The Introduction of *Pinus contorta* in Sweden

Implications for forest diversity

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Cover: A 15-year old *Pinus contorta* stand. Dorotea, Sweden
(photo: S. Bäcklund)

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Abstract

An increasing demand for forest-based products calls for further development and intensification of forest management. The use of non-native tree species in forestry is a common and expanding silvicultural practice worldwide but the effect of non-native trees on native biodiversity and ecosystem functioning is still poorly understood. The general aim of this thesis is to increase our knowledge about what effects large-scale introduction of a non-native tree species have on forest biodiversity over a chronosequence of forest stand ages. The non-native *Pinus contorta* and the two native tree species *Pinus sylvestris* and *Picea abies* were studied over three age classes (15, 30, 85 years old) of managed forests in northern Sweden to compare the stand- and tree structures, the cover and composition of functional groups of ground vegetation, and the species- and functional diversity of epiphytic lichens. Differences in ground vegetation cover were linked to both tree species and different stand and tree characteristics, but the differences were not consistent over the age classes. Stands of *P. contorta* had higher cover of vascular plants than the native tree species, and the cover increased with increasing stand age. Trees of *P. contorta* generally were of larger size than native tree species of comparable age, and also had greater branch surface area in young and middle aged stands, indicating more available substrate for epiphytes. However, the species richness of epiphytic lichens in *P. contorta* stands was comparable to *P. sylvestris* and the highest species richness was found in *Picea abies* stands. Although the forests shared many species, the composition progressively diverged with increasing forest age. Presence of dead branches, greater bark crevice depth and canopy cover generally had positive effect on functional trait diversity, and the reproductive strategy and growth form were the most influential traits on differences in functional diversity between tree species at early successional stages. Generally, the results suggest that abiotic and biotic factors common to all young managed forests act as environmental filters that cause similarly low levels of functional diversity and functional insurance among their epiphytic lichen communities. In conclusion, the planting of *P. contorta* does not create “green deserts” from the perspective of epiphytic lichens or understory vegetation. However, most stands of *P. contorta* are still younger than 50 years, and to assess the implications on forest diversity over a full rotation cycle, future studies should focus on describing diversity in old *P. contorta* stands.

Keywords: Boreal forests, managed forests, Pinus contorta, species richness, lichens, vascular plants, canopy cover, branch density, life history.

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Dedication

Till familj och vänner

Allt flyter (Panta rei)
Herakleitos

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 Bäcklund, S., Jönsson, M.T., Strengbom, J. & Thor, G. (2015). Composition of functional groups of ground vegetation differ between planted stands of non-native *Pinus contorta* and native *Pinus sylvestris* and *Picea abies* in northern Sweden. *Silva Fennica* 49(2), article id 1321.

II Bäcklund, S., Jönsson, M.T., Strengbom, J., Frisch, A. & Thor, G. (2016) A pine is a pine and a spruce is a spruce – the effect of tree species and stand age on epiphytic lichen communities. PLoS ONE 11(1): e147004.

III Jönsson, M.T., Bäcklund, S., Strengbom, J. & Thor, G. Differing patterns of lichen species and functional-trait diversity in managed forests. (manuscript).

IV Bäcklund, S., Jönsson, M.T., Strengbom, J. & Thor, G. Tree and stand structures of non-native *Pinus contorta* in relation to *Pinus sylvestris* and *Picea abies* in managed forests in boreal Sweden. (manuscript).

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The contribution of Sofia Bäcklund to the papers included in this thesis was as follows:

I Main author, field work and analysis. Developed research questions and design and wrote the paper together with MJ, JS and GT.

II Main author, field work and analysis. Developed research question and design and wrote the paper together with MJ, JS, AF and GT.

III Second author and field work. Developed research question and participated in writing together with MJ, JS and GT.

IV Main author, field work and analysis. Developed research question and design and wrote the paper together with MJ, JS and GT.

1 Introduction

1.1 Forestry and the relocation of tree species

Forest management generally aims to maximize the benefits of a planted tree species. The preferred tree species can be of both native and non-native origin, and many tree species have been used outside their native range (e.g. Richardson, 1998). Reasons for introducing plantations of non-native trees include a higher growth rate than that of native tree species, early onset of maturity, and resilience to pests and diseases (Richardson, 1998). However, replacing native forests with non-native forests can both alter associated native species composition and cause considerably lower species richness (Brown *et al.*, 2006). Introductions may especially be problematic when they result in a very different stand and tree structure than that of the preceding vegetation (Bremer & Farley 2010).

1.2 Boreal forests and forestry

The boreal biome covers about 30% of the world's forested area and is dominated by coniferous trees (Hansen *et al.*, 2010). Under natural conditions, boreal forests are structured and shaped by disturbance and succession (Kuuluvainen, 2009). Wildfires of varying severity can cause large scale disturbances, but wind and/or pest outbreaks may occasionally also have large impact (Kuuluvainen, 2009; Esseen *et al.*, 1997; Östlund *et al.*, 1997). As the succession progress after major disturbance events, additional, frequent, small-scale disturbances (e.g. small pest outbreaks, dying trees) cause gaps in the forest cover which enables regeneration of trees, resulting in a wide age distribution of trees in natural forests (Kuuluvainen, 2009; Esseen *et al.*, 1997).

Large parts of the boreal biome are intensively managed (Hansen *et al.*, 2010; FAO, 2010), and over vast areas disturbance have been more or less replaced by forestry management practices (Cyr *et al.*, 2009; Kuuluvainen, 2009). Therefore, structures common in natural forests (e.g. wide age distribution, large old trees, and cohorts of deciduous trees) have decreased (Östlund *et al*., 1997) and have been largely replaced by more or less even-aged monocultures (Fig. 1) with few deciduous trees and comparably small structural variation (Kruys *et al*., 2013; Paillet *et al*., 2009; Esseen *et al*., 1997).

Figure 1. Even-aged monoculture of 85-year old *Pinus sylvestris* outside Dorotea, Sweden. Photo: S. Bäcklund

In Fennoscandia, the most common forest types are managed forests of Norway spruce *Picea abies* (L.) H. Karst. and Scots pine *Pinus sylvestris* L. (Esseen *et al*., 1997) The common management practise is final harvest, soil preparation, regeneration by planting, seeding, or natural regeneration, followed by one or more thinning events. The fire frequency in the forests has decreased, partly due to effective fire suppression and partly due to a dense network of forest roads (Östlund *et al.*, 1997). Small disturbance gap dynamics have little impact on the forest structure because the forests are harvested at a relatively young age compared to natural forests (Fricker *et al.,* 2008). The rotation period is usually between 60-120 years depending on site conditions and choice of tree species (Fricker *et al.*, 2008; Korosuo *et al.*, 2014). The amounts of dead wood, both standing dead wood and downed dead wood, have decreased and large and old trees are rare (Stokland *et al.*, 2012; Brassard & Chen, 2006; Linder & Östlund, 1998) Generally, the forests are denser than the forests a century ago and the proportion of young forests are much higher (Linder & Östlund, 1998).

To improve structural diversity in managed forests, groups of trees, old and/or deciduous trees and snags are often retained at final harvest to be part of the new stand (Gustafsson *et al.*, 2012). Retention forestry may be a powerful way to restore boreal production forest to more natural conditions, although the delivery time can be long (Lämås *et al.*, 2015).

1.3 Species and functional trait diversity in managed forests

Structural diversity in forests is important to uphold high species diversity (Lõhmus & Lõhmus, 2008; Johansson *et al.*, 2007; Dettki & Esseen, 1998). A diverse structure of tree species and tree ages provide different habitat niches that can be colonized by various organisms, and the structures and associated species change over time during forest succession (Kuuluvainen, 2009; Schoonmaker & McKee, 1988). Both native and non-native managed forests include variations in factors relating to the stand (e.g. canopy cover, tree basal area, humidity, soil) and the tree (e.g. bark structure, bark pH, branch vigour, branch size) that may affect epiphytic species differently and thereby also the overall diversity patterns.

Much research on biodiversity issues has been focused on species richness (i.e. how many different species that exist within the area of interest) and species composition (i.e. the identity of species and their relative abundance) in relation to different environmental gradients. Currently however, the focus is shifting towards a mechanistic understanding of the biology behind such observed patterns in biodiversity. Within this more mechanistic framework, biodiversity is expressed as functional diversity (FD). The traits link directly to the environment and the traits of a species will determine its performance in relation to environmental conditions (Violle *et al.*, 2007). Studies on FD can contribute to a deeper understanding of the mechanistic process that control species distributions (Villéger *et al.*, 2008; McGill *et al.*, 2006), and are thereby an important complement to species diversity studies. The FD is the variation of traits within the community, and it is composed of three different parts; functional richness, i.e. the range of trait variability in a community, functional evenness, i.e. the abundance distribution of different traits, and finally, the functional dispersion which describe the degree of dissimilarity in abundance distributions (Mason *et al.*, 2005). Functional traits are any morphological, physiological and phenotypic feature of an organism that determines its ability to grow, reproduce or survive and thus directly, or indirectly, impact its fitness (Violle *et al.*, 2007; Petchey & Gaston, 2002). Traits can be further divided into response traits that determine sensitivity to environmental factors (e.g. growth form, environmental tolerance) and effect traits that determine ecosystem functioning (e.g. traits that influence nitrogen cycling or photosynthesis efficiency) (Laliberté & Legendre, 2010; Lavorel & Garnier, 2002; Díaz & Cabido, 2001).

1.4 *Pinus contorta*

Lodgepole pine, *Pinus contorta* Dougl. var. *latifolia* Engelm*.,* is a coniferous tree species native to North America which under natural conditions regenerates after large, stand replacing fires (Despain, 2001). The serotinous cones allow the seeds to survive the fire and germinate in the newly disturbed soil (Despain, 2001). However, not all cones are serotinous and during the first 20-30 years *P. contorta* produces non-serotinous cones that enable long-distance seed dispersal (Despain, 2001). Once established, *P. contorta* is able to outgrow any competitors (Fricker *et al.*, 2008; Despain, 2001). Although *P. contorta* is tolerant to various environmental conditions, it has trouble regenerating under an existing tree cover (Fricker *et al.*, 2008; Despain, 2001). *Pinus contorta* has been planted widely outside its native North American distribution range, mainly to increase forest production, but also as an erosion control (Sykes, 2001). It is known to colonize land marginal to other tree species where competition (i.e. shading) is low (Despain, 2001). In some areas, primarily in the southern hemisphere, *P. contorta* has become invasive in grasslands and open forests (Richardson, 2006; 1998), and New Zealand has suffered major problems with unwanted dispersal of *P. contorta* into grass- and shrublands (Ledgard, 2001). In the Chilean Patagonia, planting of *P. contorta* has been recognized as a major threat to native ecosystems, both because it potentially will invade grasslands and outcompete native vegetation, but also because it may cause increased fire intensity (Langdon, *et al.*, 2010). In the boreal biome, *P. contorta* has been introduced in several countries (Backman & Mårald, 2015; Langdon *et al.*, 2010; Richardson, 2006), but so far it does not appear to be invasive (Sanderson *et al.*, 2012). However, because of the wide ecological amplitude of *P. contorta*, there is a risk of unwanted dispersal far outside the intended area (Despain, 2001; Sykes, 2001).

1.4.1 *Pinus contorta* in Sweden

The first introductions of *Pinus contorta* to Sweden were made around 1920 (Engelmark *et al.*, 2001). Large scale introduction to Swedish forestry started in the 1970s, with the objective to mitigate an anticipated timber shortage (Elfving *et al.*, 2001). *P. contorta* has higher productivity compared to the native *Pinus sylvestris* regardless of site index, and the rotation time could thereby be shortened by approximately 10-15 years (Elfving *et al.*, 2001). Despite of some early setbacks with low stability and fungal outbreaks (Karlman 1981), *P. contorta* is still used in Swedish forestry. Since 2010, the area annually regenerated with *P. contorta* is 6–8 000 ha (Forest statistics 2014). Today *P. contorta* covers about 550 000 hectares and it constitutes 1.2% of the tree volume on productive forest land in Sweden (Forest statistics 2014). Planting of *P. contorta* is primarily allowed between latitude 60^{o} and 68^{o} north, but with some restrictions. Planting is not allowed in the vicinity (<1 km) of nature reserves or national parks, neither is it allowed above certain altitudes (depending on the latitude) (Swedish Forest Agency, 2016). The Swedish Forest Agency can allow exceptions, e.g. for scientific reasons (Swedish Forest Agency, 2016).

Few studies have evaluated the implications of planting *P. contorta* as a non-native tree species. Studies on ground vegetation suggest a simplification and homogenization of the flora, and that the ground vegetation cover is skewed towards higher bryophytes cover under *P. contorta* compared to *P. sylvestris* (Roberge & Stenbacka, 2014; Nilsson *et al.*, 2008). There are also reports of altered community composition of epigaeic beetles (Roberge & Stenbacka, 2014), and Gundale *et al.* (2014) showed that the absence of soil borne pathogens increases growth in the introduced range which might affect the risk of *P. contorta* becoming invasive. Nilsson *et al.* (2008) included some arboreal lichens on downed wood in their study, but found no major differences between *P. contorta* and *P. sylvestris*. There are no studies focusing on the effect of *P. contorta* on epiphytic lichens. However, as lichens are confined to the substrate they inhabit (Lie *et al.*, 2009), there is likely a potential effect of replacing native tree species with *P. contorta.* Part of the uncertainties of the effects from the introduction of *P. contorta* are linked to the fact that the existing planted stands are still young, and studies covering a complete forest management cycle are therefore not possible. Nonetheless, it is important to study the effect on native biodiversity also in younger *P. contorta* forests. Altered species composition and biotic interactions at younger stand ages may influence the succession of species in older stand ages.

1.5 Ground vegetation in boreal forests

Ground vegetation is an important component of forest biodiversity and changes in ground vegetation can influence ecosystem processes (Nilsson & Wardle, 2005) and has therefore been used as an indicator of changes in biodiversity and ecological integrity following e.g. shifts in the dominant tree species (Suchar & Crookston, 2010; Humphrey *et al.*, 1999). Ground vegetation in non-native managed forests is, however, not necessarily that different compared to native forests (Brockerhoff *et al.*, 2008). A shift of the dominant tree species will have more profound effects on associated vegetation if the introduced tree species differ largely from the native tree species it replaces (Meers *et al.*, 2010). For example, we might expect a change in native understory species if the introduced tree species create substantial changes in canopy closure or litter composition (Vilà *et al.*, 2011). Needle litter has been found to be chemically different in stands of *P. contorta* to that of *P. sylvestris* (Ågren & Knecht, 2001). In addition, as *P. contorta* also produce more litter than the native species, *P. contorta* stands can have a thicker litter layer than stands planted with native species (Nilsson *et al.*, 2008). A thick layer of litter can alter the amount of light reaching the soil surface which may prevent plant propagule germination and establishment (Leishman & Westoby, 1994). Taken together this suggests that composition of the ground vegetation, and ecosystem processes and functions linked to it, may differ in stands planted by *P. contorta* compared to stands planted with native species (Fig. 2).

Figure 2. Ground vegetation in the only 85-year old *Pinus contorta* stand, Dorotea, Sweden. Photo: S. Bäcklund.

The development of forest structures and the composition of the ground vegetation change in predictable fashion with time since disturbance (Johnsson *et al*., 2014; Kuuluvainen, 2009; Clark *et al*., 2003). Grasses are often abundant the first years after clear cutting, but as the canopy closes, grass cover gradually declines and other more shade-tolerant species become abundant (Widenfalk & Weslien, 2009). Bryophyte cover is known to increase with time since disturbance in boreal forests (Lindgren *et al*., 2006). The cover is generally high (above 40-50% in young forests) and increasing to about 80% in older managed stands (Uotila & Kouki, 2005). Dwarf shrubs, especially *Vaccinium myrtillus*, have also been shown to increase in abundance for up to at least 80-100 years in managed stands in the middle boreal vegetation zone (Uotila & Kouki, 2005). In addition, Nilsson *et al*. (2008) found a positive correlation between stand age and lichen cover in both *P. contorta* and *P. sylvestris* stands in Sweden.

1.6 Lichens in boreal forests

Lichens are major contributors to the biodiversity of boreal forests (Ellis, 2012). They can be found on a wide variety of substrates, including rocks, trees and on the ground, and they are a diverse group of different growth forms and functional traits (Hauck, 2011). Lichens can provide shelter for insects, be used as nesting material for birds, and they function as food for e.g. snails and reindeers (Ellis, 2012; Esseen *et al*., 1997). Moreover, lichens might play a major role in the cycling of nutrients of the boreal forest (Ellis, 2012).

Lichen diversity in boreal forests is influenced by factors of varying importance depending on spatial scale (Lie *et al.*, 2009; Nascimbene *et al.*, 2009), e.g. on large spatial scales, climatic gradients and altitude are important, whereas on a finer scale, stand age and tree species might provide better explanations to the observed patterns of diversity (Lie *et al.*, 2009; Nascimbene *et al.*, 2009). At the scale of a single tree, factors like pH, bark texture and branch quality can be important to understand the species composition of epiphytic lichens (Hauck, 2011; Lie *et al.*, 2009). Ground living lichens (terricolous lichens; e.g., *Cladonia* spp.) are influenced by ground properties, competition from other vegetation and the amount of light reaching the ground through the canopy (Crittenden, 2000). Coxson & Marsh (2001) found that lichen ground cover can increase during stand development in naturally developed pine-lichen woodlands, but in more productive forests, as studied in Paper I in this thesis, where lichens are not the dominating ground-cover type, no such temporal trend may be expected.

Intensive forest management has resulted in lower species abundance of epiphytic lichens as well as lower biomass of pendulous lichens (e.g. ArtDatabanken 2015; Dettki & Esseen 1998; Esseen et al., 1996,). Epiphytic lichens can be affiliated with certain tree species, and many studies suggest that a mixture of tree species, which is rarely found in managed forests, is important to preserve lichen species diversity (Nascimbene *et al.*, 2010; Lõhmus & Lõhmus, 2008; Dettki & Esseen. 1998). It has also been shown that choice of tree species is important for lichen diversity in plantation forestry, where lower lichen species richness was found on non-native *Eucalyptus* in Spain, but the likewise non-native pine species had higher species richness, although not as high as native oak (Calviño-Cancela *et al.*, 2013).

2 Thesis Aim

The general aim of this study is to increase our knowledge about what effects a non-native tree species have on native biodiversity when introduced as a forestry tree over large areas, and how these effects develop over a chronosequence of forest stand ages. The specific questions for each paper were:

I How does cover and composition of functional groups of ground vegetation differ between *Pinus contorta* and the native conifers *Pinus sylvestris* and *Picea abies*? Are differences influenced by the age of the stand?

II How are epiphytic lichens influenced by the non-native *Pinus contorta*? Is choice of tree species important for the epiphytic lichen species richness and composition?

III How does species and functional trait diversity patterns differ for epiphytic lichens in non-native *Pinus contorta* and native conifers *Picea abies* and *Pinus sylvestris*?

IV How do the stand- and tree structures of non-native *Pinus contorta* differ from the native conifers *Picea abies* and *Pinus sylvestris*?

3 Methods

3.1 Study area

The study area is located in the northern boreal zone (Ahti *et al.*, 1968) and centered within a 30 km radius around the town Dorotea (64°15'N, 16°24'E) in northern Sweden. The annual mean temperature is +1°C (+13°C in July, and −13°C in January) and the length of the growing season is approximately 140 days. Mean annual precipitation is ca 700 mm of which about 35-40% falls as snow (SMHI). The dominating soil type is podsolized till (Markinfo, 2016). The vegetation in the area is predominantly ericaceous dwarf shrubs (mainly *Vaccinium myrtillus* and *V. vitis-idaea*). The tree cover primarily consists of managed coniferous forests of *Pinus sylvestris* and *Picea abies* as monocultures or mixed forest. *Pinus contorta* has been planted to a large extent, and the proportion of the forested area planted with *P. contorta* is about 10% (Jansson, 2011). Deciduous trees, mainly *Alnus incana*, *Betula pendula*, *B. pubescens*, *Populus tremula* and *Salix* spp. are present in the study area, but mostly in small groups or as single trees. The forests are owned to about 70% by a single forest company, SCA, which enabled us to gain access to a stand database with almost total landscape coverage. Productive stands younger than 60 years old cover about 71% of the land owned by SCA in the study area, stands older than 110 years constitute 13%, while mires and other low-productive land not used for forest production covers about 0.9%. The mean altitude of the studied stands is 355 m above sea level (minimum 260 m and maximum 583 m) and the forests consist of various successional stages covering the entire forestry rotation period of approximately 100 years.

3.1.1 The use of chronosequences

A common technique to extract temporal trends in ecological research is to use differently aged samples (Pickett, 1989). The space for time approach is useful when studying changes over time in long lived ecosystems such as forests, where long term studies sometimes are not possible (Walker *et al.*, 2010: Uotila & Kouki, 2005). The drawback is that the chronosequence is a collection of differently aged forest stands, and that the temporal trends is not the development of a specific stand. Hence, the chronosequence is mainly useful when applied on forests with a rather predictable successional trajectory (Walker *et al.*, 2010; Uotila & Kouki, 2005).

3.2 Data collection

3.2.1 Stand selection

Data was collected during field seasons of the years 2009-2011. Stands were randomly selected from the land owner's database. Suitable stands were (i) dominated (>70%) of one of the three focal tree species, (ii) within one of the three selected stand age classes and (iii) of dry-mesic-moist soil moisture type that had vegetation that could be classified as vegetation types "pine forest of cowberry type" or "spruce forest of bilberry type" according to Pålsson, (1998). We collected data from 400 trees: 152 *Pinus sylvestris*, 140 *Picea abies* and 108 *Pinus contorta*. The trees were from three different age classes, 15 (±2 yrs), 30 (±5 yrs) and 85 (±5 yrs) years with 48 trees from each age class and tree species in 15- and 30-year old stands, and 56 *P. sylvestris*, 44 *P. abies* and 12 *P. contorta* trees in the oldest stand age class. In each study stand, the longest transect through the stand was derived from stand maps.

3.2.2 Stand data

In each stand, ground data was collected at 24 evenly spaced points along the aforementioned transect. Stand and tree data were collected at four random points out of the 24 points for ground data collection. Stems per hectare (stems ha^{-1}; the number of trees within a circle with radius 2.82 m in 15- and 30-year old stands, and 5.64 m in 85-year old stands, multiplied by 100 or 10 respectively), basal area (m^2; measured by the help of a relascope), canopy cover (%; visual estimation of the percent sky covered by tree canopy, made by the same two persons throughout the study) was measured. On the closest living tree from the position along the transect, tree height (m), diameter at breast height (cm; i.e. at 130 cm above ground level), bark crevice depth (mm; at breast height) was measured. We counted the number of dead and living branches in one metre intervals starting from the ground (0-99 cm, 100-199 cm etc.) and ending where the tree diameter was ≤5 cm in 15- and 30-year old stands, and up to 6 m in 85-year old stands. The average length and diameter of dead and living branches was estimated separately. To be included, a branch had to be at least 10 cm long and 0.8 cm in diameter (25 cm^2).

3.2.3 Ground plots

Ground vegetation was surveyed in 24 one by one metre ground plots, evenly distributed along the longest transect through each stand, starting and ending 25 m from the edge to avoid edge effects. Within the 1 × 1 m plot, a mesh grid with 10 × 10 cm squares was used to count the percent cover, i.e. each grid square was 1% (Fig. 3). Average spacing between ground plots was 29 m. The position of a plot was moved to the nearest acceptable position if it contained saplings taller than 50 cm, boulders covered more than 10% of the plot, or was wet (i.e. contained water-filled holes or patches of *Sphagnum* spp.).

Within each of the 24 plots, percent cover of macrolichens, bryophytes, vascular plants (ground and field layer) and ground without vegetation (bare mineral soil, needles or coarse/fine woody debris) was recorded. Lichens were recorded by species, with some exceptions. Bryophytes were recorded as total percent cover and consisted predominantly of *Hylocomium splendens* and *Pleurozium schreberi*. Vascular plant cover was recorded in three groups: total vascular plants (TVP), eudicots, and grasses. TVP cover includes all vascular plants in the ground- and field layer. Eudicots mainly consist of the dwarf shrubs *Vaccinium myrtillus* and *V. vitis-idaea*. Grasses mostly consist of thin-leaved grasses such as *Deschampsia flexuosa*.

Figure 3. Part of a ground plot showing the mesh grid used to estimate vegetation cover. Photo: S. Bäcklund

3.2.4 Lichen inventory

All trees used to describe tree characteristics (data on e.g. diameter, height) was also inventoried for lichens (i.e. four trees per stand).

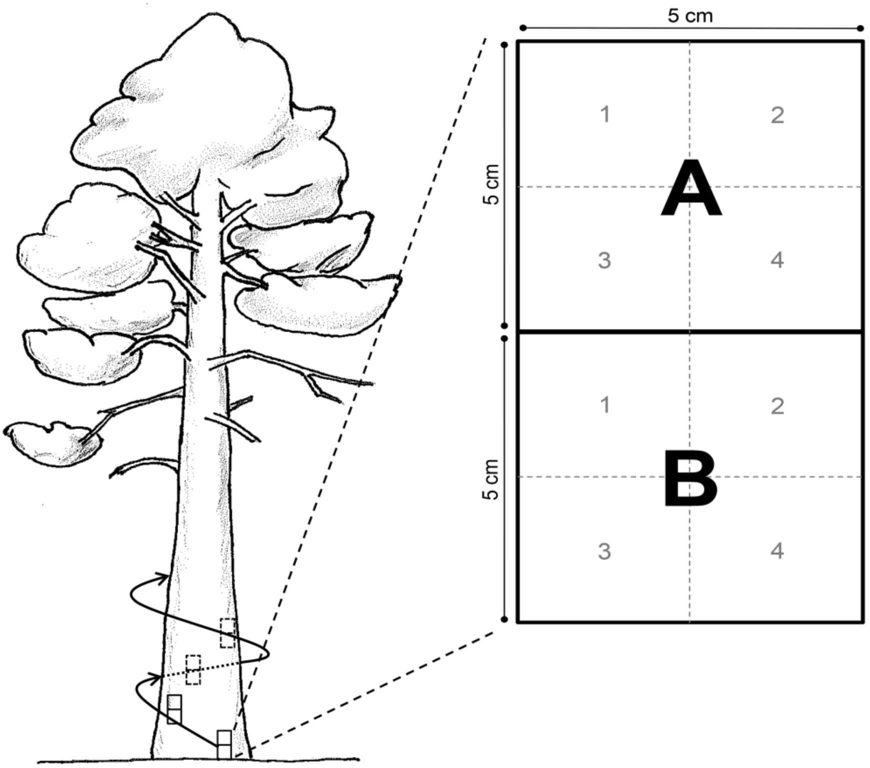

Figure 4. Schematic illustration of the tree plot used for lichen inventory on stems. Two adjacent plots (A and B) were used, each divided into four subplots for abundance measure. The plot was rotated upwards around the tree, starting from ground level, with one cardinal direction (N, E, S, W) between each consecutive plot.

Young trees and middle aged trees (15- and 30-years old) were inventoried up to the point where the trunk diameter was ≤5 cm. In most cases, it was necessary to cut down the tree to facilitate the inventory. The 85-year-old trees were inventoried up to 5.5 m in height with the help of a ladder. The inventory was conducted using a double plot of 2 × 25 cm^2 (5 × 5 cm width × height per plot; Fig. 4). For the first 2 metres from the ground, the plot interval was 25 cm (i.e. plots were located at 0 cm (base), 25 cm, 50 cm, etc.). Starting from 2 metres, the plot interval was extended to 50 cm (i.e., plots were placed at 250 cm, 300 cm, 350 cm, etc.). The plot was rotated clockwise by one cardinal direction (North, East, South, and West) between each consecutive plot (Fig. 4). The starting cardinal direction for the sampling was shifted for each tree, also in a clockwise direction. In the 85-year-old stands, all plots were sampled in the same cardinal direction for each tree, with the cardinal direction shifted clockwise for each of the four sampled trees in each stand.

The abundance of individual lichen species was estimated by their occurrence frequency within the sampling plot by dividing the sampling plot into four subplots of 2.5 × 2.5 cm (Fig. 4). The presence of all lichen species (including crustose, foliose, and fruticose) was counted once per subplot, i.e., the maximum abundance per plot was 4 for each species. Lichens were sometimes brought to the lab for later identification. In addition to abundance data of individual species, the total cover (%) for all lichen species combined was noted for each 5 × 5 cm plot.

3.2.5 Branch inventory

Branches were collected and brought back to the lab for inventory. Both living and dead branches were collected (when present) from each metre interval (up to the sixth metre in the 85-year old stands) of every tree. The branches were collected as close to the starting cardinal direction (from the tree plot inventory) as possible.

Prior to the lichen inventory, the branch was divided into 25 cm^2 plots. The species identification was conducted by using a dissecting microscope and when necessary the appropriate chemicals (C, K, PD) and/or a microscope. All lichen species (crustose, foliose and fruticose) was counted once per plot and the data was used in paper IV.

3.2.6 Selection and compilation of lichen functional traits

In Paper III, information on six life-history traits, four environmental tolerance traits, and two niche-width traits that all were likely to affect a species' habitat association was compiled for all species found on stems and branches (Table 1). The methods and source for compiling these traits were also included in Table1.

Table 1. *Lichen traits used in analyses. "Life history" and "Specialization" traits were compiled by GT and "Environmental tolerance" traits were modified and evaluated for local conditions after Nimis and Martellos (2008).*

	Trait	Categories	Method and source
Life history	Thallus type/growth form	Crustose; foliose* or fruticose*	Expert knowledge
	Reproductive strategy	Meiospores (in asci); fragmentation; isidia; soredia/leprose/goniocysts*	Expert knowledge
	Spore colour	Brown; colourless	Expert knowledge
	Pigments in thallus	Dark brown to black pigments; yellow to red pigments, no pigments	Expert knowledge
	Apothecia	Dark brown to black pigments; yellow to red pigments; no pigments/no apothecia	Expert knowledge
	Lichen substances (e.g., acids)	Substances present; substances absent	Expert knowledge
Environmental tolerance	Maximum tolerance for solar irradiation	(1) very shaded situations; (2) shaded situations; (3) plenty of diffuse light but scarce direct solar irradiation; (4) sun-exposed sites, but avoiding extreme solar radiation; (5) very high direct solar irradiation	Modified after Nimis and Martellos (2008)
	Maximum tolerance for pH of the substratum	(1) on very acid substrata; (2) on acid substrata; (3) on subacid to subneutral substrata; (4) on slightly basic substrata; (5) on basic substrata	Modified after Nimis and Martellos (2008)
	Maximum tolerance for aridity	(1) hygrophytic, in sites with a very high frequency of fog; (2) rather hygrophytic, intermediate frequency of fog; (3) mesophytic; (4) xerophytic, but absent from extremely arid stands; (5) very xerophytic	Modified after Nimis and Martellos (2008)
	Maximum tolerance for eutrophication (including deposition of dust and nitrogen compounds)	(1) no eutrophication; (2) very weak eutrophication; (3) weak eutrophication; (4) rather high eutrophication; (5) very high eutrophication	Modified after Nimis and Martellos (2008)
Specialization	Ecosystem niche width	Non-forest habitat; managed coniferous forest; old coniferous forest*	Expert knowledge: (1) no or very weak affinity, < 1 % of the population; (2) weak affinity, 1-25 % of the population; (3) moderate affinity, 26-80 % of the population; (4) strong affinity > 80 % of the population
	Micro-habitat niche width	Epiphytic; lignicolous; saxicolous; terricolous	Expert knowledge: (1) no or very weak affinity, < 1 % of the population; (2) weak affinity, 1-25 % of the population; (3) moderate affinity, 26-80 % of the population; (4) strong affinity > 80 % of the population

*Individual trait omitted from the analyses due to very high correlation (R > 0.8) with other traits (Appendix 2).

3.3 Data analysis

In Paper I-IV one-way Analysis of Variance (ANOVA) with Tukey's family error rate at the 95% confidence interval was used to analyse differences among tree species within age classes.

In Paper I, beta regression models were used to compare ground vegetation cover between stands of *P. contorta* and the two native conifers. The beta distribution is appropriate for modelling percentage cover data (i.e. when having a response variable only taking values between 0 and 1) since it adequately describes the frequency distribution of cover for the various vegetation groups studied and does not require transformation of the response variable (Eskelson *et al.*, 2011). In the full model, tree species, stand age class, canopy cover, and the two-way interactions between these variables were used as explanatory variables. Thereafter, a stepwise backward selection was performed and the least significant variables were removed one at a time until the lowest Akaike's information criterion (AIC) was achieved. AIC is a measure of relative model fit, and is proportional to the likelihood of the model penalized for the number of model parameters (Burnham & Anderson, 2002). A plausible model was defined according to Burnham & Anderson, (2002), i.e., that a model is plausible if the alternative model's AIC is less than two units higher than the AIC for the "best" model with the lowest AIC. Hence, all alternative plausible models were presented in the supplementary files of Paper I.

In Paper II, tree level species richness was modelled by using generalized linear mixed models (GLMM). Forest stand was used as random factor to deal with non-independence of the data, and we fitted Poisson models with logarithmic link functions (e.g. Bolker *et al.*, 2009; Gelman & Hill, 2007). Tree species, stand age, basal area, branch density, canopy cover, diameter at breast height, and bark crevice depth, were used as explanatory variables. All two-way interactions between stand age and tree species as well as the structural explanatory variables were included in the full model. All explanatory variables were standardized to allow for comparisons of their respective effect size (Gelman, 2008; Gelman & Hill, 2007). In all models, we accounted for varying sampling effort on different trees by including the number of tree plots surveyed as an offset variable. Model averaging was used to assess the relative strength of support for all biologically relevant models, as recommended when the Akaike weights (wi) of the "best models" are less than 0.9 (Grueber *et al.*, 2011). The information theoretic approach was used for model selection (Barton, 2011), and AIC was adjusted for small sample size (AICc). The relative variable importance (RVI) was estimated on a scale of 0 to 1 by summing the AICc weights across all sub-models in which the variable occurred. The RVI will be higher for variables that contribute more to model fit. The precision of the model-averaged parameter estimates account for model selection uncertainty, which is included in the estimated range of the confidence intervals. Species composition was analysed by using several different techniques. We used one-way analyses of similarity (ANOSIM) to investigate differences in lichen species composition on the different tree species and age classes (Clarke *et al.*, 2006; Clarke, 1993). The analyses were based on a Bray-Curtis similarity matrix built on average abundance values of each species as averaged by plot numbers from four individual trees per stand (Clarke *et al.*, 2006). ANOSIM generates an R-statistics that gives a measure of how similar groups are. Values most commonly range from 0 to 1, and a large positive R signifies large differences between groups, while a value close to zero indicates there is little difference between groups (Hammer *et al.*, 2001). Levels of significance (*p*-values) of the differences between assemblages were obtained by a permutation procedure with 10,000 replicates on the similarity matrices (Hammer *et al.*, 2001). Non-metric multidimensional scaling (NMDS) is an ordination technique suitable for community data and does not have any assumptions of normality or linearity (Peck, 2010), and we used NMDS to generate a visual configuration of the species composition patterns. Correlation coefficients between five environmental variables (canopy cover, branch density, bark crevice depth, basal area and diameter at breast height) and the NMDS scores were calculated and presented as vectors from the origin in the ordination plots. Finally, we used similarity percentage analysis (SIMPER) to evaluate which lichen species were responsible for the observed difference among groups of samples (Clarke, 1993). Species that consistently contributed significantly to the average dissimilarity between stand types were considered discriminating species, i.e., characteristic of specific stand types.

In Paper III, different indices were calculated for stems and branches separately. Species richness and evenness (Shannon diversity (H) divided by the logarithm of the number of taxa (Magurran, 2004) was calculated and the values were standardized by the area sampled. Trait diversity for the lichen community was calculated as the functional dispersion metric (FDis), which is the mean distance of each species from its community centroid in a multivariate space defined by the functional traits tested (Lealiberte & Legendre, 2010). Functional evenness (FEve) was calculated, and it is the evenness of abundance distribution in a functional trait space (Laliberté & Legendre, 2010). To quantify the impact of single traits on significant abundance weighted trait dispersion differences between tree species, the trait diversity was recalculated with each of the twelve traits excluded in turn, and reanalysed for differences among groups. We also used multiple linear regressions to test how abundance-weighted FDis for each age class were related to tree species, bark crevice depth for stem lichens or presence of dead branches for branch lichens, basal area, and canopy cover. Model selection was based on AIC. Starting models was simplified using stepwise variable selection (performed in both directions) minimizing the AIC.

All regression models (Paper I-III) and the diversity calculations in Paper IV were done in R (R Development Core Team 2013). ANOVAs were done in MiniTab 16 and 17, and the species composition analyses in Paper II were done in Past software package version 2.12 (Hammer *et al.*, 2001).

The single 85-year stand of *P. contorta* was included in the regression models in Papers I and II, but was not included in comparisons among tree species within age classes. However, although not included in the significance testing, data from the single stand was included in figures and tables to provide a visual comparison to the other 85-year old stands.

4 Results and discussion

4.1 Forest structures

Pinus contorta was larger (i.e. had larger diameter and height and greater basal area) than the native tree species of corresponding age (Fig. 5). This agrees well with previous studies where *P. contorta* have been found to exceed *P. sylvestris* in growth regardless of site index (e.g. Elfving *et al*., 2001). The branch surface area of 15- and 30-year old *P. contorta* also exceeded both native tree species. Even at similar branch densities, the branches of *P. contorta* were both longer and thicker. Thus, in stands of similar age and stem densities, *P. contorta* stands have larger canopies and the stands appear denser. Also, *P. contorta* have more needle biomass than *P. sylvestris* (Ågren & Knecht, 2001), thereby adding to the effect of denser stands. As a result of larger stems and canopies, young stands of *P. contorta* offer more substrate/habitat for epiphytes and other tree living organisms. However, denser stands and canopies imply more shaded light conditions. Thus, despite that such stands have higher substrate availability, the poor light environment may render it unsuitable for many species (Färber *et al*., 2014; Hilmo *et al*., 2009). The effect of shading also transmits to the ground vegetation, which can explain observed shifts of ground vegetation to more shade tolerant species (Roberge & Stenbacka, 2014; Meers *et al*., 2010). In 85-year old stands, the surface area of branches was largest in *P. abies* stands, while the stands of *P. sylvestris* and *P. contorta* had very few branches below the limit of the inventory. Hence, in older stands, *P. abies* had the more shaded stand and stem conditions.

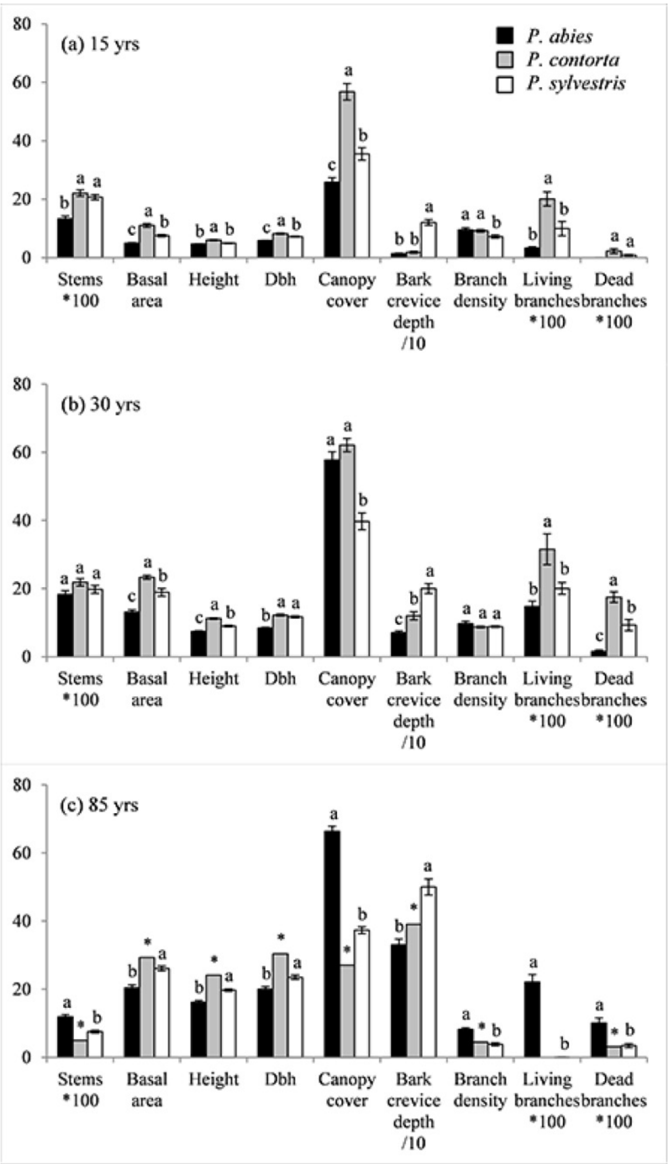

Figure 5. Stand- and tree characteristics for the different stand types (±SE) *Picea abies*, *Pinus contorta* and *Pinus sylvestris* in (a) 15-, (b) 30-, and (c) 85-year old forest stands. Significant differences among tree species within age classes are given by different letters. Note that 85-year old *P. contorta* was not tested since only one stand was available (denoted by *). To fit all characteristics in the same figure, Stems (stem ha^{-1}), Living branches (branch surface area m^2 ha^{-1}) and Dead branches (branch surface area m^2 ha^1) was divided by 100, and Bark crevice depth (mm) was multiplied by 10. Units for Basal area (m^2 ha^{-1}), Height (m), Dbh (cm), Canopy cover (%), and Branch density (No branches m^{-1}) were not changed to fit the figure.

The distribution of dead and living branches within the canopy differed between *P. abies* and the two pine species *P. contorta* and *P. sylvestris*. *Picea abies* had both dead and living branches in all metre intervals in all age classes, except in 15-year old stands where no dead branches at all were found. The two *Pinus* spp. had dead branches in all age classes, but the onset of the living crown was positioned higher up the stem as the stand age increased (Fig. 6). In 85-year old stands, almost no living branches were found in stands of *P. sylvestris* and *P. contorta* below the 6 m limit of the branch inventory. Self-pruning and branch size can to some extent be controlled by management, i.e., through initial planting distances and timing of thinning events (Egbäck *et al.*, 2012), but the difference between *Picea abies* and *Pinus* spp. is mainly a result of differing inherited growth forms of secondary tree species *P. abies* vs. pioneer tree species *Pinus* spp.

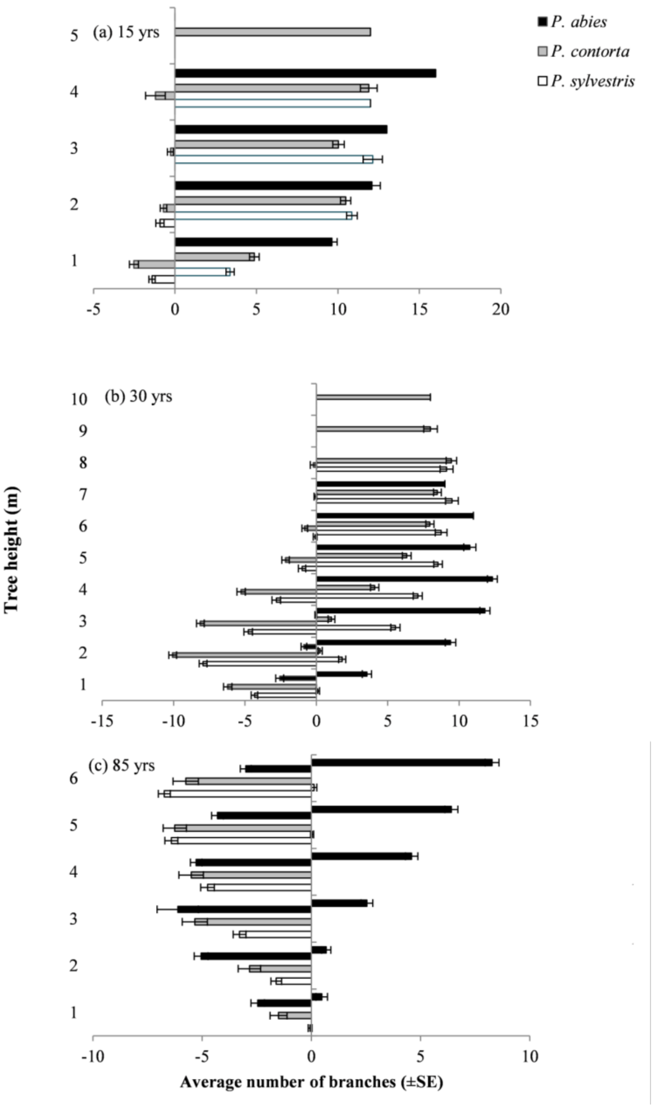

Figure 6. Average number of branches (±SE) in each meter interval for the different stand types *Picea abies*, *Pinus contorta* and *Pinus sylvestris* in (a) 15-, (b) 30-, and (c) 85-year old forest stands. Dead branches are shown as negative values (to the left side of the y-axis) and living branches are shown with positive values (to the right side of the y-axis). Note that the scale on the y-axis differ for the different age classes depending on the height of the trees (and the maximum inventory height in 85-year old stands).

The variation in light conditions within the stand can create a vertical differentiation of niches (Färber *et al.,* 2014), but different niches can also be created by the small scale variation of the single tree, i.e. the bark crevice depth

(Hauck, 2011; Nascimbene *et al.*, 2009). Habitat conditions differ between the surface of the bark vs. the bottom of the bark crevices, and habitat heterogeneity will increase with increasing depth of bark crevices (Hauck, 2011). We found bark crevice depth to increase with stand age in all tree species, thereby supporting previous literature on the successional development of micro-habitats (Ellis, 2012; Lõhmus & Lõhmus, 2008). *Pinus contorta* had intermediate bark crevice depth compared to the two native species, suggesting that the variation of habitat conditions is within the range of the two native tree species.

The variation of bark crevice depth and other stand properties among stands of *P. contorta* was neither more nor less variable than the native tree species, and the variation among stands within each age class was similar for all of the tree species (Fig. 7). If *P. contorta* is managed according to current laws and forestry practices regarding nature conservation within the managed forests (e.g. retention of tree groups and single trees, snags and other tree species) at final harvest, the variation within stands should increase, but the variation between stands will probably remain unchanged.

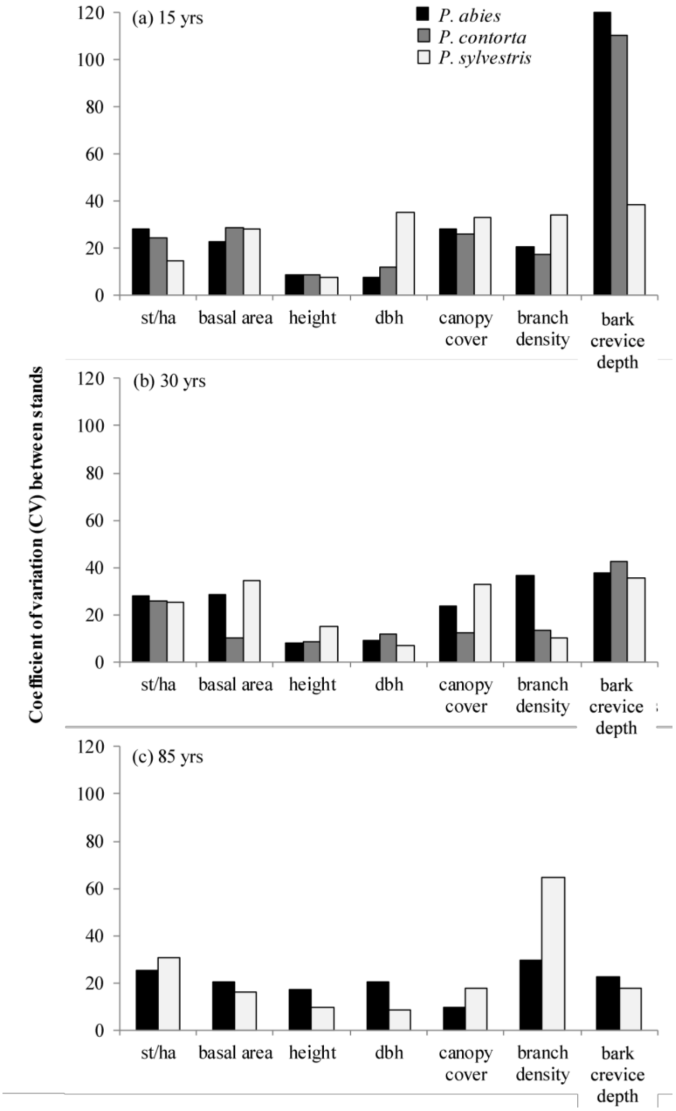

Figure 7. Among stand variation expressed as the coefficient of variation (CV). Data is shown for the different stand types *Picea abies*, *Pinus contorta* and *Pinus sylvestris* in (a) 15-, (b) 30-, and (c) 85-year old forest stands. No between-stand data for 85-years old *P. contorta* since only one stand was available.

If the variation within stands increase, the forests are likely to be able to sustain more species (Lõhmus & Lõhmus, 2008; Dettki & Esseen, 1998). However, if there is little variation between stands, connectivity between conservation areas, retention patches, or other forests areas with greater structural complexity, is important to allow for dispersal (Renhorn & Esseen, 1998) and/or the ‘life-boating’ function to maintain species over the forest regeneration phase (Perhans *et al.*, 2009).

4.2 Ground vegetation

Both tree species and stand age had significant effects on functional groups of ground vegetation. In *Picea abies* forests, the cover of dwarf shrubs can be expected to increase with stand age up to at least 80-100 years (Uotila & Kouki, 2005), which corresponds to findings in Paper I that the cover of eudicots as well as total vascular plant cover increased with increasing stand age in *Pinus contorta* stands and stands of the two native tree species. However, a Swedish study comparing *P. contorta* and *P. sylvestris* found no correlation between increasing stand age and increasing cover of vascular plants (Nilsson *et al.*, 2008). Instead, they found a positive correlation between lichen and bryophyte cover under both *P. contorta* and *P. sylvestris.* In Paper I, no effect of stand age on lichen cover was found, and the effect of stand age on bryophyte cover differed between *P. sylvestris* (positive) and *P. contorta* (negative).

The cover of vascular plants was higher in *P. contorta* stands than in stands of the native tree species in all age classes (Fig. 8), which contradicts another study where the vascular plant cover was lower in *P. contorta* stands compared to *P. sylvestsris* (Roberge & Stenbacka, 2014). The use of different age classes between the studies might not allow for direct comparisons, but the difference in result between the two studies is still interesting. In contrast to Roberge & Stenbacka (2014) there is nothing in Paper I that indicates lower vascular plant cover under *P. contorta*. Roberge & Stenbacka, (2014) also reported bryophyte cover to be higher in stands of *P. contorta* than *P. sylvestris*, which I also found, but only in the youngest age class. Although there were no large differences in bryophyte cover, it seems plausible that bryophytes could expand their cover in young to middle-aged stands of *P. contorta*, as the overall more shaded conditions of *P. contorta* compared to *P. sylvestris* might favour bryophytes (Uoutila & Kouki, 2005).

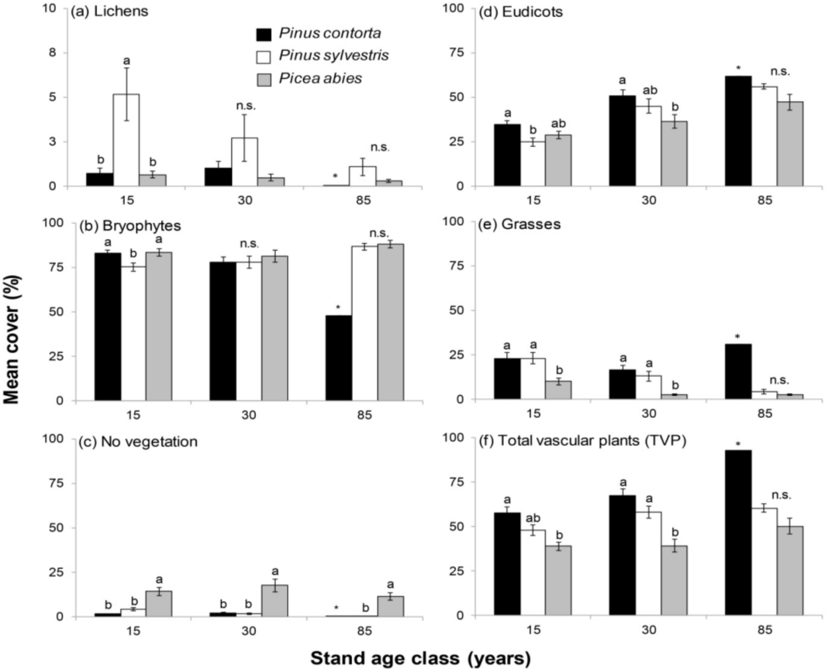

Figure 8. Mean cover (%), ±SE, for the six different types of ground vegetation in stands of *Pinus contorta*, *Pinus sylvestris* and *Picea abies* of different stand age classes. Note that the scale is different on the y-axis in (a) Lichens. Significant differences within age classes are indicated by different letters (Tukey's test; $p<0.05$), ns = not significant. The star (*) denotes the single 85-year old P. contorta stand which was not included in the significance test.

4.3 Epiphytic lichens

Studies on epiphytic lichens are often focused to the lowest 2 m of the trunk (cf. Johansson *et al*., 2009). In this thesis, data was collected from the whole trunk in young and middle aged stands and up to 6 m height in old stands. The result is a dataset of more than 70,000 lichen occurrences from 400 trees in 96 stands of managed boreal forests.

The species richness of epiphytic lichens on *Pinus contorta* was lower than that of *Picea abies*, but similar to that of *Pinus sylvestris*. Total species richness was higher in old stands compared to young and middle aged stands for all tree species, but when correcting for sampled area, species richness increased with increasing age in stands of both *Pinus* spp. whereas species richness in *P. abies* stands decreased from 15- to 85-year old stands (Fig. 9).

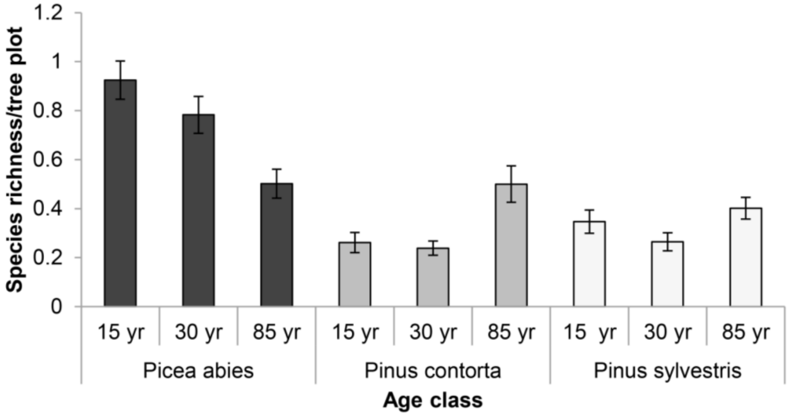

Figure 9. Average number of lichen species per tree plot in the different stand types. Error bars represent the standard error.

The same pattern was also found for total cover of lichens (Fig. 10), with increasing cover per sampled area throughout the chronosequence for *P. contorta* and *P. sylvestris*, but decreasing cover for *P. abies* from stand age 30 to 85.

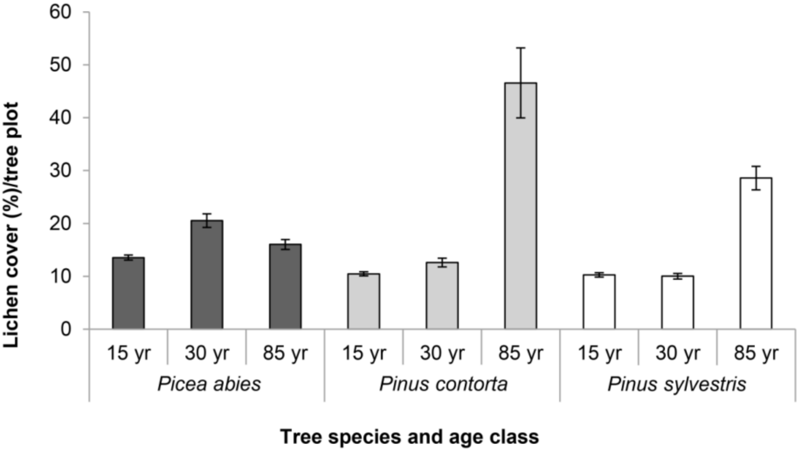

Figure 10. Average lichen cover per tree plot in the different stand types. Error bars represent the standard error.

One explanation for the decreasing species richness, as well as decreasing total cover, of epiphytic lichens in *P. abies* stands is that the low light conditions on the trunks of mature *P. abies* are likely not favourable for growth of foliose lichens, thus stabilizing or decreasing species richness and lichen cover in mature *P. abies* stands (Hilmo *et al.*, 2009).

In *Pinus* spp. stands, light was not a limiting factor, and light demanding epiphytic lichens are often found in pine stands with comparably low shading (Calviño-Cancela *et al.*, 2013). Moreover, because of the favourable light conditions, foliose lichens were able to expand their cover with increasing age in *Pinus* spp. stands.

The lichen species of managed forests mainly consist of generalist species (Svensson *et al.*, 2014), and *P. contorta* shared most lichen species with *P. sylvestris* and *P. abies*. However, the composition of lichen species differed among the tree species, and *P. abies* had a distinct composition in all age classes (Fig. 11). In stands of *P. abies*, stand and tree properties that relate to light availability (branch density and canopy cover) was the most important, whereas in *Pinus* spp. stands, stand and tree properties related to the amount of available substrate (diameter at breast height, basal area and bark crevice depth) were more important. In 30-year old stands, *P. contorta* and *P. sylvestris* had distinct lichen species composition. The bark crevice depth was the most important variable for explaining the species composition on *P. sylvestris*, and basal area and diameter on *P. contorta*. The bark crevice depth was larger in *P. sylvestris* than in *P. contorta* (Fig. 5), and the coarser bark of *P. sylvestris* likely provide a more diverse habitat for lichens (Hauck, 2011, Ulizcka & Angelstam, 1999).

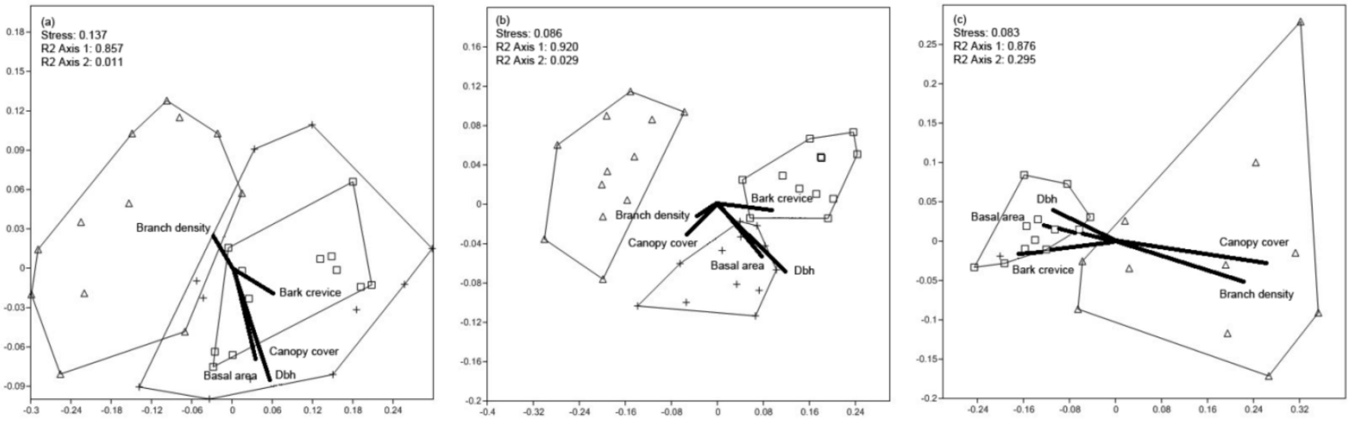

Figure 11. Nonmetric multidimensional scaling (NMDS) ordination graph of lichen species composition in managed stands of *Picea abies* (triangles), *Pinus contorta* (crosses) and *Pinus sylvestris* (squares). Panel (a) show 15-year old stands, panel (b) 30-year old stands, and panel (c) 85-year old stands. Correlation coefficients between five environmental variables and the NMDS scores are presented as vectors from the origin. The lengths of the vectors are arbitrary scaled to make a readable biplot, so only their directions and relative lengths should be considered. The following terms have been abbreviated: bark crevice depth (Bark crevice) and diameter at breast height (Dbh).

Although the majority of lichen species found was commonly occurring generalist species, some species were unique to a particular tree species or stand age. The calicioid species were only found in 85-year old *P. abies* stands. Calicioid lichens are often associated with old-growth forests and some of the species in our study can also be found on old pines (Kuusinen *et al*., 1996). However, the association with old-growth forests is not consistent (Lõhmus & Lõhmus, 2011) and as shown in Paper II, suitable habitat conditions can be found in relatively young (85-year old) managed stands of *P. abies*. There were few specific species on any of the *Pinus* spp., but findings of *Ochrolechia microstictoides* were restricted to 85-year old *Pinus* spp. Another species often reported to be more frequent on *P. sylvestris*, *Imshaugia aleurites* (e.g. Hyvärinen *et al*., 1992), was absent from 85-year old *P. abies* stands but had some occurrence in 30-year old *P. abies* stands.

The trait diversity across lichen communities was generally low on stems (Fig. 12), still, there were differences among tree species. Despite the lower species richness of *P. contorta*, trait diversity in 30-year old stands was similar to or higher than 30-year old stands of both native tree species.

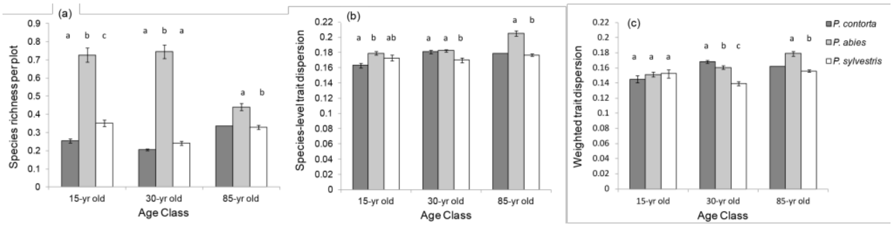

Figure 12. Species and functional-trait diversity of lichens on stems in three age classes of managed non-native *Pinus contorta* and native *Picea abies* and *Pinus sylvestris* forests in northern Sweden. (a) Species richness. (b) Functional dispersion (FDis), calculated at the species level unweighted by abundance. (c) Functional dispersion (FDis), calculated at the species level weighted by plot-level abundance. Significant differences between tree species, based on Tukey's pairwise comparisons when tree age classes were held constant, are indicated by different letters at P <0.05. Data shown are mean ±S.E. The single 85-year old *P. contorta* stand was not included in analyses.

This suggests that there is a lower degree of 'functional redundancy' (Díaz & Cabido, 2001) in the non-native *P. contorta* compared to the native tree species. A large number of functionally similar lichens (as in the native tree species) increase the probability that some species will survive and maintain functionality in a changing environment. On the other hand, greater functional trait diversity (as in *P. contorta*) implies that the chance of some species responding to environmental change and thereby surviving may require lower species richness for 'functional insurance' (Díaz & Cabido, 2001). However, regardless of the origin of the tree species, the resilience of young managed forests might be low due to the generally low trait diversity of these forests. Interestingly, lichens which colonize older stands of the shade-tolerant *P. abies* seem to have a greater extent of unique traits compared to lichens which colonize old stands of the shade-intolerant *P. sylvestris*. This suggests that, over successional stages, the lichen community of *P. abies* might become less functionally redundant but maintain some degree of functional insurance. The trait diversity on branches was also generally low, although the abundance-weighted trait diversity was lower on *P. abies* branches despite the higher species richness per branch plot (Fig. 13).

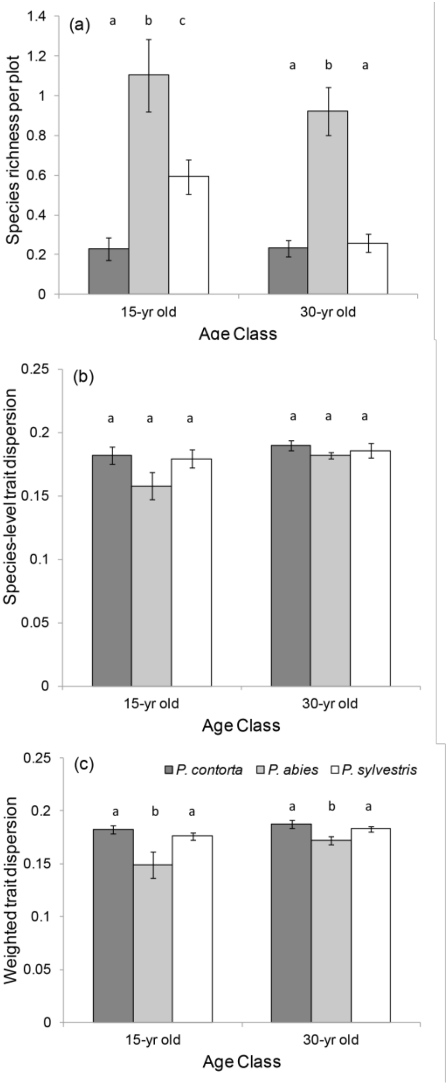

Figure 13. Bar charts of mean ±SE for (a) species richness per plot, (b) unweighted functional-trait dispersion, and (c) abundance-weighted functional trait dispersion of lichens on branches in 15 and 30-yr old managed non-native *P. contorta* and native *P. abies* and *P. sylvestris* forests in northern Sweden. Significant differences between tree species (Tukey's tests; P <0.05) are indicated by different letters.

The functional evenness on branches was also generally high and did not differ between tree species for any age class. Although species richness was higher on branches and stems in native *P. abies* stands and 15-year old *P. sylvestris* stands, the functional diversity was similar to or higher in non-native *P. contorta*.

4.4 Summary of specific questions

Short summary of the specific questions in thesis aims.

- **How does cover and composition of functional groups of ground vegetation differ between *P. contorta* and the native conifers *Pinus sylvestris* and *Picea abies*? Are differences influenced by the age of the stand?**

  The ground vegetation was influenced by both stand age and tree species. Vascular plant cover increased with increasing stand age, and the cover of vascular plants was higher in stands of *P. contorta* in all age classes.

- **How are epiphytic lichens influenced by the non-native *P. contorta*? Is choice of tree species important for the epiphytic lichen species richness and composition?**

  Lichen species richness in managed stands of *P. contorta* is similar to corresponding stands of *P. sylvestris*. The two pine species share many species but differ slightly in composition. The main difference in species richness and species composition is between *P. abies* and both *Pinus.*

- **How do the species and functional trait diversity patterns differ for epiphytic lichens in non-native *Pinus contorta* and native conifers *Picea abies* and *Pinus sylvestris*?**

  Species richness was highest on branches and stems in native *Picea abies* stands, but the functional trait diversity was similar or lower compared to non-native *P. contorta* stands. Generally, the functional trait diversity was low in lichen communities of both native and non-native managed forests. Presence of dead branches, greater bark crevice depth and canopy cover had a positive effect on functional trait diversity.

- **How do the stand- and tree structures of non-native *Pinus contorta* differ from the native conifers *Picea abies* and *Pinus sylvestris*?**

  Overall, *Pinus contorta* is larger (height, diameter at breast height, and basal area) than both native tree species. *P. contorta* also had larger surface area of branches in 15- and 30-year old stands. This means that the canopy of *P. contorta* is larger than the native tree species at comparable age and stand densities.

5 Conclusions and future directions

The effects of non-native *P. contorta* on ground vegetation in Sweden do not result in complete changes of vegetation type. The largest difference between *P. contorta* and the two native tree species was seen in eudicot cover, where *P. contorta* had significantly higher cover. From the perspective of epiphytic species, young and middle aged stands of *P. contorta* are not "biological deserts" and the higher growth rate of *P. contorta* does not affect species richness in comparison with the native *P. sylvestris*. The main differences in epiphytic lichen species richness and composition are between *P. abies* and both of the *Pinus* spp. Nevertheless, the relatively small differences found in species richness, species composition and functional diversity can also be related to the filtering effect of common abiotic and biotic forest characteristics of managed forests. As the possible variation is smaller than in natural forests, the introduction of a non-native tree species might only have subtle influence on an ecosystem already affected by intensive forestry. Even so, the introduction of *P. contorta* in Sweden has created forests of different structure than the native forests and planting of *P. contorta* generally provide greater stem and branch surface area than that of the two native conifers.

There are very few old stands of. *P. contorta* in Sweden, and studies covering the full rotation cycle is not yet possible. To fully understand the impact of this large scale introduction, future studies should focus on describing forest diversity in older stands of *P. contorta* when such stands become available in the near future.

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