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**Author(s):** Simone Bianchi, Saija Huuskonen, Jari Hynynen, Teppo Oijala, Jouni Siipilehto & Timo Saksa

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## Development of young mixed Norway spruce and Scots pine stands with juvenile stand management in Finland

Simone Bianchi <sup>a</sup>, Saija Huuskonen <sup>a</sup>, Jari Hynynen<sup>a</sup>, Teppo Oijala<sup>b</sup>, Jouni Siipilehto<sup>a</sup> and Timo Saksa <sup>a</sup>

<sup>a</sup>Natural Resources Institute Finland (LUKE), Helsinki, Finland; <sup>b</sup>Metsä Group, Jyväskylä, Finland

### ABSTRACT

In Fennoscandia, mixtures of Norway spruce (*Picea abies* Karst.) and Scots pine (*Pinus sylvestris* L.) are of increasing interest, since they may deliver simultaneously a wide variety of benefits. However, there is still lack of information on how young mixed stands in managed production forests would develop under even-aged management with artificial regeneration of spruce. We inventoried ten such stands (age range: 8–26), with soil properties, tree characteristics, and locations recorded in three plots. In each plot, five sample trees of both species were selected, and their past diameter and height growth were reconstructed through stem analysis. We compared species-specific mean stand parameters, and we modeled the individual tree growth. Spruce and pine had reached similar mean size, with only slight differences. The spatial distribution of the two species was even across the plots. Only 8% and 1%, respectively, of the total pine and spruce trees were damaged, with browsing the most common damage cause (62% for pine). The modeling results suggest that pine had only a small competitive advantage on spruce, and less so in higher fertility sites. Our observations showed that it is possible to develop single-storied pine–spruce mixture with the help of careful management.

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Mixed stands; young stands; browsing; GAM

## Introduction

Sustainable forest management recognizes that forests should be managed for a wide variety of ecological, economic, and social benefits at the same time (Cubbage et al. 2007). Increasing the diversity of forest ecosystems is one possible way to obtain multiple benefits from managed stands (Malcolm et al. 2001; Spiecker 2003; Felton et al. 2016; Macpherson et al. 2017). Mixed forest management could be beneficial due to improved resilience and increased biodiversity, and thus being more adaptive to environmental changes and ensuring the stability of raw material supply (Felton et al. 2016; Huuskonen et al. 2021). Increasing species diversity also allows a widening of product portfolio for forest-based bioeconomy. Commercial wood production can benefit from the phenomenon of over-yielding (i.e. mixed stands having higher growth rates than pure stands of the individual species components) (Zhang et al. 2012; Bielak et al. 2014). Mixed stands may have higher carrying capacity caused by a higher resource-use efficiency, as observed frequently in Central Europe (Pretzsch and Schütze 2016). However, research results in Northern Europe show that growing mixtures does not notably affect the amount of stem wood yield in managed production forests (Felton et al. 2016; Huuskonen et al. 2021). Furthermore, the enhanced range of ecosystem services provided by mixed forests may improve the acceptability of commercial use of forests.

However, for mixed stand management, there are also concerns related to the complexity of management and decreased cutting revenues, the latter due to differences in stumpage prices or increased costs of forest operations. Browsing is also an increasing problem in Fennoscandia (Nevalainen et al. 2016), and there are concerns about increasing damage in mixed stands if susceptible species are introduced, such as pine and many broadleaves (Felton et al. 2016). Moreover, there is the concern that pine would have overtaken spruce in the early stages and made the latter not a viable component for the mature stand (Ekö 1985; Nilsson et al. 2019). As a result, silviculture in Fennoscandia has favored the coniferous tree species Norway spruce (*Picea abies* (L.) Karst., from now onwards spruce) and Scots pine (*Pinus sylvestris* L., from now onwards pine) as pure stands (Korhonen et al. 2017; Official Forest Statistics of Sweden. 2020). However, pine–spruce mixtures can still be commonly found in Nordic countries (Johansson 2003).

Nordic countries have valuable series of long-term experiments to study the effect of forest management practices on growth and yield. However, most of the experiments have been established in pure monoculture stands, and there are few research studies evaluating how mixed stands grow. Some of them have recently been reported by Holmström et al. (2018). More extensively, Huuskonen et al. (2021) concluded that no facilitative or complementary mixture effects have been found in mixed pine and spruce stands in

**CONTACT** Simone Bianchi  [simone.bianchi@luke.fi](mailto:simone.bianchi@luke.fi)

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Fennoscandia. In northern Fennoscandia, the pine mixture increased the total yield compared with spruce, being the highest in pure pine stands (Agestam 1985; Ekö 1985; Lindén and Agestam 2003). In southern and central Fennoscandia, on medium- and high-fertility sites, the yield of pure pine stands was 10%–30% lower than that of pure spruce stands (Agestam 1985; Lindén and Agestam 2003). We want to stress that those above-mentioned studies were based on mixed-species stands, which regenerated decades ago. Thus, we are currently lacking information on the growth of young mixed pine and spruce stands managed according to more recent silvicultural methods. For the purpose of this study, we define modern management methods as: regeneration with improved seedling material, in the case of spruce with container seedlings; using modern soil preparation methods (e.g. spot mounding); and tended with early cleaning (EC) and precommercial thinning (PCT). EC is needed in newly regenerated stands to control the competition of abundant fast-growing broadleaves, which typically is done when the stand reaches one meter in height. PCT is needed to control the overall structure and density of the stand, which usually is done (depending on tree species) when the height reaches 3–6 m and thinning the stand to the density of 1600–2200 stems per hectare.

Commonly, pine–spruce mixtures can be established by planting spruce and planting, sowing or by natural regeneration of pine; less often the two species are planted together, since it can be more expensive and demanding greater efforts (Johansson 2003). In a country-wide survey across Sweden, Nilsson et al. (2006) found that naturally, regenerated pine seedlings were too small compared with planted spruce seedlings to be competitive enough to survive in the future stand. Thinning in young pine–spruce mixtures stands is highly important for their long-term development and has a great impact on tree composition. However, there is a lack of research into the establishment and tending of young mixture (Fahlvik et al. 2015; Novák et al. 2017).

The previously mentioned scarce pine–spruce mixture studies have been focused on growth and yield investigation. Even less knowledge exists on the effects of mixture on wood quality in terms of stem form or defects. Lindén and Agestam (2003) reported no differences in stem defects between mixed pine–spruce and monoculture stands. They also reported that pine had a lower height to diameter ratio in

the mixture than in monocultures, but in their case, the pines had a dominant position over the spruce. Pretzsch (2016) states that even more than species mixture is the structural heterogeneity that influences the wood quality.

The aim of our study was to assess the potential for growing pine and spruce mixtures managed with modern techniques. We analyzed cross-sectional measurement data from selected well-managed young mixed pine and spruce stands in production forests. We analyzed the current state and the past growth of measured sample plots. Specifically, we considered the following research questions: (1) Is the current size of pine trees larger than spruce trees in terms of height or diameter? (2) Are there differences in the past growth dynamics between the tree species in terms of height or diameter? (3) Are there differences in the tree species-wise spatial distribution? (4) Was pine more vulnerable to lower external quality and browsing damage compared with spruce?

## Methods

### Study area and measurements

For selecting well-managed young pine–spruce mixed stands, we used the following criteria: (1) proportion of mixture at minimum 20% by the number of stems; (2) stand area no less than two hectares; (3) development class: sapling class (average dominant height from 1.3 to 7 m) or young stand (average diameter from 8 to 16 cm); (4) regenerated originally as mixed pine and spruce stands; and (5) without full species segregation. As result, we selected ten mixed pine and spruce stands in Southern and Central Finland (Table 1 and Figure 1).

The sites were owned by Finsilva (company) or private forest owners. The vegetation type varied from *Vaccinium* type (VT) for two stands, suggesting low-fertility and dryish conditions, to *Myrtillus* type (MT) for six stands (one of which on peatland), suggesting medium-fertility and fresh conditions; and *Oxalis-Myrtillus* type (OMT) for two stands, herb-rich sites suggesting high fertility (Cajander 1949; Tonteri et al. 1990). The stands were even-aged, from 8 to 26 years old. Spruce was planted in all stands, in the six youngest stands with improved material. Pine was direct seeded in six stands (in five cases with improved material),

**Table 1.** Summary of stand information.

Stand	Location	Temp. sum	Age	Type	Soil preparation	Est. Method (pine)	Improved material	JSM	C/N h	C/N m
1	Keuruu	1168	13	VT	Disc trenching	Seeding	Pine, spruce	EC, PCT	0.36	0.28
2	Keuruu	1168	14	MT	Mounding	Seeding	Pine, spruce	EC, PCT	0.29	0.19
3	Keuruu	1168	14	MT*	Mounding	Seeding	Pine, spruce	EC, PCT	0.29	0.27
4	Ähtäri	1177	16	MT	Mounding	Seeding	Pine, spruce	EC, PCT	0.31	0.37
5	Viitasaari	1259	10	VT	Mounding	Seeding	Pine, spruce	EC	0.33	0.44
6	Viitasaari	1259	18	OMT	Prescribed burning, patch scarification	Natural	–	EC, PCT	0.27	0.24
7	Viitasaari	1310	26	MT	Ploughing	Natural	–	PCT (2)	0.30	0.29
8	Viitasaari	1299	24	MT	Patch scarification	Seeding	–	PCT (2)	0.34	0.42
9	Viitasaari	1299	12	MT	Mounding	Natural	Spruce	EC	0.31	0.30
10	Joutsa	1330	8	OMT	Inverting	Planting	Pine, spruce	EC	0.24	0.21

Note: Temp. sum is the sum of degree days above 5°C; VT, MT, and OMT are the *Vaccinium*, *Myrtillus*, and *Oxalis-Myrtillus* site types, respectively (\* stand 3 located on peatland site); Est. method is the establishment method for pine (spruce being always planted); Improved material specify for what species it was used improved breeding material; Juvenile stand management (JSM) depicts EC and PCT; C/N h and C/N m are the carbon/ratio values, respectively, for humus and mineral layers.

regenerated naturally in three stands, and planted in one stand (with improved material). In all stands, juvenile stand management practices were done according to the Finnish silvicultural guidelines for private forests (Rantala 2011). In five stands, both EC and PCT were carried out once, in three stands only EC once, and in two stands only PCT twice. For each stand, the long-term average of annual effective temperature sum (in degree days, d.d., threshold

value:  $+5^{\circ}\text{C}$ ) was calculated for the time period 1990–2018. The calculation of temperature sum was based on latitude, longitude, and elevation of each stand, and it was estimated by the climate data, with a  $10 \times 10$  km grid resolution (Venäläinen et al. 2005).

Three circular plots with an area of  $300\text{ m}^2$  were established in each stand. In the office, the plots were located using the stand maps across a transect. In the field, if the

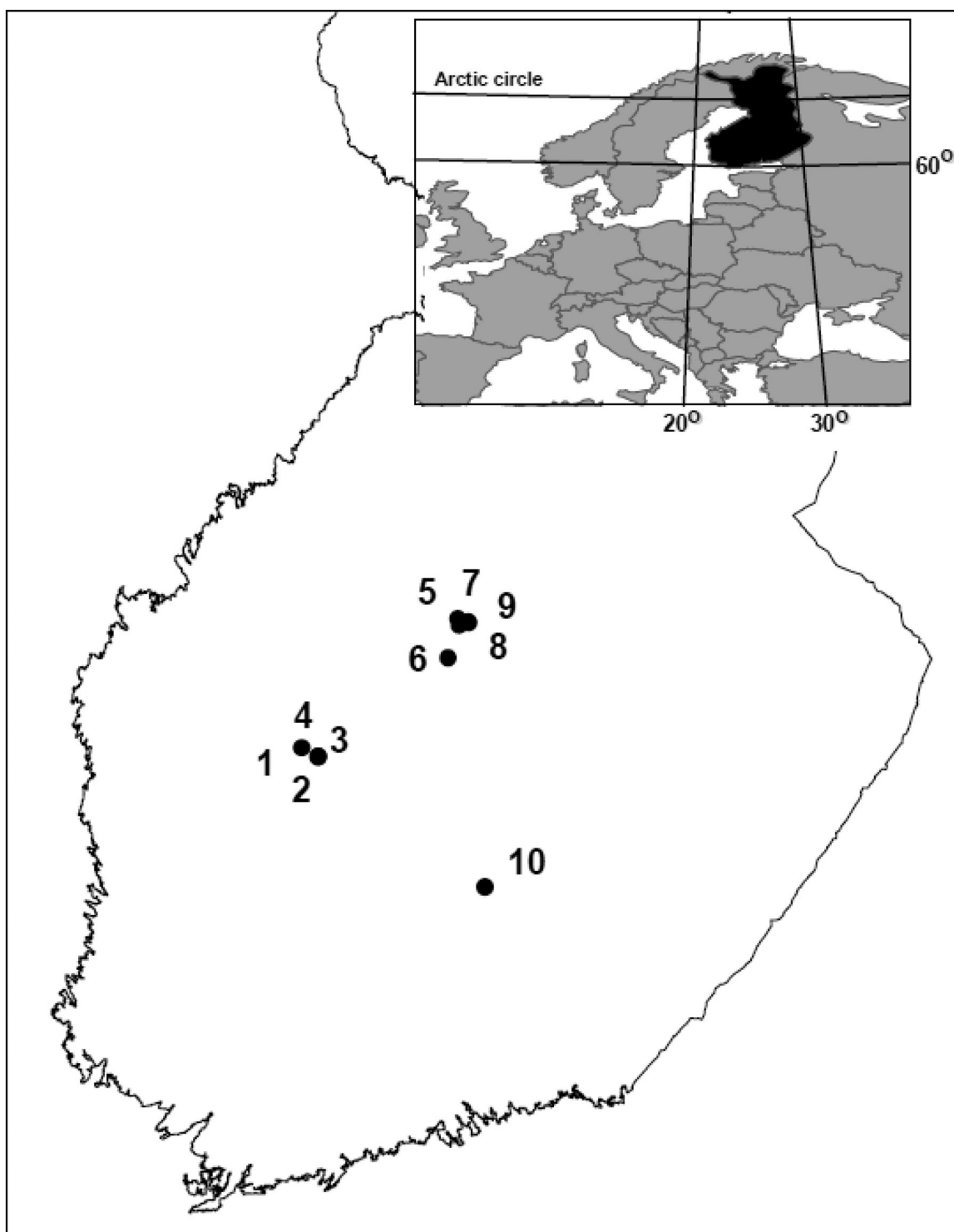


Figure 1. Location of study sites in Finland.

plots showed less than 20% of mixture for the secondary species, they were horizontally displaced to the north and then following the other cardinal directions until the criteria above were met. This intermediate random and subjective selection of the sample plots was due to the need to study actual mixtures in the local neighbors, where the two species have developed together.

In each plot, seven soil cores were systematically taken with a steel auger (diameter: 58 mm). The humus layer and mineral soil were separated from each other, and the seven replicates were combined in plastic bags to form one composite sample for each layer. The sample was brought to the laboratory and stored at 2°C–3°C before analysis. The content of carbon and nitrogen was assessed separately for the humus and mineral layers. The ratio between the carbon and nitrogen content (C/N ratio) was then calculated for both layers. Please note that smaller values of this ratio mean higher fertility of the soil (i.e. more nitrogen is present).

The location (calculated with the distance and direction from the center point of plot), diameter at breast height (dbh, 1.3 m from the base, cm) and height (m) of each tree were measured. In sapling stands, all trees above 0.5 m height were measured in 2019. In young stands, only trees with a height of more than 1.3 m were measured. Where PCT was not yet carried out, only future crop trees were measured. Crop trees were selected as the ones assumed to reach merchantable stem size at the time of the first commercial thinning. The criterion for a crop tree varied according to the management history of the stand. In managed stands, all the coniferous trees with a height of more than 10 cm were classified as future crop trees. If PCT was not yet done in stand, the most vigorous coniferous trees per sample plot (equals to 3000 trees per ha) were chosen as crop trees. In addition, broadleaved trees were accepted as crop trees if growing in open space.

In each plot, 10 sample trees were selected: five pine and five spruce trees. The selection was based on the individual tree basal area distribution by species in each plot, which was split into five portions of equal range, and one sample tree was selected for each portion. Only good quality (e.g. not forked or damaged), single stem trees were considered as sample trees, with a final subjective choice by the field crew. For the sample trees, the height of the crown base and external stem quality were also recorded. The quality was assessed by identifying visual defect classes: branchiness, forked, curved or multiple stems, and other defects.

Core increment samples at breast height (1.3 m) and stump height (0.1 m) were collected. Sample trees were then cut, and past annual height increment was estimated by means of identifying past whorls on the stem (considering each distance between successive whorls as one-year growth). Past diameter growth and the total age of the trees were measured by means of the annual ring increment (considering each distance between successive rings as one-year growth). Annual size development for both height and diameter under bark for each past year was so reconstructed. In addition, the number and diameter of branches (mm)

(separated for dead and living) was measured for the whorls closest to the heights of 2, 4, and 6 m from stump.

Due to small uncertainties in the age estimation of the sample trees, we could not be sure about their real origin (i.e. some sample trees, especially the largest, could have been natural advanced regeneration present at the time of stand establishment). Furthermore, due to another problem linked to the correlation between stand age and regeneration material (improved regeneration material was used mostly on the youngest stands), we decided to not investigate this effect in any of the modeling activities.

### Average stand characteristics

Stand mean characteristics were calculated using the KPL software (Heinonen 1994). The dominant height was calculated as the mean height of the 100 thickest trees ha<sup>-1</sup>. Stand characteristics were then analyzed according to the framework suggested by del Río et al. (2016) using R Statistical Software (R Core Team 2019). Given the few occurrences of birches in the study areas (less than 2% of the total stems), all the characteristics have been calculated comprising those trees when necessary, but only the detailed values for the pine and spruce compartments are shown in the results. For the species proportion, the stem number and the total basal area were compared for the pine and spruce components. For the species-specific size distribution, the mean diameter, mean height, and dominant height values of pine and spruce were compared with Welch's two-sample *t*-tests and by a visual analysis of diameter and height frequency polygons.

### Spatial analysis

For the horizontal spatial pattern, the Clark and Evans aggregation index (Clark and Evans 1954) was calculated, i.e. the ratio of the observed mean distance between nearest neighboring trees to that expected for a Poisson point distribution, using the package *spatstat* (Baddeley and Turner 2005) from R Statistical Software. Values above 1 suggest an even (or dispersed) distribution, while less than 1 an aggregated (or clustered) distribution. A cumulative distribution function method was used as edge correction.

For the species intermingling, the spatial diversity status *Ms* according to von Gadow et al. (2012) was calculated using the package *RANN* from R (Arya et al. 2019). Neighborhood clusters of five trees were considered and the values were calculated as follows:

$$MS_i = \frac{S_i}{n_{\max}} \times M_i, \quad (1)$$

where  $M_i$  is the spatial mingling index according to von Gadow and Fuldner (1993) (i.e. the proportion of neighbors which do not belong to the same species as the reference tree), corrected by the ratio between the actual number of tree species in the neighborhood of reference ( $S_i$ ) and the maximum possible number of species in the stand ( $n_{\max}$ ). No edge correction method was possible for this index.



## Growth analysis

### Size development

Annual size development, for both height ( $h$ ) and stump diameter ( $dsh$ ), as a function of age was modeled separately for individual pine and spruce trees. We did not consider diameter at breast height, since trees reached it at quite different ages, causing too much variation in the starting point of the analysis. For each species, only the two sample trees with the largest stump diameter for each plot (i.e. dominant sample trees) were used for this modeling to minimize as much as possible the effect of the undetermined past competition. Models based on non-linear functional equations, both asymptotic (i.e. Chapman-Richard) or non-asymptotic (i.e. power-law), resulted in very heterogeneous and still non-linear residual distributions. Failure to fit the data to a functional form was likely due to the short timespan recorded (i.e. full growth pattern not observed) and high heterogeneity in the data (progressively less trees with higher age were present in the data). Alternatively, we tested generalized additive models (GAM), models that are based on non-parametric regression and smoothing techniques (Hastie and Tibshirani 1990). Specifically, we used the package *gam4* (Wood and Scheipl 2020) from R Statistical Software to include random effects.

$$\text{size}_t = b_0 + f(\text{age}_t) + b_1 \times V_1 \dots + b_n \times V_n + u_{ai} + u_{ai,pj} + u_{ai,pj,tk} + \varepsilon_{ai,pj,tk,ml} \quad (1)$$

where size is the individual tree size at age  $t$  (either  $h$  or  $dsh$ );  $b_0$  is a fixed intercept;  $f(\text{age}_t)$  is the smoothing term;  $V_1 \dots V_n$  are additional explanatory variables;  $b_1 \dots b_n$  are linear coefficients to be determined during model fitting;  $u_{ai}$ ,  $u_{ai,pj}$  are random nested effects, respectively, for each stand  $i$  and plot  $j$  to account for the spatial correlation of trees in the same areas and plots, and  $u_{ai,pj,tk}$  is the another nested random effect for each tree  $k$  to account for the autocorrelation of the same measurements on the same subject; and  $\varepsilon_{ai,pj,tk,ml}$  is the error for each measurement  $l$ . Among the linear predictors, we considered for site characteristics the temperature sum ( $dd$ ) and the carbon/nitrogen ratio of both the humus and mineral soil layer (C/N h and C/N m, respectively, keeping in mind that higher C/N values indicate lower fertility); and for stand management, only the soil preparation method (superficial or deep). Then, we selected the model according to various criteria: lower AIC value, less variables (parsimony), and sound biological interpretation. Preliminary analysis showed that stand 5 had excessive browsing, which negatively influenced the size of pine trees, so it was removed from this and the following growth analysis.

### Recent growth

We considered as recent growth the individual cumulative growth of the last three growing seasons, both for height ( $ih$ ) diameter at stump height ( $idsh$ ). With this approach, we could study growth also in relation to the stand competition thus using all the five sample trees per plot, and at the same time smooth the possible variation in weather conditions or

other random annual events. We used species-specific generalized linear mixed models (GLMMs) using the package *lme4* (Bates et al. 2015) from R Statistical Software:

$$\Delta \text{size} = b_0 + b_1 * V_1 + \dots + b_n * V_n + u_{ai} + u_{ai,pj} + \varepsilon_{ai,pj,ml}$$

where  $\Delta \text{size}$  is the individual tree growth as described above (either  $ih$  or  $idsh$ , tested both with the original values and after logarithmic and square-root transformations);  $b_0$  is a fixed intercept;  $V_1 \dots V_n$  are the explanatory variables;  $b_1 \dots b_n$  are coefficients to be determined during model fitting;  $u_{ai}$ ,  $u_{ai,pj}$  are random nested effects, respectively, for each stand  $i$  and plot  $j$  to account for the spatial correlation of trees in the same areas and plots; and  $\varepsilon_{ai,pj,ml}$  is the error for each measurement  $l$ . Related to tree characteristics, we considered as predictors: the size before the growth (either  $h$  or  $dbh$ ); height to diameter ratio ( $hdr$ , the ratio between the tree total height and dbh, calculated as before the growth using reconstructed tree size data); and live crown ratio ( $lcr$ , the ratio between the tree live crown and total height, which could be calculated only after the growth). Related to the stand characteristics: stem per hectare ( $sph$ ); stand basal area as symmetric competition index ( $batot$ ); and the sum of the basal area of the larger trees as asymmetric competition index ( $bal$ ) (Wykoff 1990). All the previous variables were calculated for all trees and separated for both species component. We acknowledge that those values are not the ones for stand three years before the measurements, but we can consider them as the closest proxies. For the site characteristics: the temperature sum ( $dd$ ); the carbon/nitrogen ratio of both the humus (C/N h) and mineral layers (C/N m). For the stand management, the soil preparation methods (as above), and the time after the last cut ( $lag\_cut$ ), indicating the number of years after the last EC or PCT. We also tested interaction terms between soil fertility (C/N) and the various competition indices. We used a Gaussian distribution function with a logarithmic link (preliminary results showed that it returned lower AIC values than an identity link). Again, we selected the model according to various criteria: lower AIC value, less variables (parsimony), and sound biological interpretation. To compare the effect of the predictors within and across species in the final selected models, we followed a standardization procedure to calculate the beta coefficients and their 95% confidence interval using the *standardize* function of package *arm* (Gelman and Su 2020).

## Results

### Average stand characteristics

In the study areas, the proportion of pine was 35% of the total stem number and 39% of the basal area, on average. In all plots, spruce was more abundant in terms of stems per hectare, and in six cases, there were double the number of spruce than pine trees. Compared with stem numbers, the differences in basal area were less marked due to the generally slightly higher mean diameter of pine. Pine tree diameter was on average 1 cm larger compared with spruce, albeit with differences at stand level. For the mean height, there

**Table 2.** Summary of stand information.

Stand	Species	Stems (ha <sup>-1</sup> )	Basal area (m <sup>2</sup> ha <sup>-1</sup> )	Mean dbh (cm)	Mean height (m)	Dominant height (m)	CE	Ms	Browsing damage (%)
1	Total	2200	4.8	5.1	4.1	5.3	<b>1.36</b>		
	Pine	49%	56%	<b>5.4</b> ± 1.7	4.2 ± 0.8	5.2		0.47	0
	Spruce	52%	46%	4.7 ± 1.2	4.1 ± 0.9	5.2		0.47	0
2	Total	2078	7.8	6.7	5.0	6.3	<b>1.25</b>		
	Pine	44%	51%	<b>7.3</b> ± 1.6	5.1 ± 0.7	6.1		0.36	1.2
	Spruce	54%	47%	6.3 ± 1.4	4.9 ± 0.9	6.4		0.33	1.0
3	Total	2322	7.1	6.0	4.6	6.0	<b>1.23</b>		
	Pine	33%	32%	6.0 ± 1.8	4.3 ± 0.9	5.6		0.43	7.4
	Spruce	63%	66%	6.2 ± 1.6	<b>4.7</b> ± 1.0	<b>6.3</b>		0.27	3.1
4	Total	2289	9.1	6.9	5.3	6.7	<b>1.31</b>		
	Pine	31%	36%	7.4 ± 2.1	5.4 ± 1.1	6.7		0.68	12.5
	Spruce	69%	65%	6.7 ± 1.6	5.3 ± 1.1	6.7		0.30	0.7
5	Total	2000	1.7	3.4	2.4	4.1	1.13		
	Pine	25%	6%	2.3 ± 0.6	1.4 ± 0.4	1.9		0.51	40.9
	Spruce	74%	94%	<b>3.6</b> ± 1.7	<b>2.7</b> ± 1.1	<b>4.1</b>		0.20	0
6	Total	2278	14	8.5	6.7	8.2	<b>1.16</b>		
	Pine	26%	33%	<b>9.7</b> ± 2.2	6.9 ± 1.1	7.8		0.51	7.5
	Spruce	72%	66%	8.2 ± 2.3	6.6 ± 1.4	8.3		0.21	0
7	Total	2389	27.3	11.5	10.8	13.5	1.02		
	Pine	45%	41%	11.0 ± 3.3	10.4 ± 1.3	11.9		0.39	12.5
	Spruce	49%	55%	<b>12.3</b> ± 3.5	<b>11.1</b> ± 2.2	<b>13.6</b>		0.43	2.9
8	Total	2089	21.6	11.0	9.5	11.5	1.08		
	Pine	44%	51%	<b>12.1</b> ± 2.8	<b>10.0</b> ± 1.2	11.0		0.35	3.7
	Spruce	56%	49%	10.2 ± 3.2	9.2 ± 2.0	<u>12.0</u>		0.31	1.0
9	Total	2511	5.9	5.1	3.9	5.6	<b>1.17</b>		
	Pine	36%	41%	5.3 ± 2.4	3.8 ± 1.2	5.5		0.60	2.5
	Spruce	64%	59%	5.0 ± 1.6	4.0 ± 1.1	5.7		0.38	0
10	Total	2889	4.6	4.2	3.8	5.0	1.08		
	Pine	31%	41%	<b>4.9</b> ± 1.4	3.9 ± 0.7	4.6		0.43	4.9
	Spruce	68%	59%	3.9 ± 1.6	3.7 ± 1.0	5.3		0.19	0

Note: In the mean DBH and height columns, underlined numbers indicate values significantly higher than the other species with  $p < 0.05$ , bold for  $p < 0.01$ , underlined and bold for  $p < 0.001$  (using a Welch two-sample  $t$ -test). CE is the Clark and Evans aggregation index: bold font indicates values significantly higher than 1 (italic for  $p < 0.05$ ). Ms is the species-specific spatial diversity status.

were less evident differences between pine and spruce, with the former on average 0.4 m taller than the latter. Table 2 shows the summary statistics of the selected stands.

Related to the average tree size, only in two stands (5 and 7) spruce was on average larger than pine according to the results of the Welch two-sample  $t$ -test, as shown in Table 2. In two other stands (3 and 9), there were no significant differences in the mean, while pine was on average the largest in the remaining six stands. However, in the latter, the differences seem mostly due to a higher abundance of small spruces than to the presence of many pines larger than spruces as it can be observed in the diameter distribution histograms (Figure 2). This was confirmed by the differences in the dominant height, which showed significantly higher values for spruce in five stands, and no differences in the remaining ones. However, looking at the mean height distribution, there was a lower differentiation between species, which were occupying the same vertical strata almost equally (Figure 3). The exceptions identified by the Welch two-sample  $t$ -test were stands 3, 5, and 7 where spruce was higher on average, and stand 8 the only case where pine resulted higher, slightly contrary to the trend observed for diameters. For further information to the readers, we show in Figure 4 the tree height time-series for all sample trees in all plots (but for stand 5).

### Spatial distribution

Trees were evenly distributed within the stand, and the species were mingled together. The Clark and Evans

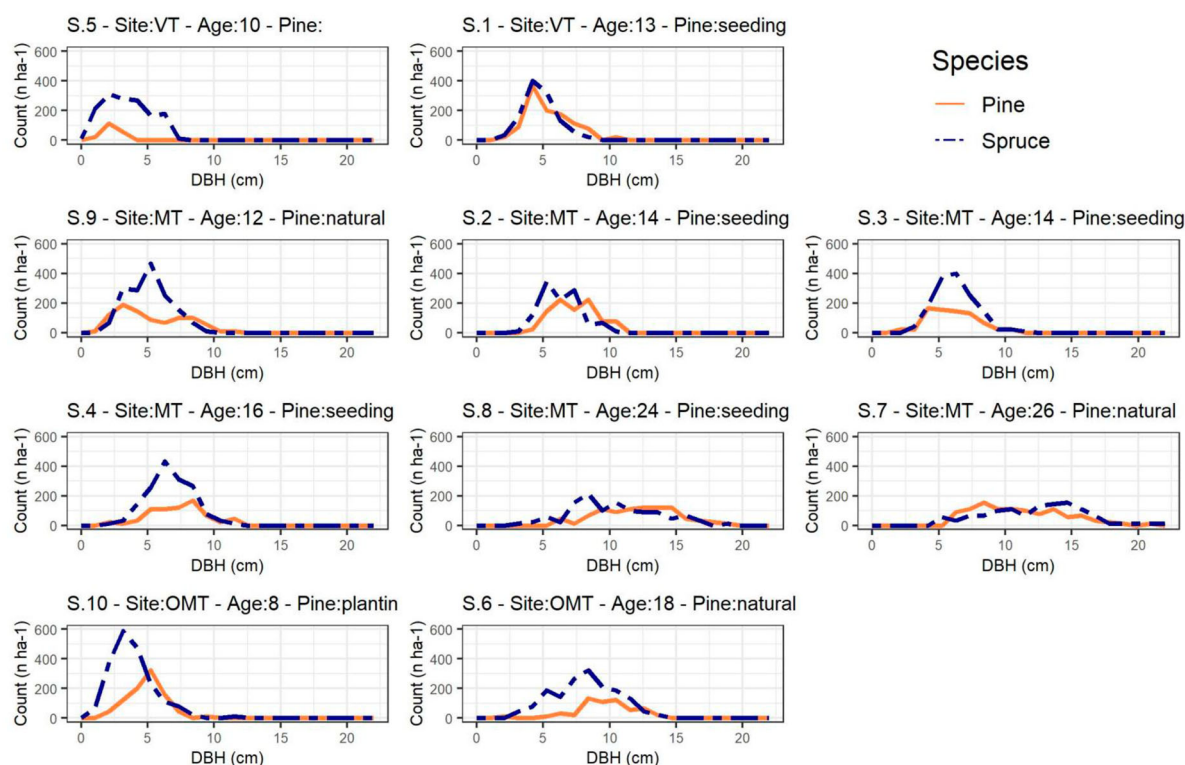
aggregation indices were above one in all cases, suggesting an even distribution pattern, even if only in six cases it was significantly so with a  $p$  value of  $< 0.05$  (Table 2). The spatial mingling index was lower for spruce only when it was clearly more abundant than pine. The general medium-high values for pine in all cases suggested that there was no species segregation.

### Damage, branchiness, and tree quality

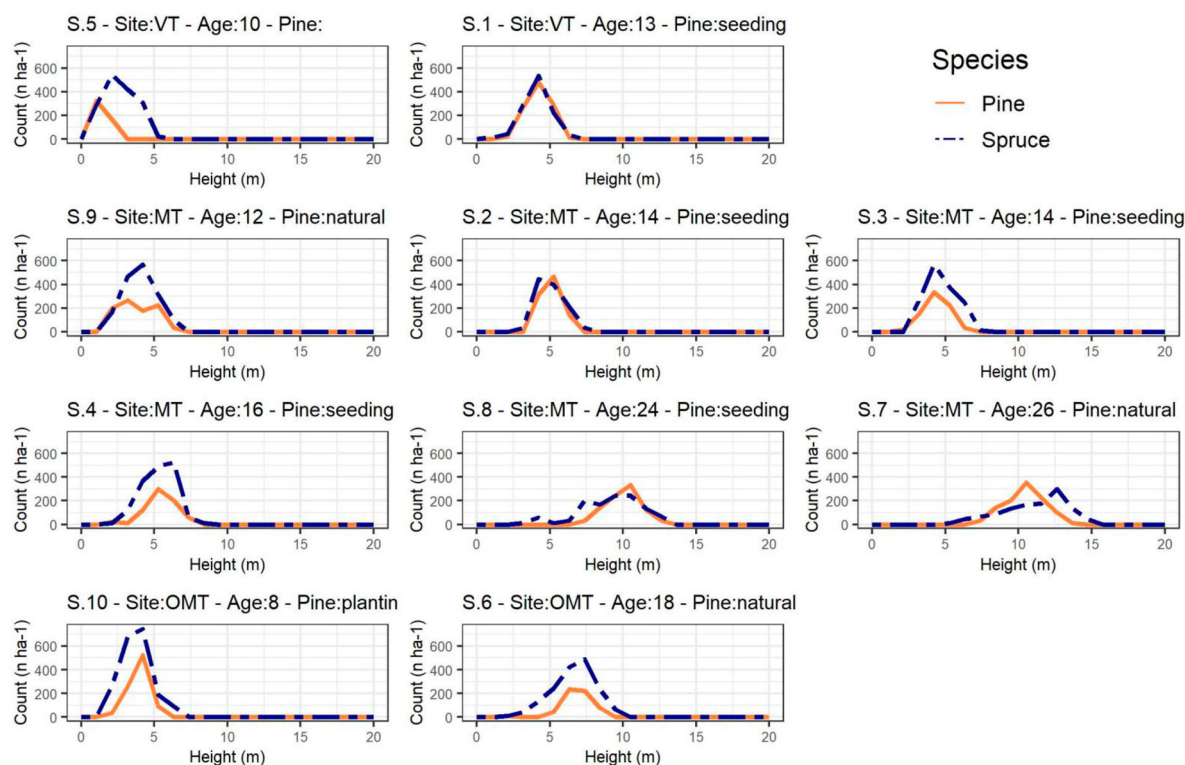
Damage was noted for only 8% of pine trees and 1% of spruce trees. For pine trees, the reason for damage was browsing in 62% of the cases. It must be noted that pine trees were heavily affected by browsing in stand 5 (around 40% of the total), so that pines were relatively short due to the loss of leader. Signs of browsing damage were evident also on around 10% of the total pine trees in stand 4, but they were negligible in the other stands for pine and in all cases for spruce. Among other causes of damage, there was snow (7% of the total damaged trees), but on the remaining trees, the cause was not recognized.

Regarding the crown characteristics, live crown ratio was on average higher on spruce trees than pine. Moreover, in the latter, there was a stronger reduction of live crown with increasing tree age (Figure 5, graph a). Regarding branchiness, pine had a higher number of branches with larger diameter on the average than spruce, for both the dead and alive branches (Figure 5, graphs b and c). For spruce, only in the oldest stands (7 and 8), there was the presence of dead branches on the stem, while for pine dead branches were

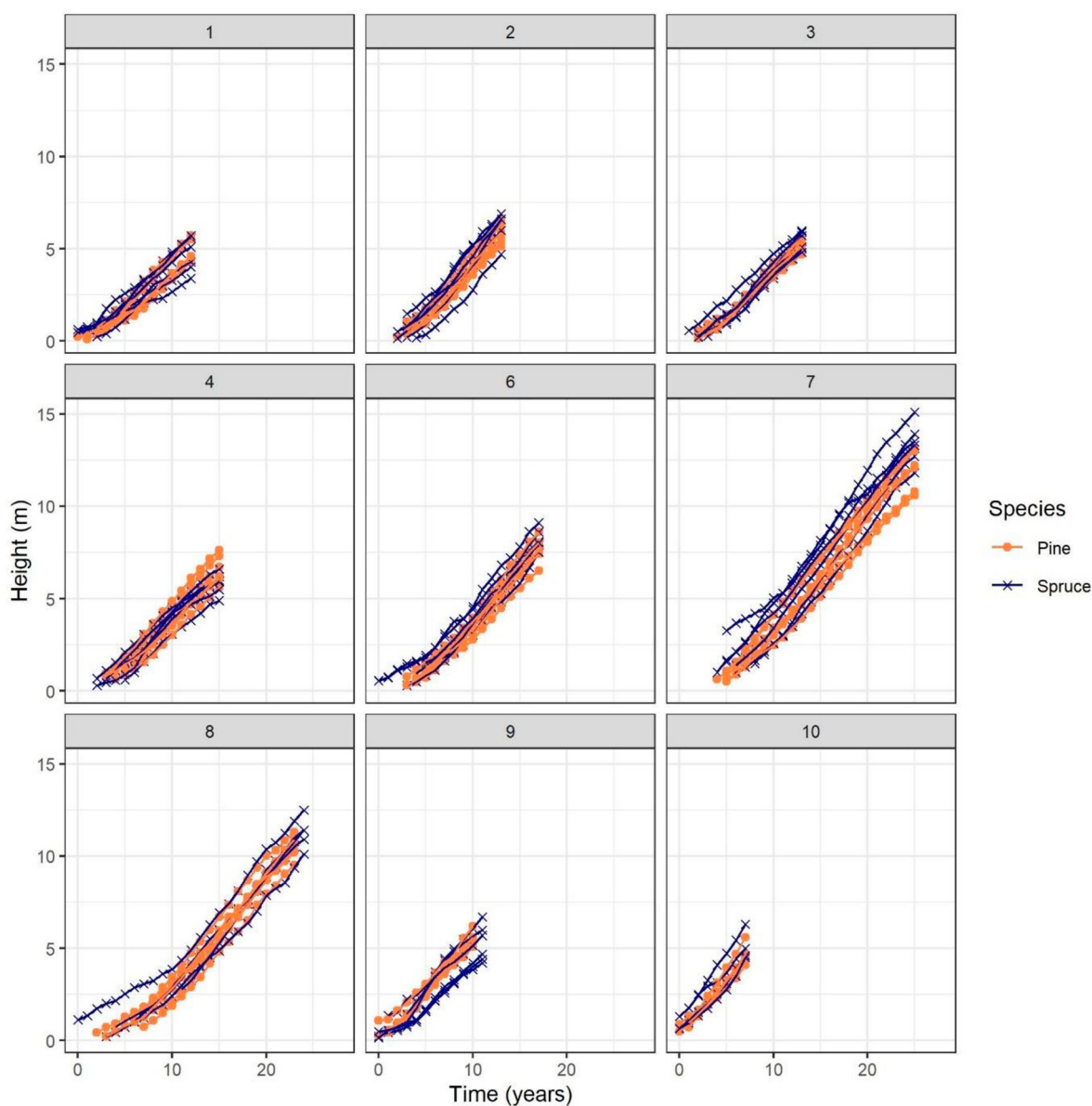




**Figure 2.** Diameter distribution at stand level for each species. Stands are ordered by site type and stand age. The labels recall the information about the stand number (e.g. S1), site type, stand age (in years), and pine establishment method (natural, seeding, and planting). VT is the dryish site (*Vaccinium* forest type), MT is the fresh site (*Myrtillus* forest type), and OMT is the herb-rich site (*Oxalis-Myrtillus* forest type) according to Cajander (1949) and Tonteri et al. (1990).



**Figure 3.** Height distribution at stand level for each species. Stands are ordered by site type and stand age. The labels recall the information about the stand number (e.g. S1), site type, stand age (in years), and pine establishment method (natural, seeding, and planting). VT is the dryish site (*Vaccinium* forest type), MT is the fresh site (*Myrtillus* forest type), and OMT is the herb-rich site (*Oxalis-Myrtillus* forest type) according to Cajander (1949) and Tonteri et al. (1990).



**Figure 4.** Tree height as a function of stand age (not tree age) for all the sample trees in each stand.

present in all stands but for the youngest stands (1, 5 and 10). The external quality of trees did not show defect in 58% of the cases. More defects were recorded for pine (56%) compared with spruce (33%). Only 6% of the pines were classified as having excessive branches, but nearly 40% of the pines show a curved stem. Additionally, 10% of the pines were classified as having multiple defects. For spruce, the curved stem was the most common defect (29%).

### Growth analysis

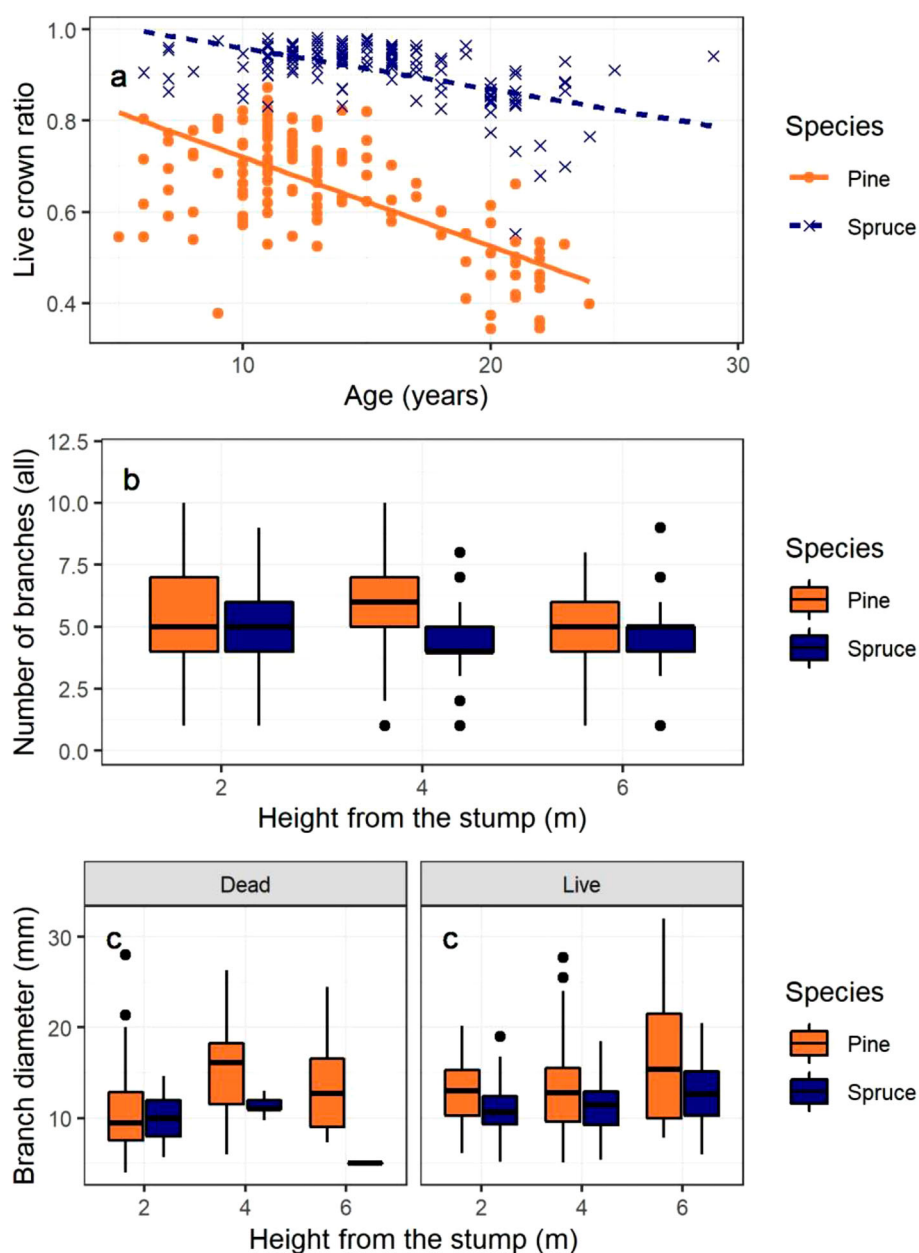
#### Size development

The models for annual size development for each species (GAMs with mixed effects) did not find significant any additional predictor but the smoothing term for age (Table 3). The simulated values fitted well against the observations (Figure 6): the adjusted R squared in the height models was 92% for pine and 75% for spruce, and in the

diameter at stump height models 94% for pine and 86% for spruce. When we used the models to simulate size development as a function of age, the species-specific trends were very similar both for height and diameter at stump height (Figure 7). There was a tendency of spruce growing more in diameter at older ages, but it was supported by less data.

#### Recent growth

We also successfully fitted species-specific GLMMs for the recent growth (last 3 years) of both height and diameter at stump height (Table 4). In both species, the fitted values against the observations for the height growth models tended to diverge more from the identity line than for diameter (Figure 6): the adjusted pseudo-R squared in the height models was 20% for pine and 41% for spruce, and in the diameter at stump height models 36% for pine and 26% for spruce. After the standardization process, the effect of the predictors could be directly compared (Figure 8). All models

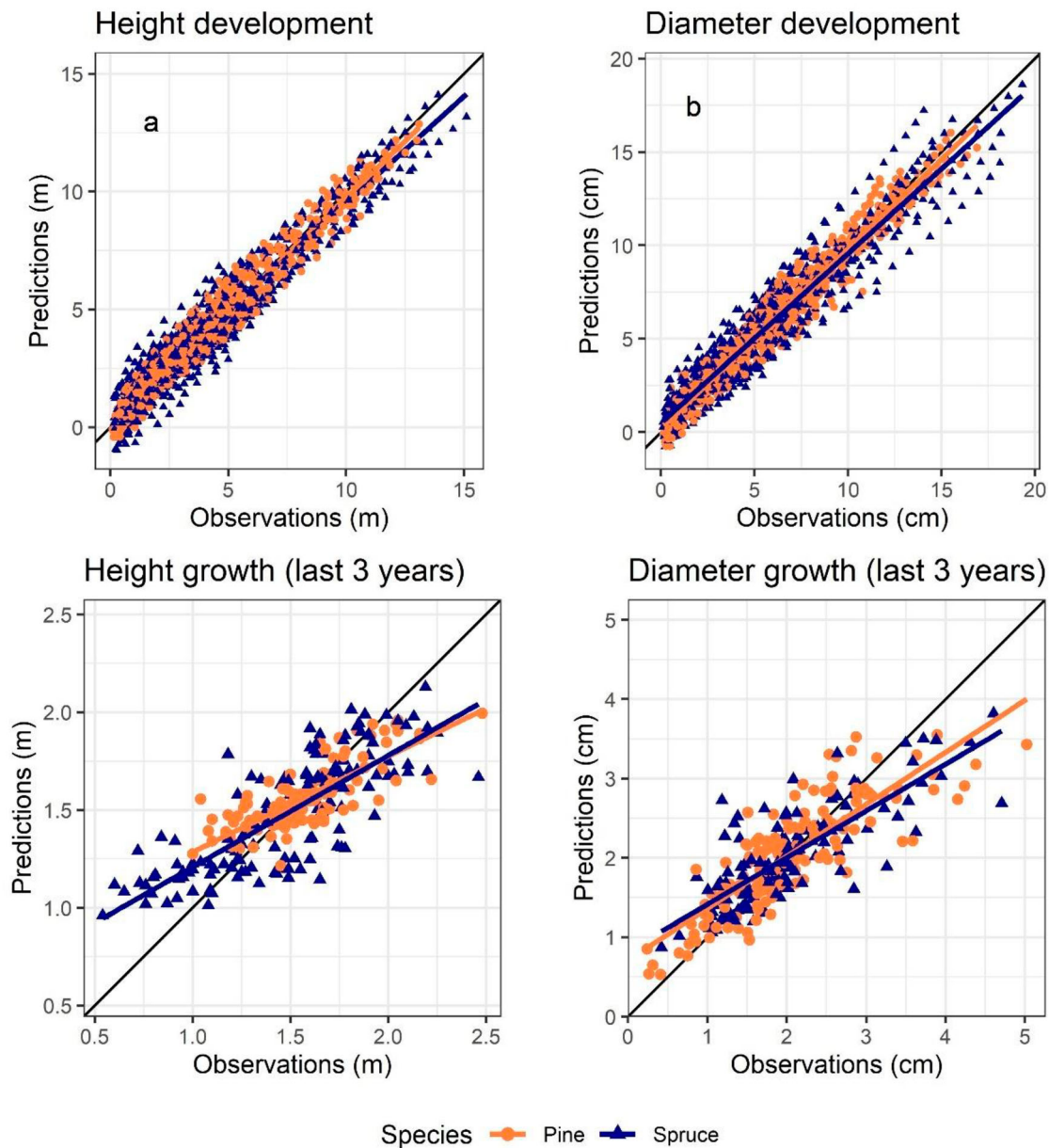


**Figure 5.** Sample trees crown characteristics. Live crown ratio as a function of age (graph a). Total number of branches as a function of height from the stump (graph b). Diameter for dead and alive branches as a function of height from the stump (graph c).

**Table 3.** Details of GAM for the annual size development (height and stump diameter) for both species as a function of age.

Height/Pine				Height/Spruce			
Fixed effects	Estimate	Std.error	p value	Fixed effects	Estimate	Std.error	p value
(Intercept)	5.4587	0.0967	<0.0001	(Intercept)	5.1415	0.2317	<0.0001
s(age, 4)	2.954		<0.0001	s(age, 4)	2.856		<0.0001
R <sup>2</sup> (adjusted)	0.94			R <sup>2</sup> (adjusted)	0.87		
Random effect				Random effect			
Stand	0.2026			Stand	0.7528		
Plot	0.3498			Plot	0.3654		
Tree	0.7417			Tree	1.1747		
Diameter/Pine				Diameter/Spruce			
Fixed effects	Estimate	Std.error	p value	Fixed effects	Estimate	Std.error	p value
(Intercept)	4.2049	0.1081	<0.0001	(Intercept)	4.0352	0.2451	<0.0001
s(age, 4)	2.908		<0.0001	s(age, 4)	2.911		<0.0001
R <sup>2</sup> (adjusted)	0.87			R <sup>2</sup> (adjusted)	0.74		
Random effect				Random effect			
Stand	0.6460			Stand	0.3351		
Plot	0.0000			Plot	0.0000		
Tree	2.8464			Tree	1.2200		

Note: The term "s" indicates the spline regressor (with the number of knots used within parenthesis): in that case, the estimate represents the degree of freedoms.



**Figure 6.** Predictions versus observations for the height (graph a) and diameter at stump level (graph b) size development. Predictions versus observations for the height (graph c) and basal area growth at breast height (graph d) of the last 3 years.

showed that size was among the most influential predictor for growth (for spruce only, using a logarithmic transformation reduced the AIC) and with a similar standardized effect. Symmetric competition was significant in the height models only for pine and in the diameter models for both species: for the latter, the standardized coefficient was higher for pine but still mostly overlapping. Site fertility, expressed in different ways by OMT, temperature sum and C/N of the humus layer in the different models, was generally more influential for spruce than for pine.

## Discussion

### Approach

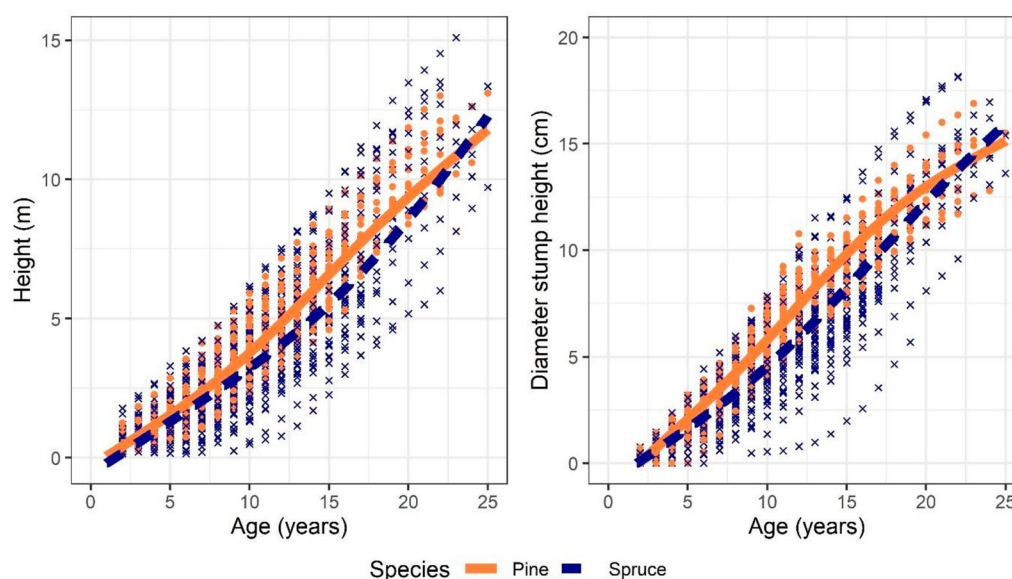
The aim of this study was to investigate the development of young and well-managed mixed pine–spruce stands.

Especially we were interested to assess their potential to maintain their mixed stands status also in the future. Cross-sectional data from ten stands were collected. Results showed that with more recent regeneration practices and juvenile stand management activities, pine and spruce trees had developed evenly in terms of height and diameter, with only slight differences. It is, therefore, possible to establish and grow single-storied pine and spruce mixed stands when modern practices have been carried out.

### Average stand characteristics

According to the growth and yield tables for naturally regenerated stands, when comparing single-species stands, pine has faster early development, while spruce grows faster later





**Figure 7.** Model simulations (lines) of height and diameter annual size development against observations (points), as a function of age.

in the mature stages (Koivisto 1959). Lindén and Agestam (2003) analyzed mixed stands around 40 years old, where both species were planted as seedlings. They found no stratification among species, although pine trees were slightly taller and thicker than spruce. In this study, we found thicker pine trees on average in most of the plots, although the average height was rather similar. The dominant height was slightly higher for spruce in many plots. The more recent results from Nilsson et al. (2006), where spruce was planted and pine naturally regenerated, mostly on *Myrtillus* vegetation type (MT), shown on the contrary pine trees were too short to be a viable component. Our results suggest a rather equal development until this stage.

### Damage, branchiness, and tree quality

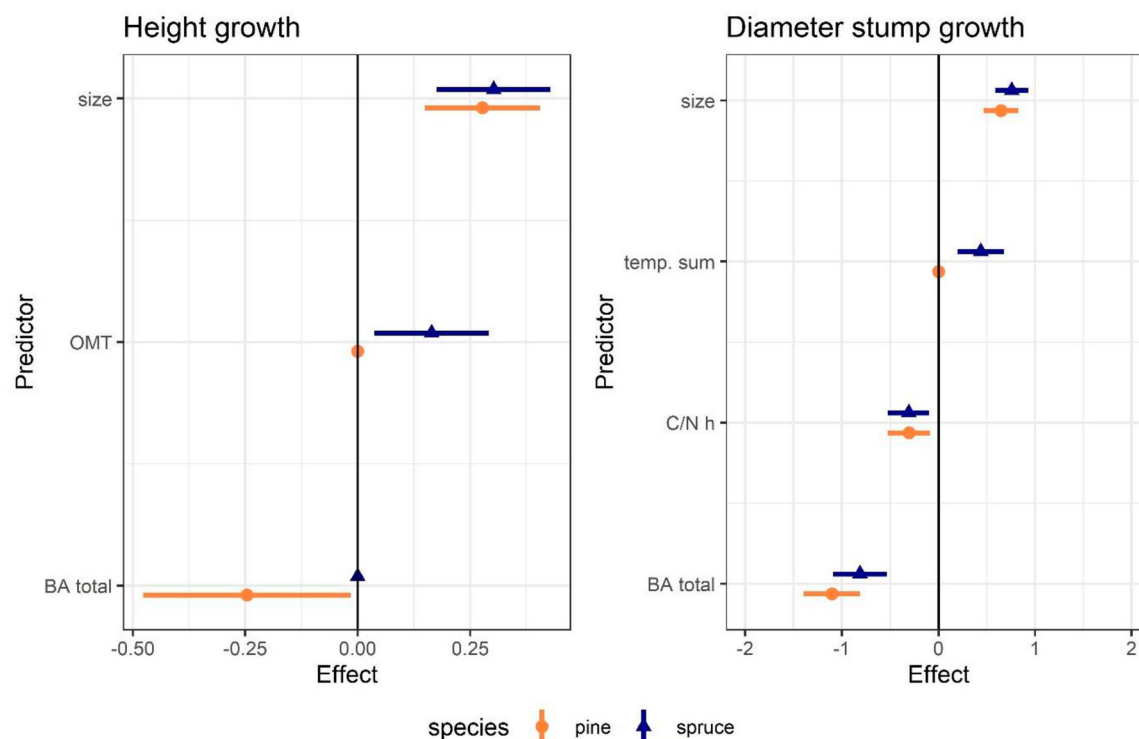
The level of damage was low, for pine 8% and for spruce only 1%. Our results showed that pine was affected by browsing

almost exclusively, with high rates of damage only in two stands. However, spruce trees were not damaged by browsing in those stands. In other words, the risk of browsing was not transferred from the most susceptible species (pine) to the least one (spruce). This is in line with the findings of Milligan and Koricheva (2013), where the high consumption of the most preferred species, pine, and the low consumption of the least preferred, spruce, did not vary with tree species richness. Other studies in Finland have observed that moose browsing increased with the number of tree species in a stand, especially with the presence of broadleaves in the mixture (Nevalainen et al. 2016; Vehviläinen and Koricheva 2006). In the stand most affected by browsing in this study, pine development was stunted while compared with spruce. Even if our results did not show any frost damage, it is known that in low-lying sites or on flat terrain, there is risk for frost damage of spruce seedlings (Luoranen et al. 2018). Based on the 8th Finnish National

**Table 4.** Details of GLMMs for recent (last three years) growth for both species; h and dsh are height (m) and diameter, respectively, at stump height (cm) before the growth, OMT is a dummy variable for the *Oxalis-Myrtillus* sites, dd is the temperature sum, C/N h is the carbon/nitrogen ratio of humus layer, BA total is the total stand basal area ( $\text{m}^2 \text{ha}^{-1}$ ).

Height/Pine				Height/Spruce			
Fixed effect	Estimate	Std.error	p value	Fixed effect	Estimate	Std.error	p value
(Intercept)	0.34426	0.09431	0.0002	(Intercept)	−0.24491	0.14462	0.0904
H	0.05331	0.01259	<0.0001	log(h)	0.35914	0.07680	<0.0001
–	–	–	–	OMT	0.16424	0.06492	0.0114
BA total	−0.01588	0.00759	0.0364	–	–	–	–
Random effect	St.dev			Random effect	St.dev		
Stand	0.04820			Stand	0.06725		
Plot	0.06240			Plot	0.08064		
Diameter/Pine				Diameter/Spruce			
Fixed effect	Estimate	Std.error	p value	Fixed effect	Estimate	Std.error	p value
(Intercept)	2.00205	0.45219	<0.0001	(Intercept)	−3.22337	1.33187	0.0155
dsh	0.10339	0.01445	<0.0001	log(dsh)	0.84744	0.09685	<0.0001
–	–	–	–	dd/1,000	3.29491	0.93004	<0.0001
C/N h	−3.91975	1.43644	<0.0001	C/N h	−3.98273	1.41507	0.0049
BA total	−0.07125	0.00964	0.0063	BA total	−0.05239	0.00919	0.0004
Random effect	St.dev			Random effect	St.dev		
Stand	0.09421			Stand	0.12709		
Plot	0.09524			Plot	0.05991		





**Figure 8.** Coefficients of the standardized predictors of the GLMMs fitted for height and diameter at stump level growth (of the last 3 years). The point (or triangle) represents the mean, and the lines represent the 95% confidence intervals. Predictors are size, either height (m) or diameter at stump height (cm) before the growth; OMT, a dummy variable for *Oxalis-Myrtillus* type; BA total, the total basal area of the plot ( $\text{m}^2 \text{ha}^{-1}$ ); temperature sum; and C/N h, the carbon/nitrogen ratio of the humus layer. The standardized coefficients should be considered dimensionless and useful only for direct comparison against each other and across species within each growth dimension considered. Negative values have a negative effect on growth, and vice versa.

Forest Inventory (NFI8) results, frost was the most common damage for young spruce stands even overall in spruce stands the damage were at lowest level (Yli-Kojola and Nevalainen 2006, pp. 1986–94). Based on NFI11 results, the frost (which causes top killing) was the fourth general damage cause in spruce stands (<3%) (Korhonen et al. 2017).

As expected, spruce trees had longer live crowns than pine trees, due to the higher shade-tolerance characteristics of the former (Mason et al. 2004), i.e. self-pruning was lower. Pine on average had also more dead branches than spruce, which showed dead branches only in two stands aged around 25 years. Earlier Mäkinen et al. (2003) noticed self-pruning in spruce only after ages of more than 50 years. Stand density has not been shown to affect self-pruning on young spruce stands (Mäkinen and Hein 2006). Fast tree growth can result in thicker branches and slower self-pruning (Kellomäki 1983). Our results showed no clear trend for branch number and stem heights. Results are in line with earlier studies of Mäkinen and Colin (1999). However, Björklund (1997) found that the number of branches per whorl reached the maximum at 2–3 m height and then diminished toward the stem apex.

In our stands, the external quality of trees showed defects in 41% of all the trees, with more defects recorded for pine (56%) than for spruce (33%). Curved stem was the most common defect in pine (40% of the total pine trees) followed by excessive branchiness (6% of the trees). Curved stems were observed to be the most common defect for young

pine stands also in Huuskonen et al. (2008), using extensive inventory data. The former study covered the whole country with different site types and regeneration methods, finding on average 46% of pines with some defects.

### Spatial analysis

The Clark and Evans aggregation index suggested an even spatial distribution in all stands, although not in all cases the index was significantly above one. Regarding the species mingling index, the values suggested the two species were spatially mixed. Mingling indices are sensitive to the proportion of a species in a stand, as well as its dispersion throughout the stand. Low proportions of a given species dispersed evenly (randomly) over a stand will show a high degree of mingling, while on the contrary, even a low overall presence of a species may result in a low degree of mingling if trees are found in comparatively small patches (Graz, 2004). Regardless, the generally higher values of pine compared with spruce suggest an even dispersion across the stand for pine, not in patches. We could not assess if this was a result of the stand establishment activities or the stand tending interventions. We deem the observed spatial pattern to have positive implications in the stand management, providing for example more flexibility in the species selection during future thinning operations (Felton et al. 2016). However, the small plot size could have affected the results.

## Growth analysis

The models for annual size development for each species did not find significant any additional predictor but age. Additionally, the general trend showed that the development was very similar both in terms of height and diameter at stump height. When we considered all the sample trees for the recent growth (last 3 years), we could also include the effect of competition in the modeling. In this case, spruce seemed to withstand better competition than pine, similar to other studies in Fennoscandia (Andreassen and Tomter 2003). Species-specific competition was not significant in any model, contrary to other studies in Finland (Hynynen et al. 2014; Pukkala et al. 2013, 1998). It may be that at this early age, inter-specific competition effects were not very strong. For example, in other environments, species mixture positively affected basal area growth only at higher stand densities (Brunner and Forrester 2020). In the sites with the higher growing potential of our study (assessed either with higher temperature sum, located in *Oxalis-Myrtillus* vegetation type site, or with lower carbon/nitrogen ratio of the soil, according to the model), spruce trees enhanced their growth faster than pine trees. This suggests that it is easier to maintain both species as a future component of mixed stands in more productive sites. Similarly, Vettenranta and Miina (1999) found in Finland the growth of spruce on fertile sites more rapid than that of pine, and the contrary on poor sites. In the boreal zone of Sweden, it is also reported that pine has higher growth than spruce on poor sites, and the contrary on rich sites (Holmström et al. 2018). Competition–fertility interaction terms were not significantly increasing the fit, as other examples in sub-boreal forests (Coates et al. 2013). We must also remind that even if we observed species-specific variations in the various models presented, spruce and pine have on average developed similarly in all stands. This suggests that the range of stand establishment and juvenile management activities carried out in the sites have reached the objective of maintaining viable both species component until now. As comparison, Holmström et al. (2018) found spruce to suffer the overtopping of pine in mixture, but their study stands were more than 50 years old and have been established with older methods (both pine and spruce were artificially seeded), while spruce was always planted in our study.

This study reports research results of a case study and provides for the first time a thorough analysis on the current status and past growth dynamics of young managed mixed stands at the stand and tree levels. However, we acknowledge that this study was limited in the choice of study material. The stands were subjectively selected, due to the small pool of potential managed mixed stands in the first place. There was variation across the stands regarding the management activity (soil preparation, establishment method, breeding material, and stand tending), which made it difficult to disentangle the drivers of the observed dynamics. Since the plots were located only where mixture was found, the data were not representative of the full stand. Long-term experiments should be established with a clear matrix of different silvicultural options to find out the most effective methods for establishing and managing

mixed stands. In the meantime, our results provide valuable information for practical forestry, showing that both species can be preserved in the mixture and grow evenly if careful management is applied, and in more fertile sites. This might be of special interest in areas of high browsing, so that the pine component happens to be highly damaged, the spruce one can be then be favored by management.

## Conclusion

This study provided valuable information on the development and current state of well-managed mixed spruce–pine stands. Our results suggest that the growing of pine and spruce mixtures may be a viable option in the management of coniferous production forests. The current regeneration and tending methods resulted in quite similar early development of pine and spruce in managed young stands. Furthermore, similar early growth rates and even spatial distribution of spruce and pine provide alternative options for future cuttings and how tree species could be favored in tree selection. Pine trees will likely need same management operations as in pure stands to ensure a good stem quality, due to relatively high observations of excessive branchiness and curved stems. Browsing caused the most damage for pine, but spruce had hardly any damage. In areas with high pressure of browsing, growing mixed spruce–pine stands could be a viable management option in suitable sites. The combined results of the tree-level modeling analyses suggest that spruce growth profits more than pine growth in higher productive sites.

## Disclosure statement

No potential conflict of interest was reported by the author(s).

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## ORCID

Simone Bianchi  <http://orcid.org/0000-0001-9544-7400>

Saija Huuskonen  <http://orcid.org/0000-0001-8630-3982>

Timo Saksa  <http://orcid.org/0000-0002-1776-2357>

## References

- Agestam E. 1985. A growth simulator for mixed stands of pine, spruce and birch in Sweden. Umeå, Sweden: Swedish University of Agricultural Sciences.
- Andreassen K, Tomter SM. 2003. Basal area growth models for individual trees of Norway spruce, Scots pine, birch and other broadleaves in Norway. For Ecol Manag. 180:11–24. [https://doi.org/10.1016/S0378-1127\(02\)00560-1](https://doi.org/10.1016/S0378-1127(02)00560-1)
- Arya S, Mount D, Kemp SE, Jefferis G. 2019. RANN: fast nearest neighbour search (Wraps ANN Library) Using L2 Metric.
- Baddeley D, Turner R. 2005. Spatstat: an R package for analyzing spatial point patterns. J Stat Softw. 12:1–42.

- Bates D, Mächler M, Bolker B, Walker S. 2015. Fitting linear mixed-effects models using lme4. *J Stat Softw.* 67:1–48. <https://doi.org/10.18637/jss.v067.i01>
- Bielak K, Dudzińska M, Pretzsch H. 2014. Mixed stands of Scots pine (*Pinus sylvestris* L.) and Norway spruce [*Picea abies* (L.) Karst.] can be more productive than monocultures. evidence from over 100 years of observation of long-term experiments. *For Syst.* 23:573. <https://doi.org/10.5424/fs/2014233-06195>
- Björklund L. 1997. The interior knot structure of *Pinus sylvestris* stems. *Scand J For Res.* 12:403–412.
- Brunner A, Forrester DI. 2020. Tree species mixture effects on stem growth vary with stand density – An analysis based on individual tree responses. *For Ecol Manag.* 473:118334. <https://doi.org/10.1016/j.foreco.2020.118334>
- Cajander AK. 1949. Forest types and their significance. *Acta For Fenn.* 56:1–71.
- Clark PJ, Evans FC. 1954. Distance to nearest neighbor as a measure of spatial relationships in populations. *Ecology.* 35:445–453. <https://doi.org/10.2307/1931034>
- Coates KD, Lilles EB, Astrup R, Kitzberger T. 2013. Competitive interactions across a soil fertility gradient in a multispecies forest. *J Ecol.* 101:806–818. <https://doi.org/10.1111/1365-2745.12072>
- Cubbage F, Harou P, Sills E. 2007. Policy instruments to enhance multifunctional forest management. *Forest Policy Econ.* 9:833–851. <https://doi.org/10.1016/j.forpol.2006.03.010>
- del Río M, Pretzsch H, Alberdi I, Bielak K, Bravo F, Brunner A, Condés S, Ducey MJ, Fonseca T, von Lüpke N, et al. 2016. Characterization of the structure, dynamics, and productivity of mixed-species stands: review and perspectives. *Eur J For Res.* 135:23–49. <https://doi.org/10.1007/s10342-015-0927-6>
- Ekö P. 1985. A growth simulator for Swedish forests, based on data from the national forest survey [stand model]. *Rapporter-Sveriges Lantbruksuniversitet, Institutionen för Skogsskötsel* (Sweden).
- Fahlvik N, Ekö PM, Petersson N. 2015. Effects of precommercial thinning strategies on stand structure and growth in a mixed even-aged stand of Scots pine, Norway spruce and birch in southern Sweden. *Silva Fenn.* 49(3):1–17. <https://doi.org/10.14214/sf.1302>
- Felton A, Nilsson U, Sonesson J, Felton AM, Roberge JM, Ranius T, Ahlström M, Bergh J, Björkman C, Boberg J, et al. 2016. Replacing monocultures with mixed-species stands: ecosystem service implications of two production forest alternatives in Sweden. *Ambio.* 45:124–139. <https://doi.org/10.1007/s13280-015-0749-2>
- Gelman A, Su Y-S. 2020. *arm: data analysis using regression and multilevel/hierarchical models.*
- Graz FP. 2004. The behaviour of the species mingling index M sp in relation to species dominance and dispersion. *Eur J For Res.* 123:87–92. <https://doi.org/10.1007/s10342-004-0016-8>
- Hastie TJ, Tibshirani RJ. 1990. *Generalized additive models.* London (UK): CRC press.
- Heinonen J. 1994. KPL—a computer programme package for computing stand and single tree characteristics from sample measurements. *Finn For Res Inst Res Papers.* 504:80.
- Holmström E, Goude M, Nilsson O, Nordin A, Lundmark T, Nilsson U. 2018. Productivity of Scots pine and Norway spruce in central Sweden and competitive release in mixtures of the two species. *For Ecol Manag.* 429:287–293. <https://doi.org/10.1016/j.foreco.2018.07.008>
- Huuskonen S, Domisch T, Finér L, Hantula J, Hynynen J, Matala J, Miina J, Neuvonen S, Nevalainen S, Niemistö P, et al. 2021. What is the potential for replacing monocultures with mixed-species stands to enhance ecosystem services in boreal forests in Fennoscandia? *For Ecol Manag.* 479:118558. <https://doi.org/10.1016/j.foreco.2020.118558>
- Huuskonen S, Hynynen J, Ojansuu R. 2008. Stand characteristics and external quality of young Scots pine stands in Finland.
- Hynynen J, Salminen H, Ahtikoski A, Huuskonen S, Ojansuu R, Siipilehto J, Lehtonen M, Rummukainen A, Kojola S, Eerikäinen K. 2014. Scenario analysis for the biomass supply potential and the future development of Finnish forest resources (No. 302), Working Papers of the Finnish Forest Research Institute. Finnish Forest Research Institute, Vantaa, Finland.
- Johansson T. 2003. Mixed stands in Nordic countries—a challenge for the future. *Biomass Bioenergy.* 24:365–372. [https://doi.org/10.1016/S0961-9534\(02\)00165-4](https://doi.org/10.1016/S0961-9534(02)00165-4)
- Kellomäki S. 1983. Strength of Scots pine branches. *Silva Fenn.* 17: 175–182.
- Koivisto P. 1959. Growth and yield tables. *Commun Inst For Fenn.* 51: 1–44.
- Korhonen KT, Ihalainen A, Ahola A, Heikkinen J, Henttonen HM, Hotanen J-P, Nevalainen S, Pitkänen J, Strandström M, Viiri H. 2017. Suomen metsät 2009–2013 ja niiden kehitys 1921–2013.
- Lindén M, Agestam E. 2003. Increment and yield in mixed and monoculture stands of *Pinus sylvestris* and *Picea abies* based on an experiment in Southern Sweden. *Scand J For Res.* 18:155–162. <https://doi.org/10.1080/02827580310003722>
- Luoranen J, Saksa T, Lappi J. 2018. Seedling, planting site and weather factors affecting the success of autumn plantings in Norway spruce and Scots pine seedlings. *For Ecol Manag.* 419–420:79–90.
- Macpherson MF, Kleczkowski A, Healey JR, Quine CP, Hanley N. 2017. The effects of invasive pests and pathogens on strategies for forest diversification. *Ecol Modell.* 350:87–99. <https://doi.org/10.1016/j.ecolmodel.2017.02.003>
- Mäkinen H, Colin F. 1999. Predicting the number, death, and self-pruning of branches in Scots pine. *Can J For Res.* 29:1225–1236.
- Mäkinen H, Hein S. 2006. Effect of wide spacing on increment and branch properties of young Norway spruce. *Eur J For Res.* 125:239–248.
- Mäkinen H, Ojansuu R, Sairanen P, Yli-Kojola H. 2003. Predicting branch characteristics of Norway spruce (*Picea abies* (L. Karst.) from simple stand and tree measurements. *Forestry.* 76:525–546.
- Malcolm DC, Mason WL, Clarke GC. 2001. The transformation of conifer forests in Britain — regeneration, gap size and silvicultural systems. *For Ecol Manag.* 151:7–23. [https://doi.org/10.1016/S0378-1127\(00\)00692-7](https://doi.org/10.1016/S0378-1127(00)00692-7)
- Mason W, Edwards C, Hale S. 2004. Survival and early seedling growth of conifers with different shade tolerance in a Sitka spruce spacing trial and relationship to understorey light climate. *Silva Fenn.* 38. <https://doi.org/10.14214/sf.404>
- Milligan HT, Koricheva J. 2013. Effects of tree species richness and composition on moose winter browsing damage and foraging selectivity: an experimental study. *J Anim Ecol.* 82:739–748. <https://doi.org/10.1111/1365-2656.12049>
- Nevalainen S, Matala J, Korhonen KT, Ihalainen A, Nikula A. 2016. Moose damage in National Forest inventories (1986–2008) in Finland. *Silva Fenn.* 50. <https://doi.org/10.14214/sf.1410>
- Nilsson O, Hjelm K, Nilsson U. 2019. Early growth of planted Norway spruce and Scots pine after site preparation in Sweden. *Scand J For Res.* 34:678–688. <https://doi.org/10.1080/02827581.2019.1659398>
- Nilsson U, Örlander G, Karlsson M. 2006. Establishing mixed forests in Sweden by combining planting and natural regeneration—effects of shelterwoods and scarification. *For Ecol Manag.* 237:301–311. <https://doi.org/10.1016/j.foreco.2006.09.053>
- Novák J, Dusek D, Slodiák M, Kacálek D. 2017. Importance of the first thinning in young mixed Norway spruce and European beech stands. *J For Sci.* 63:254–262. <https://doi.org/10.17221/5/2017-JFS>
- Official Forest Statistics of Sweden. 2020. Swedish University of Agricultural Sciences, Umeå, Sweden.
- Pretzsch H. 2016. Wood quality in complex forests versus even-aged monocultures: review and perspectives. *Wood Sci Technol.* 36:845–880.
- Pretzsch H, Schütze G. 2016. Effect of tree species mixing on the size structure, density, and yield of forest stands. *Eur J For Res.* 135:1–22. <https://doi.org/10.1007/s10342-015-0913-z>
- Pukkala T, Lähde E, Laiho O. 2013. Species interactions in the dynamics of even- and uneven-aged boreal forests. *J Sustain For.* 32:371–403. <https://doi.org/10.1080/10549811.2013.770766>
- Pukkala T, Miina J, Kurttila M, Kolström T. 1998. A spatial yield model for optimizing the thinning regime of mixed stands of *Pinus sylvestris* and *Picea abies*. *Scand J For Res.* 13:31–42. <https://doi.org/10.1080/02827589809382959>
- Rantala S. 2011. Finnish forestry practice and management. *Metsäkustannus: Helsinki.*

- R Core Team. 2019. R: a language and environment for statistical computing.
- Spiecker H. 2003. Silvicultural management in maintaining biodiversity and resistance of forests in Europe—temperate zone. *J Environ Manag.* 67:55–65. [https://doi.org/10.1016/S0301-4797\(02\)00188-3](https://doi.org/10.1016/S0301-4797(02)00188-3)
- Tonteri T, Hotanen J, Kuusipalo J. 1990. The Finnish Forest Site Type Approach: Ordination and Classification Studies of Mesic Forest Sites in Southern Finland. Springer Stable. <http://www.jstor.org/stable/2.> *Vegetatio* 87, 85–98.
- Vehviläinen H, Koricheva J. 2006. Moose and vole browsing patterns in experimentally assembled pure and mixed forest stands. *Ecography.* 29:497–506. <https://doi.org/10.1111/j.0906-7590.2006.04457.x>
- Venäläinen A, Tuomenvirta H, Pirinen P, Drebs A. 2005. A basic Finnish climate data set 1961–2000 - description and illustrations 27.
- Vettenranta J, Miina J. 1999. Optimizing thinnings and rotation of Scots pine and Norway spruce mixtures. *Silva Fenn.* 33:73–84. <https://doi.org/10.14214/sf.671>.
- von Gadow K, Földner K. 1993. Zur bestandesbeschreibung in der forsteinrichtung. *Forst und Holz.* 48:602–606.
- von Gadow K, Zhang C, Wehenke L, Pommerening A, Corral-Rivas J, Korol M, Myklush S, Hui G, Kiviste A, Zhao X. 2012. Forest structure and diversity. In: Pukkala T., von Gadow K., editor. *Continuous cover forestry.* Dordrecht: Springer Netherlands; p. 29–84.
- Wood S, Scheipl F. 2020. gamm4: generalized additive mixed models using “mgcv” and “lme4”.
- Wykoff WR. 1990. A basal area increment model for individual conifers in the Northern Rocky Mountains. *For Sci.* 36:1077–1104.
- Yli-Kojola H, Nevalainen S. 2006. Metsätuhojen esiintyminen Suomessa 1986–94.
- Zhang Y, Chen HYH, Reich PB. 2012. Forest productivity increases with evenness, species richness and trait variation: a global meta-analysis. *J Ecol.* 100:742–749. <https://doi.org/10.1111/j.1365-2745.2011.01944.x>