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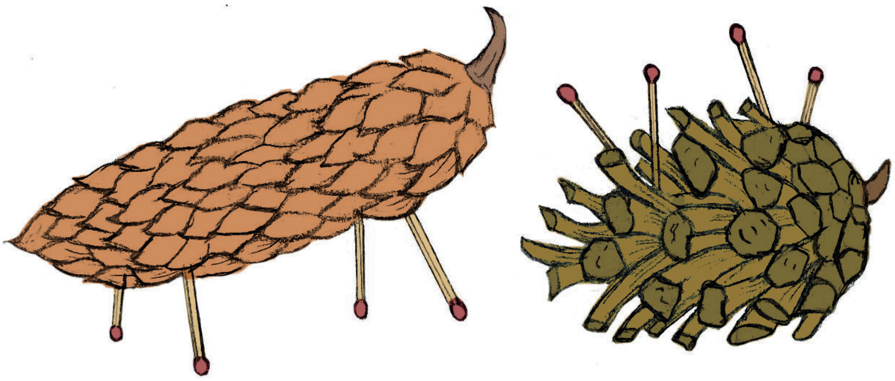
Implications for biodiversity in production forests

Lisa Petersson



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Abstract

The production forests of southern Sweden are mainly dominated by either Scots pine (*Pinus sylvestris*) or Norway spruce (*Picea abies*). Public concerns are now being raised regarding a decrease in the area on which Scots pine is being regenerated, and an increased reliance on Norway spruce production stands. The main reasons for a shift in regenerated tree species include concerns regarding higher ungulate browsing pressure on Scots pine regeneration, together with the expectation that Norway spruce provides more favourable management and profits. The aim of this thesis was to examine the potential consequences of a tree species shift from different perspectives, but with a primary focus on implications for biodiversity. To do so the diversity of vascular plants, bryophytes, lichens and birds were contrasted in three age classes (30, 55, 80 years of age) of Scots pine and Norway spruce production stands in southern Sweden. Although there was an overlap from many of the common species, the community composition of species groups varied between the stand categories contrasted. (**I**) The cover of understory vascular plants was higher in all stand age classes of the Scots pine stands, compared to Norway spruce. The semi-light conditions, created by Scots pine's less dense canopy, seems favourable to at least some keystone species, including, for example, the ericaceous shrub *Vaccinium myrtillus*. The denser canopy of Norway spruce limited vascular plant cover and species richness. (**II**) The darker and more humid Norway spruce stands were instead more favourable to a higher diversity of bryophyte species than was found in Scots pine stands. Scots pine associated forest floor species included a higher species richness and cover of terricolous lichens and bryophytes associated with dryer and lighter environment. (**III**) Scots pine and Norway spruce production forests support overlapping but still distinct bird communities, of which 80-year spruce stands had the highest average bird species richness, and largest total number of species recorded. These stands were associated with more broadleaves and higher stand complexity, i.e. vertical zonation, tree size variation and availability of dead wood. Study (**IV**) reviewed the biodiversity and ecosystem services consequences of a shift in tree species. Few benefits can be expected (e.g. reduced stand-level browsing damage), and these benefits will likely come at the expense of a range of negative outcomes for biodiversity, production, aesthetic and recreational values, as well as increased stand vulnerability to storm, frost, and drought damage, and potentially higher risks of pest and pathogen outbreak. Overall the findings of this thesis should clarify for forest owners, forest managers, and policymakers the many potentially adverse biodiversity and ecosystem service implications that could be expected if sites traditionally regenerated with Scots pine production stands are instead converted to Norway spruce.

Keywords: biodiversity, plant communities, conifer, hemiboreal zone, *Vaccinium myrtillus*, browsing pressure, light transmittance, tree species

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Ersätta tall med gran. Påverkan på den biologiska mångfalden i produktionsskogar

Sammanfattning

Produktionsskogarna i södra Sverige domineras oftast av antingen tall (*Pinus sylvestris*) eller gran (*Picea abies*). Eftersom antalet tallföryngringar har minskat den senaste tiden, har farhågor väckts inför ett alltför ensidigt beroende av granen som produktionsträd. De huvudsakliga anledningarna till att tallen minskar beror dels på det höga betestrycket i samband med föryngring, men också på uppfattningen att granen är ett förhållandevis lättskött trädslag som även tros kunna generera en högre inkomst. Målet med den här avhandlingen var att utifrån olika perspektiv undersöka vilka potentiella risker som finns vid ett trädslagsskifte, och framför allt att ta reda på hur det kan komma att påverka den biologiska mångfalden. Som ett led i detta, har kärlväxter, mossor, lavar och fåglar inventerats, i tre åldersklasser (30, 55 och 80 år) av tall- och grandominerade produktionsbestånd i södra Sverige. Trots att flera av de vanligt förekommande arterna återfanns i både tall- och granbestånd, så var det tydligt att de olika beståndsklasserna hyste olika artsamhällen. (**I**) Täckningsgrad av kärlväxter var högre i alla åldersklasser av tallbestånden jämfört med granbestånden. De halvljusa förhållandena som uppstår under tallens glesare trädkrona tycks framförallt gynna nyckelarten blåbär (*Vaccinium myrtillus*). Granens tätare krona verkar istället begränsa både kärlväxters utbredning och diversitet. (**II**) Den mörkare och fuktigare miljön i granbestånden var istället en mer gynnsam miljö för en större mängd olika mossarter, trots att täckningsgraden av mossor var lika hög i både tall- och granbestånd. De talldominerade bestånden präglades framförallt av en högre andel och mångfald av marklavar, samt sådana arter av mossor som anpassat sig till en torrare och ljusare miljö. (**III**) Produktionsskogar av tall och gran hyser till viss del överlappande, men samtidigt distinkta fågelsamhällen. Det högsta antalet arter, samt den största mängden observerade individer fanns i de 80-åriga granbestånden. Samma bestånd hade också en större andel lövträd och en mer komplex beståndsstruktur än resten av produktionsbestånden, till exempel fanns det där en jämförelsevis större mängd vertikala zoner, en högre variation av trädstorlekar samt en större tillgång på död ved. I studie (**IV**) sammanfattades konsekvenserna av ett trädslagsskifte för ett urval av olika artgrupper och ekosystemtjänster. En ökad granandel tycks kunna leda till vissa fördelar, som en minskad mängd betesskador vid föryngring. Samtidigt kommer förändringen att medföra en rad olika negativa konsekvenser för biodiversitet, produktion av skogsråvara, estetiska värden och rekreationsmöjligheter. En högre andel gran kommer också att leda till en ökad utsatthet för storm-, frost- och torkskador, och eventuellt även en ökad risk för utbrott av sjukdomar och patogener. Förhoppningen är att slutsatserna från den här avhandlingen, angående de många risker som förknippas med, och som kan förväntas av, en utökad plantering av gran på tallmarker, ska komma till nytta, för så väl beslutsfattare, som skogsägare och andra skogliga aktörer.

Nyckelord: biodiversitet, vegetation, barrskog, hemiboreala zonen, blåbär, betestryck, betesskador, ljustillgång, trädslag

Dedication

Till Daniel

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 Petersson, L.*, Holmström, E., Lindbladh, M., and Felton, A. (2019). Tree species impact on understory vegetation: Vascular plant communities of Scots pine and Norway spruce managed stands in northern Europe. *Forest Ecology and Management* 448:330-345.

II Petersson, L.*, Nilsson, S., Holmström, E., Lindbladh, M. and Felton A. Forest floor bryophyte and lichen diversity in production stands of Scots pine and Norway spruce stands (manuscript)

III Lindbladh, M.*, Petersson, L., Hedwall, P.-O., Trubins, R., Holmström E., and Felton, A. (2019). Consequences for bird diversity from a decrease in a foundation species—replacing Scots pine stands with Norway spruce in southern Sweden. *Regional Environmental Change* 19:1429-1440.

IV Felton, A.*, Petersson L., Nilsson, O. Witzell, J. Cleary, M., Felton, A. M., Björkman, C., Sang, Å. O. Jonsell, M., Holmström, E., Nilsson, U., Rönnberg, J., Kalén, C. and Lindbladh, M. (2019). The tree species matters: Biodiversity and ecosystem service implications of replacing Scots pine production stands with Norway spruce. *Ambio*. https://doi.org/10.1007/s13280-019-01259-x

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The contribution of Lisa Petersson to the papers included in this thesis was as follows:

I LP developed the research idea together with AF, EH and ML. LP performed the fieldwork and the statistical analyses. LP wrote the manuscript in collaboration with the co-authors.

II LP developed the research idea together with AF, EH and ML. LP performed the fieldwork and the statistical analyses. LP wrote the manuscript in collaboration with the co-authors.

III LP participated in planning and performing the fieldwork together with AF and ML. LP participated in writing the manuscript, which was led by ML.

IV LP participated in developing the research idea and wrote major portions of the manuscript, which was led by AF.

1 Introduction

In southern Sweden, public concerns are being raised regarding a decrease in the area on which Scots pine (*Pinus sylvestris*) is being regenerated, and an increased reliance on Norway spruce (*Picea abies*) production stands (SFA 2017). A primary concern arising from these changes is the resultant impact on forest biodiversity, because effective forest biodiversity conservation in Sweden relies on habitat contributions from both protected forests and forests managed for the production of wood biomass (Felton et al. 2019a). Furthermore, the impacts of these changes on both common and rare forest-dependent species could negatively affect the delivery of ecosystem services (Brockerhoff et al. 2017). Ecosystem services are the benefits people obtain, either directly or indirectly, from ecosystems (MEA 2005). The overall goal of this thesis was to examine the implications for forest biodiversity from the use of Scots pine or Norway spruce production stands, as well as to review the scientific literature regarding the potential effects of this shift in tree species for ecosystem services.

1.1 Forests and forestry in Sweden

The majority of Sweden's terrestrial area is covered by forests, equating with 69%, or 28 million hectares (SFA 2014). Approximately half of this forested area belongs to small scale private forest owners, and the rest belongs to forest companies and public owners, e.g. the Swedish state (SFA 2014). Most of the forest is used for the production of saw-timber and wood pulp, and the Swedish forest industry is one of the most mechanized and efficient wood product producers in the world. As a result, forestry is a key determinant of the resultant forest biodiversity and forest-derived ecosystem services provided by forest lands in Sweden, including the provision of forest products, recreational values, biodiversity, water regulation and carbon sequestration (Felton et al. 2019a).

Today, silvicultural operations such as clearcutting, soil scarification and the planting of even-aged monocultures have largely replaced what were once forest ecosystems driven by natural and semi-natural disturbance (Lindbladh et al. 2014, Svensson et al. 2018). Natural disturbances, including fire, storms, pests and pathogens, previously enabled a complex forest system combining even-aged, patch and gap scale dynamics, whereby different forest successions created high spatial and temporal heterogeneity of forest structures and disturbance histories at landscape levels (Kenkel et al. 1997, Kuuluvainen 2009, Kuuluvainen and Aakala 2011). The efficient extinguishing of forest fires, combined with highly effective and largely consistent forest management, has instead increased levels of biotic-homogenization at stand and landscape scales (Bradstock et al. 2005, Rolstad et al. 2017). Whereas the intensive management of forests can provide a large amount of wood biomass, it can also limit the biodiversity and ecosystem services provision of forest lands (Felton et al. 2016). Notably, since the early 1990s, Sweden's Forest Act has given equal status to environmental and production objectives (Gov. bill 1992/93:226). In addition to providing important habitat for forest biodiversity, Sweden's production forests also provide environments for recreation and non-wood forest products. Forest recreation is a widespread tradition in Sweden (Fredman et al. 2014), which includes visits to forests to experience the pleasure of nature, physical activities, and the hunting or collection of forest products (Lisberg Jensen and Ouis 2014), with likely benefits to mental health and wellbeing (Oh et al. 2017, Buckley et al. 2019). In this regard, the use of broadleaved trees and Scots pine are often considered to benefit the aesthetic value of a stand, especially close to residential areas. In terms of forest products, production stands can be important habitats for bilberry (*Vaccinium myrtillus*) – which is one of the most economically important wild berry species in Sweden (Lindhagen and Bladh 2013, Sténs and Sandström 2013), and edible mushrooms – for which annual collection is estimated to exceed 15 million liters in some years (Yrjölä 2002). Game animals add to the list of benefits supported by production forest lands, for which the annual gross value of the recreational benefits and the food provided is estimated to exceed 300 million USD (Boman and Mattsson 2012).

Here we provide a brief background to the development of todays' landscape in southern Sweden. This material sets the scene for the reader with the respect to the context within which current forest management is conducted.

1.2 Early development of forests in southern Sweden

Scots pine was one of the first tree species to reach southern Sweden after the last glaciation, and arrived together with other pioneer species, including birch (*Betula* spp.), goat willow (*Salix caprea*) and aspen (*Populus tremula*) almost 15 thousand years ago (Berglund 1996, Price 2015). Among the earliest forest types to develop, were forests dominated by Scots pine and birch, together with elements of aspen and goat willow. Later broadleaved species, such as lime (*Tilia cordata*), oak (*Quercus robur*/*petraea*), elm (*Ulmus glabra*) and beech (*Fagus sylvatica*) arrived (Björse and Bradshaw 1998). Still some thousand years ago the forests of southern-most Sweden were dominated by Scots pine and these broadleaf species. These type of forests were characteristic of the hemiboreal zone (Ahti et al. 1968) of Sweden until the arrival of Norway spruce. Norway spruce reached the northern parts of Götaland approximately 2000 years ago (Giesecke and Bennett 2004), migrating from refugia in eastern Europe (Tollefsrud et al. 2015). Meanwhile, it was not until the 20th century that Norway spruce became dominant in southern Sweden (Lindbladh et al. 2014). One reason for the slow expansion of Norway spruce from the north, relates to the prevalence of a natural and anthropogenic induced disturbance regimes favouring Scots pine (Bradshaw and Lindbladh 2005, Rolstad et al. 2017).

1.3 Human impacts on the landscape

Forest lands and forest products have been comprehensively used ever since humans first arrived to the Nordic lands around 10 000 years ago (Kardell et al. 2003). For a long time, some of the most important uses of these forests, was the grazing and collecting of fodder for livestock. In southern Sweden, abundant findings of pollen from juniper (*Juniperus communis*), through paleoecology studies, indicate that the forest landscape for a long time was characterized as open/semi-open (Björse and Bradshaw 1998). To improve grazing, areas of forests were regularly burned (Östlund 2000). Starting around 2800 years ago, the previous forested land of southern Sweden, was gradually transformed into a mosaic of hay-meadows, arable fields, grazing pastures and forest land (Myrdal and Morell 2011).

In the 19th century, the increased demand for timber, pot ash and tar expanded the commercial use of wood products (Kardell and Wennerberg 2004). In the second half of the 19th century, the agriculture of Sweden reached its largest extent in terms of open farmland (Myrdal and Gadd 2000). The combination of a higher demand for forest products, and the expansion of agricultural land, led to a substantial decrease in forest area in southern Sweden, leaving only those areas untouched that were difficult to access (Angelstam et al. 1997, Lindbladh et al. 2011). In the beginning of the 20th century, the introduction of chemical fertilizers in agriculture and the transition of forage production to arable land were important parts of the intensification of agriculture in southern Sweden (Myrdal and Morell 2001). As a consequence, the least productive areas were abandoned and, often as the result of natural succession, re-emerged as forest land (Dahlström et al. 2006). A large-scale transformation of the landscape started during the decades following after the Second World War, as many of the small farms were closed down or combined into larger units (Lindborg et al. 2008, Myrdal and Morell 2011). In connection to the land abandonment, plantations of Norway spruce were established on more fertile sites, which were often formerly crop land (Kardell and Henckel 1994, Lindbladh et al. 2014). The fact that until relatively recently most of the forested land of southern Sweden consisted of a mosaic of open semi-natural grasslands or semi-open forest land affected by forest grazing (Eriksson et al. 2002), is important to consider when evaluating the biodiversity contribution of today's forest landscape.

1.4 Scots pine and Norway spruce production stands in southern Sweden

The tree species composition of production forest stands in southern Sweden consist today of primarily Norway spruce or Scots pine. The current gap between the standing volume of Scots pine (29.8 %) and Norway spruce (47.3 %) (SFA 2014) is expected to increase in the future (Claesson et al. 2015). One reason for this is that Scots pine regeneration in southern Sweden has been below 10 % of the total regenerated area, during the last 10 years (SLU 2017). When accounting for the low proportion of Scots pine survival during the regeneration phase, often due to ungulate browsing and pine weevil (Bergqvist et al. 2014, Johansson et al. 2015), the proportion of area successfully regenerated with Scots pine is even lower. Recent data (2015-2018) indicates that the proportion of forest area in southern Sweden where Scots pine has succeeded (>1500 Scots pine stems ha^{-1}, 1-4 m in height), is only 1.53 % of the regenerated forest land (M. Ara, unpublished data, November 2019) .

Scots pine is a pioneer tree species, which establishes by rapidly colonizing open land, often after natural or anthropogenic disturbance events such as forest fires, storm-fellings, and clear-fellings (Lundmark 1988). Scots pine can establish across a wide range of soil and hydrological conditions which are often unfavourable for other tree species, due to the resultant stress, extremes of acidity and alkalinity, as well as waterlogging and drought (Connolly and Kelly

2000). In very nutrient poor sites where few other tree species can compete, Scots pine can form pure stands (Engelmark and Hytteborn 1999). High demand by individual trees for light and their low competitive ability, is however often associated with self-thinning and natural pruning as the stands get older. The resultant increase in combustible dry material (logs, snags, branches) can in turn feed forest fires, and is one reason why forest fire initiation rates can be higher in Scots pine compared to Norway spruce stands (Heidi et al. 2005). Additional adaptations for early succession environments include a deep rooting system, which makes Scots pine resistant in wind exposed locations, and thick bark, which protects older trees from fire, enabling seed set even after severe fire disturbance (Lundmark 1988). After such events, Scots pine can start a new forest succession via the establishment of pure even-aged stands (Kuuluvainen 2009).

In contrast, the later-successional tree species Norway spruce, often regenerates beneath the canopy of other trees, outcompeting earlier establishing pioneer species by overgrowth and shadowing (Lundmark 1988). To be able to grow in readily established forest stands, the needles of Norway spruce can adapt to growing in dark conditions (Gebauer et al. 2011). Furthermore, as different needle types are better suited to different light environments, Norway spruce can replace its needles if the environment changes to enable more efficient photosynthesis; e.g. in response to thinning (Gebauer et al. 2011) and natural gap formation. The higher density of the Norway spruce canopy (Goude et al. 2019) provides additional assistance to its competitive abilities by limited opportunities for other tree species to establish. A further effect of this dense canopy is to help maintain a humid microclimate on the forest floor, which helps prevent the outbreak of forest fires for which Norway spruce has limited tolerance (Lundmark 1988). Relative to Scots pine, Norway spruce is also more sensitive to wind throw and uprooting due to its shallow root system (Peltola et al. 2000).

Even though Scots pine essentially prefers the same site conditions as Norway spruce, i.e. mesic, fertile soils, Scots pine is regarded as being unable to compete with Norway spruce on such site conditions, and is only considered to be a superior competitor to Norway spruce on nutrient poor, dry or very wet sites (Leijon 1979, Engelmark and Hytteborn 1999). Nevertheless, Scots pine increment growth can be equal to or even better than Norway spruce in at least northern regions of Sweden (Ekö et al. 2008, Nilsson et al. 2012). When comparing the growth of Scots pine and Norway spruce in central Sweden, Scots pine produced 126 % more stem wood biomass compared to Norway spruce

(Holmström et al. 2018), while comparison of data from the Swedish national forest inventory indicates that Scots pine growth equates with only 60 % of that by Norway spruce in southern Sweden (Ekö et al. 2008). Although there is a lack of studies comparing the growth of Scots pine and Norway spruce in southern Sweden (but see Nilsson et al. (2019), for early regeneration growth comparisons) there seems to be a general perception that Norway spruce provides higher production returns than Scots pine in this region (Lodin et al. 2017).

1.5 Reasons for the tree species shift

Lodin et al. (2017) interviewed forest owners in southern Sweden regarding their thoughts about why they preferred Norway spruce as the crop tree for regeneration. They found that forest owners thought that the easier management of Norway spruce relative to alternative tree species (e.g. Scots pine and broadleaf trees), together with clear management regimes and established and reliable markets, were important factors when deciding which tree species to plant. These questions were asked in the context of regeneration decisions after the storm 'Gudrun' felled the equivalent of approximately 70 million cubic meters of timber primarily comprised of Norway spruce (Valinger and Fridman 2011).

A key additional reason for choosing Norway spruce is because regeneration failures are often linked to more intensive browsing pressure on the saplings of native tree species alternatives, including Scots pine (Wallgren et al. 2013). Even though large herbivores, including moose (*Alces alces)* and roe deer (*Capreolus capreolus*), generally prefer to consume the leaves, stems and shoots of broadleaf tree species over Scots pine seedlings (Månsson et al. 2007, Bergqvist et al. 2014), the lack of deciduous forage in the landscape and the increased ungulate populations in this region may be a reason why the browsing pressure on Scots pine has increased (Angelstam et al. 2000, Petersson et al. 2019a). Despite the fact that Scots pine is considered better suited to low productive sites, the regeneration of Norway spruce is now also occurring on these sites (SFA 2019). As a result, the proportion of the standing volume of Norway spruce in southern Sweden is predicted to increase even more in the future (Claesson et al. 2015).

1.6 Indicators for biodiversity in forested ecosystems

Biodiversity refers to the variability among all living organisms as found within genes, species, and ecosystems (CBD 2011). Trees are the foundation of forest ecosystems, providing the resources and environments on which many other organisms depend. Because of the large variation in the characteristics of different tree species, different combinations of trees will have distinct impacts on light, water and soil nutrients (Barbier et al. 2008). The presence of a diversity of trees is often important for biodiversity, not just because of the associated variation in resources and habitats provided within a forest, but also because many organisms are dependent on specific host tree species for their survival (Sundberg 2019).

In addition to the implications of different tree species, there are other disturbance and structural related aspects of forest systems that are important determinants of forest biodiversity. For example, time-since disturbance, or forest age, is an important factor for the establishment of many species. Old structures and the occurrence of old trees can increase species richness and the number of red listed species (Fritz and Brunet 2010). In addition to providing more time for colonization (Hedwall et al. 2013), and increased area for colonization (height and girth), older and/or larger trees can develop attributes not found in younger trees, including numerous cavities, vertically heterogeneous crowns, crenulated bark, and large lateral branches (Lindenmayer and Laurance 2016). The reproductive success of some species can be closely tied to the availability of old large trees, as in the case of excavated nesting holes, or large diameter branches supporting birds' nests (Stokland 2003). There is also a correlation between forest age and the occurrence of late decomposition stages of dead wood (Bond and Franklin 2002). Several thousand species, including many threatened species of bryophytes and fungi are dependent on different decomposition stages of dead wood sourced from different tree species (Berg et al. 2002, Stokland et al. 2012). In managed forest stands, the stand age rotation length limits the time of both large diameter older tree species, and the dead wood that is allowed to develop. Consequently, the occurrence of late decomposition stages of dead wood is usually lower in production forest stands, than in natural forests, and tends to decrease in forests with a longer history of intensive forest management (Stokland et al. 2012).

Not all forest associated species are dependent on long forest continuity. There are also numerous species that depend on the early succession stages of forests following a disturbance. Storm felling, forest fire and diseases resulting from insect or fungus attack are considered the most important natural disturbances in the hemiboreal forests (Niklasson and Drakenberg 2001). In most cases natural forest stand replacements are initiated by forest fires and in Norway spruce stands, wind storms are also of importance for the gap dynamics (Kuuluvainen and Aakala 2011). Naturally occurring disturbance-succession cycles are important for understanding both ecological and evolutionary functions in forest systems (Kuuluvainen 2009, Kuuluvainen and Aakala 2011). Large amounts and varieties of dead wood are often provided by these types of disturbances (Stokland 2003, Jonsson et al. 2016), and some insect and plant species are specialized on the structures and conditions provided in burned forest land (Hjältén et al. 2009). Furthermore minor disturbances, such as wind throws, browsing and selective cutting can also promote the establishment of many species (Stokland 2003).

2 Thesis aim

The aim of this thesis was to examine the implications for forest biodiversity, and review the scientific evidence relevant to projecting impacts on different ecosystem services, from the use of Scots pine or Norway spruce production stands. To meet this goal, production stands of Scots pine and Norway spruce of three distinct age categories were compared on similar sites and within the same region of southern Sweden.

The most important questions raised were:

I. What are the differences between Scots pine and Norway spruce production stands in southern Sweden in terms of understory vascular plant abundance and species composition? What are the tree species specific drivers likely underlying these differences?

II. What are the differences between Scots pine and Norway spruce production stands in southern Sweden for forest floor bryophyte abundance and species composition? How do the Scots pine and Norway spruce forest floor environments differ?

III. What are the differences between Scots pine and Norway spruce production stands in southern Sweden, in terms of bird species diversity and community composition, and how do these contrast with conifer-dominated reserves within the same region?

IV. What are the potential implications for biodiversity and a range of forest-derived ecosystem services from the two tree species Scots pine stands to Norway spruce, as synthesized from the published scientific literature?

3 Material and methods

3.1 Method used for the empirical studies (I-III)

In paper I-III, empirical studies were conducted for comparing biodiversity found in production stands of Scots pine and Norway spruce. To do so we contrasted aspects of biodiversity found within Scots pine and Norway spruce dominated production stands, in order to get an idea about consequences of Scots pine decline for biodiversity. In study I-II, we focused on the understory vegetation, i.e. vascular plants, bryophytes and terricolous lichens. Bird communities were surveyed in study III.

3.1.1 The study area: Småland, southern Sweden

The study area was located in Småland, southern Sweden within the two adjacent counties of Kalmar and Kronoberg (Fig. 1). This part of Sweden is characterized by a mosaic of agricultural land, forest stands, mires and lakes. The area is dominated by silicate rich bedrock, i.e. granite and rhyolite, with occasionally occurring patches of mafic bedrock (e.g. gabbro and amphibolite). The soil cover was to a large extent formed during the last glacial period. Soil texture is typically medium grained till and degraded fluvio-glacial sediment, but there are also areas with peat and exposed base rock.

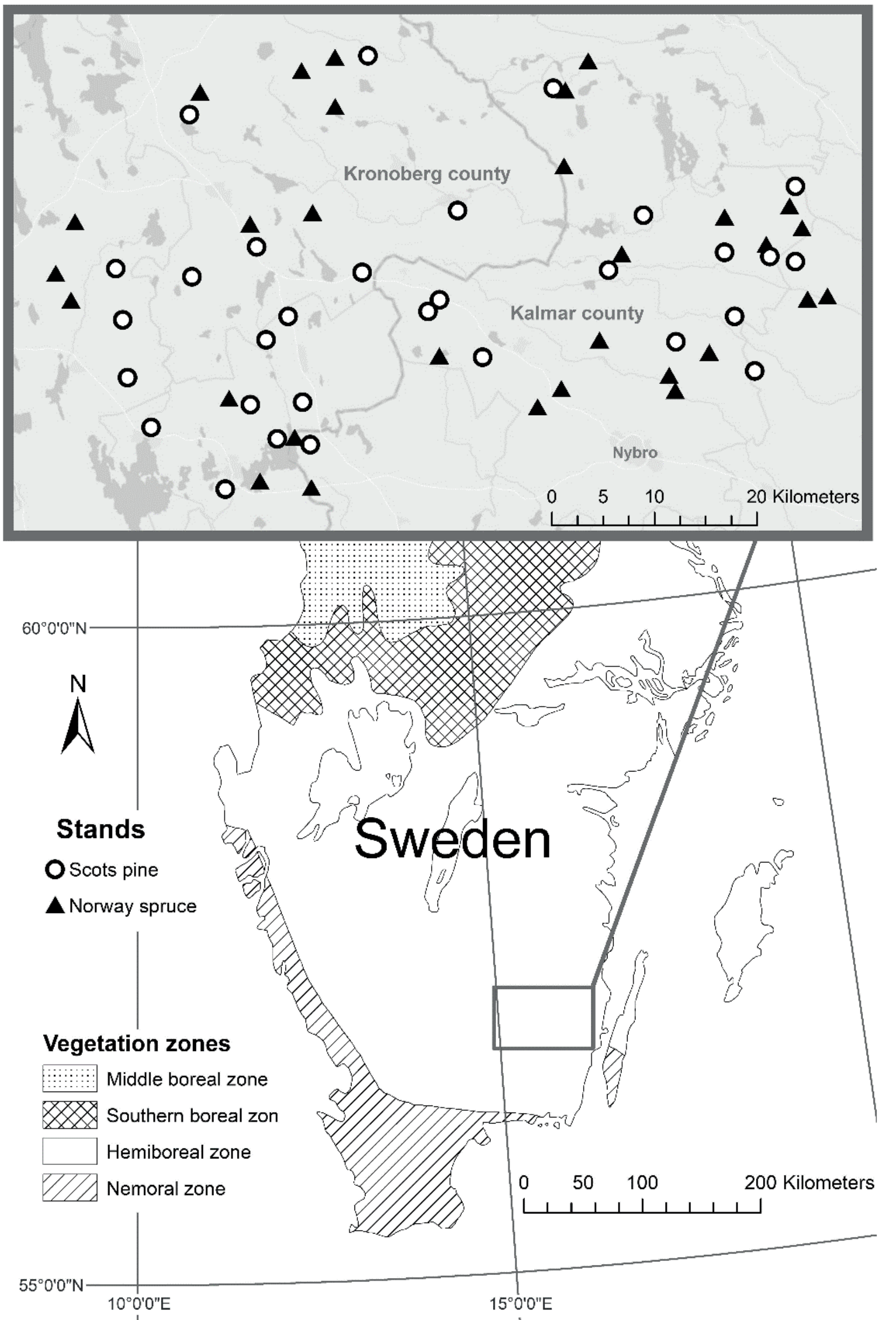

Figure 1. The study area is located in the hemi boreal zone of southern Sweden. The upper part of the figure shows the location of the Scots pine (circles) and Norway spruce (triangles) stands (Petersson et al. 2019b).

3.1.2 Site selection

In total 30 Scots pine and 30 Norway spruce dominated stands were selected from the land ownership databases of Sveaskog (forest company owned by the Swedish state) and Södra skogsägarna (private forest owners association). To capture early- middle- and late rotation periods, three age categories of stands were chosen: 30 (+/-5), 55 (+/-5) and 80 (+/-5) year old.

The following additional selection criteria were used to limit the range of confounding variables and increase the importance of the primary tree species in dictating resultant outcomes for forest biodiversity. By so doing we increased the applied relevance of our findings to the ongoing transformation of Scots pine production stands to Norway spruce.

- The dominant tree species – Scots pine or Norway spruce – had to constitute at least 80 % of standing volume (m^3 ha^{-1}).

- The sites were located on till soils, with an underlying bedrock of either granite or rhyolite (SGU, bedrock map, soil type map 1:25 000-1:100 000).

- Forest plan site index (SI) was restricted to G24-G29 m for Norway spruce (SI referring to projected mean height of the dominant trees at the stand age 100 years). The Scots pine SI was transformed into the corresponding value for Norway spruce according to Hägglund and Lundmark (2003).

- Sites should have a continuity of forestry according to historical maps (Economic map 1941-1949).

3.1.3 Vegetation sampling (I-II)

In every stand, a total of 10 plots were surveyed. The first four survey points were placed in the central parts of the stands, and the six additional were added from them in random directions (Fig 2). Survey points were located beforehand using GIS to avoid onsite selection bias. Points were concentrated within the centre of each stand, to reduce edge effects. This constraint also helped to ensure that survey points were not displaced over larger areas in larger stands, which could have biased outcomes due to an increased range of environments surveyed. The presence of all understory species of bryophytes, terricolous lichens and vascular plants were registered in 100 m^2 circular plots centred on the survey points (radius 5.64 m). In the same plots, dead wood and the abundance of tree saplings was also measured. To quantify the abundance of the different understory species, 2×2 m quadrats were placed in the very centre of each circle. Here, the abundance of the understory species was measured in percentage cover. Forest structure variables, i.e. basal area, stem density and light transmittance was measured around all vegetation plots within a radius of 7-15 meters.

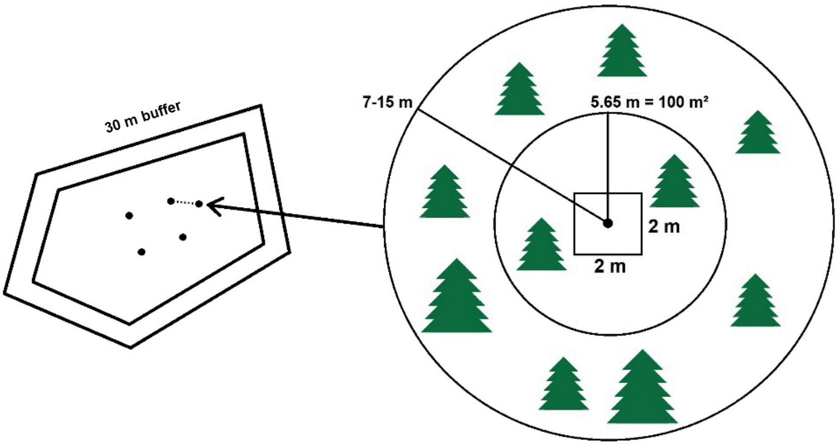

Figure 2. Schematic drawing of the vegetation and stand structure survey. Left part of picture: The first four points were placed in the very central part of the stand, before the additional six plots were added in random directions. Right part of picture: The setup of each plot, with different variables being measured within different sized plots.

3.1.4 Bird inventory (III)

The bird survey was conducted during spring and summer of 2017. In this study, the 55 and 80 year old stands of Scots pine and Norway spruce were included, together with ten additional stands selected from conifer-dominated forest reserves (> 75 % basal area of coniferous trees) located in the study area. Reserves were included to capture the available species pool of conifer-associated bird communities. Bird surveys were performed using the point count method (Bibby 2000) and restricted to those individuals engaged in territorial behaviour (primarily singing) within 40 m of the four central plot points of the stands (Fig. 2). Three persons participated in the survey, visiting each plot four times: twice in the end of March/beginning of April, and twice in the end of May. Surveys were similarly conducted in the nature reserves, and measures of forest structure as described above were used.

3.2 Method used for the review study (IV)

The aim of paper IV was to summarize the available research concerning the differences between Scots pine and Norway spruce in terms of biodiversity and ecosystem service provision, in order to evaluate potential consequences of a tree species shift. The choice of topics assessed was targeted towards those issues frequently raised by forest stakeholders, including production outcomes, damage risk, recreation, and biodiversity (Lidskog and Sjödin 2014, Lodin et al. 2017, SFA 2017), as well as being dictated by the expertise of participating researchers. We examined how the shift from Scots pine to Norway spruce would affect different ecosystem services, and different taxonomic groups of biodiversity:

- **Cultural services**
  Aesthetics and recreation

- **Provisioning services**
  Wood production and quality

- **Regulatory services**
  Biotic and abiotic risks, climate suitability

- **Biodiversity**
  Vascular plants, bryophytes, epiphytic lichens, birds, saproxylic beetles and large herbivores

We used Boolean search terms, to find relevant studies. The databases used were Web of science (http://isiwebofknowledge.com), Google scholar (http://scholar.google.com) and Scopus (https://www.elsevier.com/solutions/scopus). In addition, we collected additional papers through reference lists and from colleagues. We also obtained information from books and reports. We prioritized studies conducted in even aged monocultures of Scots pine or Norway spruce in Fennoscandia.

3.3 Nomenclature, indicator species and red lists

Throughout the thesis, the English common names are used for birds, mammals and trees, except where introduced. For bryophytes, lichens and other vascular plants than trees, the scientific names are used according to Dyntaxa (Dyntaxa 2019). The Ellenberg indicator values for bryophytes were extracted from Bernhardt-Römermann et al. (2018). The most recent red list of threatened species for Sweden was used in this thesis, together with the European red list for bryophytes in Europe (Westling and Gärdenfors 2015, Hodgetts et al. 2019).

4 Result and discussion

4.1 Different environmental drivers explain understory vascular plant abundance and species richness (I)

In this study, abundance and diversity of the vascular plant understory of Scots pine and Norway spruce stands was examined. Scots pine stands had a consistently higher cover of vascular plants, for which the dwarf shrub species *Vaccinium myrtillus* and *V. vitis-idaea* (Fig 4, 5) provided the highest percentage coverage. These two species of ericaceous shrubs were also present in most of the Norway spruce plots, but only with low coverage. We also found that light transmittance was consistently higher in the Scots pine stands, compared to the Norway spruce stands (Fig 3). As we tested the relationship between light transmittance and the abundance of vascular plants in Scots pine stands, there was no significant result, suggesting that light transmittance in these stands was consistently sufficient for field layer development. In contrast, within the Norway spruce stands there was an increase of vascular plant cover with increasing light transmittance, and also an increase in species richness. The finding of higher vascular plant cover in Scots pine stands, compared to Norway spruce stands is consistent with findings from northern Sweden, Finland and France (Tonteri et al. 1990, Augusto et al. 2003, Bäcklund et al. 2015). Other studies have also found that the cover of *V. myrtillus* in Scots pine stands is highest at a basal area of 30-40 m^2, after which it decreases (Eldegard et al. 2018). Very few Scots pine plots exceeded that high basal area in this study with the result that we could not confirm or challenge this finding (Fig. 3).

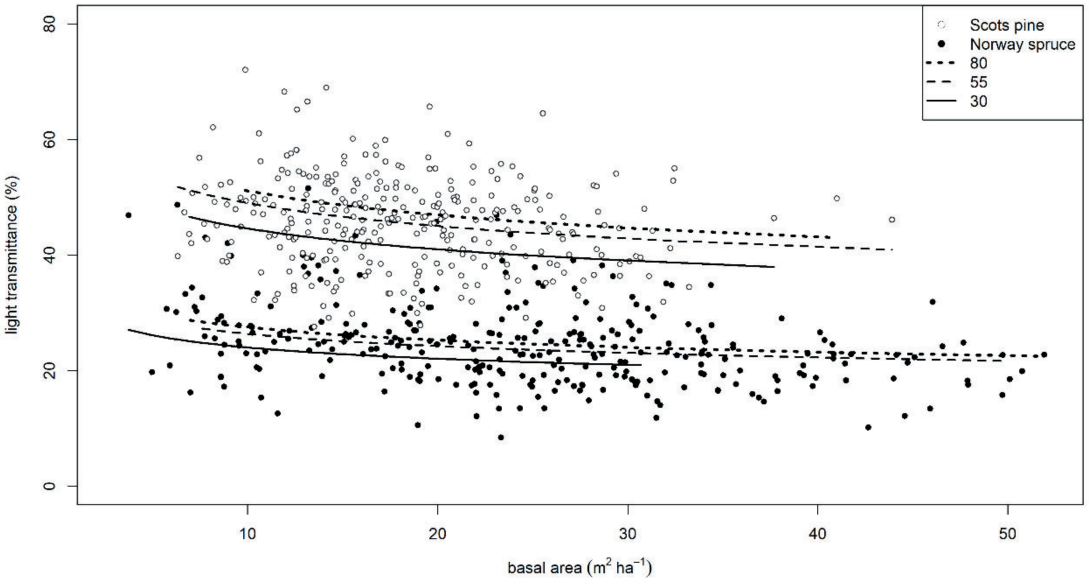

Figure 3. Basal area plotted against light transmittance in 600 sites, representing 60 stands of Scots pine and Norway spruce. The trend lines show the predicted light transmittance as the average for each combination of Scots pine and Norway spruce and the different stand ages (30, 55 and 80 years old) (Petersson et al. 2019b).

There was also higher density of tree saplings in the Scots pine stands (Fig. 6), although this was accompanied by high variation in this density between stands. Consistent with the percentage cover of vascular plants, the density of tree saplings increased with higher light transmittance in the Norway spruce stands, whereas there was no impact from light on their density in the Scots pine stands.

Figure 4. The dwarf shrub *Vaccinium myrtillus* was the most abundant vascular plant species in the Scots pine stands (Photo: Lisa Petersson).

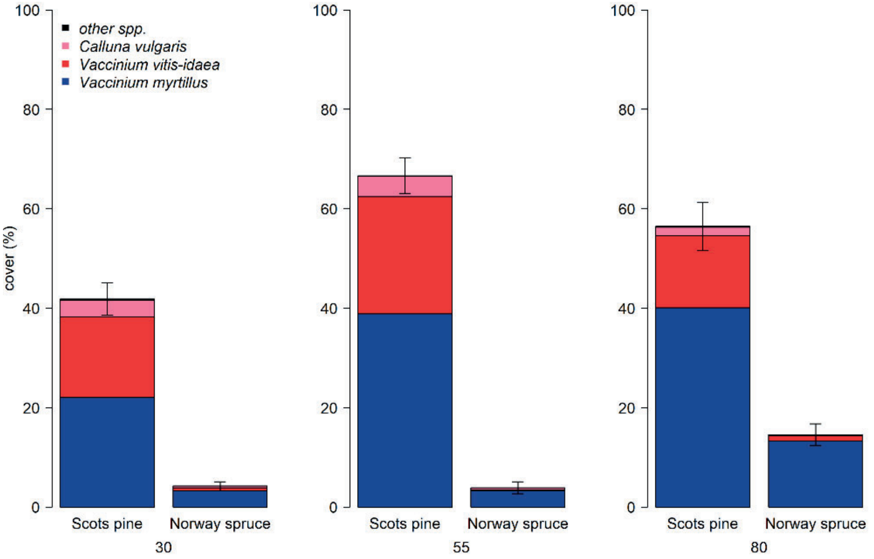

Figure 5. Dwarf shrub cover was higher in Scots pine stands for all stand age classes. The most abundant dwarf shrub species was *V. myrtillus*, followed by *V. vitis-idaea*, *Calluna vulgaris, Empetrum nigrum* and *V. uliginosum*. D (Petersson et al. 2019b).

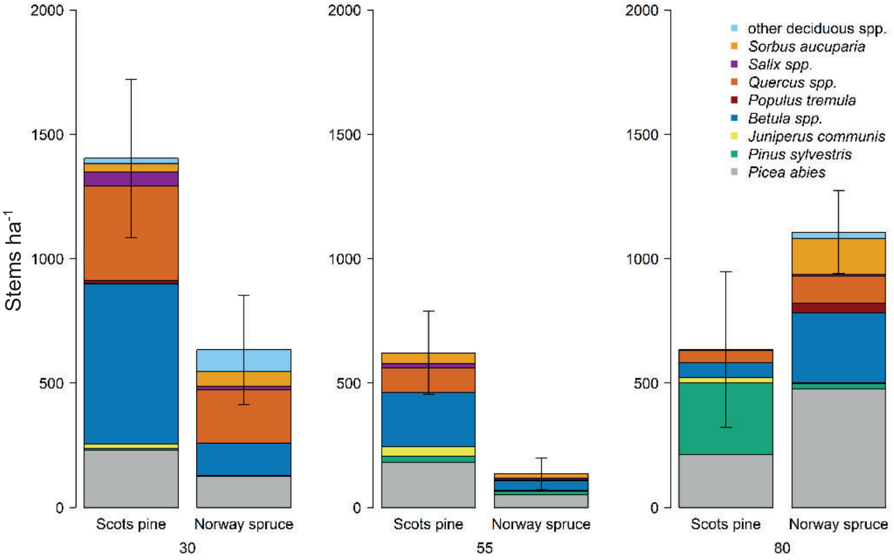

Figure 6. Density of tree saplings (stems ha^{-1}) and the standard deviation in Scots pine and Norway spruce stands (Petersson et al. 2019b).

Changes in the vascular plant cover supported by production forest lands in this region can have cascading flow on impacts for biodiversity and ecosystem services. The dwarf shrub *V. myrtillus* is generally considered to be a keystone plant for forest biodiversity; meaning that a decline in their stand or landscape scale abundance will have corresponding impacts on a large number of additional species (Mills et al. 1993). For example, many species rely heavily on *V. myrtillus* as forage, including some ungulates, the bank vole (*Myodes glareolus*) and capercaillie (Storch 1993, Selas et al. 2011). In addition, there are more than fifty insect species (mainly *Lepidoptera*) that are dependent on *V. myrtillus* as a host plant (Sundberg 2019). Other studies have shown that the development of denser forests, has caused a decline of dwarf shrubs in southern Sweden during the last twenty years (Hedwall and Brunet 2016). Furthermore, *V. myrtillus* plays an important role for the provision of non-wood forest products and for recreational values (Saastamoinen et al. 2000).

Even though Scots pine stands seemed to provide more favourable environments for the percentage cover of vascular plants, the species richness of vascular plants was higher in Norway spruce stands. Correspondingly, the lowest species richness of vascular plants was found in the oldest category of Scots pine stands.

This result may be linked to the theory of climax communities (Clements 1936). At the pioneering stage of forest development, e.g. after clearcutting, early colonizers tend to establish rapidly. As the succession proceeds, competitive and long lived species tend to outcompete the early succession species (Kuusipalo 1985). If communities then remain undisturbed for a long time they can become dominated by a few strong competitive species, with corresponding implications for the species richness of the resultant communities (Widenfalk and Weslien 2009). This is thought to occur, for example, in the late successional stages of Scots pine forests in southern boreal mesic sites (Tonteri et al. 1990).

Historical land-use is also known to have an effect on forest biodiversity, even after long time periods since land use changes occurred (Ibbe et al. 2011, Jonason et al. 2016). Despite trying to account for this by using historical maps (origin from 1941-1949) to avoid including sites without a long continuity of forestry, there seemed to be differences between land use history between the two stand types. For instance, some of the Norway spruce stands had remnants of Scots pine stumps, showing they were at least partly once occupied by trees of Scots pine. In other Norway spruce stands, the occurrences of vascular plant species indicative for semi-natural grasslands, e.g. *Hypericum maculatum*, *Lathyrus pratensis*, *Vicia cracca*, *Geum urbanum* and *Rumex acetosa*, gave the impression that former hay-meadows or pastures had been planted, or alternatively of late succession ingrowth. Notably, similar observations were not made in any of the Scots pine stands. Other studies have found that vascular plants originating from semi-natural grasslands can survive in managed forests (Milberg et al. 2019), and seeds stored in the seed bank can sprout again, for instance after trees have been uprooted (Lyhagen 2006). In this regard, vascular plant species richness may temporarily stay higher in forest stands with a history of different land use. Especially since higher species richness tends to emerge when different communities are combined. It is unclear to what extent these effects will endure several regenerations of intensively managed production forests.

4.2 Bryophyte and terricolous lichen communities indicate different forest floor conditions (II)

In this study we examined the bryophyte and lichen diversity of the forest floor in Scots pine and Norway spruce stands. We found that although the percentage cover of bryophytes was the same in both stand types, species richness was higher in the Norway spruce stands. The two pleurocarp species *Pleurozium schreberi* and *Hylocomium splendens* were the most prevalent bryophytes in both Scots pine and Norway spruce stands as indicated by percentage cover. Notably, the cover of terricolous lichens was higher in the Scots pine stands and highest in the intermediate aged stands. The two species *Cladonia rangiferina* and *C. arbuscula* largely dominated these results. Overall however, the cover of these two lichens was relatively low compared to what can be found in younger Scots pine stands, and in northern Fennoscandia (Bråkenhielm and Persson 1980, Herder et al. 2003).

The multivariate analysis (CCA) revealed different community compositions in the Scots pine and Norway spruce stands (Fig. 7a). The species associated with the Scots pine stands (Fig. 7b) were often adapted to a drier environment, as indicated by the pointed leaves of *Racomitrium heterostichum*, *R. lanuginosum*, *Campylopus introflexus* and the undulate leaves of *Dicranum spurium*, that form small water retaining chambers (Watson 1914, Hallingbäck and Knorring 2006). The larger number of Norway spruce associated species, instead represented a large variety of life forms, including several species dependent on dead wood.

In an additional analysis, Ellenberg indicator values for bryophytes (Bernhardt-Römermann et al. 2018) were used to map differences between Scots pine and Norway spruce forest floor environmental conditions. We found that the bryophyte communities in the Norway spruce stands had a higher proportion of taxa with an affinity for low light and high humidity conditions, relative to the communities found within Scots pine stands. In relation to the Norway spruce stands, Scots pine associated communities were more associated with a continental climate, higher temperatures and had lower nitrogen requirements.

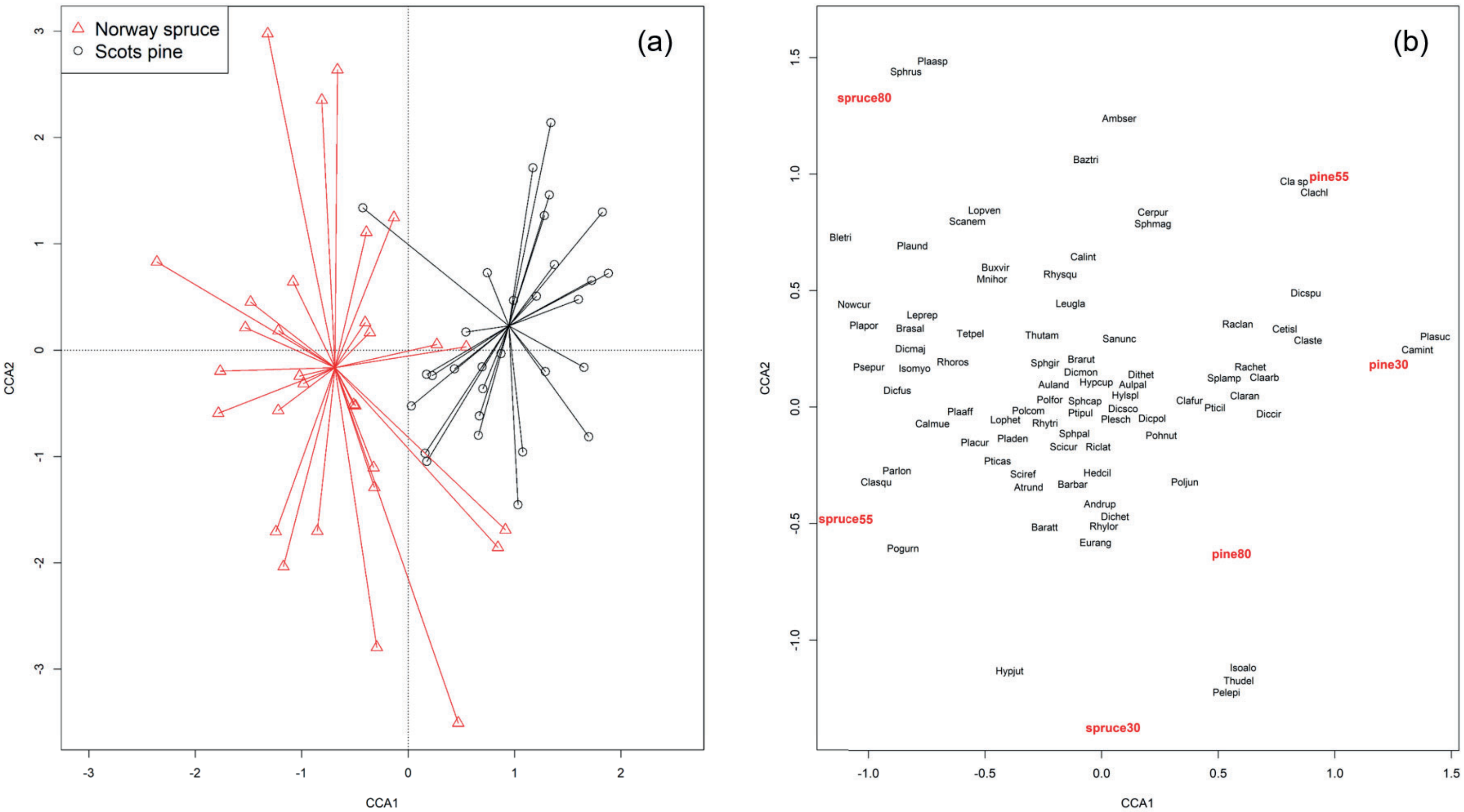

Figure 7. CCA plot (a) shows the location of each stand depending on the forest floor community composition of the 30 Norway spruce (triangles) and 30 Scots pine (circles) forest stands. CCA plot (b) shows the forest floor community composition, consisting of 85 species of bryophytes and lichens in the same Norway spruce and Scots pine stands. The plot also shows the location of the six different stand classes in the ordination plot. Forest floor species name codes consist of the three first letter s of the genus and the three first letters of the species' epithet.

4.3 Old forest structures support bird diversity (III)

In this study we found that Scots pine and Norway spruce stands supported largely overlapping but nevertheless distinguishable bird communities. In total 32 different species of birds were recorded in the production stands during the surveys, but only a few species were unique to the different stand types. Notably, the highest species richness was recorded in the 80 year old Norway spruce stands, for which species richness was higher on average than in the nature reserves assessed. This result was unexpected, as unmanaged stands usually provide a larger diversity of habitats and associated bird communities than managed forest stands (Rosenvald et al. 2011). However, whereas the reserves did harbour some large diameter trees and significant volumes of dead wood, these areas nevertheless supported few other indicative features of true old-growth forests, i.e. tree sapling undergrowth and large tree species diversity. Although the reserves supported a lower bird diversity than expected, they made a larger contribution to the diversity at landscape scale (gamma diversity) (Whittaker 1960) than the production forest stands.

One possible explanation for higher bird species richness in Norway spruce relative to Scots pine production stands, may result from the larger amount of vertical zonation. It has long been established that different bird species prefer spending time in different vertical zones within forests (Colquhoun and Morley 1943, Pedley et al. 2019). For example, different species can allocate higher or lower proportions of their time within distinct higher or lower tree strata (Sturman 1968, Pedley et al. 2019). In this respect, the self-pruning of Scots pine trees consequently results in fewer available branches at lower strata. In contrast, the branches of Norway spruce trees often extend further down the stem providing greater vertical opportunities for e.g. foraging (Edenius and Meyer 2002). Other reasons why the old Norway spruce stands had higher bird diversity may stem from larger forest structure complexity, i.e. variance in stem DBH and the comparably larger availability of dead wood (Hewson et al. 2011). These variables have been found to be important in previous research assessing drivers underlying the diversity of forest bird communities within different forest types (Rosenvald et al. 2011, Eldegard et al. 2014, Lindbladh et al. 2017). In either regard it is important to emphasize that the eldest category of Norway spruce stands examined is also the age and forest type category of production stand least likely to persist if rotation lengths are shortened in the future (Felton et al. 2017).

4.4 Red listed taxa (I-III)

The three red listed plant species encountered were all found in Scots pine stands. The hawkweed *Hypochaeris maculata* (VU in Sweden) was found in three plots and the bryophyte *Splachnum ampullaceum* (NT in Europe) was found on two occasions. They are both associated with open forest conditions with high light levels, as indicated by their habitat distribution, that ranges from pasture land to open forests. The third red listed plant species, the orchid *Goodyera repens* (NT in Sweden), was found once in a Scots pine stand. It requires forests with long continuity (Edqvist 2011), but tolerates a wide range of environments, from mesic-moist Norway spruce forests, to dry sandy Scots pine forests; although it seems to be more associated with Scots pine across its European range (Connolly and Kelly 2000, Edqvist 2011).

Of the six bird species unique to Scots pine, only tree pipit (*Anthus trivialis*) and spotted flycatcher (*Muscicapa striata*) were recorded in higher numbers. Both are among the ten most common birds in the country, with national abundances of over 1 million pairs (Green 2019). Hence, it is difficult to argue that the decrease in Scots pine poses an imminent risk to any particular bird species. Two red listed species were found in the production stands assessed in this study: goshawk (*Accipiter gentilis*) (NT) and goldcrest (*Regulus regulus*) (VU). The goshawk was encountered once each in the 80 year old Scots pine and Norway spruce stands. Goshawks prefer hunting in older forests, and the decline of old forests is one possible reason for their population decline (Widén 1997). In stark contrast, the goldcrest was the second most abundant bird species encountered in the survey and was found in all stand categories surveyed (55, 80 year old and nature reserves). During the last ten years goldcrest is one of the bird species that has increased the most in Sweden, but from a longer time perspective the population has declined, and hence its vulnerable status (Green 2019).

4.5 The tree species matters for multiple reasons (IV)

Our results highlighted the importance of tree species choice in production forest stands for a wide variety of biodiversity and ecosystem service related outcomes. First, this tree species shift had complicated and scale dependent implications for forest biodiversity that were inconsistent across the taxonomic groups assessed (Table 1). Whereas the stand-level diversities of large herbivores and vascular plants were projected to decrease, the opposite was projected for bryophytes and birds, with uncertain outcomes projected for epiphytic lichens and saproxylic beetles. These stand-level distinctions in biodiversity outcomes were however not reflected at landscape scales, for which negative outcomes were projected for most taxa due to the increased homogeneity of forest lands, and the underlying and important differences in community composition. With respect to red listed species, negative outcomes could only be projected for the vascular plants and epiphytic lichens, with uncertain or neutral outcomes projected for the other taxonomic groups assessed.

Table 1. Expected changes at the stand level for species diversity, community composition and red listed species from the shifting of Scots pine to Norway spruce. The outcomes are graded: positive- "↑", negative- "↓", neutral/no change- "◯", and uncertain outcomes ↕. The species diversity includes the combination of both species richness and abundance. The delta symbol "Δ" indicates a change in community composition, a key consideration when determining landscape-scale biodiversity impacts. "Effect modifiers" indicate forest management that strongly impacts on outcomes. The confidence levels (i.e. *, **, ***) represent "possible", "probable", and "highly probable" outcomes, but are not relevant to "uncertain" outcomes (Felton et al. 2019b).

Biodiversity		Expected general change		Effect modifier
	Stand –level species diversity	Community composition	Red listed species	
Vascular plants	↓**	Δ***	↓*	Stand density / canopy cover
Bryophytes	↑*	Δ***	↕	Rotation length, coarse woody debris retention
Epiphytic lichens	↕	Δ***	↓*	Rotation length
Saproxylic beetles	↕	Δ***	↕	Dead wood occurrence Stand insolation / temperature
Birds	↑*	Δ***	◯**	Broadleaf retention levels, rotation length
Large herbivores	↓**	◯*	N/A	Stand density / canopy cover; broadleaf retention

The ecosystem services outcomes were specifically evaluated with respect to the impacts of stand conversion on provisioning services, cultural services and regulatory services; the latter of which was assessed in terms of abiotic and biotic risks (Table 2). First, in terms of cultural services, the outcomes of Scots pine stand conversion to Norway spruce was consistently negative. From forest aesthetics and stress recovery, to hiking, hunting, and berry picking, the replacement of Scots pine stands with Norway spruce appears to decrease the cultural values of production forest. The primary caveat in this regard is that in urban landscapes, Norway spruce may provide higher utility for stress recovery due to its insulating properties (Hauru et al. 2012).

Whereas it could be expected that positive production outcomes would be an outcome of this assessment, both biomass production and product diversity were projected to decrease with the conversion of Scots pine stands to Norway spruce. Furthermore, these negative outcomes were not overcome by a clear wood price benefit for Norway spruce. Compounding these results, production outcomes can also be challenged by the wide range of increased disturbance risks found to be associated with Norway spruce. The use of Norway spruce on Scots pine sites was deemed to increase stand-level vulnerability to storm, drought, and frost damage, as well as the risks posed by bark beetle and root rot. Notably the only clear advantage of planting spruce in terms of regulatory services, was the previous mentioned reduction in the risk of browsing damage to regenerating seedlings and saplings. Even in this regard an important caveat is needed. If the proportion of Scots pine decreases in a landscape, browsing pressure on the few remaining Scots pine seedlings may increase further (Wallgren et al. 2013, Bergqvist et al. 2014). In other words, stand-scale reductions in browsing damage may compound browsing related damage at landscape scales (Wallgren et al. 2013, Bergqvist et al. 2014). This likewise raises concerns that conversion pressures favouring Norway spruce will in-turn increase with Norway spruce conversions, thereby providing a positive feedback loop with the associated adverse biodiversity and ecosystem services outcomes identified.

Table 2. Expected implications at the stand level of Scots pine conversion to Norway spruce for different ecosystem services. The outcomes are graded in terms of positive outcomes "↑", negative outcomes "↓", and uncertain outcomes ↕. The "Effect modifier" indicates management with a strong impact on the outcomes. Different confidence levels (i.e. *, **, ***) represent "possible", "probable", and "highly probable" outcomes. These are not relevant when the outcomes are "uncertain" (Felton et al. 2019b)

Ecosystem services	Positive or negative outcomes	Effect modifiers
Provisioning		
Biomass production	↓*	Varies with type and extent of disturbance (e.g. browsing pressure vs. storm damage)
Product diversity	↓*	
Wood prices	↕	
Cultural		
Forest aesthetics	↓**	
Hiking	↓**	
Hunting	↓*	
Bilberry picking	↓***	
Stress recovery	↓**	Potential to improve in urban areas
Regulatory services		
Abiotic risks		
Projected outcomes due to:		
Climate damage	↓**	Extent of future GHG emissions
Storm damage	↓***	When thinning and harvest takes place
Drought damage	↓***	
Fire damage	↕	Ignition risk may be lower in spruce, but damage higher if a fire occurs; unknown implications of spruce on dry sites
Frost damage	↓***	
Biotic risks		
Projected outcomes due to:		
Browsing damage	↑***	However, conversion may increase / focus landscape scale damage
Spruce bark beetle damage	↓***	
Other bark beetle damage	↓**	Tree stress may allow other bark beetles to become pest species
Root rot damage	↓***	Higher spruce stem densities are likely to increase risks

5 Main conclusions from each paper

(I) The vascular plant communities associated with Scots pine and Norway spruce stands was distinct in terms of community composition. Vascular plant cover was higher in the Scots pine stands, but species richness was higher in the Norway spruce stands. The available light transmittance seems to be a key factor for vascular plant abundance and species richness in the Norway spruce stands. Meanwhile, available light transmittance seemed to be consistently sufficient in the Scots pine stands, as no effect was associated regarding variation in light transmittance and vascular plant abundance and species richness in these stands.

(II) Bryophyte abundance was the same in Scots pine and Norway spruce stands, but the cover of lichens was higher in the Scots pine stands. Although a small number of pleurocarpous bryophyte species dominated the forest floor of both Scots pine and Norway spruce stands, multivariate analysis revealed different community compositions. Species richness of bryophytes was higher in the Norway spruce stands. The bryophyte indicator species analysis showed that Scots pine and Norway spruce micro habitats are different from each other when it comes to light, moisture, temperature, continentality, acidity and nitrogen.

(III) There was a large, but not complete overlap in bird community composition in Scots pine and Norway spruce stands. The highest species richness was found in 80 year old Norway spruce stands, which was also higher than the species richness found in the reserves. Stand level diversity was generally higher in the Norway spruce stands, but both stand types are important to maintain biodiversity at the landscape level. In addition, the reserves made a larger contribution to avian diversity at landscape scales than the production forest stands.

(IV) The ongoing shift from Scots pine to Norway spruce is associated with negative landscape scale outcomes for biodiversity, and a wide range of ecosystem services, spanning provisioning, cultural and regulatory categories. Although some positive aspects at stand level were identified for some taxa, the effect at landscape levels were primarily negative. Biomass production was limited and likely further constrained by the multiple biotic and abiotic risks associated with Norway spruce, which are likely to increase with climate change. The one clear exception was the likely reduced stand-level risks of browsing damage in Norway spruce stands. In terms of cultural services, the outcomes of Scots pine stand conversion to Norway spruce was consistently negative.

6 General conclusion

The results of this thesis indicate that although there was an overlap in many of the commonly occurring species, the community composition of vascular plants, cryptogams and birds diverged, at least to some extent between Scots pine and Norway spruce stands, and with large differences in the abundance of some taxa. The different traits associated with the two tree species, seemed to be an important determinant of the environmental conditions provided in these production forest alternatives. In the Norway spruce stands, denser canopies limited development of the vascular plant layer and associated species richness. At the same time, the more humid environment of Norway spruce benefited a larger variety of bryophyte species. With respect to the bird communities encountered, similar or higher species richness in Norway spruce production stands was countered by the non-overlapping community composition supported by these two stand types. If Norway spruce is replacing Scots pine at landscape scales, this can be expected to limit landscape scale diversity. More generally, an expanded use of Norway spruce at the expense of Scots pine will have a direct negative effect on species dependent on semi-open forest conditions. This includes the dwarf shrub species *V. myrtillus*, which is an important key-stone species for many additional species and highly appreciated for its recreational and non-wood forest product values. Furthermore, most taxa were projected to have negative population outcomes due to any resultant increase in the homogeneity of production forest lands. As a result, differences between Scots pine and Norway spruce stands in the habitats provided, environments created, and species supported, mean that long term costs to at least some aspects of landscape-scale biodiversity can be expected if such conversions take place.

More broadly our results suggest that an expanded use of Norway spruce at the expense of Scots pine is associated with negative outcomes for a range of ecosystem services. Both biomass production and wood product diversity were projected to decrease if Scots pine stands were converted to Norway spruce.

Compounding these results, production outcomes may also be challenged by increased disturbance risks associated with Norway spruce. The use of Norway spruce on Scots pine sites is also likely to increase stand-level vulnerability to storm, drought, and frost damage, as well as the risks posed by bark beetle and root rot. Also, if the proportion of Scots pine decreases in a landscape, browsing pressure on the few remaining Scots pine seedlings may increase further (Wallgren et al. 2013, Bergqvist et al. 2014), and thereby increase incentives to avoid regeneration with Scots pine.

In summary, the findings of this thesis will ideally help to clarify for forest owners, forest managers, and policy makers the many adverse biodiversity and ecosystem services implications that can be expected if Scots pine stands are replaced with Norway spruce.

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