

## What is the potential for replacing monocultures with mixed-species stands to enhance ecosystem services in boreal forests in Fennoscandia?



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### ARTICLE INFO

#### Keywords:

Mixed-forest stand  
Review  
Forestry  
Ecosystem services  
Tree species

### ABSTRACT

The boreal forests of Fennoscandia are largely dominated by Norway spruce and Scots pine. Conifer monocultures have been favoured in forest management during the last decades. Recently, concern has risen that forests consisting of only one tree species could be vulnerable to biotic damage. Additionally, environmental and societal changes are placing new demands on forest utilization, thus shifting the focus to alternative forest management options providing a wider scale of ecosystem services. It has been proposed that mixed forests are better than monocultures with respect to biodiversity, risk management and recreational value. By synthesising research studies, we provide an overview of current knowledge on how to combine wood production and other ecosystem services in mixed boreal forests in Fennoscandia. We addressed the following questions in more detail: what are the effects of mixed forests on soil properties, understorey vegetation, biodiversity, wildlife, resistance to and resilience against damage, forest productivity and the multiple use of forests? Furthermore, what are the silvicultural possibilities for establishing and managing mixed forests?

Based on this review, mixed forests appear to provide a higher output of most ecosystem goods and services, including higher biodiversity and improved risk management, soil properties and multiple-use values. The most serious challenge is the browsing by cervids, which damages sapling stands. There is potential to establish single-storied mixed forests with current regeneration methods and material. Further research is particularly needed on the silvicultural practices suited for mixed boreal forests.

### 1. Introduction

A crucial question concerning current forest management is how to manage our forests now and in the future to attain a wider range of ecosystem services. Environmental and societal changes are creating new demands for the utilization of forests. On one hand, the need for renewable raw materials from the forests is increasing due to the growing bioeconomy. On the other hand, the role of forests in mitigation and adaptation to climate change, preserving biodiversity, regulating water and nutrient cycling, and providing recreation and health for citizens is being emphasized. According to the 6th Ministerial Conference on the Protection of Forests in Europe, forests should

contribute to the green economy, including the increased provision of wood and other forest products and ecosystem services, but at the same time they should mitigate climate change, conserve biodiversity and provide socioeconomic and cultural benefits (Forest Europe, 2011). Consequently, the integration of ecological, economic and social functions of forests in practice needs more effort.

Ecosystem services are benefits that people obtain from ecosystems and that enhance human wellbeing (Daily, 1997, Millennium Ecosystem Assessment (MA), 2005, Nahlík et al., 2012, Reyers et al., 2013). In boreal forests, timber production has been prioritized as the main ecosystem service. However, the focus is shifting to forest management aiming to provide a wider range of ecosystem services

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<https://doi.org/10.1016/j.foreco.2020.118558>

Received 29 June 2020; Received in revised form 29 August 2020; Accepted 31 August 2020

Available online 15 October 2020

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(National Forest Strategy 2025). The Millennium ecosystem assessment (2005) classifies ecosystem services into four categories: supporting services (e.g. photosynthesis, soil formation and nutrient cycling), regulating services (e.g. water purification, climate regulation, and pest and pathogen regulation), provisioning services (e.g. food, water, timber production and non-timber forest products) and cultural services (e.g. spiritual, recreational and aesthetic values). Biodiversity is the machinery through which ecosystems provide the different services and adapt to changing conditions. In this review we addressed a range of ecosystem services (soil properties, understorey vegetation, biodiversity, pathogens and pests, multiple-use of forests, stand establishment and precommercial thinning and growth and yield) important in Fennoscandian boreal forests and covering elements of all the four categories of the MA framework and the role of mixed forests providing ecosystem services.

Numerous studies have emphasized the importance of biodiversity for the functioning of forest ecosystems (e.g. Erskine et al. 2006, Brassard et al. 2013, Gamfeldt et al. 2013). Tree species diversity can increase ecosystem productivity (so-called overyielding), when mixtures are compared to respective monocultures, as a result of complementarity or selection effects (Loreau and Hector 2001, Zhang et al., 2012). Complementarity means, that the combination of different species can allow a niche partitioning between species above or below ground and thus a more efficient use of light or soil resources. Complementarity can occur also when interactions between species are positive (i.e. facilitation). The selection effect means that increasing species diversity may also increase the probability of including a species with a high overall ecosystem service potential, such as biomass production, when compared to the other species present (Loreau and Hector 2001, Tobner et al. 2016).

Monocultures have been studied more and are generally better known than mixed forests, and a general and explicit definition of a mixed forest is challenging. Many different approaches have been used to define mixed forests taking into account the proportion of tree species (e.g. Sterba 1987, Bartelink and Osthorn 1999), stand structure (e.g. Leikola 1999), development stage of the stand (e.g. Spies 1997, Smith et al. 1997) and the tree species richness (e.g. de Bello et al. 2007). Additionally, the spatial and temporal scales should be taken into account when defining mixed forests. One consistent definition was given by Bravo-Oviedo et al. (2014): "A mixed forest is a forest unit (i.e. stand), excluding linear formations, where at least two tree species coexist at any developmental stage, sharing common resources (light, water, and/or soil nutrients). The presence of each of the component species is normally quantified as a proportion of the number of stems or of basal area, although volume, biomass or canopy cover as well as proportions by occupied stand area may be used for specific objectives. A variety of structures and patterns of mixtures can occur, and the interactions between the component species and their relative proportions may change over time." Bravo-Oviedo et al. (2014), however, did not define any specific thresholds for the proportions of the tree species so that a forest could be considered to be a mixed forest. They concluded that this broad-term definition would need more explicit criteria in working situations. Such criteria are defined in national forest inventories (NFIs), for example. In this study, we focus on tree species mixtures at the stand level. A forest stand is a management unit that is homogenous with respect to site properties and structure of the growing stock (development stage, tree species composition and silvicultural operations recently accomplished and needed).

According to the Finnish NFI in pure or almost pure stands the dominance of one tree species is more than 95%. In slightly mixed stands the dominance of one tree species is 75–95% and in actual mixed stands less than 75% (Korhonen et al. 2017). In sapling stands the dominance is based on the number of stems, and in mature stands it is based on volume.

A general presumption concerning the conversion of monocultures to mixed forests is that it will result in a higher delivery of ecosystem

goods and services (Ratcliffe et al. 2017, Astrup et al. 2018, Jonsson et al. 2019). In addition, it can result in synergies between ecosystem services (van der Plas et al. 2017). This means that, for example, if a forest has a high timber production it can also mean that the forest makes a positive contribution to climate regulation. Generally, multifunctionality has been positively correlated with productivity in a larger European transect across six major European forest types (Baeten et al. 2018). Mixed forests can provide several or many ecosystem functions at the same time, and as van der Plas et al. (2016) suggested, mixed forests are a "Jack of all trades, but masters of none". This means that mixed forests can offer more ecosystem services than monocultures, but not necessarily at the same level of multifunctionality, implying that if moderate ecosystem functioning levels are desired, mixed forests can offer a wider range of ecosystem goods and services, but monocultures can outcompete them in a specific service or good. Consequently, when high levels of multifunctionality are desired, an increase in species richness in mixed forests has a negative effect on the achieved multifunctionality (van der Plas et al. 2016). In addition, multifunctionality of mixed forests does not only depend on the species richness as such, but also on the actual species combination.

The boreal forests of Fennoscandia are largely dominated by two coniferous tree species, Norway spruce (*Picea abies* (L.) Karst., hereinafter spruce) and Scots pine (*Pinus sylvestris* L., hereinafter pine). Of the broadleaved tree species only silver birch (*Betula pendula* Roth) and pubescent birch (*B. pubescens* Ehrh.) are economically important. Early successional forests on fertile sites are usually dominated by broadleaved trees and mature forests by conifers, whereas less fertile sites are dominated by Scots pine during all successional phases. Conifer monocultures have been favoured in forest management during the last decades. Thus, even early successional forests are commonly conifer-dominated. As a consequence, also future forests in Fennoscandia are supposed to be conifer monocultures.

Recently, there have been rising concerns about the fact that large forest areas are dominated by only one tree species, as forests consisting of only one tree species can be highly vulnerable to biotic damage. Spruce, especially, is susceptible to many serious pests and pathogens (e.g. European spruce bark beetle or *Heterobasidion* spp.) which are likely to spread more in the future, partly due to changes in climate. In addition, spruce changes the soil fertility unfavourably and may have negative biodiversity impacts by lowering the soil pH and reducing the understorey vegetation (Smolander and Kitunen 2011, Augusto et al. 2015).

On average, less than one fifth of the forest land area in Finland, Sweden and Norway is covered by mixed forests (Table 1) (Forest Europe 2015). The number of tree species in boreal forests is low.

**Table 1**

Forest land area (1,000 ha) and share (%) of pure and mixed forests and number of tree species occurrence in Finland, Sweden and Norway (Forest Europe 2015). In mixed forests neither coniferous, nor broadleaved species account for more than 75% of the tree crown cover. The tree species occurrence is not directly related to the definition of mixed forests since even one single tree of another species on the measured plot resulted in higher tree species diversity.

	Finland		Sweden		Norway	
Predominantly coniferous forest	16,685	(75%)	20,216	(72%)	5713	(47%)
Predominantly broadleaved forest	1445	(7%)	2660	(9%)	4318	(36%)
Mixed forest (1000 ha)	4088	(18%)	5197	(19%)	2071	(17%)
Tree species occurrence						
1	7788	(35%)	2948	(11%)	5674	(47%)
2-3	12,908	(58%)	22,727	(81%)	6046	(50%)
4-5	1484	(7%)	2305	(8%)	369	(3%)
6+	38	(0%)	94	(0%)	13	(0%)
Total forest land area (1000 ha)	22,218		28,073		12,102	

Forests comprising six or more tree species are very rare in the Nordic forests (Table 1, Forest Europe 2015). Currently, approximately 14% of the forest land area in Finland is covered by mixed stands of which 42% are dominated by pine, 33% by spruce and 25% by broadleaved trees (Korhonen et al. 2017). Thus, even mixed forests in Finland are mostly dominated by conifers. In Finland, mixed forests have been more common in the past because of slash-and-burn cultivation and when mainly selective cuttings were done and cutting areas were not actively regenerated. Based on the Finnish NFI1 (1921–1924), the proportion of mixed forests (dominant tree species comprises less than 80%) was 57% and in the NFI2 (1936–1938) 64% of productive forest land area (Ilvessalo 1951).

Environmental and societal changes have resulted in new demands on forest utilization, thus shifting the focus in production forests to alternative forest management options providing a wider range of ecosystem services. One solution could be to increase the area of mixed forests. However, comprehensive knowledge of the ecosystem services provided by mixed boreal forests is lacking. In addition, we do not know how to manage boreal forests to increase the proportion of mixed forests. Therefore, in this review we will answer the following questions: what are the effects of mixed forests on the following ecosystem services: soil properties, understorey vegetation, biodiversity, resistance and resilience against damage, forest productivity and multiple use of forests (Sections 2–6)? Furthermore, what are the silvicultural possibilities to establish and manage mixed forests (Sections 7–8)? In Discussion, the state-of-art and the implications for forest management are summarized.

An excellent general overview of the pros and cons of specific forest management alternatives (spruce monocultures vs. spruce/birch or spruce/pine) in southern Sweden was recently given by Felton et al. (2016). We will also continue and expand this review by considering the relevant alternative management options in more northern boreal forests and will discuss management options in relation to soil fertility and stand age. The aim of our work is to provide an overview of current knowledge on how to combine wood production and other ecosystem services in mixed boreal forests in Fennoscandia. This study does not provide a systematic literature review but a discussion about ecosystem services in mixed stands in Fennoscandia. Researchers with expertise in a range of relevant disciplines summarized the current state of scientific evidence regarding the implications of mixed forest stands for soil properties, understorey vegetation, biodiversity, pathogens and pests, multiple-use of mixed forests, establishment and precommercial thinning and growth and yield.

## 2. Soil properties and processes

### 2.1. Soil effects of broadleaved trees vs. conifers

Tree species may affect the soil directly and indirectly. The various mechanisms include the amount and composition of both above- and below-ground litter, root activities, the associated microclimatic conditions, as well as the ground vegetation that develops under the tree cover (Augusto et al. 2015).

The degree of shading by tree canopies affects both light and temperature conditions in the soil. Birch stands, for example, are warmer and lighter than spruce stands. In addition, tree canopies also contribute to the thickness of the snow cover and depth of soil freezing, the snow cover being thinner and the soil frost stronger under spruce than under birch (Ylivakkuri 1960). Additionally, the precipitation undergoes changes when passing through the forest canopy (Hyvärinen 1990, Augusto et al. 2015), resulting in different soil impacts of different tree species.

The litter amount and composition differ between tree species. Surface layer waxes and a high concentration of lignin and other polyphenolic compounds make needle litter difficult to decompose whereas higher nutrient concentrations and more easily leached and

decomposable water-soluble compounds such as simple carbohydrates make leaf litter generally easier to decompose (Mikola 1954, Viro 1955, Johansson 1995, Kiikkilä et al. 2013). Although broadleaved litter (e.g. from birches or alders [*Alnus* sp.]) decomposes faster during the first year, the differences in mass-loss tend to decline over time (Prescott et al. 2000, 2004). There are some clear differences between tree species in plant structural compounds, cellulose, hemicellulose, and lignin. However, a major differentiation between tree species occurs in the composition of secondary plant compounds, for example mono-, sesqui- and diterpenes are typical for conifers, while birch contains higher terpenes (Dev 1989). With regard to tannins, which are an important group of phenolic compounds, spruce and pine contain condensed tannins, but birch has low amounts of condensed but also hydrolysable tannins. All these differences in the composition affect the soil properties and processes. Root activities include the rate and pattern of nutrient and water uptake and root exudation. Large amounts of labile carbon (C) compounds from birch roots are connected with rapid mineral nitrogen (N) uptake and can stimulate soil microbes to acquire nutrients from the soil to a larger extent than it would be the case with spruce (Parmelee et al., 1993, Priha and Smolander 2003).

Not only trees but also the understorey vegetation affects the soil underneath. Moss litter has a lower pH and decomposition rate than the dead parts of most herbs and grasses (Mikola 1954), and thus tree species indirectly control soil properties by affecting the understorey vegetation (discussed in the next chapter).

There are only a few studies available on the boreal region that have quantified the soil effects of individual tree species by using truly replicated and sufficiently old experiments on similar geological formations. Thus, we focus our discussion on studies that at least partly fulfil these criteria, and because of the sparse amount of mixed forest literature we first discuss the tree species effects on the soil in monocultures.

A few older studies concluded that an increase in the birch proportion increased the soil pH, nutrient concentrations and earthworm populations and replaced mor-humus with mull (Miles and Young 1980, Mikola 1985). In contrast to the soil improving effects of birch, spruce seems to change the soil fertility gradually in a more unfavourable direction by lowering the soil pH and by enhancing podsolization. Indeed, several studies have revealed that the soils under birch, compared to soil under conifers, have lower C-N ratios but a higher soil pH, more exchangeable nutrients and microbial biomass C and N, as well as higher C and N mineralization rates (Menyailo and Hungate 2005, Priha and Smolander 1999, Priha et al. 2001, Smolander and Kitunen 2002, Smolander et al. 2005, Kanerva and Smolander 2007, Lindroos et al. 2011, Smolander and Kitunen 2011). The species effects seem to be most consistent in regard to the pH and C-N ratio, but microbial activities such as N mineralization are more variable. A few studies have also shown the positive effect of birch on biological N fixation by free-living soil microbes (e.g. Nohrstedt 1985), and on the amounts of *Frankia*, an N-fixing root nodule symbiont of alder (Smolander 1990). Birch also appears to affect the microbial community structure (Priha et al. 2001, Grayston and Prescott 2005) and soil enzyme activity (Adamczyk et al. 2014).

The tree species effects on the N availability in boreal mineral soils are of special interest, since N is the main nutrient which limits forest growth (Högberg et al. 2017). Although these soils contain large amounts of N, the plant-available proportion is small, consisting of ammonium- and nitrate-N and small-molecular-weight organic N, mainly amino acids (Näsholm et al. 2009). Experiments with different tree species, ranging from 20 to 72 years of age, and on different sites and locations in Finland, have shown, that the C-N ratio was lower and the amounts of exchangeable ammonium higher under silver birch compared to spruce or pine, but the effect of tree species on the net N mineralization was dependent on the site (Smolander and Kitunen 2011). The dissolved fraction of soil organic matter plays an important role in nutrient cycling and pedogenesis. Interestingly, the dissolved

organic N: mineral N ratio was always lower in birch soil, indicating that in the soil under birch, N is rather mineralized all the way to mineral N in contrast to coniferous soils where it remains more in organic dissolved forms (Smolander and Kitunen, 2011). Accordingly, organic N dominates N supply in coniferous soils and the significance of organic N as an N source is emphasised (Inselsbacher and Näsholm 2012, Näsholm et al. 2009). In addition, soils under conifers show a higher abundance of certain secondary plant compounds than soils under birch, and these compounds can inhibit N cycling processes, at least according to laboratory experiments (Kanerva et al. 2008, Adamczyk et al. 2009, Smolander et al. 2005, 2006, 2012). For example, high amounts of volatile monoterpenes were observed in the soil atmosphere of coniferous forests, in contrast to negligible amounts in birch forests, and an exposure of birch soil to resin (that was emitting monoterpenes), or different individual commercial monoterpenes inhibited net N mineralization and nitrification (Smolander et al. 2006, Uusitalo et al. 2008, Adamczyk et al. 2015).

Although birch, as compared to conifers, seems often to rank first when evaluating properties important for soil fertility, there is an interaction between the tree species and the site, i.e. tree species effect depend on the site properties (Augusto et al. 2015, Ribbons et al. 2018). This appears to be particularly the case with conifers, implying that the ranking between spruce and pine depends more on site characteristics such as soil fertility, and stand age than it would be the case between birch and conifers (Smolander and Kitunen 2011). Before canopy closure, soil properties may be more favourable (in terms of nutrient availability and pH) in spruce than in pine stands. After canopy closure, however, the understorey vegetation under spruce changes from dwarf shrubs, herbs and grasses to a fairly even moss layer and a thick litter layer of partly undecomposed needle litter which reduces the soil quality, whereas in pine forests no drastic changes occur.

Grey (*Alnus incana* [L.] Moench) and black alder (*A. glutinosa* [L.] Gaertn.) are interesting tree species in regard to soil improving effects due to their root nodule symbioses with *Frankia*, an N-fixing bacterium (e.g. Viro 1955, Virtanen 1957, Mikola 1966). Estimates for the annual N fixation of grey alder range from 40 to 150 kg per ha (Hytönen and Saarsalmi 2015), and grey alder leaf litter can provide the soil with 60 to 100 kg N per ha annually (Mikola 1966). By accumulating N in the soil, grey alder can give a long-term boost for other, commercially more valuable tree species (Mikola et al. 1983). Additionally, alders generally increase the rate of N cycling and the above ground net primary production in N-limited forests and probably also the C accumulation (e.g. Binkley et al. 1992, Vogel and Gover 1998).

Two interesting questions are connected to tree species effects on soil and their consistency. First, how long does it take for visible effects and second, how deep into the soil do they extend? Greenhouse studies conducted with seedlings assessing the rhizosphere effect showed that differences between species developed already after some months (Priha et al. 1999a, 1999b). However, no studies are available where the development of tree species effects would have been systematically monitored. Original site properties are important in buffering against changes and also have an indirect effect by affecting the vegetation and tree growth. In afforested sites of agricultural fields, the humus layer properties were relatively similar after 20 years, despite the tree-specific differences in the litter layer (Priha and Smolander, 1997, Menyailo et al., 2002a, 2002b). On former forest sites, however, the tree species effect was visible already after a shorter time period (Mikola 1985, Smolander and Kitunen 2011).

Recent studies indicate that soils in pure birch forests have lower C stocks than soils under spruce or pine (e.g. Hansson et al. 2011). However, according to Dawud et al. (2017), increasing soil C stocks with increasing birch proportion in mixed forests in Eastern Finland have been found, a pattern that deviates from the general picture at other European sites where the soil C stock increased with increasing conifer proportion. This might be the result of complementarity, as mixing species increases the C stock compared to respective

monocultures. A similar one-tree-species effect was observed by Guckland et al. (2009) where the forest floor C increased with an increasing proportion of beech (*Fagus sylvatica* L.). In boreal forests the roots of the understorey vegetation play a more important role than in temperate forests, since their biomass can be of the same magnitude than that of the tree roots (Leppälampi-Kujansuu et al. 2014, Finér et al. 2017). This seems to be an important factor, especially with increasing birch proportions, which can result in a higher abundance of the understorey, particularly in comparison to spruce stands (Ampoorter et al. 2014).

Boreal mineral soils show a characteristic pattern in soil formation leading to a distinctive horizontal pattern, called podzol. Due to humid conditions, organic matter, as well as iron and aluminium, are leached from the upper mineral soil (eluvial horizon) right under the litter and humus layer, to deeper mineral soil layers (illuvial horizon). How deep then do the various effects of the tree species extend? Usually the largest effects are seen in the litter and humus layer and less in the deeper mineral soil (Priha and Smolander 1999, Priha et al. 2001, Kanerva and Smolander 2007, Kanerva et al. 2008, Lindroos et al. 2011). On a longer time scale, a vertical differentiation between tree species develops but broadleaved species result in more mixed surface layers, the main reason being probably bioturbation by soil animals (e.g. Taylor et al. 2018).

## 2.2. Mixed forests

There are only a few studies comparing boreal mixed forests to respective monocultures and fulfilling the prerequisite that the trees are growing on originally similar soils. Based on studies conducted on monocultures, we can expect that boreal broadleaved trees would improve soil properties, whereas conifers, in particular spruce, would reduce the soil productivity. Based on the sparse literature, we can conclude that the way the tree species change the soil of monocultures probably holds true also in mixed stands. However, their quantitative effects cannot be directly extrapolated from the results from monocultures, as various interactions between the different tree species and the soil exist (Scherer-Lorenzen et al. 2007). For instance, differences in the vertical root distribution and allelopathic effects due to secondary plant compounds may result in unexpected effects.

Mixed forests are known to have the potential to increase ecosystem C storage, and there are evident indications of increasing the above-ground C (Paquette and Messier 2011, Fichtner et al. 2018). However, there do not seem to exist any clear belowground patterns, as this relationship has been observed to be context dependent, being affected by the species identity, functional traits (e.g. complementary shade-tolerance or root systems) and climatic conditions (Vesterdal et al. 2013, Blaško et al. 2020).

In addition to water and nutrient uptake, tree roots are of great importance for C cycling and accumulation, since a substantial proportion of the annual tree net primary production is allocated below ground, and the majority is allocated to the fine roots (Helmisaari et al. 2007, Yuan and Chen 2010). The allocation to fine roots, with a rather short lifespan and thus high turnover, can be even more than 60% of the annual net primary production (Högberg et al. 2002). There are studies conducted in temperate forests, indicating that the competition of tree species, when growing together, can result in differences in horizontal or vertical root distribution (e.g. Leuschner et al. 2001). Mixing tree species with contrasting rooting traits can thus result in a more effectively used soil space, and temporal or spatial niche partitioning in the soil can increase root biomass (Brassard et al. 2013). One example could be that birch and spruce, when grown together, increase the complementarity instead of engaging in competition by spatial niche separation, and thus could increase the fine root biomass and soil C in deeper soil layers. This is because some tree species have inherently different rooting depths, e.g. spruce has a shallower root system than pine or birch (Kalliokoski et al., 2008). However, the



hypothesis that broadleaved tree species and conifers are generally complementary in their nutrient uptake from the forest floor and mineral soil in mixed stands forests was not supported by a Swedish study (Brandtberg et al. 2004).

Swedish studies concluded that in spruce stands, a birch admixture of 12.5% or more (of basal area) increased the soil pH, base saturation and exchangeable concentrations of calcium and magnesium in the litter layer of the forest floor after 10 years (Saetre 1999, Brandtberg et al. 2000). The soil fauna was also affected by the birch admixture. Microbial biomass and the average mineralization rates of C, N and P were not significantly affected but were higher under birch than under spruce (Saetre 1999). Litter decomposition seems to be enhanced when litters are mixed (Prescott et al. 2000). Mixing birch and spruce litters seemed to result in increased decomposition and fluxes of dissolved organic C and N and phenolic compounds (Kiikkilä et al. 2012, 2013). A Finnish field experiment indicated that an admixture of about 30% of silver birch in a spruce stand stimulated the net N mineralization and changed the composition of organic matter but the response varied between different soil characteristics (Smolander A. and Kitunen V., submitted). We may conclude that, even though no significant effects of tree species in mixed stands occur immediately or in the short run, the soil horizontal and vertical variation probably will increase with time with differences in both above- and belowground litter as well as root activities.

### 3. Understorey vegetation

During the last decade, several review articles have assessed the influence of mixing tree species and tree species composition on the biodiversity of the understorey vegetation in boreal and temperate forests (e.g. Barbier et al. 2008, Felton et al. 2010, Cavard et al. 2011, Felton et al. 2016).

Overstorey trees have an immense influence on understorey vegetation (Zhang et al. 2017, Kumar et al. 2018). Each tree species has a specific impact. These differences between tree species lie in their influences on resource availability and other environmental conditions, including light, water, soil nutrient status and other soil properties as well as soil processes, litter quality and quantity, microclimate, precipitation throughfall and competition (Messier et al. 1998, Saetre et al. 1997, Saetre 1999, Smolander et al. 2005, Barbier et al. 2008, Lindroos et al. 2011, Augusto et al. 2015). The tree species not only affect the occurrence and biomass of the understorey species, but they can have functional effects, as well.

As a result, plant communities under different tree species differ in many ways. In boreal forests, both shade-tolerant and acidophilous species, as well as species which can cope with a thick raw humus layer, thrive in spruce stands (Augusto et al. 2003, Tonteri et al. 2005, Hotanen et al. 2008). Dwarf shrubs are more abundant under pine, which provide more optimal light conditions than spruce (Tonteri et al. 2005, Petersson et al. 2019). Many epigeic lichens are much more abundant in old pine forests than in spruce or birch forests, as they need plenty of light and are slow-growing (Tonteri et al. 2005, Petersson et al. 2019). Grasses thrive best in birch forests as do many herbs, too (Tonteri et al. 2005, Wallrup et al. 2006, Hotanen et al. 2008). Bryophytes and lichens, however, are less abundant in birch forests compared to spruce or pine forests (Saetre et al. 1997, Bartels and Chen 2013), as they are likely to suffer from excessive amounts of leaf litter (Tonteri et al. 2005).

It has often been stated that the composition of understorey vegetation in a mixed forest lies in the midway between communities found under the respective monocultures (Kembel and Dale 2006, Macdonald and Fenniak 2007), meaning that each occurring tree species contributes all or some of the species associated with it. No studies have suggested that there would be plant species occurring in mixed forests only (Cavard et al. 2011).

Many studies reported that tree species admixtures increase the

understorey species richness and biomass (Barbier et al. 2008, Gamfeldt et al. 2013). A larger mixture effect is usually found when the tree species involved differ as much as possible in their effects on the understorey vegetation by changing the light transmission, soil, litter, root turnover or microclimate (Cavard et al. 2011, Jonsson et al. 2019). These differences are expected when shade-tolerant and shade-intolerant (Messier et al. 1998), early successional and late successional species (Hill et al. 2005), or broadleaved species and shade-intolerant coniferous species are combined (Légaré et al., 2011). A common understanding is that different tree species in an admixture create different microhabitats, which makes the coexistence of a larger number of species possible (Saetre 1999, Cavard et al. 2011).

Recent studies include experimental research where the influence of tree species admixtures on the composition and diversity of understorey vegetation has been divided into two components (Amppoorter et al. 2014, 2015, 2016). First, the mixed forest ecosystem is influenced by properties of the participating tree species, which is called the species identity effect. Second, tree species combinations can produce non-additive effects that cannot be explained by the identities alone. This is called the species richness effect. For instance, mixed forests often produce more species-rich understorey vegetation with a higher biomass than any of the participating tree species in a monoculture would, and the strength of this effect is dependent on the size and spatial location of the tree species patches in the forest. The most common explanation also in this case is that a mixed forest contains more different microhabitats than the respective monocultures do, and more understorey species can find optimal sites to grow than in monocultures. Additionally, the grain size is important in mixed forests—a stand comprised of small monoculture patches will have a larger variation of environmental conditions than a stand where tree species are planted in a complete admixture. Amppoorter et al. (2016) even suggest creating chessboard patterns of monocultures if the target is to increase the diversity of understorey vegetation at the stand level.

In boreal forests the degree of tree species admixture usually is succession-dependent, as birch trees are a shade-intolerant pioneer species (Kuuluvainen and Aakala 2011). Early-successional forests on herb-rich to mesic sites tend to contain a lot of naturally born birch trees, but these are usually removed as a silvicultural measure, while conifers remain. Even if they are not removed, the late-successional spruce is likely to overgrow the shorter-lived birch trees, which tends to reduce the birch effect in older forests. Therefore, the birch proportion in the stand is likely to be larger in early successional stages than in mature forests.

Hedwall et al. (2019) showed that the influence of the tree admixture is dependent on the stand density: in a spruce–birch admixture the cover and species richness of vascular plants increased with an increasing proportion of birch, but the effect was suppressed by increasing stand density. They also found the opposite pattern for bryophytes and lichens. Depending on the understorey vegetation structure, the admixture could also have different effects at different stand ages. If the abundance of dwarf shrubs decreases for some reason, extra space may be available for grasses and herbs. Even forest thinning can cause unexpected changes in understorey species abundances (Tonteri et al. 2016).

### 4. Biodiversity

There are a few previous review papers assessing the significance of mixed forests on biodiversity. Felton et al. (2010) examined the potential biodiversity benefits of replacing spruce monocultures with mixed spruce–birch stands in southern Sweden. Felton et al. (2016) widened the scope and examined the benefits of mixed spruce–birch and spruce–pine stands for biodiversity (along with other ecosystem services) compared to spruce monocultures in Sweden. Cavard et al. (2011) reviewed the importance of boreal mixed forests on understorey plants, birds, soil fauna and ectomycorrhizal fungi based on both North

**Table 2**

The numbers of species in different taxonomic groups associated with the main boreal tree genera in Finland. All species = total number of species using each tree species (or several tree species), specialists = species only using one tree genera, red-listed = species classified as threatened or near-threatened in the latest red list of Finland (Rassi et al. 2010). Data on Macrolepidoptera from Huldén et al. (2000), saproxylic beetles from Heliövaara et al. (2004, 2014) and the author's own expertise, and polypores Niemelä (2016) and Reijo Penttilä (pers. comm).

Species group	Species category	<i>Picea</i>	<i>Pinus</i>	<i>Betula</i>	<i>Populus</i>	<i>Alnus</i>	<i>Salix</i>	<i>Sorbus</i>
Macrolepidoptera	all	17	11	56	52	29	69	18
	specialists	10	4	19	12	6	17	11
	red-listed	—	—	—	2	—	1	1
Saproxylic beetles <sup>1</sup>	all	51	56	44	46	29	31	14
	specialist	15	21	5	11	1	6	1
	red-listed	4	13	8	15	8	8	2
Polypores	all	107	95	84	88	66	65	40
	specialist	24	19	6	7	—	5	—
	red-listed	33	31	10	19	7	11	3
Total	all	175	162	184	186	124	165	72
	specialist	49	44	30	30	7	28	12
	red-listed	37	44	18	36	15	20	6

<sup>1</sup> Includes only the families: Buprestidae, Cerambycidae, and Elateroidea.

American and European studies.

The previous Nordic reviews have concentrated mainly on the significance of a birch admixture in spruce-dominated forests. However, in addition to birches, several other broadleaved tree genera and species occur in the North European boreal forests, including aspen (*Populus tremula* L.), alders (*Alnus incana*, *A. glutinosa*), goat willow (*Salix caprea* L.) and rowan (*Sorbus aucuparia* L.).

In this section we will bring forth the following new aspects on the theme of the significance of other boreal broadleaved tree species than birch on biodiversity. On the landscape scale, does it matter whether different tree species grow in different stands or as an admixture in the same stand? How does the amount and quality of broadleaved admixture affect the potential biodiversity benefits?

According to the National Forest Inventory of Finland (Korhonen et al. 2017), pine constitutes 50% of the volume of growing stock, while spruce accounts for 30%, birches 17% and other broadleaved trees (mainly aspen) account for the remaining 3%. The relative importance of these tree genera as host trees for different taxa was estimated based on three species groups: Macrolepidoptera, saproxylic beetles and polypores (Table 2).

In spite of their low numbers, the infrequent broadleaved tree species host almost equal numbers of species than each of the three dominating tree genera, spruce, pine, and birches (Table 2). A considerable part (on average about 15%) of those species associated with infrequent tree species consist of specialists depending on one tree genus. The number of red-listed species on infrequent tree species is also large; the importance of aspen as a host for red-listed species is particularly pronounced. Since the infrequent tree species do not generally form pure stands, their proportion as admixed species in mixed stands is crucial for the local and regional persistence of their associated species.

Broadleaved trees provide food for many vertebrate species, too, and some of these species can be considered true specialists of mixed forest which require the intermixing of two or more tree species at the stand level. The flying squirrel (*Pteromys volans* L.) and the hazel grouse (*Tetrastes bonasia* L.) are prominent examples of species which favour spruce-dominated forests with a broadleaved component. Both species feed on broadleaved trees and need spruce for cover against avian predators. Flying squirrels eat leaves, buds, and catkins of broadleaved trees, particularly aspen and alders (Hanski 1998). Hazel grouse feed on buds and catkins of alder, especially during winter (Swenson, 1993, Åberg et al. 2003). It is possible that there are species that use different admixed tree species within a stand for different purposes among invertebrate or fungal species too.

The proportion of a broadleaved admixture affects the species richness of the taxa living in tree canopies. Invertebrate fauna dwelling

on spruce branches had, on average, 20% lower species richness and 40% lower abundance in spruce-dominated stands (proportion of spruce > 70%) than in mixed stands dominated by broadleaved trees (Salingre and Heliövaara 2001). The abundance of canopy invertebrates may, in turn, affect the winter survival of canopy-gleaning passerine birds, including several species of tits (*Parus* spp.), the goldcrest (*Regulus regulus* [L.]) and the tree-creeper (*Certhia familiaris* L.) (Pettersson et al. 1995). The diversity and abundance of epiphytic macrolichens and number of resident bird species were higher in mixed forests than in old coniferous or managed forests in central Sweden (Uliczka and Angelstam 2000), where the number of bird species correlated positively with the proportion of broadleaved trees in a stand. The authors concluded that the conservation of mature stands which also contain broadleaved (non-commercial) trees favours both lichens and birds and probably a wide range of other plants and animals.

Mixed forests have several structural characteristics that make them more suitable habitats for most species than coniferous monocultures. The vertical and horizontal canopy structure is more variable in mixed forests than in monocultures. Together with the multi-species composition of trees, this structural variation is obviously the key factor which increases the overall species richness in mixed forests (Ishii et al. 2004, Gao et al. 2014). Therefore, any addition of a broadleaved admixture will increase the stand-level species richness. However, many species groups living on broadleaved trees require special kinds of host trees, such as old trees or dead trees (see Table 2), and for these species an increase in the broadleaved admixture as such is not sufficient to meet their habitat requirements.

Trees suitable for making cavities are an important resource for many species (Andersson et al. 2018). Invertebrate species, old broadleaved trees with heart-rot and snags are important for cavity nesting birds (such as woodpeckers, owls, and tits) and bats (Siitonen 2001, Vatka et al. 2014). Additionally, the flying squirrel utilizes the cavities of large broadleaved trees (Hanski 1998). The number of cavity trees is notably lower in managed forests than in unmanaged forests and, therefore, saving broadleaved trees in all stages of the forest management chain starting from regeneration maintains habitats for species dependent on cavity trees (Vatka et al. 2014, Andersson et al. 2018).

Species living on old broadleaved trees, such as epiphytic lichens, and saproxylic species living on dead broadleaved trees may show metapopulation dynamics (Snäll et al. 2003). These species may have threshold values for the minimum amount of their host tree at the stand or landscape scale. Suitable living and dead host trees constitute distinct habitat patches. However, living hosts will eventually die and fall down, and dead trees will decay and disappear. Therefore, these species must colonize new suitable host trees at the same average rate as the old host trees become unsuitable, otherwise the local population will go

extinct. The colonisations can take place within the same stand or between adjacent stands. If the density of host trees is too small, the species will not persist in the long term.

In line with these predictions, Fedrowitz et al. (2012) showed that epiphytic cyanolichens confined to aspen exhibited patch-tracking metapopulation dynamics. Three of the studied species faced a high risk of disappearing from the studied patch of old forest because the colonization rate of new host trees did not compensate the rate of local extinctions caused by tree fall. Low colonisation rates can be compensated only by a higher density of potential host trees.

The habitats of most vertebrate species are composed of multiple patches scattered over an area that is larger than a single forest stand. For these species, a sufficient proportion of broadleaved admixtures can be manifested both on the stand, landscape, and even regional scales. For instance, alder is an important food resource for the hazel grouse, and the abundance of alder defines the territory size of the species. The proportion of broadleaved trees in habitats occupied by hazel grouse is generally 5–40% (Åberg et al. 2003). In addition, the number and distribution of territories is dependent on the amount of alder at the landscape level (Swenson, 1993). Several bird species exhibit thresholds for the sufficient amount of patches dominated by broadleaved trees at the landscape scale. Long-tailed tits (*Aegithalos caudatus*) had a significantly higher occurrence probability in landscapes where the proportion of broadleaved habitat was 15% than in landscapes with only 5% of suitable habitat (Jansson and Angelstam 1999).

However, already a rather low proportion of broadleaved admixture seems to benefit forest bird diversity. In managed boreal forests, an increase from 0% to 5% in the broadleaved admixture increased the number of bird species while no effect of higher proportions of broadleaved trees could be detected (Jansson and Andrén 2003). In another study the inclusion of even relatively small proportions (less than 15%) of broadleaved tree species had a positive effect on bird species richness (Lindbladh et al. 2017).

## 5. Pathogens and pests

### 5.1. Pathogens

Mixed forests are usually considered to have a reduced risk of tree diseases as compared to monocultures (e.g. Pautasso et al. 2005, Haas et al. 2011). The increased susceptibility of monocultures is due to the availability of large amounts of similar aged host trees of the same species which may be suitable for a particular pathogen. Additionally, theoretical evolutionary ecology analysis (see Ennos 2001) suggests that monoculture management of forests leads to reduced resilience against pathogens. Functional diversity (Schmidt 1978) is a suitable term here, ‘functional’ implying all mechanisms allowing forests to resist epidemics of diseases and pests.

There are several possible general advantages of mixed forests against specialist pathogens (Thomsen 2016): (1) fewer host trees means lower risk of build-up of inoculum and higher likelihood of disease escape, (2) non-hosts act as barriers to the spread of pathogens (especially via root systems) and (3) if one tree species is decimated by a disease, the whole stand is not lost.

However, generalist pathogens hosted by several tree species may have an extended basis for population growth in mixed forests. Well known and ultimate cases of this sort include rust fungi, which alternate between two unrelated tree species. For example, pine seedlings in recently regenerated mixed forests including pine and aspen are extremely vulnerable to damage caused by the pine twisting rust *Melampsora pinitorqua* (Braun) Rostr. (Desprez-Loustau and Dupuis 1994). Other examples are highly general pathogens that may inhabit several tree species. Good examples are generalist *Armillaria* species that may disperse during thinning from stumps of broadleaved trees to conifers and cause root rot (Simard et al. 2005), although opposite observations have also been made (Gerlach et al. 1997). Furthermore,

exotic tree species grown together with native ones may support local pathogens. This was exemplified in Sweden, where the North American pine *P. contorta* var. *latifolia* (S. Watson) which is susceptible to *Gremmeniella abietina* (Lagerb.) Morelet was planted in the vicinity of the native *P. sylvestris* and caused elevated pathogen pressure on the latter species (see Ennos 2001).

Despite the general acceptance for the good health of mixed forests and examples supporting this theory, the analysis by Nguyen et al. (2016) on foliar diseases at northern latitudes did not fully support this view. They showed that the impact of species diversity on tree disease incidence was weak, and overall pathogen damage instead increased with tree diversity, although the incidence decreased in conifers. This was supported in the finding by Müller and Hallaksela (1998), who showed that the diversity of endophytic fungi in spruce needles correlated with the proportion of spruce trees. In mixed stands, the pathogens may concentrate on fewer focal host trees (host concentration effect), but on the other hand, the presence of heterospecific, non-host neighbours may also reduce the probability of colonization of the focal trees by providing a physical barrier to spore deposition (see Nguyen et al. 2016).

The best scientific evidence regarding benefits of mixed forests against pathogens in the boreal zone concerns *Heterobasidion* root rot. The ability of *Heterobasidion* spp. to grow from tree to tree through root contacts can make conifer monocultures especially susceptible. The smaller size of the *Heterobasidion* clones in mixed than in pure spruce stands indicates that admixed trees restrict the vegetative spread of *H. parviporum* (Niemelä and Korhonen), possibly by reducing the number of root contacts between spruce trees (Piri et al. 1990). In boreal spruce stands the effect of pine admixture seems to be more beneficial than that of birch admixtures (Piri et al. 1990, Lindén and Vollbrecht 2002).

Although most studies have shown positive effects of mixed stands on spruce health by reducing *Heterobasidion* infections (e.g. Huse 1983, Bruchwald 1984, Piri et al. 1990, Lindén and Vollbrecht 2002), several studies failed to show a clear correlation between the incidence of root rot on spruce and the proportion of admixed trees (e.g. Kangas 1952, Kató 1967, Siepmann 1984). Korhonen et al. (1998) suggested that this might be due to the management history of the site determining the root rot incidence and outweighing the positive effect of the tree species composition. Although admixed trees would not protect spruce from *Heterobasidion* infections, they – being resistant to *H. parviporum* – reduce the transmission of *Heterobasidion* root rot to the following tree generation by leaving less inocula, i.e. decayed spruce stumps, per areal unit.

Unlike *H. parviporum*, which is almost exclusively confined to spruce, the other *Heterobasidion* species causing root rot in boreal conifer forests, *H. annosum* (Fr.) Bref., has a broad host range. Its main host is pine, but it also attacks other coniferous trees, including spruce, and even broadleaved trees growing in infected pine stands. Although *H. annosum* is able to spread vegetatively in mixed pine stands, a birch mixture has silvicultural advantages by reducing the establishment of new *Heterobasidion* infections. This is because birch stumps are more resistant against *Heterobasidion* spore infection than conifer stumps (Lygis et al. 2004, Gunulf et al. 2012). Thus, removing admixed birch during summer thinnings instead of conifers reduces the risk of stump infections, which in turn protects the remaining spruces from *Heterobasidion* root rot (Lindén and Vollbrecht 2002).

### 5.2. Insect pests

Several reviews and meta-analyses support the view that mixed stands have lower levels of insect damage, similar to fungal diseases (e.g. Jactel and Brockerhoff 2007, Jactel et al. 2009, 2017, Bauhus et al. 2017). This hypothesis is apparently based more on correlative studies than on experiments (Liebhold 2012). According to Koricheva et al. (2006), empirical evidence supporting the lesser susceptibility of mixed stands to herbivores is largely circumstantial, and rather controversial.

Long-term experiments demonstrate that forest diversity does not generally and uniformly reduce insect herbivory (Vehviläinen et al. 2007). Furthermore, the few experiments that exist have usually been of short duration and have not addressed the frequency or intensity of pest outbreaks, but some surrogate variable, e.g. the level of herbivory or defoliation (Jactel and Brockerhoff 2007). The theory of increased susceptibility of monocultures seems to have most support in the case of specialized insects (mono- or oligophages) in mixtures of broadleaved and coniferous trees (Castagneyrol et al. 2014). Damage by generalist pests may, in contrast, increase in mixed forests (Plath et al. 2012).

Here we focus on the most important host tree and pest insect combinations in Finland during past or future climates (Neuvonen and Viiri 2017, Fält-Nardmann et al. 2018a), and discuss them in respect of the plausible mechanisms that may be applicable to mixed forests.

The factors influencing the damage incidence by the European spruce bark beetle (*Ips typographus* L.) are complex, and there are predisposition assessment systems rating the site- and stand-related hazards of bark beetle infestation (Netherer and Nopp-Mayr 2005). An increasing proportion of broadleaved trees within spruce stands may reduce the vulnerability to bark beetle damage via different mechanisms: (1) by reducing the probability of storm damage (Felton et al. 2016; but there seems to be conflicting evidence for this, see Mason and Valinger 2013), which is often a prerequisite for consequential tree killing due to bark beetles (Eriksson et al. 2007, Komonen et al. 2011, Viiri et al. 2011); or (2) by interfering with the host finding of *Ips typographus* (Byers et al. 1998, Zhang et al. 1999). Additionally, Netherer and Nopp-Mayr (2005) presented, based on relevant literature and discussions with expert scientists, that there should be a nearly linear positive relationship between the proportion of spruce in the stand and the relative score for bark beetle damage predisposition (see also Overbeck and Schmidt 2012). In their field data the proportion of stands infested by spruce bark beetles was about 37%, 8% and 2% in stands with the proportion of spruce > 70%, 25–70% and < = 25%, respectively (Netherer and Nopp-Mayr 2005). However, Grodzki (2011) found that in outbreak conditions there were no clear trends in the relative mortality of spruce in relation to the proportion of broadleaved trees in the stand.

The large pine weevil (*Hylobius abietis* L.) causes economically significant damage to spruce and pine seedlings. Additionally, broadleaved species, such as silver birch, can be utilized as nutrition, but not to any large extent (Toivonen and Viiri 2006). The females lay eggs in fresh coniferous stumps and their immediate vicinity (Nordlander et al. 1997), and during swarming, pine weevils can fly kilometres to new breeding sites. The pine weevil benefits from clear-cut based forestry and the regeneration method currently exploited in the Nordic countries. A more extensive use of natural regeneration and growing of mixed forests might reduce pine weevil damage.

Pine sawflies (mainly *Neodiprion sertifer* Geoffr. and less commonly *Diprion pini* L.) are the most common pine defoliators in Finland (Varama and Niemelä 2001, Neuvonen and Viiri 2017). On the basis of extensive data from Finnish NFI and ICP Forests (International Co-operative Programme on Assessment and Monitoring of Air Pollution on Forests), the probability of pine sawfly damage in forests growing on mineral soils increases with decreasing site fertility, being 1.5- to 4-fold higher in semi-xeric and poorer heath forests than in mesic heath forests (Nevalainen et al. 2015). As the tree species richness generally increases with site fertility, this might limit the feasibility of growing mixed forests on sites with poor fertility with the highest susceptibility to damage.

The Nun moth (*Lymantria monacha* L.) is a generalist species which has historically caused extensive damage to coniferous forests in Central Europe (Bejer 1988). It has spread to Southern Finland during the last decades (Fält-Nardmann et al. 2018b), and it is common below the 62nd parallel (Melin et al., 2020) and has even caused small scale damage in the Southwest Archipelago of Finland (Heino et al. 2014). Heiermann and Schütz (2008) did not find significant differences in

light-trap catches of *L. monacha* in forests with varying proportions of beech and spruce, although the relative abundance of the species was 30% lower in mixed stands than in spruce monocultures. Practical experience from Germany suggests that spruce-pine mixtures are especially vulnerable to damage caused by *L. monacha* (Altenkirch et al. 2002). In summary, mixed coniferous forests should be avoided, but conifer-broadleaved mixtures may reduce the risk of *L. monacha* damage (see also Castagneyrol et al. 2014).

### 5.3. Browsing by cervids affecting early development of mixed forests

In Northern Europe, there can be high numbers of browsing cervids, and the species composition varies by countries and regions. The southwestern part of Finland has high populations of white-tailed deer (*Odocoileus virginianus* Zimmermann), moose (*Alces alces* L.) and roe deer (*Capreolus capreolus* L.). In the central and eastern areas moose are present in high numbers accompanied by locally significant populations of roe deer, and in the northern part of the country the most numerous cervid species are moose and semi-domesticated reindeer (*Rangifer tarandus* L.) (Finnish Wildlife Agency 2020, Natural Resources Institute Finland 2020, Reindeer Herders' Association 2020). All these cervids potentially influence the regeneration and early succession of their preferred browsing trees which, in most cases, are broadleaved species (Ammer 1996, Rooney 2001, den Herder and Niemelä 2003, Heikkilä and Tuominen 2009, Ramirez et al. 2018).

Maintaining broadleaved admixtures in boreal coniferous stands, using the most preferred broadleaved species by cervids in their diet, such as aspen, rowan and oak (*Quercus robur* L.) faces serious problems in forest areas with high cervid densities (Kouki et al. 2004, Götmark et al. 2005, Härkönen et al. 2008a, Edenius and Ericsson 2015). The relatively high preference for silver birch by moose (Bergström and Hjeljord 1987) is economically the most problematic issue for growing boreal mixed forests. Although silver birch is able to survive the sapling stage despite browsing, large-scale browsing damage results in serious quality flaws, reducing tree quality and thus also the utilization of silver birch as an industrial timber (Härkönen et al. 2009, Nevalainen et al. 2016). In addition, using high quality seed material for forest tree breeding in artificial regeneration might be compromised due to higher moose preference for planted and faster growing trees due to the improved seed material (Heikkilä 1991, Jia et al. 1997).

The increasing proportion of tree species which are preferred by cervids may bring along an increasing risk of damage to other, less preferred tree species growing in the same stand. In this sense, especially the admixture of aspen and birch can increase the damage risk to pine and spruce seedlings (Milligan and Koricheva 2013, Nevalainen et al. 2016). Furthermore, when growing a broadleaved mixture in pine stands it is essential to prevent the broadleaved from overtopping pines to avoid increasing damage for pine (Heikkilä and Härkönen 1993, Härkönen et al. 2008b, Nikula et al. 2008, Bergqvist et al. 2014).

All the main concerns of cervid browsing in regard to growing mixed forests can be associated with the cervid density. In order to reduce cervid populations to levels with low or no negative impacts for forestry, we need critical thresholds for animal numbers when browsing damage can prevent regeneration or lead to serious quality loss of preferred tree species. In evaluating the cervid density effects on forests, species compositions of regional cervid guilds are critical due to differing browsing impacts of different species (Ramirez et al. 2018), but no such analyses have been made in boreal conditions.

## 6. Multiple-use of mixed forests

The multiple use of forests means that they are used for more than one purpose, and thus multiple-use forest management aims at simultaneously producing several goods and services. Non-wood forest products (NWFPs) and scenic beauty value are used here as examples of goods and services when mixed stands and monocultures are compared



with respect to ecosystem services.

Wild forest berries and mushrooms are economically important NWFPs and are widely collected for both household consumption and sale in the Nordic countries. The abundance and yield of both berries and mushrooms are primarily affected by site conditions, but also the growing stock and silvicultural operations affect their yields by modifying the stand structure.

Bilberries (*Vaccinium myrtillus* L.) are typical and abundant in conifer-dominated forests of medium fertility, but good bilberry production requires a moderate supply of light (Raatikainen et al. 1984, Kuusipalo 1988, Salemaa 2000a, Nielsen et al. 2007). The highest bilberry yields are found in mature conifer stands with a canopy coverage between 10 and 50% (Raatikainen et al. 1984). The bilberry coverage is also affected by the tree species composition (Kühlmann et al. 2001, Miina et al. 2009, Hedwall et al. 2013, Eldegard et al. 2019). Due to higher light availability, the bilberry yields in pine-dominated stands are higher than those dominated by spruce (Kuusipalo 1988). The bilberry yield decreases heavily when the stand basal area of a spruce stand exceeds a certain level (Miina et al. 2009). According to a simulation-optimization study by Miina et al. (2010), the mean annual bilberry harvest of a pine-spruce-birch mixture was three-fold compared to that of a spruce monoculture, but lower than that in a pine monoculture. According to Jäppinen et al. (1986), the bilberry yields in mature mixed stands were higher than in either spruce or pine monocultures (cf. Gamfeldt et al. 2013). However, pine monocultures with suitable light conditions were characterized by the smallest variation in the annual berry yields. To increase bilberry yields, a higher share of pine and birch in shaded spruce stands, and more conifers in light birch stands could be applied.

Cowberries (*Vaccinium vitis-idaea* L.) are typical in pine-dominated forests on nutrient-poor mineral soil sites. The species is well adapted to grow under a tree canopy, but a good supply of light is needed for good cowberry yields. Cowberry yields are high at the beginning and end of the forest rotation in seed-tree and small pine seedling stands, if competition from herbs and grasses is not too severe, and in sparsely populated stands of large and old trees (Salemaa 2000b). To increase the cowberry yields, longer rotation lengths, higher thinning intensities and more frequent thinnings could be applied in pine stands (Miina et al. 2016). Additionally, the tree species composition has a significant effect on the abundance of cowberries; the coverage being higher in pine-dominated stands than in stands dominated by spruce or broadleaved trees (Hedwall et al. 2013, Turtiainen et al. 2013). The priority of pine over other tree species is reasonable since the best cowberry sites in Finnish forests are largely pine-dominated. Thus, mixing the tree species would have negative effects on cowberry yields but on the other hand, spruce and birch do not naturally grow to a large extent on the best cowberry sites.

In Finland, there are 31 species listed as commercially edible mushrooms, of which ceps (*Boletus edulis* Bull. and *B. pinophilus* Pilát & Dermék), milk-caps (*Lactarius* spp.) and yellow chanterelle (*Cantharellus cibarius* Fr.) are the most popular (Marsi 2018). These mushrooms are mycorrhizal fungi which differ in their ecology and host tree species, and whose seasonal fruiting body production is largely controlled by autumn precipitation (e.g. Ohenoja 1993). According to a three-year inventory in Eastern Finland, the yields of commercial mushrooms were higher in mature mixed pine-spruce stands than in spruce monocultures (Jäppinen et al. 1986). In Northern Finland, pine-birch stands were more diverse in mycorrhizal species than birch monocultures (Ohenoja 2000). However, the highest mushroom yields were observed in pine monocultures of dryish heath forest site type (Finnish classification *Vaccinium* type according to Cajander 1949), where *Lactarius rufus* (Scop.) Fr. was a frequent and productive species. As a conclusion, the highest total yields of edible mushrooms are usually found in monocultures, but in mixed stands of several tree species the species number of mushrooms is the highest due to their symbiotic nature.

Besides berries and mushrooms, forests offer a range of tree-origin

NWFPs such as spruce and pine shoots, birch sap and leaves, pine and spruce resin, as well as chaga mushrooms (*Inonotus obliquus* (Ach. ex Pers.) Pilát), growing most commonly on birches. Naturally, these NWFPs are available only if the tree species producing these NWFPs exist in the stand. Thus, it is straightforward that tree species mixtures have a positive effect on tree-origin NWFPs (Kurttila et al. 2018).

The scenic quality of Finnish forests has been explained by stand characteristics including the tree species composition (Silvennoinen 2017). According to Pukkala et al. (1988) and Tyrväinen et al. (2003), pine and birch stands are preferred by most Finnish people, and spruce monocultures are the least favoured monocultures. Mixed stands are less popular than monocultures. Mixtures of broadleaved trees (spruce with birch and/or aspen) are especially disliked, but mixtures of pine and spruce are appreciated equally to spruce monocultures (Tyrväinen et al. 2003). On the contrary, Pukkala et al. (1988) found that an admixture of other tree species improves both beauty and recreation values of spruce monocultures. In young monocultures, pine, birch, and spruce are equally preferred, but in older forests, pine and birch are preferred over spruce. In general, most Finnish people value large stems and relatively open forests, and a high number of spruces decreases the scenic beauty most probably due to the poor visibility in dense spruce monocultures. Based on simulation-optimizations, Pukkala (2018) found that the scenic beauty value was higher in mixed forests, based on broadleaved-oriented management, when compared to conifer-based managed forests.

## 7. Establishment and precommercial thinning in mixed forests

### 7.1. Establishment of mixed forests

Mixed stands can have several different structures. Basically, they can be two-storied, and uneven- or even-aged. In this section we will focus on even-aged spruce and birch mixtures. In mixed stands, each species responds uniquely to the prevailing conditions (Grossnickle 2000). Broadleaved seedlings typically outgrow spruce seedlings during the first years of a rotation period (Mielikäinen 1985, Nyström 2000, Fahlvik and Nyström 2006, Kaila et al. 2006), and different growth dynamics between species should be equalized in even-aged mixed stand management. Spruce needs an advantage in establishment, and the growth of birch has to be controlled in juvenile stands.

Modern establishment methods such as spot mounding, the use of container-grown seedlings, and genetically improved seeds improve the early growth of spruce compared to previous methods, as well as compared to the growth of naturally regenerated birch (Hallsby and Örlander 2004, Saksa et al. 2005, Kaila et al. 2006, Uotila et al. 2010, Lehtosalo et al. 2010, Rikala 2012, Uotila and Saksa 2014, Luoranen and Viiri 2016, Jansson et al. 2017). Thus, planted spruce can have a head start on natural seed-origin birch, and ordinary establishment methods for spruce can work well when establishing even-aged mixed stands.

Natural regeneration allows reduced planting densities in order to decrease establishment expenses (Holmström 2015, Holmström et al. 2016a). However, to encourage natural regeneration and to fill possible stand gaps with naturally regenerated birch, site preparation is needed, and it should preferably expose mineral soil (Raulo and Mälkönen 1976, Uotila et al. 2010, Holmström et al. 2016a). Some drawbacks are still possible: (1) there is a risk of diminished revenues in wood production if natural regeneration fails (Agestam et al. 2006, Holmström 2015, Holmström et al. 2016a, 2017), (2) increased expenses may be incurred during pre-commercial thinnings due to higher seedling densities as a result of improved germination in the exposed mineral soil (Raulo and Mälkönen 1976, Uotila et al. 2010), and (3) negative environmental effects may occur, such as C loss from the humus layer (Simola 2018) or nutrient leaching (Ahtiainen and Huttunen 1999, Piirainen et al. 2007) due to soil preparation.

## 7.2. Precommercial thinning (PCT)

In general, precommercial thinning (PCT) in mixed forests, even if they are even-aged, is more challenging than it is in monocultures (Fahlvik 2005, Agestam et al. 2006, Holmström 2015). The additional feature of PCT in mixed stands is to even out the growth of the different species and to determine the level of the species proportions in the mixture. The target seedling stand densities can vary from monocultures, as mixtures cope with higher stand densities (Pretzsch and Forrester 2017). The species mixture and stand composition in mixed stands can be greatly influenced by PCT (Agestam et al. 2006, Fahlvik et al. 2015, Holmström 2015, Holmström et al. 2016b). Furthermore, the spatial pattern of a species mixture can vary: for example, mosaic-like structures of small monocultural plots can be used instead of a uniform distribution of different tree species throughout the stand (Fahlvik et al. 2015). However, the over-yielding effect can diminish when the different species are more segregated (Pretzsch and Forrester 2017). Unconditional considerations, such as the spatial distribution of the trees, tree vitality and quality somewhat restrict the possibilities for controlling the mixture compositions during PCT (Fahlvik et al. 2015). Moreover, cervid browsing can substantially restrict admixing spruce with broadleaved trees (Holmström et al. 2016b).

The height difference between the tree species retained in PCT determines whether the stand becomes a mixed even-aged or two-storied birch and spruce stand, or a spruce dominated stand where birch will vanish by self-thinning (Fahlvik et al. 2005). At the time of PCT, equally sized birch and spruce can grow at a similar rate (Fahlvik et al. 2005, Lehtosalo et al. 2010, Uotila and Saksa 2014), or birch can grow faster (Mielikäinen 1985, Luukkonen 2018) or slower (Fahlvik et al. 2005, Fahlvik and Nyström 2006, Kaila et al. 2006). The dynamics of the species composition in spruce–birch stands depends also on the birch species; silver birch generally grows faster than pubescent birch (Mielikäinen 1985, Fahlvik and Nyström 2006, Lehtosalo et al. 2010), but the site fertility (Mielikäinen 1985) and climate (Pretzsch and Forrester 2017) can affect the growth rates of birch species.

Recommendations for the height difference between spruce and birch retained in PCT, varies from 1.5 m for the benefit of spruce to 1 m for that of silver birch (Mielikäinen 1985, Fahlvik et al. 2005, Äijälä et al. 2014). Generally, spruce seems to need an advantage in Finland, whereas in Sweden it is birch. Contradicting recommendations could be explained by different growing conditions, as silver birch may benefit from more continental climate in Finland (Pretzsch and Forrester 2017). The results of Mielikäinen (1985) also emphasize the differences between birch species, as silver birch grows quicker than pubescent birch in young stands.

Spruce–birch mixtures created in PCT typically have equal or slightly lower growth and yields than spruce monocultures (Fahlvik et al. 2005, 2011, Holmström et al. 2016b, 2016c), although Mielikäinen (1985) reported volume and profitability gains in mixed even-aged spruce–silver birch stands compared to spruce stands. A slightly reduced profitability of spruce–birch mixed stands has been found compared to pure spruce stands (Fahlvik et al. 2011). The decrease in total volume growth and profitability can be minimized by reducing the proportion of birch towards the end of the rotation (Valkonen and Valsta 1999; Fahlvik et al. 2011), and due to the use of mounding in soil preparation, improved genetic material and container seedlings in planting, the juvenile growth of planted spruce is faster than earlier, resulting in advantages of spruce also in mixtures in this respect.

## 8. Growth and yield in mixed forests compared to monocultures

### 8.1. Mixed stand effects in managed forests in Fennoscandia

Mixed stands are assumed to be capable of utilizing growth factors (nutrients, water and light) more efficiently than single species stands,

and better mitigate the effects of risks, such as drought, resulting in a more sustainable and higher growth and yield. Mixtures of tree species in forest stands have been reported to increase the biomass production for some tree species combinations (e.g. Gamfeldt et al. 2013, Condés et al. 2013, Pretzsch et al., 2015a, Lu et al. 2016), especially in Central and Southern Europe. According to growth and yield studies in the Nordic countries, the effect of species mixtures on productivity has been found to be minor or negligible for most common tree species in the region, i.e. spruce, pine, silver birch and pubescent birch (e.g. Agestam 1985, Mielikäinen 1985, Hynynen et al. 2011, Holmström et al. 2018).

One explanation for the difference between the Nordic and Central European studies, in addition to different tree species structure, is the difference in the stocking levels of the studied stands. In the studies by Pretzsch et al. (2015b) and Lu et al. (2016) the stands were close to full density, or only moderately thinned, while in the Nordic studies stocking levels were lower due to more intensive thinnings.

Presently the two most interesting management models for a single-storied mixture of species in the Nordic forestry are the use of naturally regenerated broadleaves, mainly birch, in planted stands of spruce or pine (Agestam et al. 2006). In addition to single-storied mixed stands, two storied stands with birch overstorey and spruce understorey, are relatively common.

### 8.2. Growth and yield in mixed stands

In the Nordic countries, the growth and yield of mixed stands can be evaluated in the following groups (single-storied spruce–birch, pine–birch and pine–spruce stands, two-storied birch–spruce and pine–spruce stands, and continuous cover forestry in mixed stands) according to the tree species and vertical canopy structure.

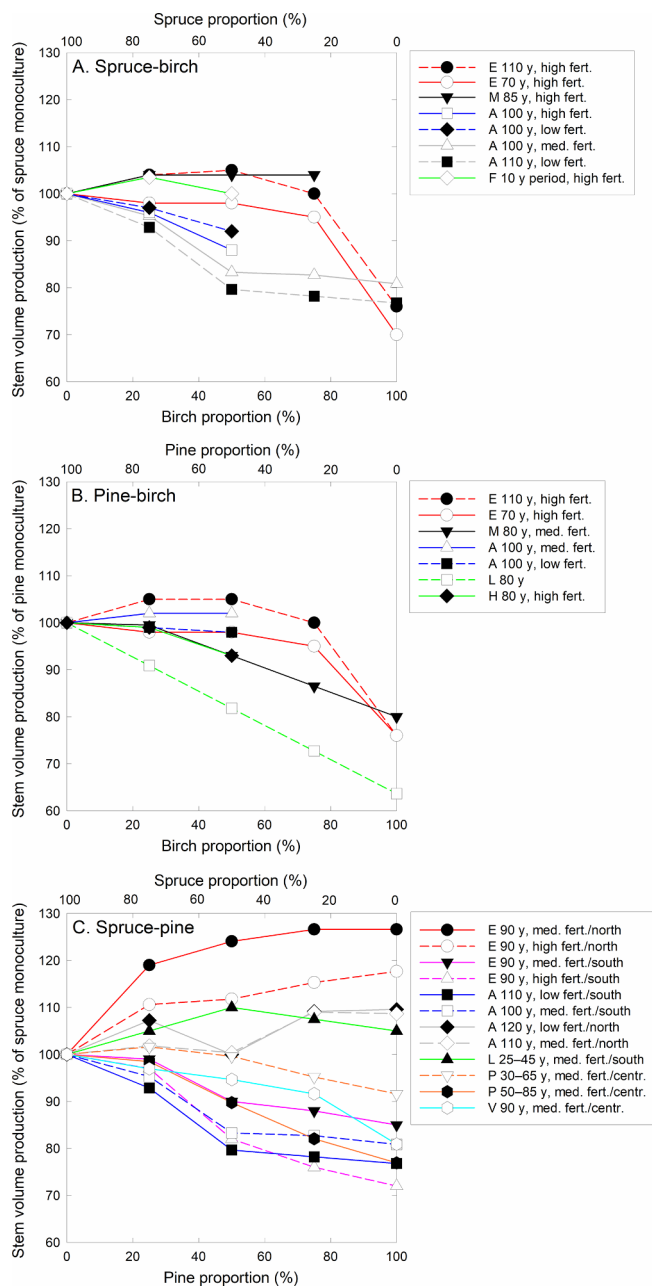
#### Single-storied spruce–birch stands

In the boreal zone of Northern Europe only a few studies have resulted in higher total wood production in the mixed stands of spruce and silver birch compared to pure spruce stands (Fig. 1). Positive mixture-effects have been reported on fertile sites by Mielikäinen (1980), by Ekö (1985) during long rotation, by Frivold and Frank (2012), and in experiments by Agestam and Frivold (Lindén and Agestam 2003, Fahlvik et al. 2011). On the other hand, Agestam (1985) simulated a low negative effect with birch mixtures on sites of medium fertility, and even a 20% growth loss with a birch mixture of 50% or higher on sites of low fertility. According to most studies, the proportion of birch should be reduced in commercial thinnings in order to avoid growth losses. Only Ekö (1985) resulted in opposite numbers; the overall recommendation for the birch proportion is 50% in young stands and no more than 20% after thinnings. One reason for the contradictory results in these studies is that two birch species (silver birch and pubescent birch) were not separated in the analyses. According to Hytönen et al. (2014), the volume increment of pubescent birch was 33% lower than that of silver birch. In mixed stands, Mielikäinen (1980) found that the total production was 9% higher with a silver birch mixture of 50% compared to a similar mixture of pubescent birch. In simulations, the growth and yield of pure stands of birch have been 19–24% lower compared to pure spruce stands, but the models have been based on the data including both birch species (Agestam 1985).

#### Single-storied pine–birch stands

Both pine and birch are regarded as light demanding pioneer tree species. The early growth of birch is known to be faster. In young mixed pine and birch stands with a dominant height of 2–6 m, the mean annual height increment of natural seed-origin birches and planted pines was 43 cm and 38 cm, respectively (Valkonen and Ruuska 2003). The birch mixture significantly reduced the diameter increment of pine trees but not the respective height increment.

Because of the different growth rhythm and shorter life span of birch, the competition dynamics of these tree species will change in the course of their life (Mielikäinen 1980, Hynynen et al. 2011). Compared



**Fig. 1.** Effect of the mixture-% on the volume yield in a) mixed Norway spruce - Silver birch stands, b) mixed Scots pine - Silver birch stands and c) mixed Norway spruce - Scots pine stands at varying rotations (years), site fertilities (low, medium and high fertility) and locations (south, centre, north) according to Ekö 1985 (E), Mielikäinen 1980 and Mielikäinen, 1985 (M), and Agestam 1985 (A), Hynynen et al. 2011 (H), Lindén 2003 (L) and Pukkala et al. 1994 (P) and Vetterranta 1999 (V).

to the young stands above, the difference in annual height increments between birch and pine was reduced but still remained until the ages of 35–68 years being 48 cm and 45 cm for dominant birches and pines, respectively. During the following 19-year period the difference in the annual dominant height increment was the opposite and was 21 cm for birch and 23 cm for pine.

A small loss in growth or no mixed-stand-effect ( $\pm 2\%$ ) was found with birch mixtures of 25% in pine stands by Mielikäinen (1980), Agestam (1985) and Lindén (2003) (Fig. 1). With a birch mixture of 50% the corresponding growth loss was 0–18%. Compared to pure pine stands, the simulations by Ekö (1985) showed similar growth losses in middle-aged mixed pine-birch stands and higher growth losses in

younger stands, but a positive mixed-stand-effect at older ages. However, the simulation results by Ekö (1985) are incompatible with the growth rhythm of birch with a high increment in young ages and regress after middle age (Mielikäinen 1980).

According to measurements on long term plots (Hynynen et al. 2011), the negative effect of birch mixtures in pine stands on the total volume growth was stronger than that found in simulations. Both the height and diameter increment of pine suffered due to abundant birch mixtures. The height increment depends on light-competition, and the dominant birches were higher than the pines at the beginning of study period. Although pines approached the height increment of birches, they remained overshadowed in birch dominated stands. Additionally, the different water and nutrient requirements of pine and birch (Mälkönen 1974, 1977) can favour birch in mixed stands on fertile sites. Therefore, pines growing alongside birches suffer more from belowground competition compared to those growing in pure pine stands. However, on poorer sites pine overwhelms both birch species.

#### Single-storied pine-spruce stands

Additionally, in mixed pine-spruce stands, the growth reactions are very site-sensitive. In the north the pine mixture has been shown to increase the total yield, being at its highest in pure pine stands (Ekö 1985, Agestam 1985, Lindén and Agestam 2003) (Fig. 1). On sites with medium and high fertility in southern and central Fennoscandia, the yield of pure pine stands was 10–30% lower than that of pure spruce stands (Ekö 1985, Agestam 1985, Pukkala et al. 1994, Vetterranta 1999). On these sites, a pine mixture of one fourth did not lower the yield, but with an increasing pine proportion it was 5–20% lower than in spruce stands. Recently, based on the long-term experiments in mixed pine-spruce stands, Holmström et al. (2018) reported that pine monocultures produced 126% more stem wood biomass than spruce. In addition, pine benefitted from the mixture of spruce and tended to grow as it would in a reduced spacing pattern. However, spruce suffered from competition from pine resulting in a lower mean diameter compared to the spruce monoculture. Based on preliminary results of analysis for temporary sample plot data of young pine-spruce mixtures (unpublished data from Natural Resources Institute Finland), single storied pine and spruce mixtures can be developed evenly with proper juvenile stand management practices. Thus, no facilitative or complementary mixture effects were found in mixed pine and spruce stands.

#### Two-storied birch-spruce stands

Birches usually form the overstorey in a young spruce stand, because of their rapid juvenile growth compared to spruces (Mielikäinen 1985, Mielikäinen and Valkonen 1995). Traditionally, naturally regenerated birches and other broadleaves have been used as shelter to protect spruces against summer frost, and at the same time to produce firewood (Leikola and Pyllkö 1969, Leikola and Rikala 1983, Andersson 1984, Heikurainen 1985). The negative effects of sheltering birches on the growth and mortality of planted spruce have been found to be relatively low (Heikurainen 1985, Bergan 1987, Tham 1988, 1994, Mielikäinen and Valkonen 1995).

Tham (1988, 1989, 1994) studied the growth and yield of spruce, silver birch and pubescent birch in mixed stands, where naturally regenerated birch was grown for 20–35 years above spruces. Silver birches were found to be from 2 to 4 m higher than spruces, but the height difference between pubescent birch and spruce was lower. Using simulations over 50-year-long rotations, Tham (1994) obtained the highest total volume increment (mean annual increment  $7.7 \text{ m}^3 \text{ ha}^{-1} \text{ a}^{-1}$ ) with 1,600 spruces per hectare and 600 silver birches per hectare, and by removing sheltering birches at age of 30 years. The increment of pure spruce stands without birch shelter was 19–23% lower. A denser birch or spruce storey did not increase the total volume increment but changed the relative growth rates of the tree species. The effect of sheltering pubescent birches on the total volume increment was small, because the slightly reduced volume increment of the birches (20%) was compensated by a higher increment of spruce.

Tham (1988) pointed out that it is important to ensure through



tending and pre-commercial thinning that the spruces rapidly reach a height of 1–2 m, which is the phase when the birches should be spaced to 500–800 trees per hectare. However, if there is a risk of summer frost, the number of birches should be higher depending on the size of birch (Andersson 1984) and a later PCT is needed.

The results above apply to stands with spruces and birches more or less of the same ages, and the birch forms the overstorey because of its faster juvenile growth. Another frequent combination is an older birch generation above spruces, when distinctly younger spruces have established themselves naturally or artificially below the birches. According to Mielikäinen & Valkonen (1995), the development of the dominant height of the spruce understorey falls 2–4 m behind that of spruces in single-storey pure or mixed stands, but almost reached it in 15–20 years after the release of spruces at the age of 10 years. During the first 2–3 years after the release, the height growth of spruces was equal or even lower than before, but it increased often in the third year and became faster in the next 3–4 years. Cajander (1934), Skoklefeldt (1967), Bergan (1987) and Koistinen and Valkonen (1993) noted similar results on the release response of understorey spruce. After a recovery period, the released spruces grew even faster than the free-growing spruce seedlings of the same size (Bergan 1987, Tham 1988). However, the current height development of planted spruces, with improved planting material and regeneration methods, is faster than that observed in the earlier studies above.

The height increment of undergrowth spruces has not been clearly influenced by the density of the birch overstorey (Mielikäinen and Valkonen 1995) apart from very dense birch thickets (Niemistö and Poutiainen 2004). In young and dense birch stands, there are limited growing space and shaded conditions under birches (Oliver and Larson, 1996), but in two-storey birch-spruce stands, the shading effect of birches clearly higher than spruces may not be as severe (Pukkala et al. 1991). In addition, the spruces can be hampered by the whipping overstorey birches if the difference in their age is narrower than 10–15 years (Fries 1974).

The thinning of the birch overstorey was more feasible when birches were young compared to older ones, mainly because of increased saw log production. The total volume increment (birch + spruce) was almost the same in thinned and unthinned stands, but it was 40–50% lower when all birches were removed (Mielikäinen and Valkonen 1995). The reaction to a thinning or a release has been found to be stronger concerning the diameter increment than for the height increment (Assmann 1970, Fries 1974, Andersson 1984, Niemistö and Poutiainen 2004). No effect of the density of the spruce understorey on birch growth has been found (Mielikäinen and Valkonen 1995, Niemistö and Poutiainen 2004, Bergqvist 1999).

#### *Two-storied pine-spruce stands*

There are very few studies on two-storied pine-spruce stands. According to Pukkala and von Gadow (2012), the optimal structure of a pine-spruce stand on a sub-xeric site is two-storied, where pines are larger than spruces with some overlap between the tree species. Pukkala et al. (2013) and Laiho et al. (2014) questioned the common belief that birch is the best canopy for a spruce understorey (and the best admixture in a spruce stand). If the effects of the stand basal area and site fertility were removed, the growth of spruces was equal or even better under pine than under birch. The common belief concerning the lesser competitive effect of birch may be partly due to lower stand basal areas and better site fertility of birch stands compared to pine stands. After moderate thinning of the pine overstorey, a short-term but clearly positive effect on the growth of the understorey spruce has been observed (Niemistö 2003) suggesting that pine is also a strong competitor for the spruce understorey.

#### *Continuous cover forestry in mixed stands*

The key question in aiming for continuous cover forestry as mixed stands is how to maintain the mixed structure. Pukkala et al. (2012) suggested that it might be easier and more profitable to alternate between periods of pine and spruce dominance on medium sites, and

between broadleaves and spruce dominance on fertile sites. Another question is how to establish a pine- or birch-dominated stand after the dominance of spruce using either clear cutting or very heavy continuous cover treatment.

In continuous cover forestry in mixed stands, information about the development of various tree species in various hierarchical positions is needed. At present, it is possible to say that spruces growing under birches or pines may develop well, but birches as an understorey hardly have any chance to develop into harvestable trees. However, there are not yet enough research results and data available to give more precise recommendations.

## 9. Discussion

### 9.1. Current knowledge, its gaps and research needs

Timber production has been considered the most important ecosystem service of boreal forests for many decades. However, environmental, and societal changes have resulted in new demands on forest utilization, thus shifting the focus in production forests to alternative forest management options providing a wider scale of ecosystem services. Forest biodiversity has been emphasized as an important factor for the whole forest ecosystem. The boreal forests of Fennoscandia are characterized by a low number of tree species, and in fact, two conifers, pine and spruce dominate almost the entire forest landscape, whereas mixed forests with a similar proportion of both conifers and broad-leaved trees are scarce. The conversion of particularly coniferous monocultures, into mixed forests is generally assumed to result in a higher delivery of ecosystem good and services, especially biodiversity, improved risk management and recreational value. Thus, one important aim of current silviculture and forest management is to increase the number of mixed forests.

Our review exclusively focussed on a Fennoscandian context. However, the functioning of mixed-species forest ecosystems has also been studied elsewhere in the boreal zone. Results are available, for instance, on soil properties and processes (Légaré et al., 2005, Chomel et al. 2015, Laganière et al. 2015, Ribbons et al. 2018), understorey vegetation (Bartels and Chen, 2013, Li et al. 2012, Zhang et al. 2017, Kumar et al. 2018), biodiversity (Cavard et al. 2011, Li et al. 2012), pests (Su et al. 1996), fungi (Kernaghan et al. 2003, Nagati et al. 2018) and ecosystem productivity (MacPherson et al. 2001, Chen et al. 2003, Paquette and Messier 2011, Zhang et al., 2012, Kabzems et al. 2016, Ma and Chen 2016, Hisano et al. 2019). The work done in Europe and elsewhere shows that mixed tree species can enhance the ecosystem services provided by forests. The ways to increase the number of mixed forests in different locations greatly depend on e.g. the tree species and their growth dynamics as well as forest management practices (e.g. Chen and Popadiouk 2002, Pretzsch et al. 2017).

In boreal Europe, a relevant question is whether to replace a pure spruce forest with a spruce–birch forest (e.g. Felton et al. 2010, 2016). The addition of birch is likely to increase the amount of light on the forest floor and the nutrient cycling, improving the nutrient availability in the soil, while reducing the C/N ratio and raising the pH (Barbier et al. 2008, Augusto et al. 2015). Additionally, the numbers of microhabitats are thought to increase (Felton et al. 2010, 2016) as well as the resistance of the stand against attacks by *Ips typographus* and *Lymantria monacha*. Grasses and herbs would probably benefit from the admixture of birch (Wallrup et al. 2006). However, the number of bryophyte species and their biomass would decrease (Saetre et al. 1997) as well as the biomass of lichens (Bartels and Chen 2013).

Tree species affect the soil directly and indirectly, with numerous mechanisms including the amount and composition of above- and belowground litter, root activities, microclimatic conditions and the ground vegetation developing under the tree cover. The litter quality and composition differ between monocultures of different tree species, resulting in different tree species effects. While birch is regarded as a



**Table 3**

Main findings and research needs of replacing monocultures with mixed-species stands in boreal forests in Fennoscandia.

Questions and aspects for ecosystem services	Main findings on the effects of mixed forest stand		More research needed about
	Pros	Cons	
<b>What are the effects of mixed forests?</b>			
<b>Soil properties</b>	Broadleaves improve soil properties  Soil horizontal and vertical variation will increase with time		The long-term soil effects of tree species in mixed stands The optimal or minimum required proportions of tree species in a mixture
<b>Understorey vegetation</b>	Admixtures increase the understorey species richness and biomass  Tree-species admixture can have different effects on understorey vegetation depending on stand age		The influence of the most important tree species (spruce, pine, and birch) on the understorey vegetation when occurring as a mixture Influence of stand age on the impact of different tree species  The influence of mixture at different site types and age classes
<b>Biodiversity</b>	Infrequent broadleaves host almost equal numbers of species than each of the three dominating tree genera, spruce, pine and birches  Mixed forests have several structural characteristics that make them more suitable habitats for most species than coniferous monocultures A rather low proportion of broadleaved admixture seems to benefit forest bird diversity	Increasing the proportion of broadleaves in conifer monocultures can increase biodiversity, but as such is unlikely to improve conditions for many red-listed forest species associated with overmature and dead broadleaves	The optimal or minimum required proportions of tree species in a mixture
<b>Pathogens and pests</b>	Mixed forests (especially conifer-broadleaved mixtures) have a lower risk of pathogen and pest damage as compared to monocultures	Generalist pathogens hosted by several tree species may have an extended basis for population growth in mixed forests  Increasing proportion of broadleaved admixture can attract browsing cervids and increase the damage risks in pine and spruce sapling stands Spruce-pine mixtures may increase the risk of <i>L. monacha</i> damage	The critical thresholds for animal numbers when browsing damage can prevent regeneration or lead to serious quality loss of preferred tree species
<b>Multiple use</b>	Compared to spruce stands, admixture increases bilberry yields  Tree species mixture diversifies mycorrhizal fungus flora Admixture improves the beauty and recreation values of spruce stands	The highest mushroom yields are obtained in pure conifer stands  Mature, pure pine and birch stands are highly preferred by their beauty and recreational values	Assessing factors influencing the scenic beauty and recreational values at the landscape level
<b>What are the silvicultural possibilities to establish and manage mixed forests</b>			
<b>Establishment and precommercial thinning</b>	Applying the prevailing regeneration methods for spruce and utilizing natural regeneration of broadleaves seems to be feasible method in establishing even-aged mixed stands	Compared to monocultures, the management of mixed forests is more challenging  The height difference between birch and spruce trees retained in PCT determines whether the stand develop to a mixed even-aged or two-storied stand, or a spruce dominated stand	Regeneration methods of mixed stands utilizing both artificial and natural regeneration methods  Dynamics of mixed juvenile stands established with improved regeneration material of spruce or pine
<b>Growth and yield</b>	Growing mixtures does not notably affect the amount of stem wood yield in managed production forests In practice, all needed tools for updating forest management regimes exists	The management of mixed stands needs more attention than that of single-species stands	Tree species dynamics of mixed stands with varying intensity of forest management and density control

soil improving species, conifers, and spruce in particular, change soil fertility gradually in a more unfavourable direction (Table 3). Based on the sparse literature, we can conclude that the direction the tree species change the soil of monocultures probably holds true also in mixed stands. However, due to various interactions between trees caused by aspects such as the litter chemistry, root distribution and nutrient

uptake patterns, it is not possible to extrapolate results obtained from monocultures to mixed stands. Moreover, even if no significant effects of tree species in mixed stands occur in the short run, the soil horizontal and vertical variations probably increase with time due to differences in both above- and belowground litter as well as root activities.

In order to be able to make more accurate predictions of the effect

mixed forests have on soil properties, we need more tree diversity field studies assessing the long-term soil effects of tree species, and using experiments involving trees growing on the same geological formation and originally similar soil, being truly replicated (e.g. so-called common garden studies). There are a few but still rather young experiments assessing the effects of biodiversity on ecosystem functioning (e.g. Satakunta forest diversity experiment (<http://www.sataforestdiversity.org/>)). These should be established in different climatic conditions within the boreal zone. Additionally, various interactions between tree species should be taken into account. Furthermore, we would need more experiments addressing detailed research questions, combined in the same experiment, and monitored in situ. Practically oriented and specific topics, e.g. the minimum proportion of broadleaved trees in a spruce stand to improve soil, as well as the possibilities to use tree species living in symbiosis with N-fixing bacteria (*Alnus* sp.) to improve the soil N status, particularly in soils that are N-limited.

Generally, mixed forests will increase biodiversity. They have several structural characteristics making them more suitable habitats for most species than coniferous monocultures, and already a rather low proportion of a broadleaved admixture seems to be beneficial for many species (Table 3). According to the Finnish NFI, conifers constitute 80% of the growing stock in Finnish forests, birch 17% and other broadleaved trees the remaining 3%. In spite of their low numbers, the infrequent broadleaved tree species host almost equal numbers of species as each of the three dominating tree species (spruce, pine, and birch). A considerable part of those species associated with infrequent tree species consist of specialists depending on one tree genus only. Consequently, the number of red-listed species on infrequent tree species is large. In particular, the importance of aspen as a host for red-listed species is pronounced.

There are several proven mixed-forest specialists in vertebrate species (e.g. the flying squirrel and the hazel grouse) which require the intermixing of two tree species at the stand level, and it is possible that there are similar species among invertebrate or fungal species too. Since the infrequent tree species do not generally form pure stands, their proportion as admixed species in mixed stands is crucial for the local and regional persistence of their associated species.

The optimal or minimum required proportions of tree species in a mixture remain unknown, even though the positive influence of the mixture may be documented in many studies (Table 3). In addition, little is known about the influence of the most important tree species (spruce, pine, and birch) on the understorey vegetation in the boreal forests of Europe when occurring as a mixture. The tree species influence in mixtures on different site productivities is a relevant question, as in practice different tree species are grown on different sites.

Forest monocultures should in theory be more prone to disease epidemics and pest outbreaks than mixed stands, at least to attacks by specialist pest and pathogen species (Table 3). Although beneficial effects of tree-species diversity in reducing stand vulnerability have been observed in some cases, the scientific evidence on the reduced risks of mixed forests is not unequivocal. The spread of *Heterobasidion* root rot can be somewhat controlled by growing mixed stands, and the build-up of serious damage can be slower than in spruce monocultures. In contrast, an increasing proportion of aspen and birch admixture might attract browsing cervids and increase the damage risks in pine and spruce sapling stands.

Diversification of forests can be an advantage if new threats to specific tree species arrive—or known pests and pathogens intensify their damages due to climate change. It is very important to employ species-specific knowledge of pests and pathogens when planning and managing mixed stands. This involves avoiding growing tree species that are known to be susceptible to potential damage, or poorly adapted to the prevailing site, climatic conditions and day length, or which are known to host rust fungi during different parts of their life cycles.

The management of mixed forests is more challenging compared to

monocultures, especially the establishment and precommercial thinning in mixed-stands compared to pure spruce or pine stands, as the current widely-used and efficient regeneration chains have been developed for spruce and pine (Table 3). During the regeneration phase, spontaneous regeneration could be used in the establishment of mixed stands to reduce regeneration costs. If the aim is to convert monocultures to mixed stands in the future, it will be crucial to pay attention to the precommercial and commercial thinnings, and to allow more admixed species as potential crop trees.

One bottleneck is definitely the scarce knowledge on how to achieve a productive mixed forest, taking into account economical constraints, but also the provision of multiple ecosystem services. Research on mixed stand development is limited compared to single species stands. Studies of mixed stands often show contradictory results. One reason for this is that in many studies it is not clear what kind of single-species monoculture the mixed stand is compared with. In addition, a clear definition of a mixed stand is often lacking. The complexity of mixed stands and the high number of possible combinations of species makes it difficult to obtain generalizable results. So far, the hypothesis of higher production in mixed stands has generally not been confirmed in yield studies in Nordic countries. The separation of extra- and intra-species competition is problematic, and the tree species have different long-lasting effects on soil and other growth conditions. Forest yield studies are complicated and time consuming. Long-term experiments including mixed forest stands are rare. Many experiments suffer from various shortcomings, such as the lack of single-species control plots including all the tree species in the experiment (e.g. Assmann 1970). A common method to overcome the problems with long-term experiments and lack of control plots is the use of growth simulator applications to predict the future development.

To fulfil the demands of society, there is an urgent need to establish long-term experiments with current tree breeding material and regeneration methods to answer the question of how mixed stands should be established in the future. Another urgent question is how the current young mixed stands have developed. In order to answer that question, largescale surveys including different tree species compositions are needed.

## 9.2. Implications for forest management

There is a need to close the gap between the goals of sustainable forest management and its practical application. Current forest management measures should be improved to attain multi-functional and sustainable forest management. These goals have been set usually as National Forest Strategies and are found in silvicultural guidelines and forest certification systems. For example, according to the [National Forest Strategy 2025](#) for Finland, forests are in active, economically, ecologically and socially sustainable and diverse use. Thus, as one solution, forest management regimes which can increase the species mixture in coniferous-dominated production forests in a feasible manner should be emphasized.

Another, important issue is to increase the C sequestration by forests, in order to mitigate climate change (Luyssaert et al. 2018). There are indications that mixed forests can increase ecosystem C storage, and there are evident indications for increasing aboveground C (Paquette and Messier 2011, Fichtner et al. 2018). Belowground patterns, however, are not that clear, as they are observed to be context dependent, being affected by species identity, functional traits, and climatic conditions (Vesterdal et al. 2013).

Total species richness in a mixed forest is always higher than in a monoculture, which is due to the fact that all tree species host their own specialized herbivores, epiphytes, mycorrhizal fungi etc. The inclusion of even a few individuals of an infrequent broadleaved tree species into a stand will therefore enable the local occurrence at least some associated species. The enhanced structural diversity of stands will increase general species diversity.

There is too little information to give any quantitative prescriptions for the optimal amount of broadleaved admixture in order to maximize the biodiversity benefits at a given cost. Since most of the infrequent broadleaved tree species have low economic value, retention of these trees will bring about costs in the form of reduced production opportunities. From the silvicultural and economic points of view, the easiest options to retain and increase these species include key habitats, retention tree groups, stand edges, and marginal sites. It is probable that many species living in old living trees and dead trees have threshold values for the minimum density of host trees. Therefore, the conservation effort should be concentrated rather than evenly dispersed.

As pointed out by Felton et al. (2010), increasing the proportion of broadleaved admixture in conifer monocultures can be expected to increase biodiversity, but as such it is unlikely to improve conditions for many red-listed forest species associated with broadleaved trees. In addition to dead wood, these species require tree individuals that are clearly older than ordinary rotation times would allow. This means that, in addition to increasing the broadleaved admixture, other silvicultural means to increase biodiversity should be implemented simultaneously.

From the perspective of multiple use of the forest, for example, the bilberry yields in shaded spruce stands can be increased by a mixture of pine and birch (Miina et al. 2009). Further, it is straightforward that tree species mixtures diversify tree-origin NWFPs (e.g. spruce shoots, resin, and birch leaves), as well as mycorrhizal fungi due to the symbiotic nature of the most important edible mushrooms in Fennoscandia. However, the practical evaluation of the scenic beauty of mixed forests compared to monocultures has shown rather varying results. An admixture of other tree species improves the beauty and recreation values for spruce stands, but mature coniferous monocultures are preferred by most Finns (Tyrväinen et al. 2003). However, there are also results supporting the high scenic value of mixed-stand- or broadleaved-oriented forest management (Pukkala (2018)).

Jonsson et al. (2019) pointed out that the species composition and their relative mixing affect the potential of forests to provide ecosystem services. They also concluded that in the boreal region mixing spruce and birch results in a high level in several ecosystem services simultaneously. Astrup et al. (2018) highlighted the significance of increasing the proportion of broadleaved trees also for reducing the risk of forest fires and with enhanced surface albedo resulting also in mitigating climate change.

In summary, there seem to be good possibilities to combine wood production and increased provision of other ecosystem services simultaneously by growing mixed stands in boreal Fennoscandia, with some reservations (Table 3). However, silvicultural regimes for mixed stands need to be developed, and many research questions connected to mixed forests remain to be solved (Table 3).

## 10. Conclusions

We identified the current research-based knowledge on the potential of mixed forests in providing ecosystem services compared to monocultures in boreal forests in Fennoscandia. In this review we addressed the questions of the effects of mixed forests on soil properties, understorey vegetation, biodiversity, resistance and resilience against damage, forest productivity, and on the multiple use of forests, as well as the silvicultural possibilities to create, maintain and manage mixed forests. The conversion of coniferous monocultures in particular to mixed forests appears to provide a higher delivery of ecosystem goods and services, especially biodiversity, improved risk management, soil properties, and recreational value. However, challenges of growing mixed forests were also pointed out. The most serious of these is the browsing by cervids, and all main concerns of browsing in regard to growing mixed forests can be associated with cervid density. In addition, open questions still remain related to resilience and management practices such as the establishment of mixed stands with current

regeneration methods and material and ways to increase mixture in current stands.

## Funding

This work was supported by the Natural Resources Institute Finland strategic funded project “Mixi - Can mixed forests provide a wide range of ecosystem services in the future?”.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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