*, 2010; Reimoser & Putman, 2011; Linnell *et al.*, 2020) by altering ecosystem processes and plant community dynamics (Côté *et al.*, 2004; Speed *et al.*, 2013). Thus, human-deer interactions are increasing, especially in landscapes with high economic value (Danell *et al.*, 2003; Reimoser & Putman, 2011). For example, forests are highly managed for their timber resources, but at the same time forests are a key habitat for several deer species, where especially young forest stands are an attractive foraging habitat for deer (Reimoser & Gossow, 1996; Speed *et al.*, 2013). With increasing deer densities, damage on important production tree species, which is caused by deer (i.e. *deer damage*), is increasing and identified as a common problem in young forest stands. In forestry, deer damage on trees in young forest stands is commonly classified as three types of damage: browsing on the apical leader shoot, bark damage on the main stem, and stem breakage (see Box 1). These types of deer damage are purely based on the interest and consequences for forest production since they lead to future economic losses for the forestry sector due to reduced timber quality, stem deformations, and tree death (Gill, 1992; Ramos *et al.*, 2006).

Box 1: Examples of the three types of deer damage



From left to right: Browsing on the apical leader shoot (i.e., top shoot browsing), bark damage on the main stem (i.e., bark stripping or fraying), and stem breakage. Top shoot browsing is often the most common form of deer damage. *Pictures: S. Pfeffer*

With increasing deer densities, also potential intra- and interspecific interactions become more common, leading to competition over space use, cover, and forage resources (Putman, 1996; Bartos *et al.*, 2002; Focardi *et al.*, 2006). For example, the co-occurrence of the main deer species in Sweden – moose (*Alces alces*), roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*), and fallow deer (*Dama dama*) – seems to influence their niche partitioning and may lead to competition over shared forage resources (e.g., ericaceous shrubs, *Vaccinium spp.*). In landscapes where moose co-occur with high densities of the smaller deer species (i.e., roe, red, and fallow deer), moose has a relatively higher share of conifer tree species (e.g., Scots pine, *Pinus sylvestris*) and lower share of *Vaccinium spp.* in their diet (Spitzer *et al.*, 2021). Hence, the presence of several deer species in a forested landscape might impact damage levels on trees differently than the presence of a single or two species. Furthermore, the diet of species generally differs between seasons. Especially during winter, the intake of woody browse is increasing for all deer species (Mysterud, 2000; Spitzer *et al.*, 2020). While a dietary overlap facilitates competition, the impact of browsing on forestry may further differ between seasons.

Studies investigating the relationship between multi-species deer communities and damage levels in a European context are rare since most studies focus on one or two deer species. In this thesis, I examine the ecosystem impacts of multiple co-occurring deer species in Sweden by studying the effects of the combined presence of the main deer species on damage levels in young forest. In order to sustainably manage deer populations and reduce forest damages, a deep understanding of deer foraging behaviour is important across spatial and temporal scales.

1.3 Foraging behaviour of deer

A number of factors determine the foraging behaviour of large herbivores, such as deer, across space and time, which will eventually determine the extent of damage. Among many other factors, such as climate (e.g., temperature and snow) and risk (e.g., predation; Senft *et al.*, 1987), the spatial and temporal distribution of forage availability and quality is of primary importance (Stephens & Krebs, 1986) – across different hierarchical orders: from the individual plant scale to the regional scale (Johnson, 1980; Senft *et al.*, 1987). At larger spacial scales, landscape characteristics usually influence the establishment of home ranges (Johnson, 1980; Boyce, 2006), in which herbivores may select a mosaic of tree stands of varying age and height classes (Danell *et al.*, 1991). At finer spatial scales, forage resources are targeted (Boyce, 2006), where herbivores may select foraging patches and individual plant species within foraging patches according to their quantity and nutritional quality (Johnson, 1980; Danell *et al.*, 1991). Thus, across spatial and temporal scales, the decision making of large herbivores is constantly influenced by two main selection processes: ‘Where to go?’ vs. ‘What to eat?’.

Among various aspects (e.g., risk; Gallagher *et al.*, 2017), movement may be driven by the maximisation of energy intake, while tracking resources across space and time (e.g. green wave-surfing; Merkle *et al.*, 2016; Aikens *et al.*, 2020). Thus, the choice of a foraging patch is dependent on its availability and distribution in the landscape, which influences the intake rate of herbivores (Duparc *et al.*, 2019). Therefore, landscapes of different compositions are likely to vary in their risk to deer damage (Godvik *et al.*, 2009). Within the foraging patch, the selection of individual stems is influenced by the plant species composition (Milligan & Koricheva, 2013). Furthermore, the availability of forage at preferred foraging heights may be of importance, especially in a multi-species community where deer differ in body sizes (Nichols *et al.*, 2015).

In a multi-species setting, where species vary in body size (Müller *et al.*, 2013) and feeding type (Hofmann, 1989), the selection of resource items and habitat may differ between species due to diverse physiological requirements (Belovsky, 1997). Differences in body size determine not only the intake rate of forage (i.e., quantity), but also if forage quality is sufficient to sustain the metabolic rates and energy demands of herbivores. Thus, a trade-off between the nutritional quality and tolerance towards secondary metabolites of the forage plant species may determine herbivore food choice (Pyke *et al.*, 1977). However, the selection of forage quality happens in general at the expense of forage quantity (Senft *et al.*, 1987). Furthermore, the relationship between forage quality and quantity is scale dependent, where herbivores select for forage quantity at large spatial scales, whereas they select for forage quality at finer spatial scales (van Beest *et al.*, 2010).

Large-bodied herbivores are characterised by requiring a greater amount of forage, while being able to tolerate lower-quality forage better than small-bodied herbivores (Müller *et al.*, 2013). But diet balancing becomes important even for large herbivores (e.g. moose) since nutrient requirements cannot be met by a single plant species (Felton *et al.*, 2017; Felton *et al.*, 2020). Thus, forage species-rich areas may receive in general higher browsing pressure compared to forage species-poor areas due to an overall higher quality leading to a longer foraging time in the patch to optimize foraging (Milligan & Koricheva, 2013).

Foraging by herbivores influences the composition and structure of plants (Gill, 1992; Danell *et al.*, 2003; Rooney & Waller, 2003). Direct effects of foraging include reduced growth of the targeted individuals, whereas indirect effects may include a reduced photosynthetic activity through leave stripping or affect shoot sizes and bud-burst in the following vegetation season (Danell *et al.*, 1994; den Herder *et al.*, 2009). At the same time, herbivore foraging also influences the competition between different plant species. By browsing for example on deciduous species during summer, the growth of shade-intolerant conifer species may be positively affected (Kuijper *et al.*, 2010; Stokely & Betts, 2019). Browsing and grazing may have further indirect impacts on additional plant characteristics such as the production of secondary metabolites, which in return may influence the food choice of herbivores (Bryant *et al.*, 1991). Differences in the plant preferences of deer due to varying nutritional requirements can lead to associational effects, where the selection of the focal plant is dependent on the abundance and palatability of the neighbouring plant species (Champagne *et al.*, 2016). There are four different types of associational effects: *associational susceptibility* (increased herbivory on the focal plant due to preferred neighbour), *neighbour contrast defence* (decreased herbivory on the focal plant due to preferred neighbour), *neighbour contrast susceptibility* (increased herbivory on the focal plant due to avoided neighbour), and *associational defence* (decreased herbivory on the focal plant due to avoided neighbour). Thus, the composition and density of preferred and avoided plant species may determine the levels of deer damage in young forest stands and associational effects may be a useful tool to manage herbivore browsing (Champagne *et al.*, 2016).

1.4 Management across scales

Different management actions are undertaken to mitigate deer damage in forests; examples include supplementary feeding, fencing, and population regulations via hunting, with a large focus on the latter (Putman & Staines, 2004; Reimoser & Putman, 2011). In order to manage the interaction between the intensity of deer foraging and its consequences on forests (specifically young forest stands) appropriately, management actions need to target the correct scale.

Wildlife management is characterised by spanning across large spatial scales, while often being built on long-term knowledge (Weisberg & Bugmann, 2003). A mismatch between the scale of observations (e.g., research) and management may lead to ineffective wildlife management. In addition, long-term studies that may provide a picture at the entire landscape scale are rare, as (scientific) field studies often are conducted at very fine scales (Hobbs, 2003). Moreover, the scale of wildlife management might differ from the scale of forest management, due to the use of different boundaries dependent on species distributions, administrative units, or landownership. Thus, both management regimes implement different monitoring methods at different spatial and temporal scales.

In Sweden, moose is the deer species largest in body size and is present across the whole country (except on the island *Gotland*). The economically important tree species Scots pine is an important winter forage for moose (Cederlund *et al.*, 1980; Shipley *et al.*, 1998) and of the different deer species, moose is considered to be the main damaging agent on Scots pine in young forest stands (Bergqvist *et al.*, 2001; Nichols & Spong, 2014). Thus, the Swedish system for managing deer is centred on moose. Moose management areas (MMAs) form the focal unit of the national management system since 2012, when a new adaptive co-management system was established for moose. MMAs are supposed to cover at least one migratory moose population (Naturvårdsverket, 2011). Due to different migratory patterns of moose across the country (Singh *et al.*, 2012), MMA sizes increase from the south to the north (mean MMA size in 2020: 273,640 ± SD 414,116 ha). An extensive formal management system such as for moose does not exist for the smaller deer species (i.e., roe, red, and fallow deer).

The management of forests does not directly align with the management scale of moose. In general, forests are managed at the individual forest stand scale following the interests of individual landowners and forest companies. Since deer move across the landscape, successful co-management of deer and forests requires finding common management goals and appropriate actions to reach these goals at a common scale. Therefore, it is important that the spatial scale of monitoring and of management match.

Monitoring the impacts of deer on young forest stands is one objective of the Swedish Forest Agency (SFA, in Swedish: *Skogsstyrelsen*). In order to facilitate the use of the monitoring results within the moose management system, results are extrapolated from the forest stand to the MMA scale. In return, this requires an understanding of the ecological interactions between deer and forests at the different management scales, as well as appropriate monitoring of the relevant factors, which may differ depending on the ungulate community, forest composition, and climate.

1.5 Objectives

Due to increasing deer abundances and the more common co-occurrence of multiple deer species in Sweden, there is a need to deeper understand the impacts of deer on forestry. Moreover, it is necessary to identify how the effects of a shifting deer community interact with environmental variables and other types of human land-use to enhance the sustainable management of wildlife and boreal forests. Therefore, the overall objective of my thesis is to expand on the existing literature by investigating the drivers and effects of deer damage on economically important tree species in a multi-species deer community across scales that are driving the ecological mechanisms of foraging behaviour and that are relevant for management actions. My analyses span from the individual plant, to the community, to the landscape and the regional scale (adapted from Senft *et al.* (1987); see also Figure 4 for a graphical illustration).

Throughout this thesis, *deer damage* is defined as three types of damage affecting the wood quality of the future production stem: browsing on the apical leader shoot, bark damage on the main stem, and steam breakage (see also Box 1). I focus my research on the four most common deer species in Sweden (i.e., moose, roe deer, red deer, and fallow deer) and one main dominant conifer species (i.e., Scots pine, whereas *Paper III* also studied the effects of deer browsing on Norway spruce) in Swedish forests.

Specifically, the aims of this thesis are to:

1. Identify the predictors of deer damage at two different management scales: the management scale of moose (MMAs, *Paper I*) and the management scale of forests (young forest stands, *Paper II*), which represent the regional and plant community scale, respectively. To do this, I linked data on deer damage on Scots pine to deer densities, tree densities, winter severity, and landscape characteristics (see Figure 1).

2. Investigate in an experimental study the growth responses of conifer trees to seasonal browsing in a multi-species deer community. Specifically, I tested the individual growth and demographic response of conifers at the individual plant scale to *summer* vs. *winter browsing* in comparison to *no* and *year-round browsing* in young forest stands during the first years after clear-cutting (*Paper III*).

3. Identify the spatial vs. the temporal variation in damage levels monitored by the Swedish deer damage inventory at the landscape scale to provide insight into the mechanisms driving varying damage levels in different years (*Paper IV*).

Overall, this thesis aims to provide valuable knowledge for the co-management of deer and forests. To further provide insights into data collected within the current management system, data in *Paper I* was extracted only from publicly available databases – mainly used as a tool in the Swedish moose management system – to identify the predictors of deer damage on Scots pine at the scale of the Swedish MMAs.

Figure 1 provides a graphical overview on the data collected and the aim per paper across spatial scales. See also Figure 4 for an illustration of the specific spatial scales per paper.

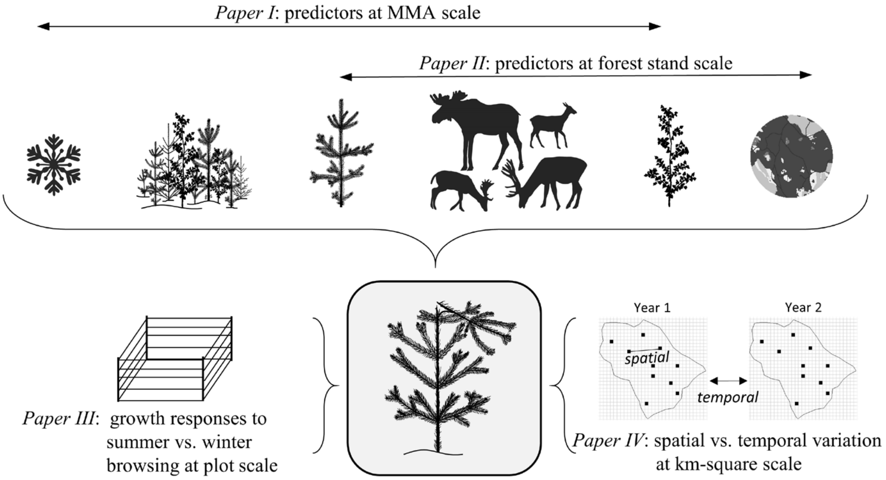


Figure 1: Graphical overview on the aim and data composition per paper to identify the environmental variables affecting deer damage and conifer growth. 'MMA' stands for moose management area.

2. Material and Methods

2.1 Study area and species

Each paper of this thesis investigated the drivers and mechanisms of deer damage on conifers at a different spatial and temporal resolution (see below in section 2.2). However, most data analysed in this thesis were extracted at the national scale spanning across Sweden's large latitudinal gradient (*Paper I*, *II & IV*), whereas *Paper III* experimentally investigated the seasonal patterns of browsing in a particular study area.

2.1.1 National scale (Paper I, II & IV)

Sweden's large latitudinal gradient (55.4° to 69.1° N; see also Figure 3a) is characterized by differences in a number of environmental variables. In the following, I list some of these variables relevant for the context of this thesis and provide a general overview of their importance.

Winter conditions

In northern Sweden, winters are colder spanning across a longer period with more snow compared to southern Sweden (see detailed maps at the Swedish Meteorological and Hydrological Institute, SMHI[1]). Thus, the duration of the growing season is shorter in the north (~170 days) than in the south (~210 days; SMHI, 2020), which may affect the availability and accessibility of forage, animal movement possibilities, and physiology.

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[1] https://www.smhi.se/data/meteorologi/kartor/manadsmedeltemperatur [2020-12-14].

Land-use & forestry

Approx. 3 million ha of Sweden's land area (total terrestrial size of ~40 million ha) are covered by agricultural land. The abundance of agricultural land is increasing from the north towards the south (SCB, 2020). In comparison to agriculture, forestry is of higher national importance. Approx. 60 % of Sweden's terrestrial area is covered by productive forest land (SFA, 2014) and the country is one of the largest exporters of pulp, paper, and timber (export value of SEK 145 billion in 2018; SFIF, 2018). In general, the ownership of forests is dominated by private landowners in southern Sweden, whereas company owned forest land is higher in northern Sweden (SFA, 2014). Scots pine, covering 39 % of the productive forest land, and Norway spruce, covering 42 % of the productive forest land, are the two dominant tree species in Sweden (Esseen et al., 1997; SFA, 2014). In general, standing volumes of Scots pine are higher in northern Sweden, whereas standing volumes of Norway spruce are higher in southern Sweden (SFA, 2014). Across the whole country, there is a large focus on even-aged forest management, where stands are clear-felled and mostly planted with one of the two main conifer species (Kuuluvainen *et al.*, 2012). Sowing and natural regeneration are two other reforestation methods, but less common than planting.

Scots pine is a light-demanding species (Bachofen *et al.*, 2019) making it sensitive to competition (Kelly & Connolly, 2000). Still, Scots pine has a high stress tolerance (e.g. climatic or edaphic stress) and is therefore able to grow under low temperatures, in dry habitats, and when soil conditions are poor (Kelly & Connolly, 2000). During winter, Scots pine is an important forage dominating moose diets (Cederlund *et al.*, 1980; Shipley *et al.*, 1998). Norway spruce on the other hand is a shade-tolerant species, which grows well on soils with moist and fertile conditions (Heiskanen, 2004). It is a browse species that is generally avoided by deer (Shipley *et al.*, 1998; Spitzer, 2019).

Deer community

The studied deer community in this thesis comprises species that differ in body size, feeding type, and occur at variable densities across the latitudinal gradient. In Sweden, the co-occurrence of multiple deer communities established due to the natural distribution of native species (e.g. moose and roe deer), but also due to the introductions of non-native species (e.g. fallow deer) and translocations of native species (e.g. red deer) towards the north (Liberg *et al.*, 2010). Moose is the deer species largest in body size and occurs across the whole country (except on the island *Gotland*, which is excluded in Figure 2). Populations of the smaller deer species (i.e., roe, red, and fallow deer) are spreading across large parts of the country (Figure 2) and their distributions and densities are increasing (Danell & Bergström, 2010; Liberg *et al.*, 2010). Roe deer have a similar distribution range compared to moose, but are in the northern areas mostly restricted to the coast in the east (Figure 2). Densities of roe deer are higher in the south than in the north (Jarnemo *et al.*, 2018; Figure 2). Red deer are established across large parts of the country (Figure 2). However, densities vary largely with lower numbers in the northern part of the country (Jarnemo *et al.*, 2018; Figure 2). Fallow deer occur mainly in the south of Sweden with high densities in certain areas (Figure 2). Some fallow deer populations occur sporadically towards the north due to translocations by humans (Jarnemo *et al.*, 2018).

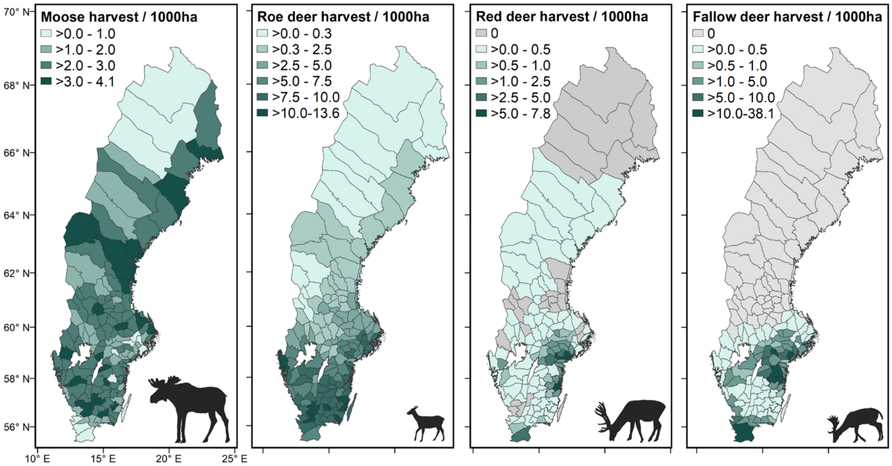

Figure 2: Harvest [$1000\ ha^{-1}$] providing a density index for each deer species per moose management area (MMA) during the hunting season 2015/16. Moose harvest was extracted from *Älgdata*[2], whereas harvest data of the smaller deer species was directly provided by the Swedish Association for Hunting and Wildlife Management (sv: *Jägareförbundet*) per hunting district[3]. See *Paper I* for details on the extraction of harvest data from hunting districts to MMAs.

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[2] https://algdata-apps.lansstyrelsen.se/algdata-apps-stat [2020-12-10]

[3] Data is also available online at *Viltdata*: https://rapport.viltdata.se/statistik/ [2020-12-10]

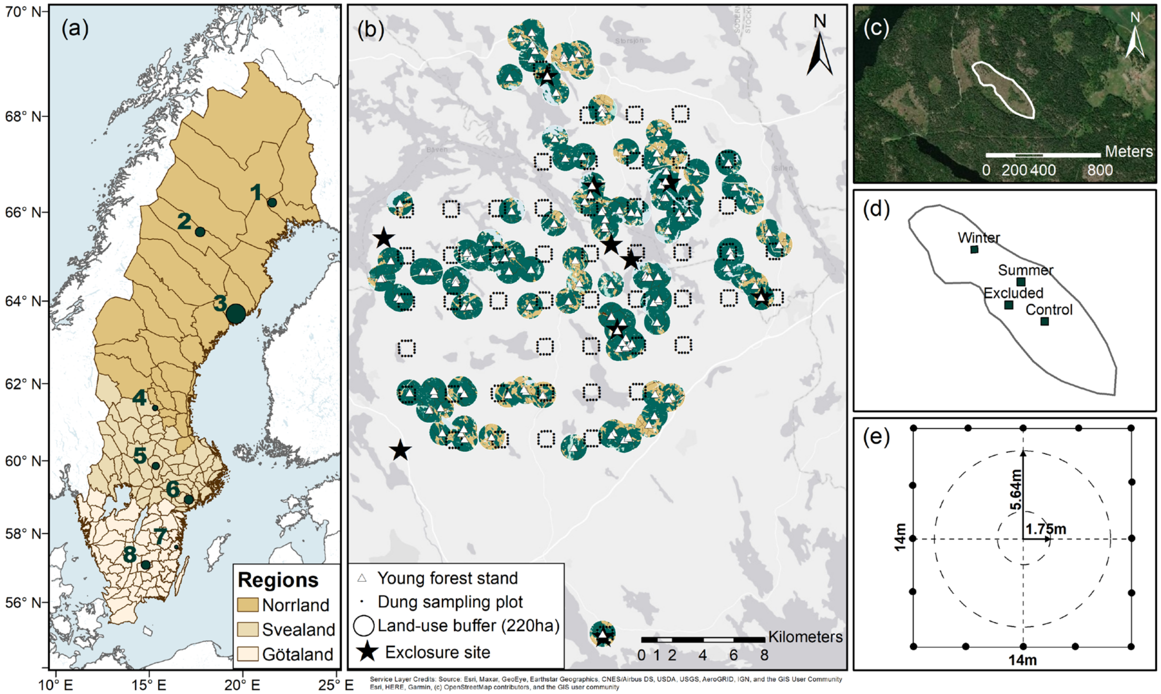
Moose and roe deer are considered as concentrate selectors with diets containing the largest share of woody browse compared to the other two deer species (Hofmann, 1989; Spitzer *et al.*, 2020). The diet of moose contains the largest share of coniferous species while preferring pine over spruce (Shipley *et al.*, 1998; Milligan & Koricheva, 2013; Spitzer *et al.*, 2020). Red deer and fallow deer are intermediate feeders that include significant proportions of grasses and forbs in their diets, especially during the growing season (Spitzer *et al.*, 2020). However, the consumption of woody browse increases for all deer species during winter showing a higher diet similarity than during summer (Spitzer *et al.*, 2020). Furthermore, ericaceous shrubs (*Vaccinium spp.*) are an important forage resource for all deer species (Spitzer *et al.*, 2021).

Regions

Due to the differences in environmental variables along the latitudinal gradient, I separated in *Paper I* and *IV* data at the national scale into three geographical regions, termed *Norrland*, *Svealand*, and *Götaland* (Figure 3a). These three geographical groupings, which broadly follow the latitudinal gradient of climate, land-use, and deer densities across the country, are often used by Swedish management institutions and forestry.

2.1.2 Local scale (Paper III)

Data collection in *Paper III* was limited to study *area 6*, which is located around Öster Malma in Södermanland county (58.74-59.06°N, 16.90-17.33°E; Figure 3b). The area lays within the boreo-nemoral vegetation zone (Ahti *et al.*, 1968). Besides the above mentioned conifer species Scots pine and Norway spruce, common deciduous tree species are birch (*Betula spp.*), willow (*Salix spp.*), rowan (*Sorbus spp.*), aspen (*Populus spp.*), and oak (*Quercus spp.*). Typically, the field layer is comprised of *Vaccinium spp.*, heather (*Calluna vulgaris*), different grasses, and mosses. The study area is dominated by ~22 % pine forest, ~16 % arable land, ~10 % spruce forest, ~10 % mixed coniferous forest, and ~8 % re-growing areas with trees < 5 m (i.e., clear-felled, storm-felled or burnt; Naturvårdsverket, 2019). All four deer species occur sympatrically in this study area – together with another ungulate, the wild boar (*Sus scrofa*).



Service Layer Credits: Source: Esri, Maxar, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community
Esri, HERE, Garmin, (c) OpenStreetMap contributors, and the GIS user community

Figure 3: Study design and data collection across spatial scales. (a) Sweden and its moose management areas (hunting season 2015/16) divided into three geographical regions (*Paper I & IV*). Circles represent the location and size of eight study areas (*Paper II*). Water bodies are illustrated in blue. (b) *Area 6* as an example illustrating the setup of squared transects with 16 dung sampling plots each and sampled young forest stands with Scots pine across years. Water bodies are illustrated in dark grey. Each young forest stand is surrounded by a land-use buffer (mean core home range size of moose; r = 0.85 km). Green colours within buffers represent forest areas, brown colours represent agricultural and open land, and blue colours represent waterbodies and wetland (*Paper II*). The location of exclosure sites is illustrated with stars (*Paper III*). (c) Satellite image of an exclosure site capturing (d) the four exclosure treatment plots. (e) Detailed setup of an exclosure plot divided into four quadrants (*Paper III*).

2.2 Data collection

2.2.1 Deer damage inventory (Paper I, II & IV)

Method of the Swedish Forest Agency (Paper I & IV)

In *Paper I & IV*, the Swedish MMAs (Figure 3a) serve as basis for the collection of data on damaged Scots pine in young forest stands via a deer damage inventory (in Swedish: *Älgbetesinventering*) conducted by the SFA since the year 2000. Literally, the inventory would translate to a *moose browsing inventory*. However, even though the SFA is focusing on the assumption that the damage is mainly caused by moose, partly because monitoring is limited to young forest stands in preferred moose browsing heights, it cannot be visually assessed which deer species caused the damage. Furthermore, the inventory is not directly assessing browsing but three types of deer induced damage relevant to forestry: browsing of the apical leader shoot, stem breakage, and bark damage on the main stem (i.e., deer damage; see Box 1). Thus, side shoot browsing is not monitored. Due to these reasons, I call the method a *deer damage inventory* (DDI) throughout my thesis.

Results of the DDI are used as an important tool within the Swedish moose management system and are thus aggregated from the sampling plot to the MMA scale, at which they are publicly available[4]. During the years 2015 and 2016, Sweden was divided into 148 MMAs (*Paper I*, Figure 3a). During 2020, Sweden was divided into 133 MMAs (*Paper IV*), since several MMAs from the previous years merged as a result of management actions within the adaptive moose management system.

The SFA places a 1 x 1 km grid across each MMA (see Figure 4). Within randomly selected grid cells (km-squares), young forest stands with a mean height of 1-4 m are identified (Figure 4). Max. 5 of these young forest stands are monitored per km-square. Within each young forest stand, circular sampling plots with a radius of 3.5 m are placed 80 m from each other in a grid (Figure 4). Hence, the number of plots is determined by the size of each young forest stand. Data collection is done directly after snow-melt and before bud-burst of deciduous trees.

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[4] https://skobi.skogsstyrelsen.se/AbinRapport/#/valj-rapport [2020-12-22]

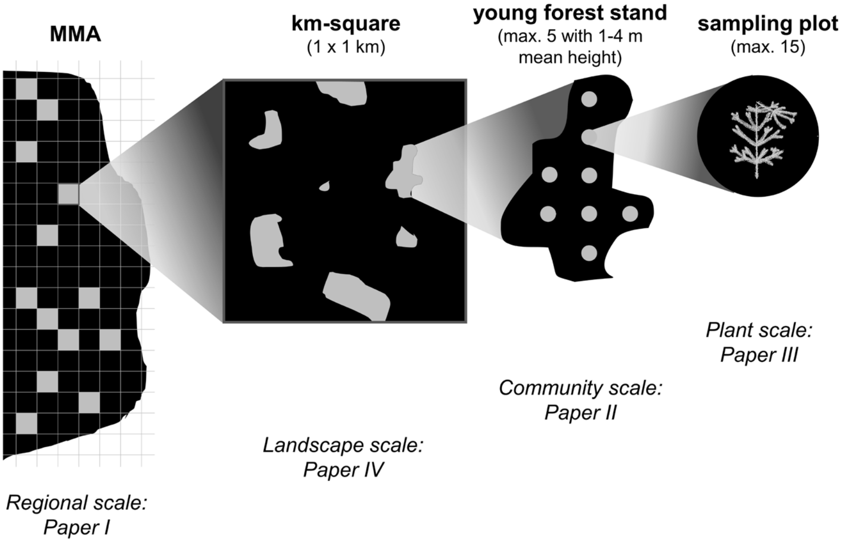

Figure 4: Graphical illustration of the sampling structure of the Swedish deer damage inventory to monitor the number of damaged Scots pine stems. At the same time, this sampling structure outlines the analyses regime across spatial scales per paper. (adapted from *Paper I* and *Paper IV*, based on an illustration of the SFA)

In each sampling plot the number of damaged and undamaged Scots pine stems and the total number of Norway spruce and birch *spp.* stems above a height of 30 cm are counted. Furthermore, all monitored stems need to be taller than half of the average height (i.e., half-average-height) of the two tallest production trees within the plot. By considering only these taller trees, it is assumed that only trees contributing to the future production stand are considered. Damaged Scots pine stems are divided into fresh winter damage (damaged during the latest winter; visible via wood of light colour, often still shimmering resin, see also Box 1) and summer damage (damaged during the growing season preceding the latest winter; visible via wood of darker colour, not yet lignified top shoot). Additionally, stems were specifically classified as production stems (i.e., estimated as retained after future pre-commercial thinning) in 2015 and 2016. These sampling criteria reflect that the DDI is a monitoring method developed for the forestry sector.

In *Paper I*, I analysed the proportion of Scots pine damaged during summer (i.e., summer damage) and winter (i.e., winter damage) at the MMA scale, as especially winter damage levels are a key variable for the decision making within the Swedish moose management system at this scale.

Furthermore, I used the total number of pine and birch *spp.* stems as an index for forage availability. I only considered the years 2015 and 2016 due to a change of the methodology to previous years. Since roughly half of the MMAs per county are monitored per year, the two years provided a dataset for 145 MMAs across the country (see *Paper I*, Fig. 1).

In *Paper IV*, I analysed the number of damaged Scots pine stems during winter at an intermediate scale: the km-square scale (see Figure 4). To evaluate the spatial and temporal variation in the number of Scots pine stems with winter damage, only the km-squares, which have been inventoried at least twice during the time period 2015-2020 (see Appendix, Table A.1 for the different year combinations), were extracted. Furthermore, I used the area of young forest stands fulfilling the DDI's criteria per km-square as an index for forage availability. Both, for *Paper I* and *IV*, I was directly provided with data of the DDI by collaborators of the SFA.

Project method (Paper II)

From 2008 to 2019, the monitoring of winter damage on Scots pine in young forest stands was part of three projects across eight study areas spread across the latitudinal gradient of Sweden (Figure 3a). However, the number of sampling years varied per study area (see Table 1). The project method of monitoring deer damage on Scots pine was very similar to the DDI of the SFA as explained above. Differences were the following: (i) Young forest stands with a mean height of 0.5-3 m were monitored in *area 3*, *6*, and *8*. (ii) Across all areas, the number of damaged and undamaged Scots pine, and the number of downy birch (*Betula pubescens*) and silver birch (*Betula pendula*) above the half-average-height were monitored in 10 sampling plots in each young forest stand regardless of size. (iii) Plots had a spacing of 20 m to each other. Additionally, we recorded, if stands were pre-commercially thinned (PCT) prior to our data collection. I extracted the sum of damaged and the sum of undamaged pine stems during winter per young forest stand. Furthermore, I summed the total number of stems per tree species (i.e., Scots pine, downy birch, and silver birch) to calculate a stem density index (100 m^{-2}) representing forage availability.

Table 1: Location, sampling regime, and deer density indices based on dung pellet group counts per study area. Mean (±SD) density indices of moose and the smaller-bodied deer species (roe, red, and fallow deer combined) are presented across all squared transects and years. (from *Paper II*)

	Study area	**Coordinates**	**Sampling years**	**Moose density [100 m^{-2}]**	**Deer density [100 m^{-2}]**
1	Råneå	66.2°N, 21.8°E	2008, 2009, 2011	0.57±0.57	0±0
2	Sorsele	65.6°N, 17.7°E	2008, 2009, 2011	0.26±0.31	0.00±0.01
3	Nordmaling	63.7°N, 19.6°E	2015-2019	0.22±0.27	0.20±0.75
4	Furudal	61.4°N, 15.3°E	2008, 2009, 2011	0.07±0.13	0±0
5	Malingsbo	59.9°N, 15.4°E	2008, 2009, 2011	0.37±0.58	0.09±0.45
6	Öster Malma	58.9°N, 17.1°E	2012-2018	0.24±0.29	5.10±4.79
7	Misterhult	57.6°N, 16.4°E	2008, 2009, 2011	0.23±0.24	1.98±1.82
8	Växjö	57.1°N, 14.8°E	2012-2016	0.26±0.25	1.78±1.59

2.2.2 Tree responses in seasonal exclosures (Paper III)

To study the growth responses of trees to summer and winter browsing in comparison to no and full browsing, an experiment at 10 sites each containing four browsing treatment plots was established in *area 6* during summer 2015 (Figure 3b). These sites are characterized by being a former clear-cut (Figure 3c). In 2014 and 2015, sites were either naturally regenerated with Scots pine or planted with Norway spruce (see details in *Paper III*). The four plots per site captured the following treatments: *No browsing* (fenced year-around), *Summer browsing* (only fenced during the dormant season, October-March), *Winter browsing* (only fenced during the growing season, April-September), and *Control* (never fenced; Figure 3d). Each plot, including the *Control*, was determined by 16 wooden posts capturing an area of 14 x 14 m (Figure 3e). When fenced, metal frames excluded larger terrestrial animals such as deer, but allowed smaller animals such as rodents (Rodentia) and hares (*Lepus spp.*) to enter all plots. Fences were established in October 2015.

The first complete data collection after installing the fences started in spring 2016 with two measurements per year: in spring (April) and in autumn (September). Two types of data were collected: (i) Up to four conifers per species per quadrant were marked within each plot (Figure 3e) to follow their individual growth. I then extracted the mean relative annual height increment for conifers, which were followed individually during at least four spring measurements (Figure 5a). However, the relative annual height increment of both Scots pine and Norway spruce did not differ between the treatment plots. Therefore, I will not discuss the variable in the remainder of this thesis (for details, see *Paper III*). (ii) The total number of stems per tree species (i.e., Scots pine, Norway spruce, downy birch, silver birch, rowan, aspen, willow, oak) was counted. Trees were divided into different height classes and monitored in the height classes 1-5 cm, 6-20 cm, and 21-30 cm within a circle of 10 m^2 at the centre of each plot. Trees in the height classes 31-50 cm, 51-100 cm, 101-150 cm, 151-200 cm, 201-250 cm, 251-300 cm, 301-350 cm, and 351-400 cm were monitored within a circle of 100 m^2 (Figure 3e). I extracted the number of conifer stems per height class in spring 2016 and after four years in spring 2020 to identify the demographic response per treatment (Figure 5b). Additionally, I extracted the number of deciduous stems and calculated the number of deciduous stems taller than the individual conifers (Figure 5c). If deciduous trees were counted within a circle of 10 m^2 only, I multiplied their number by the factor 10 to match the counts within the 100 m^2 circle. A detailed description of the data collection and extraction of the different variables is presented in *Paper III*.

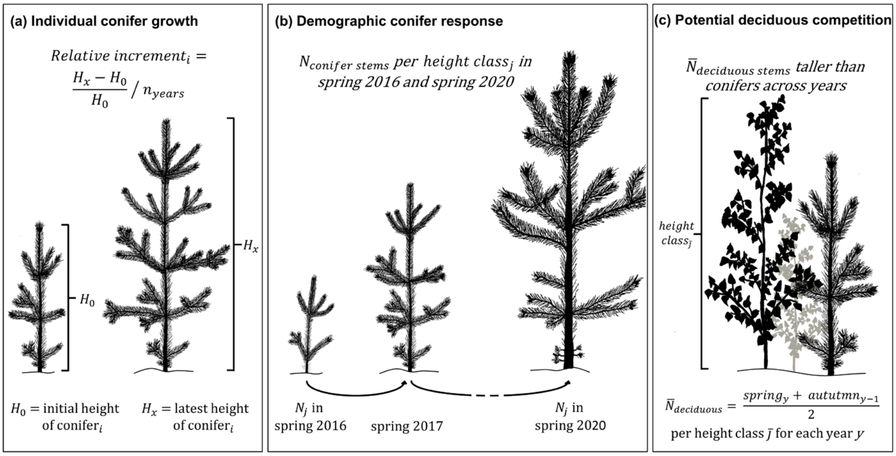

Figure 5: Graphical overview of the three response variables used for representing (a) individual conifer growth (i.e. relative increment), (b) demographic conifer response (i.e. shift to taller height classes), and (c) potential competition effects from deciduous trees (i.e. number of deciduous stems taller than conifers). (from *Paper III*)

2.2.3 Ungulate density indices (Paper I & II)

Harvest data (Paper I)

In *Paper I*, I used the number of animals shot per 1000 ha as density index for each deer species per MMA. Harvest data is the only density measure, which is available for all deer species at the national scale. Moose harvest is mandatorily reported by hunters and gathered in the database *Älgdata*[5]. I extracted the numbers of shot moose per MMA for the hunting seasons 2013/14 – 2015/16.

For the smaller deer species, harvest data is voluntarily collected by hunters and presented per hunting district (in Swedish: *Jaktvårdskrets*). The numbers of shot animals for roe deer, red deer, and fallow deer are publicly available within the database *Viltdata*[6]. In this thesis, harvest data for the hunting seasons 2013/14 – 2015/16 was directly provided by the Swedish Association for Hunting and Wildlife Management, who is responsible for maintaining the online database. I extrapolated harvest data of the smaller deer species from the hunting district to the MMA scale via the terrestrial overlap between the two units. See a detailed description for the extraction process in *Paper I*.

Both for moose and the smaller deer species, I linked harvest data from the hunting seasons 2013/14 and 2014/15 to deer damage caused in the summers of 2014 and 2015 (measured in 2015 and 2016). I linked harvest data from the hunting seasons 2014/15 and 2015/16 to deer damage caused during the same winters (measured in 2015 and 2016).

Moose observations (Paper I)

Since results of the DDI influence moose harvest goals at the MMA scale, we expected a causal link between the DDI and moose harvest. Thus, we included additionally moose observations as independent density index for moose (in Swedish: *Älgobs*). Moose observations were weakly correlated with moose harvest at the national scale ($n = 137$, Pearson's $r > 0.28$, $p \leq 0.001$). Observational data does not exist for the smaller deer species across all MMAs and results of the DDI are not formally used to set harvest quotas of these deer species.

Moose observations are voluntarily reported by hunters during the first seven days of hunting within the first month of the moose hunt (which starts

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[5] https://algdata-apps.lansstyrelsen.se/algdata-apps-stat [2020-12-10]

[6] https://rapport.viltdata.se/statistik/ [2020-12-10]

in September in the north and in October in the south). However, these first seven days do not need to follow directly one another. Observational data is presented as the number of sightings per man hour in the database *Älgdata*[7], from which I extracted values per MMA for the hunting seasons 2013/14 - 2015/16. MMAs with less than 5,000 man-hours are considered to represent unreliable results (Ericsson & Kindberg, 2011), thus I had to exclude 11 of the 148 MMAs (see in *Paper I*, Table A.2), when running models which included moose observations as explanatory variable.

Dung pellet group counts (Paper II)

In *Paper II*, I used the number of dung pellet groups as winter density index for moose and the smaller deer species for all study areas. The winter density index was represented by fresh pellet groups, which were laying on top of leaf litter and showed no signs of decomposition (Hemami & Dolman, 2005). Data collection was in parallel to the DDI in all study areas. Each study area was defined by a grid of squared transects (1x1 km) each containing 16 circular sampling locations. In almost all study areas, dung pellet groups of moose and red deer were counted within 100 m^2 and of roe deer and fallow deer within 10 m^2 per sampling location. Pellet groups needed to have a size of ≥ 20 pellets for moose and red deer and ≥ 10 pellets for roe deer and fallow deer in order to be counted. If pellet groups were counted within 10 m^2, I multiplied their number by the factor 10 to match the counts within the 100 m^2 circle. Due to the high morphological similarity of dung pellets between red deer, roe deer, and fallow deer (Spitzer *et al.*, 2019), I grouped the dung pellet groups of these smaller deer species as an overall deer density index. I calculated a dung pellet index per 100 m^2 per squared transect for moose and the smaller-bodied deer. To receive a density index for moose and the smaller deer per young forest stand, I linked each forest stand, where the DDI was performed, to the closest squared transect.

2.2.4 Young forest area (Paper I)

I extracted the area of young forest stands per MMA from the food prognosis database (in Swedish: *Foderprognos*)[8], which is also collected by the SFA. I downloaded the data in 2018, however it is currently not available on the

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[7] https://algdata-apps.lansstyrelsen.se/algdata-apps-stat [2020-12-10]

[8] https://www.skogsstyrelsen.se/statistik/statistik-efter-amne/abin-och-andra-skogliga-betesinventeringar/foderinventering/ [2018-01-31]

webpage of the SFA. The variable was used as an index of forage availability per MMA.

2.2.5 Winter severity (Paper I)

I extracted the maximum daily temperature and snow depth as an index of winter severity from the weather station closest to the centre point of each MMA from the webpage of the SMHI[9]. I then calculated the proportion of days during winter (Oct-April) with at least 10 cm, 20 cm, and 30 cm of snow and a max. daily temperature < 0 °C.

2.2.6 Land-use characteristics (Paper II)

To calculate indices for neighbouring land-use characteristics per young forest stand, I extracted the different land-use classes (see Appendix, Table A.2) around each young forest stand based on a raster of the Swedish vegetation cover (in Swedish: *Nationella marktäcke data*)[10]. We used a circular buffer of 220 ha around the centre of each young forest stand to represent the mean national core home range size of moose. We extracted moose home range sizes from existing GPS data and averaged values between our southernmost study area (Växjö: 170 ha; Neumann *et al.*, 2019b) and a GPS study location close to our northernmost study area (Gällivare: 270 ha; Neumann *et al.*, 2019a). Home ranges of the other deer species are smaller and included in this buffer.

For each buffer, we calculated the proportion of pine forest being at least 15 m tall as an index for alternative forage availability due to a potential high availability of *Vaccinium spp.* in the field layer of mature pine forests (Tolvanen, 1995). We performed the extraction of the variable from the vegetation cover raster in ArcMap (version10.6, © 1995-2017 ESRI). Furthermore, I calculated the conditional entropy per buffer (R package *landscapemetrics*; Hesselbarth *et al.*, 2019). The conditional entropy is representing an index of landscape fragmentation (see Nowosad & Stepinski, 2019). We expected that fragmentation might alter the availability of forage (Jarnemo *et al.*, 2014).

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[9] https://www.smhi.se/data/meteorologi/ladda-ner-meteorologiska-observationer/#param=airtemperatureInstant,stations=all [2020-12-21]

[10] https://www.naturvardsverket.se/Sa-mar-miljon/Kartor/Nationella-Marktackedata-NMD/Ladda-ned/ [2020-12-21]

2.3 Statistical analyses

If not stated otherwise, all analyses in this thesis were performed in R (R Core Team, 2019) considering a significance level of $\alpha = 0.05$. All explanatory variables in a numerical format were scaled according to the z-score method in all analyses (Abdi, 2007).

2.3.1 Predictors of deer damage (Paper I & II)

MMA scale (Paper I)

To identify the predictors of deer damage (i.e. apical leader browsing, bark damage, and stem breakage), I used a beta regression (R package *betareg*; Cribari-Neto & Zeileis, 2010) to test the effect of deer densities (represented by harvest data), forage availability (i.e., density of Scots pine, density of birch *spp.*, and proportion of young forest area), and winter severity (i.e., proportion of days with a maximum temperature < 0°C and at least 10 cm, 20 cm, and 30 cm of snow) on the proportion of damaged Scots pine stems per MMA. If explanatory variables had a Pearson correlation coefficient of $|r| > 0.7$ (see Appendix, Table A.3 and Table A.4), I tested their effects on the proportion of damaged pine stems separately from each other (Dormann *et al.*, 2013). Furthermore, levels of summer and winter damage were modelled in two separate models, where indices for winter severity were excluded in models for summer damage. After an analysis at the national scale, I tested the effect of all explanatory variables per geographical region (i.e., *Norrland*, *Svealand*, and *Götaland*) for both summer and winter damage. I always selected the most parsimonious model and assured the exclusion of explanatory variables with a likelihood ratio test.

Young forest stand scale (Paper II)

In *Paper II*, I identified the predictors of deer damage on Scots pine using data collected across eight study areas across the latitudinal gradient. I applied a generalized linear mixed model (GLMM; R package *MASS*; Venables & Ripley, 2002) with a binomial distribution to test the effect of forage availability (i.e., density of Scots pine, downy birch, and silver birch stems), deer densities (represented by dung pellet group counts), and neighbouring land-use characteristics (i.e., pine forest ≥ 15 m and conditional entropy) on the number of damaged vs. undamaged Scots pine stems. Additionally, I included the half-average-height (due to different sampling regimes in the different projects) as fixed effect and tested the factor PCT as interaction term with the densities of the three tree species. The combination of study area and year was included as random effect, additional to an exponential spatial correlation structure.

2.3.2 The effects of summer and winter browsing on conifer growth (Paper III)

To understand the effects of *Summer browsing* and *Winter browsing* by deer in relation to *No browsing* and a *Control* (i.e., full browsing) on Scots pine and Norway spruce in detail, I tested the effect of the four different browsing treatments on three response variables. For all three models, I tested Scots pine and Norway spruce separate from each other. In the following, I will only describe and discuss models of two of these response variables. See *Paper III*, for details on the third response variable, namely the *individual conifer growth response*.

Demographic response of conifers

I tested the effect of the interaction term *browsing treatment* * *height class* on the demographic response (i.e., number of trees per height class) of conifers in a GLMM using a poisson distribution while accounting for zero-inflation (R package *glmmTMB*: Brooks *et al.*, 2017). Similar as above, 'site' was included as random effect.

Due to low sample sizes in the taller height classes in the first spring measurements (i.e. spring 2016; see Figure 8a+c), I tested the demographic response for the latest spring measurement only (i.e. spring 2020). However, even in 2020 the number of stems in the tallest height classes was low. Therefore, I excluded the height classes taller than 300 cm for pine (see Figure 8b) and taller than 200 cm for spruce (see Figure 8d) from these analyses.

Density of deciduous trees taller than the individual conifers

I applied the same GLMM structure as for the analysis of the demographic response of conifers to test the effect of browsing treatment on the number of deciduous stems taller than individual pine and spruce while including 'site' as random effect. I rounded the response variable to an integer format in order to be used in a poisson distribution.

2.3.3 Spatial vs. temporal variation in the Swedish deer damage inventory (Paper IV)

To identify the spatial and temporal variation in damaged pine of the DDI at the km-square scale, I ran a GLMM with a negative binomial distribution accounting for zero-inflation (R package *glmmTMB*; Brooks *et al.*, 2017). I modelled the response of deer damaged pine as the number of damaged pine stems at the square scale and included a log-transformed offset with the number of available pine stems. In order to extract the variation within spatial and temporal levels, the model included a nested spatial random structure with a temporal interaction (i.e., km-squares nested within years nested within MMAs), and a crossed random term represented by the factor year. I included the total available area of young forest stands per km-square [ha] representing forage availability as fixed effect. Due to the regional differences in the predictors of deer damage identified in *Paper I*, I also tested for the variation in deer damage in the three regions separately in *Paper IV*.

3. Results

3.1 Predictors of deer damage across moose management areas (Paper I)

Pine density was the only variable that predicted both summer and winter damage on Scots pine across MMAs in 2015 and 2016 (Figure 6) and was the only predictor for summer damage. Summer damage on Scots pine decreased with increasing pine densities at the national scale and in *Svealand* ($z \leq -2.48$, $p \leq 0.013$; Figure 6b), whereas winter damage on Scots pine decreased with increasing pine densities independent of spatial context ($z \leq -2.49$, $p \leq 0.013$; Figure 6a). In general, pine density was an equally or more important predictor for damage levels than deer density indices.

Density indices of the smaller deer species were identified as significant predictors at the national scale and in the region *Götaland*, where winter damage levels increased with increasing roe deer densities and potentially also red deer densities (represented by harvest data; $z \geq 1.85$, $p < 0.064$; Figure 6a). Especially in *Götaland*, where densities of the smaller deer species are highest, their numbers were of higher importance than moose density or pine density. Winter damage levels increased with an increasing number of moose observations in *Norrland* ($z = 2.32$, $p = 0.020$; Figure 6a), where moose is the dominant deer species. The effect of moose observations was of similar magnitude than pine density.

With increasing winter severity (i.e., the proportion of winter days with at least 30 cm of snow, see details on the different indices of winter severity in *Paper I*), winter damage levels increased at the national scale and in *Norrland*, where winters are strongest.

Contrary as expected, winter damage increased with an increasing proportion of young forest area (i.e. forage availability) only at the national scale ($z = 1.99$, $p = 0.047$; Figure 6a).

Overall, predictors at the national scale differed from the predictors at the regional scale, especially for winter damage (Figure 6). This shows that management actions to reduce damage levels implemented at the national scale might be insufficient for effective outcomes at the regional scale.

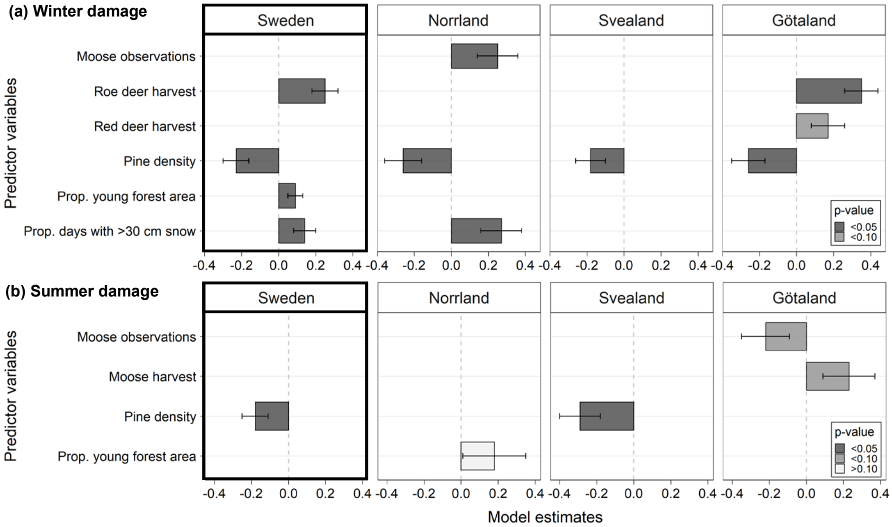

Figure 6: Model estimates (±SE) for explanatory variables predicting (a) winter damage and (b) summer damage on Scots pine at the national and regional scale. (Estimates are extracted from Table 2 and 3 in *Paper I*)

3.2 Predictors of deer damage in young forest stands (Paper II)

Similar to *Paper I*, I tested for the predictors of deer damage on Scots pine in *Paper II*, however, for winter damage only and at the scale of young forest stands instead of MMAs. Overall, tree densities were a stronger predictor of winter damage than deer densities (represented by dung pellet group counts). The effect of pine density on winter damage was comparable to the effect of moose density (see estimate sizes in Appendix, Table A.5). Across the eight study areas, winter damage on Scots pine decreased with increasing pine density ($t = -3.00$, $p = 0.003$; Figure 7b) and increased with increasing birch *spp.* density ($t \geq 3.17$, $p \leq 0.002$; Figure 7c+d). Contrary to the results at the MMA scale revealed in *Paper I,* winter damage increased with increasing moose density across study areas ($t = 2.92$, $p = 0.004$; Figure 7a), whereas higher densities of the smaller deer species did not affect winter damage at the forest stand scale ($t = 0.16$, $p = 0.877$). Winter damage in young forest stands was not affected by PCT, the half-average-height of the stand, or the neighbouring land-use characteristics ($-0.93 \geq t \leq 0.71$, $p \geq 0.351$). See Appendix, Table A.5 for the detailed results of the GLMM.

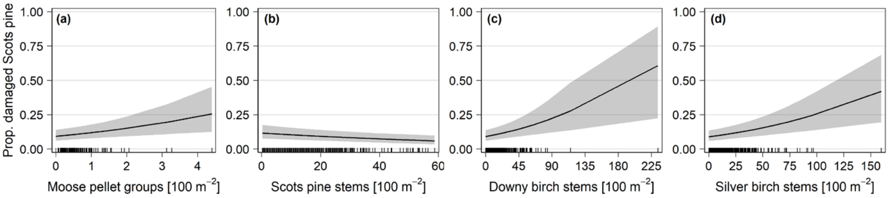

Figure 7: Predicted effects of (a) moose, (b) Scots pine, (c) downy birch, and (d) silver birch density on winter damage on Scots pine in young forest stands across study areas and sampling years. Grey shades illustrate 95% confidence intervals. Tick marks along the x-axis indicate underlying distribution of the continuous data. (from *Paper II*)

3.3 The effects of summer and winter browsing on conifer growth responses (Paper III)

Across plots and sites, a total of 151 individual Scots pine and 242 individual Norway spruce trees were monitored. Mean (±SD) annual damage levels of pine per site were 9.44 % (±7.86) in the *Control* and 11.11 % (±11.79) in the *Winter browsing* plots, whereas no deer damage occurred on pine in the *Summer browsing* plots. Thus, pine was mainly damaged by deer during winter. For spruce, mean (±SD) annual damage levels per site were in general lower than for pine with 3.43 % (±5.89) in the *Control*, 1.48 % (±2.08) in the *Winter browsing*, and 3.88 % (±8.65) in the *Summer browsing* plots. No deer damage occurred in the *No browsing* plots for both conifer species.

Demographic response of conifers

The demographic distribution (i.e. the number of trees per height class) differed between the treatment plots for both pine and spruce 4.5 years after the experimental start (see also Figure 8b+d). For pine, stems 51-100 cm tall dominated in all treatment plots ($z \geq 2.0$, $p \leq 0.050$) with the highest abundance in the *Winter browsing* plot ($z \geq 2.5$, $p \leq 0.014$). Besides of pine stems 51-100 cm tall, stems 101-200 cm tall dominated in the *Summer browsing* plots ($z \geq 4.4$, $p < 0.001$) with the highest abundances in this treatment ($z \geq 3.4$, $p < 0.001$). Pine stems 201-300 cm tall were most abundant in the *Winter* and *Summer browsing* plots compared to the *Control* and *No browsing* treatment ($z \geq 3.5$, $p < 0.001$). For spruce, stems 51-100 cm tall dominated on average in the *Summer browsing* plots ($z \geq 2.3$, $p \leq 0.022$) and stems 101-200 cm dominated in the *Winter browsing* plots ($z \geq 2.4$, $p \leq 0.015$). Spruce stems 51-100 cm tall were most abundant in the *Summer* and *Winter browsing* plots ($z \geq 2.4$, $p \leq 0.017$), whereas spruce stems 101-200 cm tall were most abundant in the *Winter browsing* plot only ($z \geq 3.9$, $p < 0.001$).

In summary, pine trees in higher height classes dominated the *Summer browsing* plots, whereas spruce trees in higher height classes dominated the *Winter browsing* plots. However, both species were similar in their demographic responses in the *Control* and *No browsing* plots showing no differences between these two treatments (see also Figure 8b+d).

Density of deciduous trees taller than the individual conifers

Densities of deciduous stems taller than Scots pine were highest in the *Winter browsing* plots ($z \geq 10.5$, $p < 0.001$; see also Appendix, Figure A.1a). Deciduous densities, which were taller than Norway spruce, were highest in the *No browsing* plots ($z \geq 6.1$, $p < 0.001$), higher in the *Winter browsing* than in the *Summer browsing* plots ($z = 8.8$, $p < 0.001$), and higher in the *Summer browsing* plots than in the *Control* plots ($z = 4.3$, $p < 0.001$; see also Appendix, Figure A.1b). This suggests, that densities of deciduous stems taller than the focal conifers potentially affect the demographic responses of both conifer species via competition.

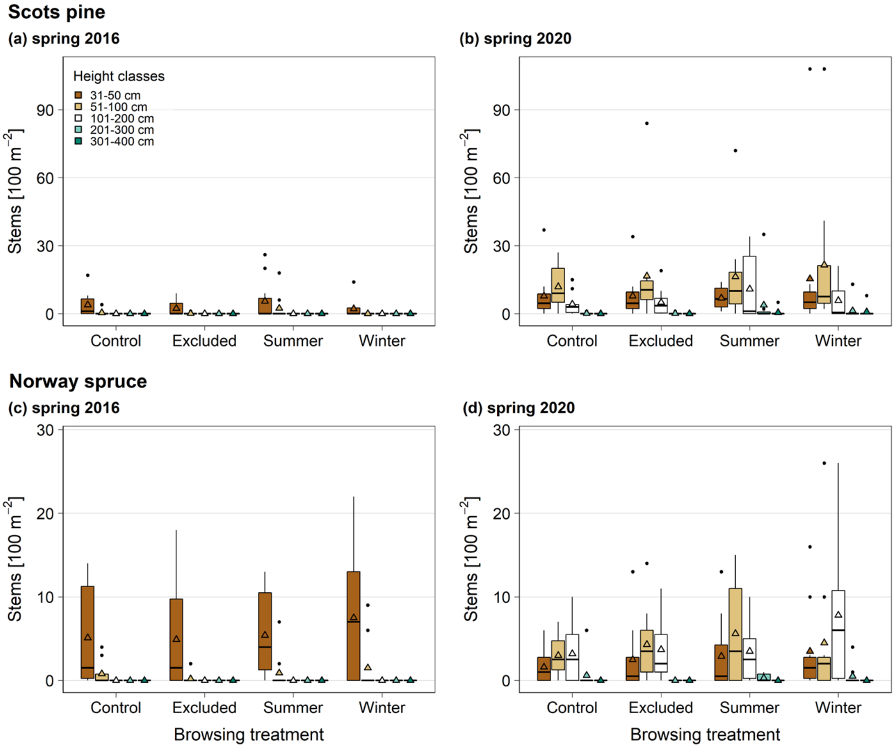

Figure 8: Demographic responses of the two conifer species presented as the number of stems [100 m^{-2}] per height class per browsing treatment across sites for Scots pine in (a) spring 2016 and (b) spring 2020 and for Norway spruce in (c) spring 2016 and (d) spring 2020. Triangles illustrate mean values. (from *Paper III*)

3.4 Spatial vs. temporal variation in the Swedish deer damage inventory (Paper IV)

The DDI monitored deer damage on Scots pine in 620 km-squares in *Norrland*, 469 km-squares in *Svealand*, and 378 km-squares in *Götaland* at least twice during the time period 2015-2020 (see Fig. 1 in *Paper IV* for a graphical overview per year). The area of available young forest stands within squares averaged 13.58 (±11.51 SD) ha in *Norrland*, 10.58 (±8.76 SD) ha in *Svealand*, and 9.71 (±7.17 SD) ha in *Götaland*. It correlated strongly with the area of inventoried young forest stands (see Appendix, Figure A.2).

The temporal variation in damage levels was lower than the spatial variation among re-inventoried km-squares within years and MMAs in all regions (Table 2). Damage levels on pine declined with an increasing area of available young forest stands within km-squares in each region (*Norrland:* $z = -5.96$, $p < 0.001$; *Svealand:* $z = -6.51$, $p < 0.001$; *Götaland:* $z = -2.93$, $p = 0.003$; Table 2). Thus, landscape characteristics such as forage availability might be one potential driver of the spatial variation in the results of the DDI.

Table 2: Predicted estimate (±SE) for the fixed effect and variance (SD) for random effects of the generalized linear mixed model testing the response of damaged pine stems with the log-transformed number of available pine stems as offset with a zero-inflated negative binomial distribution per region. 'MMA' stands for moose management area. Superscript symbols indicate significance with '**' p≤0.01 and '***' p≤0.001.

Variable		**Norrland**	**Svealand**	**Götaland**
		Estimate(±SE)	**Estimate(±SE)**	**Estimate(±SE)**
Fixed effect	Young forest area per square [ha]	-0.21 (±0.04)***	-0.27 (±0.04)***	-0.14 (±0.05)**
		Variance(SD)	**Variance(SD)**	**Variance(SD)**
Random effects	Square : (Year : MMA)	0.43 (0.65)	0.39 (0.62)	0.34 (0.58)
	Year : MMA	0.07 (0.26)	0.06 (0.25)	0.10 (0.32)
	MMA	0.07 (0.27)	0.13 (0.37)	0.15 (0.39)
	Year	0.03 (0.18)	0.03 (0.18)	0.00 (0.05)

4. Discussion

With this thesis, I had the objective to provide insights on the impacts of co-occurring deer species on economically important conifer tree species. I focussed on aspects affecting deer damage levels and the growth responses of conifers to seasonal browsing. My analyses reached across a variety of spatial scales, which represent the ecological scales relevant to understand deer foraging behaviour: from the regional scale (i.e., MMAs; *Paper I*), to the landscape scale (i.e., km-squares; *Paper IV*), to the plant community (i.e., young forest stands; *Paper II*) and individual plant scale (i.e., individual trees; *Paper III*; see also Figure 4). At the same time, I was able to connect this multi-scale perspective to the relevant spatial scales actively used within the Swedish forest and wildlife management to discuss the implications of these results for current management practices. Throughout my analyses with observational and experimental data, I concentrated on a multi-species deer approach. My results showed that the impacts of deer foraging and their relationship to deer damage in production forests are highly dependent on the investigated spatial and temporal scale. This indicates that results are scale specific and should not be generalized. In the following, I discuss in detail the mechanisms of the relevant factors across spatial and temporal scales.

4.1 General discussion

Spatial scales (Paper I, II & IV)

In general, winter damage on Scots pine increased with increasing deer densities. However, the effect of the different deer species varied widely and was dependent on the spatial context. Even though moose is considered as main damage agent on Scots pine, moose density was not always a significant predictor of deer damage. At the large regional scale (i.e., MMAs; *Paper I*), the density of the smaller deer species seemed a better predictor for winter damage than moose density for a national analysis and in *Götaland*, where deer densities are high. However, damage levels increased with increasing moose density (represented by moose observations) across MMAs in *Norrland*, where moose is the dominant deer species. At the plant community scale (i.e., young forest stands; *Paper II*), which is the main forest management scale, winter damage on Scots pine increased with an increasing density of moose in study areas spread across the whole county. At the larger management scale of deer (i.e., MMAs), moose density did not directly affect winter damage levels at the national scale (*Paper I*).

Månsson *et al.* (2007) reasoned that the missing effect of a moose density index at larger spatial scales could be due to the decreased variation in the index among areas at these larger scales. This would indicate that the effect of a moose density index might be scale-dependent. However, the different results at two different spatial scales in this thesis, could also be dependent on the use of different density indices. At the MMA scale (*Paper I*), I had to use moose harvest and moose observations as density index, whereas I was able to use dung pellet group counts at the scale of young forest stands (*Paper II*). The stronger effect of the moose density index based on dung counts might indicate that it is potentially a better index reflecting moose density at that scale. A comparison between density estimates from dung counts and camera traps in a particular study area showed that indices from both methods were similar and actually corresponded to a density estimate calculated from moose observations and harvest data (Pfeffer *et al.*, 2018). However, it is questionable if the relationship between these different density indices applies at the larger MMA scale. In general, moose harvest is seen as a reasonable index for moose density across large spatial scales as it represents the spatial variation in moose density rather well (Ueno *et al.*, 2014). Observational data on the other hand is highly dependent on the region-specific visibility, which influences the detectability (Ueno *et al.*, 2014). Thus, comparisons between regions might be less effective and provide different results.

As indicated above, the effect of the smaller deer species was especially pronounced in MMAs in *Götaland* (*Paper I*). Southern Sweden is characterised by areas with high densities of these smaller deer species and here the density of roe deer (partly also of red deer) was a stronger predictor than moose density on winter damage. Recent research showed that moose seems to compete with the smaller deer species for foraging resources such as *Vaccinium spp.* (Spitzer *et al.*, 2021). Therefore, high densities of the smaller deer species might force moose to increase its pine intake, which may result in high damage levels on Scots pine. Moose is expected to better tolerate lower quality forage than the other deer species due to its body size (Müller *et al.*, 2013). Thus, moose is the species that might increasingly consider pine as forage if competition over alternative higher quality forage is high. Thus, it is important to consider the whole deer community at the current wildlife (moose) management scale at least in areas where the co-occurrence of deer is high and if deer damage is intended to be regulated via population control.

However, at the forest stand scale (*Paper II*), densities of the smaller deer species did not affect winter damage on Scots pine. Three potential mechanisms might drive the lack of a small-deer-effect at the forest stand scale: (i) The effect of the smaller deer species might decrease with finer spatial scale, just opposite to the potential scale-dependency of a moose density index. (ii) Young forest stands might not represent the preferred foraging habitat of the smaller deer species, due to a higher risk in this open habitat (Godvik *et al.*, 2009). Pastures, habitat edges, and the field-forest ecotone are usually preferred by these smaller species (Godvik *et al.*, 2009; Tinoco Torres *et al.*, 2011). Thus, their impact at the forest stand scale might be less pronounced. However, I would like to emphasize that dung counts were extracted from the landscape surrounding the young forest stands and not directly from the specific young forest stands. Therefore, this argument might not necessarily be a relevant mechanism. (iii) The measured density index of the smaller deer species via dung counts, which was rather low across study areas, might not have represented their density appropriately. Thus, the statistical power of the variable was reduced. Dung pellets of the smaller deer species are smaller in size than dung pellets of moose (Spitzer *et al.*, 2019) and the detectability of smaller pellets might differ across the landscape (Lioy *et al.*, 2015). Thus, dung pellet group counts of smaller deer species tend to underestimate their density (Pfeffer *et al.*, 2018). However, at the studied forest stand scale, there were no alternative density estimates available. Therefore, assuming that the density estimate of the smaller deer species via dung counts reflected density levels appropriately, meaning their densities were truly low, the effect of the smaller deer species simply might have not been pronounced. Furthermore, just a limited amount of study areas was located in southern Sweden, where densities of the smaller deer species are highest. Thus, moose can most likely be considered the dominant deer species across study areas affecting winter damage levels directly.

Irrespective of spatial scale, deer densities were not the most important predictors of deer damage on Scots pine. Different variables representing forage availability indicated that forage availability seems to have a major effect on damage levels. Across scales, the availability of forage influences different selection processes of herbivores (i.e., deer), such as their selection of foraging patches (Stephens & Krebs, 1986).

At all spatial scales, deer damage on Scots pine decreased with an increasing pine density (*Paper I & II*). Findings of previous studies across Scandinavia also indicated that damage levels decreased with increasing pine availability (e.g., Andrén & Angelstam, 1993; Månsson *et al.*, 2007; Wallgren *et al.*, 2013; Herfindal *et al.*, 2015; Nevalainen *et al.*, 2016). An increasing number of pine trees is assumed to provide a higher forage availability, which might result in a dilution effect for damage levels (Bergqvist *et al.*, 2014; Díaz-Yáñez *et al.*, 2017). Even if the absolute number of damaged stems might increase with an increased availability of stems, the proportion of damaged stems will decrease leaving a higher number of stems undamaged.

In addition to pine density, an increase in the area of young forest seemed to reduce winter damage on Scots pine at the landscape scale (i.e., km-squares; *Paper IV*). At the landscape scale, previous research supports that stem breakage decreases with an increasing proportion of young forest stands surrounding the targeted forest stand (i.e., 2 x 2 km squares; Heikkilä & Härkönen, 1993). However, an increasing proportion of young forest area did not reduce winter damage at the larger regional scale (i.e., MMAs; *Paper I*); on the contrary, damage levels increased with an increasing area of young forest in MMAs across the whole country. Potentially, the positive and negative effects of young forest area might be dependent on the spatial scale due to the foraging behaviour of deer. At the landscape scale (*Paper IV*), the choice of a forest stand might be dependent on the relative availability of forest stands (Danell *et al.*, 1991). Thus, with an increasing availability of surrounding forest stands, the probability that a particular forest stand is damaged might decline (Hurley *et al.*, 2012). However, at the regional scale (*Paper I*), where there might be different mosaics of forest stands available in different areas of the region, the availability of these stands might influence the choice of movement rather than the active choice of 'what to eat'. Thus, deer might concentrate in areas with an increased density of young forest area (i.e., forage availability) within a region, especially during winter. Therefore, damage levels increase with an increase in young forest area. Thus, young forest area can be an important landscape characteristic driving the spatial variation in deer damage levels.

The effect of birch *spp.* densities on winter damage was only pronounced at the forest stand scale (*Paper II*) and not at the larger MMA scale (*Paper I*). In winter, birch density might primarily represent forage quality rather than quantity and thus its effect is stronger at the finer spatial scale (van Beest *et al.*, 2010). During winter, deer seem to select against birch *spp.* (Bergqvist *et al.*, 2018; Spitzer, 2019), which might indicate a low forage quality potentially due to missing leaves. According to Faber and Lavsund (1999), top shoots of Scots pine seem to have an equal or higher nutritional quality than alternative forage, such as birch *spp.,* even during summer. Furthermore, the lower bite size of birch *spp.* in comparison to Scots pine might determine the selection of the latter especially for moose (Shipley *et al.*, 1998). The preference of Scots pine over birch *spp.* in winter might indicate *neighbour contrast susceptibility* (i.e., associational effect), where the focal plant Scots pine is negatively influenced by the neighbouring birch *spp.*. Additionally, the increasing damage levels on Scots pine via an increasing presence of birch *spp.* might be driven by plant-plant-competition. Scots pine is a light-demanding species (Bachofen *et al.*, 2019), where its growth might be limited due to shading from e.g. birch *spp.* seedlings. Thus, Scots pine might remain longer in the preferred browsing height of deer, resulting in increased damage levels.

Also other environmental variables predicted deer damage on Scots pine differently across spatial scales. As winters are longest and more severe in northern Sweden, the effect of winter severity (i.e., the proportion of days with ≥ 30 cm snow) on winter damage levels was especially pronounced in *Norrland*. Deep snow during a longer period in winter is limiting the availability of alternative forage (Visscher *et al.*, 2006). Thus, the effect of snow might be comparable to the effect of the smaller deer species in southern Sweden. Both limit the accessibility of important alternative forage resources in the field layer (i.e., *Vaccinium spp.*) and thus lead to higher damage levels on Scots pine.

To conclude, variables representing forage availability were an equal or stronger predictor for winter damage than deer densities or winter severity irrespective of spatial scale. Furthermore, at the current scale of wildlife management in Sweden, a multi-species management approach seems necessary to mitigate deer damage levels efficiently. Therefore, a co-management of different deer species as well as deer and forests might be needed.

Temporal scales (Paper I, III & IV)

Different seasonal browsing treatments affected the demographic responses of conifers differently potentially via plant-plant-competition (*Paper III*). The demographic response of Scots pine and Norway spruce did not differ between the *No browsing* and *Control* treatments, which supports previous findings (e.g., Speed *et al.*, 2013). This indicates that the effect of a total exclusion of herbivores, which might increase plant-plant-competition (McLaren *et al.*, 2009; Kuijper *et al.*, 2010; Stokely & Betts, 2019), and year-round browsing, which gives the opportunity for herbivores to affect conifer heights throughout the year, are of similar magnitude during the first years of tree recruitment. However, the demographic response in both conifer species was different for the *Summer* and *Winter browsing* treatments relative to the *No browsing* and *Control* treatments.

For Scots pine, most individuals grew into the tallest height classes when winter browsing was excluded. This suggests a direct effect of browsing because especially during winter, Scots pine dominates moose diets (Spitzer, 2019). Simultaneously, the density of competing deciduous trees was regulated by herbivory during summer, since deciduous trees are an important component of deer diets during summer (Spitzer, 2019). This resulted in less browsing and less plant-plant competition for the light-demanding Scots pine when winter browsing was excluded.

For Norway spruce, most individuals recruited into the tallest height classes when summer browsing was excluded. Norway spruce is rarely browsed (Speed *et al.*, 2013; Szwagrzyk *et al.*, 2020), thus its growth is less influenced via the direct height control by herbivores. Moreover, Norway spruce is a shade-tolerant species, where the shading from neighbouring trees (e.g. when summer browsing is excluded) might protect spruce from microclimatic stress (i.e., frost during winter). This positively affects the growth of Norway spruce (Langvall & Örlander, 2001; Heiskanen, 2004).

Thus, seasonal fencing, rather than year-round fencing, can be an approach to mitigate deer damage during the first years of conifer growth. Moreover, fencing should potentially occur in different seasons for spruce (summer fencing) than for pine (winter fencing). Future studies should investigate the growth responses during a longer time period after reforestation.

As shown in *Paper III* and discussed above, the growth response of Scots pine differed between *Summer* and *Winter browsing* in general. Furthermore, I could identify different predictors for summer and winter damage on Scots pine, where pine density was the only predictor of summer damage, whereas pine density together with deer densities and winter severity was a predictor for winter damage (as discussed above; *Paper I*). Hence, the only common predictor for both summer and winter damage was pine density. This underlines the importance of forage availability – especially pine density – regardless of season.

However, the nutritional quality per forage species needs to be understood in detail, especially per season since seasonal variations can affect the selection of forage items to a large degree (e.g., due to fibre content; Felton *et al.*, 2018). Forage that might be avoided by deer during winter could be selected for during summer. For example, deciduous tree species are more dominant in the summer than the winter diet of deer (Spitzer, 2019) most likely due to their leaves which are present during the growing season only.

The temporal variation in deer damage on Scots pine was much lower than its spatial variation (*Paper IV*). Thus, annual differences in deer damage seem to be less influenced by environmental drivers such as climate or deer densities, which are supposedly a main driver for annual variations. Instead, the spatial variation between sampling units was highest. This indicates that landscape characteristics, such as forage availability, might be of higher importance in explaining the variation in deer damage rather than climatic influences. Since the DDI selects sampling locations within MMAs randomly per year, this might explain partly the high annual differences in damage levels. This would indicate that landscapes of different compositions are likely to differ in their risk to deer damage (Godvik *et al.*, 2009). However, the analysed dataset in *Paper IV* mainly compared the temporal variation between two years only. It should be investigated if a long-term study might reveal a different relationship between the temporal and spatial variation.

4.2 Future investigations

With this thesis, I was able to highlight relevant factors that influence deer damage and the growth of conifer tree species in a community where several deer species co-occur. Still, several questions are left unanswered and seek future exploration. In the following, I would like to list some of the future directions that seem relevant to me.

- My thesis clearly identified the role of several drivers across varying spatial scales. However, I was not able to test their effectiveness in terms of regulating deer damage levels. Future studies should actively test the outcomes of the different identified predictors across the varying spatial scales indicated.
- Furthermore, some detected drivers might regulate deer damage directly, whereas others might only have an indirect influence. In this thesis, I was not able to tackle apart these detailed mechanisms and future studies should investigate these in more detail. To name one examples: Is the relationship between deer damage on Scots pine and birch density driven through associational effects and/or plant-plant-competition?
- In order to provide more information to forest managers on the economic status of forests in relation to deer damage, an alternative approach could be to investigate the number of undamaged trees instead of the number of damaged trees. A recently published study implemented this approach (Loosen *et al.*, 2021) and I believe that further investigations could bring useful insights since the numbers of undamaged trees are most relevant from an economical perspective by contributing to the future production stand.
- Throughout all analyses, I focussed on deer damage, which is of relevance for the forestry sector. However, in order to understand the foraging behaviour of deer in further detail, not only these three types of damage should be considered. For deer, the number of available side

shoots should be also of relevance in order to maintain energy rates. It might be interesting to investigate the relationship between deer damage and side shoot browsing and potentially even the nutritional quality of the top shoot in relation to side shoots, to be able to draw further conclusions between deer foraging behaviour and deer damage across scales.

- At the plant community scale, I used density estimates based on dung pellet group counts for all species. As discussed above, the small size of dung pellet groups of the smaller deer species might decrease the detection probability of pellets. Furthermore, a high morphological overlap between the pellets of the different deer species makes it difficult to disentangle the effect of each deer species separately (Spitzer *et al.*, 2019). Thus, alternative density estimates could be considered at the named scale. Since harvest data is mainly presented at larger spatial scales, data such as from camera traps could serve as alternative tool, especially since density estimates from camera traps might be a better predictor of the densities of the smaller deer species (Pfeffer *et al.*, 2018).
- Even if my results could not detect a clear relationship between PCT and deer damage, it might be useful to investigate its effects in more detail. Furthermore, if fencing might be used as a tool to mitigate deer damage, PCT could be an important tool to reduce plant-plant-competition.

4.3 Concluding remarks of interest to management

I believe that my thesis is of high value for the current wildlife and forest management in Sweden, which both devote a lot of focus on controlling damage levels by deer in forests. By capturing a multi-scale approach, I was able to identify the potential mechanisms of deer damage at various scales that are relevant for different stakeholders. Furthermore, I considered the Swedish deer community as a whole and did not specifically focus on moose, in contrast to previous studies. Additionally, I used data collected within management, which is used for active management decisions, to demonstrate the potential strengths and weaknesses of current management practices.

According to the SFA, the proportion of damaged Scots pine per MMA should be no higher than 5 % across the country. My thesis did not reflect on the exact numbers of damage levels in Sweden; but in order to control winter damage levels on Scots pine, my work suggests that a co-management of deer and forests is of high relevance in order to mitigate deer damage on economically important Scots pine. However, deer are managed at the landscape/regional scale, whereas forests are mainly managed at the plant community/forest stand scale.

For the management of deer, my thesis clearly suggests that the whole deer community needs to be taken into account in order to develop the management system, which currently is centred heavily on moose. Regulating moose populations only does not seem to be an effective tool to reduce deer damage in forests. Especially in southern Sweden, where the co-occurrence of moose with roe deer, red deer, and fallow deer is common, a formal multi-species management approach should be tested. Furthermore, my results highlight the importance of forage availability for levels of damage. Increasing pine availability appeared to reduce pine damage from deer across all spatial scales.

However, only adapting one approach (e.g., focus on population regulations or increasing forage availability) might not be the most effective way of regulating deer damage in forests. Additionally, my findings suggest that management actions applied at the national scale may not be most effective in regulating damage levels on Scots pine. Relevant factors identified at the national scale were partly not relevant at the regional scale and the effectiveness of a factor may differ between regions. Thus, management actions need to be adapted to the relevant environmental variables at the right scale across Sweden's latitudinal gradient.

In some instances, fencing might be used as a management practice to mitigate deer damage on forests. However, it should be considered that a full exclusion of browsing might not necessarily enhance the growth of conifer tree species due to plant-plant-competition – at least during the first years during regeneration. Furthermore, the characteristics of different plant species need to be considered if seasonal fencing is supposed to be effective. The growth response of Scots pine seedlings might increase if winter browsing is excluded, whereas the growth response of Norway spruce might increase if summer browsing is excluded. The difference in growth between Scots pine and Norway spruce is most likely dependent on their varying needs for light and the varying palatability of different tree species during summer and winter.

4.4 Personal reflections

During the time of my PhD studies, I participated not only in international research conferences, but presented my research also to several stakeholders and management institutions. When participating in the meetings of management groups within the moose management system, hunter organizations, or national wildlife management conferences, I realized from the very start to the end of my PhD that the topic of this thesis is of high relevance and clearly relates to the questions encountered by stakeholders on an everyday basis. Different stakeholders might have varying opinions on how to manage the interactions between deer and the damage encountered in forestry, but to me they all seemed to agree that there is not only a 'moose-forestry-problem'. I found the interest and willingness to discuss the current issues from a multi-species deer perspective very inspiring for my personal work and I think that these discussions are a first step in developing the adaptive management system further. It might be a long-term process, but it definitely has started to evolve.

I would like to acknowledge all organizations and institutions that administrate the large amount of data collected within the Swedish wildlife management system. I would also like to thank everyone – especially the many hunters and stakeholders – that did and are still contributing to this wealth of data. In order to improve the usability of these valuable data resources, I would like to encourage a closer collaboration between the different organizations and institutions. Having extracted and worked with these data, I found it often challenging to align the different datasets from the different sources correctly. To give an example, a uniform labelling of management units (e.g., MMAs) across databases would highly improve the data usability. Overcoming such minor discrepancies and potentially providing yearly national shapefiles on the borders of management units from the past and the future, will offer further possibilities for long-term analysis of management data and its use in research as well as in management.

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Popular science summary

During the past decades, the numbers of deer (*Cervidae*) have increased in Europe and their ranges have expanded. In Sweden, moose (*Alces alces*) has historically been the dominant deer species across the country and the wildlife management system in Sweden has therefore traditionally been centred on moose. But the distribution and numbers of smaller deer such as roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*), and fallow deer (*Dama dama*) are now increasing and more than one deer species is becoming a common sight in many areas.

In areas that are highly dominated by humans and where landscapes are intensively used, the increased populations of deer are causing new challenges for agriculture and forestry. Fields, pastures, and young forest stands provide an increased amount of favourable food all year around for the expanding deer populations. By feeding on, for example, trees, deer reduce tree growth as well as wood quality. Common types of *deer damage* that reduce the wood quality are browsing on the top shoot, damaging the bark on the main stem, and breaking the stem of a tree. This leads to conflicts based on human interests because the feeding of deer may cause economic losses on a yearly basis.

From a deer's perspective, their choice of food can be dependent on the availability, quantity, and nutritional quality of the food. The choice of food is also dependent on how food plants are arranged with respect to other plants.

In this thesis, I studied mainly the role of the Swedish deer community in affecting the damage and growth of commercially important Scots pine (*Pinus sylvestris*) in young forests. Specifically, my aim was to understand how biological factors – such as the population density of deer or the availability of food – and environmental factors – such as snow – affect the probability of damage by deer on Scots pine. To explore these relationships in detail, I extracted data at many different geographical levels in Sweden. These levels are spanning from north to south and consider the entire gradient of moose management areas (in Swedish: *Älgförvaltningsområde*), but also local levels such as young forest stands in several study sites, and the food choice of individual plants in experimental seasonal exclosures. My results provide valuable insights on the processes and drivers of deer damage to Scots pine, which will offer useful knowledge for managers on how to potentially regulate deer damage.

In general, I found that deer damage on Scots pine was higher when the density of deer was high, but simultaneously, the density of just moose was not always directly related to higher deer damage. An effect of moose on damage was most pronounced in moose management areas in northern Sweden (*Norrland*), where moose is still the dominating deer species. In southern moose management areas (*Götaland*), where the numbers of the smaller deer are high, my results suggest that all deer species and their population size should be considered for regulating deer damage on Scots pine at the current wildlife (moose) management scale. Therefore, regulating only the numbers of moose may not control damage levels effectively. Moose are considered to cause most of the damage on Scots pine in young forest stands, but earlier research has shown that the feeding behaviour of moose may be affected by the densities of the other deer species because of competition over food resources (e.g. shrubs such as blueberries). This competition might increase the feeding on pine by moose in areas where densities of the smaller deer species are high.

The amount of available food affected damage levels on Scots pine in moose management areas as well as at finer levels such as the individual forest stands. The amount of food was equally or often even more important than the number of deer in order to control deer damage in young forest stands. This suggests that deer and forests should be managed jointly. With a higher number of Scots pine in young forests, the proportion of damaged pine trees during winter was lower. But with a higher number of birch (*Betula spp.*) trees, the proportion of damaged pine trees during winter increased. In winter, birch has no leaves and might therefore have a lower nutritional quality than pine. Furthermore, the size of one bite on birch is lower than the bite size of pine. These could be reasons why deer eat more pine during winter when there are more birch trees present, which results in higher damage levels.

I also found that a high number of taller broadleaved trees (such as birch) may reduce the growth of Scots pine and Norway spruce (*Picea abies*) during the first years after tree plantation. After 4.5 years, Scots pine grew taller when deer were excluded with fences during winter, whereas Norway spruce grew taller when deer were excluded during summer. The difference in growth between Scots pine and Norway spruce is most likely dependent on their need for light. Scots pine requires more light than Norway spruce to grow, whereas Norway spruce is more influenced by its micro-climate. During summer, deer feed a lot on broadleaved trees, which regulates the height and number of broadleaved trees. Therefore, Scots pine experience less light-competition from broadleaved trees when deer are present during summer but absent during winter to prevent damage. Norway spruce might benefit from a high number of broadleaved trees during winter, which may function as a protection against frost. Furthermore, a full exclusion of deer did not promote the growth of conifer trees during the initial years of conifer regeneration because of plant-plant-competition.

I also studied the variation in deer damage that is monitored via the Swedish deer damage inventory (in Swedish: *älgbetesinventering*). In general, the yearly variation in the results of the deer damage inventory seems to be driven more via the variation of landscape characteristics rather than annual fluctuations in environmental variables. This suggests that landscape characteristics, such as the availability of food, might have a higher effect on the variation in damage levels than for example snow or temperature.

In conclusion, this thesis shows that the relationship between the densities of deer and deer damage in young forests requires a management approach that does not only focus on moose. In addition, the availability of food is an important driver to regulate damage levels efficiently. Furthermore, management actions should not be generalized across space and time. Regional and local adaptations seem necessary.

Populärvetenskaplig sammanfattning

Under de senaste decennierna har antalet hjortdjur (*Cervidae*) och deras utbredning ökat i Europa. I Sverige har älgen (*Alces alces*) historiskt sett varit den dominerande hjortarten med störst spridning över hela landet. Viltförvaltningen har därför traditionellt varit inriktad på just älg. Nu ökar utbredningen och antalet av mindre hjortarter, som rådjur (*Capreolus capreolus*), kronvilt (*Cervus elaphus*) och dovvilt (*Dama dama*). Därför har förekomsten av flera hjortarter tillsammans blivit allt vanligare. Arterna har delvis olika födopreferenser, men konkurrerar ofta om samma foder. Valet av föda kan bero på födans tillgänglighet, kvantitet och näringskvalitet, men även hur olika växtarter förekommer i förhållande till varandra samt konkurrens mellan betande hjortdjur.

I områden som är starkt dominerade av människor, och där landskap brukas intensivt, gynnas ofta hjortdjur då åkrar, betesmarker och ungskogsbestånd ger en ökad mängd föda under hela året. Samtidigt orsakar växande hjortpopulationer nya utmaningar för jord- och skogsbruket, eftersom betesskador kan orsaka ekonomiska förluster. Genom att beta på träd minskar hjortdjur såväl tillväxten av träden som kvaliteten på timret från träden. Vanliga typer av betesskador som minskar kvaliteten på timmer är toppskottsbete, barkskador på huvudstammen och stambrott.

I denna avhandling har jag i huvudsak studerat hur sammansättningen av svenska hjortdjurssamhällen påverkar skador och tillväxt av kommersiellt viktig tall (*Pinus sylvestris*) i ung skog. Specifikt var mitt mål att förstå hur biologiska faktorer – såsom hjortpopulationernas täthet eller tillgången på föda – och miljöfaktorer – som snö – påverkar sannolikheten för betesskador på tall. För att utforska dessa relationer i detalj extraherade jag data på olika geografiska skalor i Sverige. Dessa omfattar hela Sverige från norr till söder, med en varierande upplösning från Sveriges älgförvaltningsområden till lokala studieområden och bete på enskilda växter i experimentella hägn. Mina resultat ger värdefull förståelse om vilka processer som påverkar mängden betesskador på tall. Något som kommer att ge användbar kunskap till förvaltningen om hur man kan reglera betesskador av hjortdjur.

Jag fann att andelen skadade tallar var högre när den sammanlagda tätheten av hjortdjur var hög, samtidigt som tätheten av enbart älg inte alltid var relaterad till högre viltskador. Effekten av älg på skador var tydligast i älgförvaltningsområden i norra Sverige (*Norrland*), där älg fortfarande är den dominerande hjortarten. I älgförvaltningsområden i söder (*Götaland*), där täthet av de mindre hjortarterna är hög, tyder mina resultat på att det är nödvändigt att ta hänsyn till alla hjortarter och deras beståndsstorlek för att begränsa betesskador på tall. En begränsning endast av antalet älgar kommer sannolikt inte kontrollera skadorna effektivt.

Älg anses orsaka merparten av skadorna på tall i unga skogsbestånd, men tidigare forskning har visat att älgens diet kan påverkas av tätheten från de andra hjortarterna på grund av konkurrens om födoresurser som bärris. Denna konkurrens kan vara mekanismen som påverkar viltskador på tall av älg i områden med många andra hjortdjur.

Mängden tillgänglig föda påverkade också skadorna på tall, såväl i älgförvaltningsområden som på mindre geografisk skala, som enskilda skogsbestånd. Mängden föda var viktigare eller lika viktig som den totala tätheten av hjortdjur för mängden betesskador i ung skog. Sammantaget tyder detta på att hjortdjur och skogar bör förvaltas gemensamt. Med ett högre antal tallar i unga skogar var andelen skadade tallar under vintern lägre, men med ett högre antal björkar (*Betula spp.*) ökade istället andelen skadade tallar. På vintern har björken inga löv och kan därför ha en lägre näringskvalitet än tall. Dessutom ger ett tallbett mer föda än ett bett på björk under vintern. Detta kan vara en av anledningarna till att hjortdjur äter mer tall på vintern när det finns fler björkträd, vilket kan resultera i mer skador.

Jag fann också att ett stort antal konkurrerande lövträd, huvudsakligen björk, kan minska tillväxten av tall och gran (*Picea abies*) under de första åren efter trädplantering. Efter 4,5 år växte tallar sig högre när hjortdjur uteslöts med staket under vintern, medan gran växte högre när hjortdjur uteslöts under sommaren. Skillnaden i tillväxt mellan tall och gran är sannolikt beroende av deras behov av ljus, och att tallen betas, vilket sällan är fallet för gran. Tall betas främst vintertid, om hjortdjur då stängs ut vintertid minskar den direkta negativa effekten på tall. Tall kräver mer ljus än gran för att växa, medan gran är mer påverkad av sitt mikroklimat. Under sommaren äter hjortdjur mycket lövträd, vilket reglerar höjden och antalet lövträd. Därför utsätts tall för mindre konkurrens från lövträd när hjortdjur är närvarande under sommaren. Gran kan istället dra nytta av ett stort antal lövträd under vintern, vilket kan fungera som ett skydd mot frost. Ett fullständigt uteslutande av hjortdjur verkade däremot inte öka tillväxten av barrträd i unga, oröjda bestånd, sannolikt på grund av konkurrensen mellan olika träd.

Jag studerade också variationen i betesskador som inventeras genom älgbetesinventeringen (*Äbin*). Resultaten visar att den årliga variationen i mängden betesskador, mätt med Äbin, snarare orsakas av variationen i landskapet än årliga växlingar i miljövariabler. Detta tyder på att landskapsegenskaper, som tillgången på föda, har en större effekt på variationen i skador än till exempel snö eller temperatur.

Sammanfattningsvis visar denna avhandling att sambandet mellan hjortpopulationers täthet och betesskador i ungskogar kräver en förvaltning som inte enbart fokuserar på älg. Dessutom är det viktigt att ta hänsyn till tillgången på föda för att effektivt kunna reglera skador. Förvaltningsåtgärder bör inte generaliseras över tid och rum, utan regionala och lokala anpassningar verkar nödvändiga.

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Appendix

Tables

Table A.1: Number of re-inventoried km-squares per year-combination per region. (from *Paper IV*)

Year combination	**Norrland**	**Svealand**	**Götaland**
2015+2016	6	0	0
2015+2017	22	47	22
2015+2018	7	3	5
2015+2019	20	24	15
2015+2020	5	5	12
2015+2016+2017	1	0	0
2015+2017+2018	1	0	0
2015+2017+2019	1	12	7
2015+2017+2020	1	0	1
2015+2018+2019	2	0	0
2016+2018	34	55	17
2016+2019	50	6	3
2016+2020	10	31	10
2016+2017+2019	7	0	2
2016+2018+2019	8	0	1
2016+2018+2020	3	2	4
2017+2018	17	0	5
2017+2019	104	251	154
2017+2020	3	5	9
2017+2018+2019	5	0	3
2017+2019+2020	0	1	0
2017+2018+2019+2020	0	0	1
2018+2019	289	0	56
2018+2020	19	26	37
2018+2019+2020	0	0	3
2019+2020	5	1	11

Table A.2: List of the 25 land-use classes of the Swedish vegetation cover (*Nationella marktäcke data*)[11] and the reclassification of land-use classes to extract the conditional entropy.

NMD landscape classes	**Classification for conditional entropy**
Open wetland	Wetland
Arable land	Agriculture
Non-vegetated other open land	Open land
Vegetated other open land	Open land
Artificial surfaces: building	Artificial surfaces
Artificial surfaces: road or railway	Artificial surfaces
Artificial surfaces: other	Artificial surfaces
Inland water	Waterbody
Marine water	Waterbody
Pine forest not on wetland *	Forest not on wetland
Spruce forest not on wetland	Forest not on wetland
Mixed coniferous forest not on wetland	Forest not on wetland
Mixed forest not on wetland	Forest not on wetland
Deciduous forest not on wet-land	Forest not on wetland
Deciduous hardwood forest not on wetland	Forest not on wetland
Deciduous forest with deciduous hardwood forest not on wetland	Forest not on wetland
Temporarily non-forest not on wetland	Forest not on wetland
Pine forest on wetland	Forest on wetland
Spruce forest on wetland	Forest on wetland
Mixed coniferous on wetland	Forest on wetland
Mixed forest on wetland	Forest on wetland
Deciduous forest on wetland	Forest on wetland
Deciduous hardwood forest on wetland	Forest on wetland
Deciduous forest with deciduous hardwood forest on wetland	Forest on wetland
Temporarily non-forest on wetland	Forest on wetland

'' NMD class representing pine forest, which was used to extract pine forest > 15 m based on a raster for object height.*

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[11] https://www.naturvardsverket.se/Sa-mar-miljon/Kartor/Nationella-Marktackedata-NMD/Ladda-ned/ [2020-12-21]

Table A.3: Pearson correlation matrix with pairwise comparisons among explanatory variables to explain winter damage including all explanatory variables (a) on the national scale, and per region; (b) *Norrland*, (c) *Svealand*, and (d) *Götaland*. Superscript symbols indicate significance levels with ‘*’ p≤0.05, ‘**’ p≤0.01, and ‘***’ p≤0.001. ‘°’ represents p≤0.1. (from *Paper I*)

		Moose observations	**Moose harvest**	**Roe deer harvest**	**Red deer harvest**	**Fallow deer harvest**	**Pine density**	**Birch density**	**Prop. young forest**	**Prop. ≥10cm snow**	**Prop. ≥20cm snow**	**Prop. ≥30cm snow**	**Prop. days <0ºC**
(a) Sweden	***n***	*137*	*148*	*148*	*148*	*148*	*145*	*145*	*148*	*148*	*148*	*148*	*148*
Moose observations	*137*	1											
Moose harvest	*148*	0.36 ***	1										
Roe deer harvest	*148*	0.3 ***	-0.08	1									
Red deer harvest	*148*	-0.09	-0.19 *	0.12	1								
Fallow deer harvest	*148*	-0.14	-0.31 ***	0.16 *	0.63 ***	1							
Pine density	*145*	-0.16 °	0	-0.69 ***	-0.11	-0.23 **	1						
Birch density	*145*	0.39 ***	0.13	0.48 ***	0.04	0.09	-0.4 ***	1					
Prop. young forest area	*148*	0.17 *	0.52 ***	-0.14 °	-0.17 *	-0.22 **	0.11	0.23 **	1				
Prop. days ≥10cm snow	*148*	-0.27 **	0.03	-0.61 ***	-0.19 *	-0.18 *	0.55 ***	-0.37 ***	0.09	1			
Prop. days ≥20cm snow	*148*	-0.3 ***	0.04	-0.65 ***	-0.21 *	-0.23 **	0.56 ***	-0.43 ***	0.08	0.86 ***	1		
Prop. days ≥30cm snow	*148*	-0.32 ***	0.03	-0.58 ***	-0.18 *	-0.19 *	0.51 ***	-0.42 ***	0.04	0.78 ***	0.93 ***	1	
Prop. days <0ºC	*148*	-0.23 **	0.09	-0.76 ***	-0.28 ***	-0.32 ***	0.69 ***	-0.48 ***	0.21 *	0.70 ***	0.72 ***	0.66 ***	1
(b) Norrland	***n***	*31*	*33*	*33*	*33*	*33*	*33*	*33*	*33*	*33*	*33*	*33*	*33*
Moose observations	*31*	1											
Moose harvest	*33*	0.13	1										
Roe deer harvest	*33*	0.48 **	0	1									
Red deer harvest	*33*	0.04	0.23	-0.1	1								
Fallow deer harvest	*33*	-0.06	0.12	-0.04	-0.08	1							
Pine density	*33*	0.23	-0.14	-0.15	-0.11	0.24	1						
Birch density	*33*	0.28	0.45 **	0.38 *	0.11	0.35 *	0	1					
Prop. young forest area	*33*	0.29	0.52 **	0.26	0.13	0.05	0.2	0.46 **	1				
Prop. days ≥10cm snow	*33*	-0.28	-0.15	-0.38 *	-0.02	-0.02	0.47 **	-0.44 *	-0.29	1			
Prop. days ≥20cm snow	*33*	-0.33 °	-0.10	-0.48 **	0.05	-0.08	0.35 *	-0.45 **	-0.27	0.91 ***	1		
Prop. days ≥30cm snow	*33*	-0.4 *	-0.10	-0.57 ***	0.04	-0.11	0.35 *	-0.44 **	-0.27	0.85 ***	0.90 ***	1	
Prop. days <0ºC	*33*	-0.35 °	-0.44 *	-0.56 ***	-0.01	-0.04	0.31 °	-0.41 *	-0.47 **	0.68 ***	0.62 ***	0.60 ***	1

Continued.

		Moose obser-vations	**Moose harvest**	**Roe deer harvest**	**Red deer harvest**	**Fallow deer harvest**	**Pine density**	**Birch density**	**Prop. young forest**	**Prop. ≥10cm snow**	**Prop. ≥20cm snow**	**Prop. ≥30cm snow**	**Prop. days <0ºC**
(c) Svealand	***n***	*54*	*59*	*59*	*59*	*59*	*59*	*59*	*59*	*59*	*59*	*59*	*59*
Moose observations	*54*	1											
Moose harvest	*59*	0.33 *	1										
Roe deer harvest	*59*	0.19	-0.39 **	1									
Red deer harvest	*59*	-0.02	-0.22 °	0.31 *	1								
Fallow deer harvest	*59*	-0.13	-0.31 *	0.29 *	0.73 ***	1							
Pine density	*59*	0.05	0.15	-0.54 ***	-0.32 *	-0.29 *	1						
Birch density	*59*	0.31 *	-0.02	0.25 °	0.08	0.10	-0.33 *	1					
Prop. young forest area	*59*	-0.07	0.51 ***	-0.58 ***	-0.13	-0.11	0.08	0.14	1				
Prop. days ≥10cm snow	*59*	-0.08	0.1	-0.44 ***	-0.14	-0.1	0.26 °	-0.27 *	0.14	1			
Prop. days ≥20cm snow	*59*	0.01	0.2	-0.57 ***	-0.28 *	-0.3 *	0.40 **	-0.28 *	0.17	0.85 ***	1		
Prop. days ≥30cm snow	*59*	-0.05	0.16	-0.55 ***	-0.23 °	-0.21	0.42 ***	-0.29 *	0.5	0.61 ***	0.82 ***	1	
Prop. days <0ºC	*59*	-0.05	0.15	-0.60 ***	-0.45 ***	-0.40 **	0.63 ***	-0.49 ***	0.31 *	0.31 *	0.46 ***	0.46 ***	1
(d) Götaland	***n***	*52*	*54*	*54*	*54*	*54*	*53*	*53*	*54*	*54*	*54*	*54*	*54*
Moose observations	*52*	1											
Moose harvest	*54*	0.54 ***	1										
Roe deer harvest	*54*	-0.03	-0.08	1									
Red deer harvest	*54*	-0.26 °	-0.21	-0.31 *	1								
Fallow deer harvest	*54*	-0.37 **	-0.46 ***	-0.31 *	0.39 **	1							
Pine density	*53*	-0.05	0.06	-0.38 **	0.53 ***	0.04	1						
Birch density	*53*	0.29 *	0.16	0.16	-0.18	-0.13	-0.06	1					
Prop. young forest area	*54*	0.32 *	0.53 ***	0.30 *	-0.2	-0.36 **	-0.16	0.46 ***	1				
Prop. days ≥10cm snow	*54*	0.02	0.11	-0.17	-0.15	-0.12	0.21	0.15	0.05	1			
Prop. days ≥20cm snow	*54*	0.03	0.12	-0.26 °	-0.11	-0.07	0.08	0.18	-0.02	0.35 **	1		
Prop. days ≥30cm snow	*54*	-0.05	0.03	-0.16	-0.05	-0.05	-0.08	0.23 °	-0.04	0.23 °	0.83 ***	1	
Prop. days <0ºC	*54*	0.24 °	0.45 ***	-0.2	-0.02	-0.13	0.26 °	0.17	0.26 °	0.4 **	0.36 **	0.15	1

Table A.4: Pearson correlation matrix with pairwise comparisons among explanatory variables to explain summer damage (a) on the national scale, and per region; (b) *Norrland*, (c) *Svealand*, and (d) *Götaland*. Deer density indices were extracted one year prior to the browsing damage inventory and thus marked with ‘^{S}’ indicating ‘summer’. Superscript symbols indicate significance levels with ‘*’ $p \leq 0.05$, ‘**’ $p \leq 0.01$, and ‘***’ $p \leq 0.001$. ‘°’ represents $p \leq 0.1$. (from *Paper I*)

		Moose observations^{S}	**Moose harvest^{S}**	**Roe deer harvest^{S}**	**Red deer harvest^{S}**	**Fallow deer harvest^{S}**	**Pine density**	**Birch density**	**Prop. young forest area**
(a) Sweden	***n***	*137*	*148*	*148*	*148*	*148*	*145*	*145*	*148*
Moose observations^{S}	*137*	1							
Moose harvest^{S}	*148*	0.28 **	1						
Roe deer harvest^{S}	*148*	0.43 ***	-0.06	1					
Red deer harvest^{S}	*148*	0.02	-0.16 °	0.14 °	1				
Fallow deer harvest^{S}	*148*	-0.04	-0.22 **	0.19 *	0.66 ***	1			
Pine density	*145*	-0.23 **	-0.1	-0.69 ***	-0.09	-0.21 *	1		
Birch density	*145*	0.34 ***	0.17 *	0.49 ***	0.04	0.10	-0.4 ***	1	
Prop. young forest area	*148*	0.07	0.51 ***	-0.16 °	-0.12	-0.19 *	0.11	0.23 **	1
(b) Norrland	***n***	*29*	*33*	*33*	*33*	*33*	*33*	*33*	*33*
Moose observations^{S}	*29*	1							
Moose harvest^{S}	*33*	0.02	1						
Roe deer harvest^{S}	*33*	0.52 **	-0.04	1					
Red deer harvest^{S}	*33*	0.18	0.23	-0.05	1				
Fallow deer harvest^{S}	*33*	0.01	0.05	-0.04	0.81 ***	1			
Pine density	*33*	0.14	-0.20	-0.11	-0.05	0.26	1		
Birch density	*33*	0.21	0.46 **	0.32 °	0.02	0.02	0	1	
Prop. young forest area	*33*	0.25	0.55 ***	0.18	0.23	0.38 *	0.2	0.46 **	1

Continued.

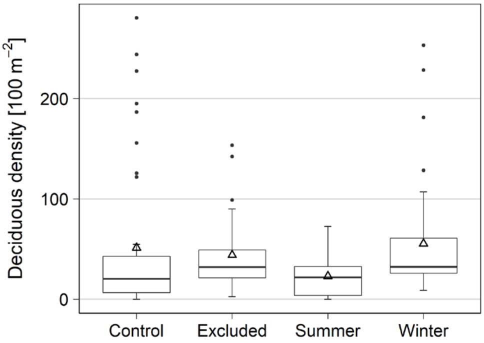
		Moose observations^S	**Moose harvest^S**	**Roe deer harvest^S**	**Red deer harvest^S**	**Fallow deer harvest^S**	**Pine density**	**Birch density**	**Prop. young forest area**
(c) Svealand	***n***	*56*	*59*	*59*	*59*	*59*	*59*	*59*	*59*
Moose observations^S	*56*	1							
Moose harvest^S	*59*	0.04	1						
Roe deer harvest^S	*59*	0.4 **	-0.32 *	1					
Red deer harvest^S	*59*	0.24 °	-0.19	0.35 **	1				
Fallow deer harvest^S	*59*	0.04	-0.26 *	0.34 **	0.77 ***	1			
Pine density	*59*	-0.11	-0.08	-0.54 ***	-0.27 *	-0.29 *	1		
Birch density	*59*	0.25 °	0.11	0.28 *	0.10	0.09	-0.33 *	1	
Prop. young forest area	*59*	-0.22	0.51 ***	-0.51 ***	-0.07	-0.08	0.08	0.14	1
(d) Götaland	***n***	*52*	*54*	*54*	*54*	*54*	*53*	*53*	*54*
Moose observations^S	*52*	1							
Moose harvest^S	*54*	0.51 ***	1						
Roe deer harvest^S	*54*	0.15	-0.19	1					
Red deer harvest^S	*54*	-0.21	-0.17	-0.25 °	1				
Fallow deer harvest^S	*54*	-0.32 *	-0.29 *	-0.25 °	0.35 **	1			
Pine density	*53*	-0.03	0.08	-0.42 **	0.52 ***	0.14	1		
Birch density	*53*	0.19	0.14	0.22	-0.20	-0.08	-0.06	1	
Prop. young forest area	*54*	0.23	0.51 ***	0.21	-0.18	-0.33 *	-0.16	0.46 ***	1

Table A.5: Likelihood of winter damage on Scots pine in relation to explanatory variables as given by the full GLMM across all study areas and years. Significant results are marked in bold. (from *Paper II*)

Explanatory Variables	Estimate(SE)	*t*-value	p
Half-average-height	0.04(0.06)	0.71	0.476
Moose density	**0.11(0.04)**	**2.92**	**0.004**
Deer density	0.01(0.09)	0.16	0.877
Scots pine density	**-0.14(0.05)**	**-3.00**	**0.003**
Downy birch density	**0.19(0.06)**	**3.17**	**0.002**
Silver birch density	**0.20(0.06)**	**3.58**	**<0.001**
PCT	-0.02(0.16)	-0.11	0.913
Proportion of pine forest >15m	-0.04(0.07)	-0.65	0.515
Conditional entropy	-0.05(0.05)	-0.93	0.351
df	710		
SD of random term	1.19		
Range of correlation structure	400.38		

Figures

(a) Scots pine



(b) Norway spruce

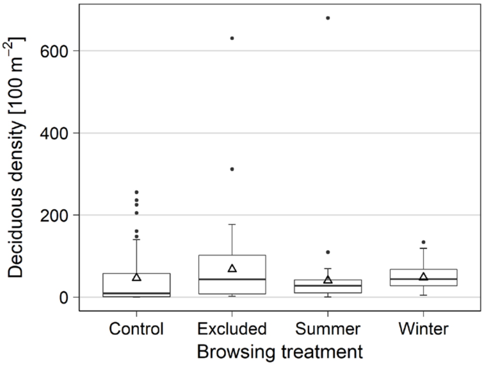


Figure A.1: Potential competition from deciduous density presented as deciduous stems taller than individually marked (a) Scots pine and (b) Norway spruce. Triangles illustrate mean values. (from *Paper III*)

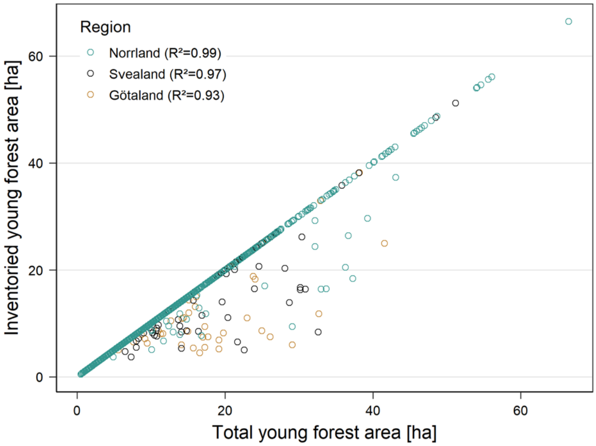


Figure A.2: Illustration of the inventoried against the total area of young forest stands per km-square per region. R^2 indicates the Pearson correlation coefficient between the two variables. (from *Paper IV*)

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During the past decades, the numbers and distributions of deer (*Cervidae*) increased across Europe leading to novel co-occurrences of several deer species. Therefore, a deep understanding on the impacts of these deer communities on boreal forests is needed across various spatial and temporal scales. This thesis uses observational and experimental data from national to local scales to investigate the drivers and effects of deer damage on economically important tree species in young forests in Sweden from a multi-species deer perspective.

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