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Early development of planted Norway spruce in recently established stands, growing pure and in admixture

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ABSTRACT

In Fennoscandia, Norway spruce (*Picea abies* Karst.) in clearcut forestry has traditionally been grown as pure species stands. There is increasing interest in mixed stands of spruce and other species such as Scots pine (*Pinus sylvestris* L.) and birch (*Betula* spp.). Mixed stands provide a wider range of ecosystem services, although there were concerns that spruce would suffer from competition and grow more slowly than in pure stands. There is still scarce knowledge of the early growth of mixed stands, especially given recent silvicultural advances. We compared the early development of spruce growing in recently established pure stands and mixed stands, either with pine or birch. For sample spruce trees, we reconstructed the past diameter and height growth through stem analysis. For spruce, we investigated differences across admixtures in terms of (Q1) age–size development, (Q2) recent diameter and height growth, and (Q3) achieved mean size. We did not observe strong negative effects in young spruce (<25 years) development growing in mixed stands compared to pure stands. The only differences were an early slower diameter development over age in the spruce–pine stands (not found in the recent growth or mean size achieved), and a higher achieved mean height in spruce–birch stands.

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Diameter growth; height growth; Finland; *Picea abies*; mixed forests

Introduction

The boreal forests of Fennoscandia are commonly managed with rotation forestry, practiced with relatively large clearcuts followed by artificial and/or natural regeneration. Forest management has favored pure coniferous species of either Norway spruce (*Picea abies* (L.) Karst., henceforth spruce) or Scots pine (*Pinus sylvestris* L., henceforth pine). The natural regeneration of undesired species, especially broadleaved species such as silver birch and pubescent birch (*Betula pendula* Roth and *Betula pubescens* Ehrh. respectively, henceforth birch), was often removed during juvenile stand management.

There is an increased societal demand that forests be managed to provide a wider range of ecosystem services, including both goods (such as timber and non-timber forest products) and functions (such as biodiversity, recreation, and carbon sequestration). Increasing the diversity of forest ecosystems is one possible way to obtain multiple benefits from managed stands (Felton et al. 2016). Mixed species forests are therefore gaining interest worldwide, including in Fennoscandia. Mixed species stands are deemed to deliver more ecosystem services, from biodiversity to carbon storage and timber production (Jonsson et al. 2019). Mixed species are also considered both more resistant and resilient to certain sources of forest damage agents, including various pests and diseases (Haas et al. 2011; Thomsen 2016), although not in every case (Huuskonen et al. 2021 and references therein). Spruce is especially susceptible to drought and some pests (such as European bark beetle and *Heterobasidion* sp.) that may increase in the future climate. Introducing more species to the stand may decrease the overall risk. Mixed stands are therefore generally considered better for both adaptation to and mitigation of climate change. In Central and Southern Europe, overyielding has also been observed – that is, mixed species stands having higher wood production than corresponding pure stands of the same age on the same site (Pretzsch and Forrester 2017). However, such a phenomenon has not been found in Fennoscandia, probably because of the lower stand densities in managed boreal forests (Huuskonen et al. 2021).

There are also some concerns related to mixed stands. Browsing damage may also spill over to spruce if more palatable trees are present (Felton et al. 2016). Silvicultural management is more complicated and less studied. There were general concerns that spruce could suffer from the competition of other faster growing species. For spruce–pine mixtures, it has been reported that spruce grows more quickly than pine in more fertile soils and milder climates, and vice versa in less fertile soils and colder climates (Vettenranta and Miina 1999; Holmström et al. 2018; Nilsson et al. 2019). In spruce–birch mixtures, the faster early growth of broadleaved trees lets them extend their canopy above the spruce. The stand would develop as two-storied, with the conifer trees at risk of suppression, but if well managed, the birch may even provide a beneficial shelter that could be

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useful against frost, for example. However, to avoid suppressing spruce growth too much, such a shelter must be removed in a timely fashion, and harvesting operations may damage the remaining spruce trees (Niemistö and Valkonen 2021; Niemistö et al. 2024).

The studies related to mixed species in Fennoscandia are based on stands regenerated decades ago. We therefore currently lack information about the growth of young mixed spruce stands managed according to more recent silvicultural methods (Bianchi et al. 2021). For example, there have been advances in the forest regeneration material (e.g. container spruce seedlings of improved genetic) and soil preparation methods (e.g. spot mounding). There is also better silvicultural care during juvenile phases, carrying out activities such as early cleaning (EC) and precommercial thinning (PCT). In Bianchi et al. (2021), Huuskonen et al. (2022) and Männistö et al. (2024), we have therefore compared the early growth dynamics of spruce growing as admixture with either pine or birch in more recently established stands. We found that spruces had a slower initial growth than either pine or birch, but they were eventually able to reach or even surpass the size of the admixture species. These results demonstrated that spruce could coexist in the same canopy layer as a secondary species in managed stands, showing more options were available for growing species admixtures in Fennoscandia, especially for the most promising spruce–birch mixture. However, concerns remain about lower spruce productivity compared to pure stands.

In Bianchi et al. (2021), Huuskonen et al. (2022), and Männistö et al. (2024), we collected a valuable database of young spruce growing in recently established stands with different mixtures, and we carried out inter-specific comparisons. To expand the knowledge further, in the present study, we analyze these data with a new dataset of similarly young and recently established pure spruce stands. The rationale was to investigate intra-specific differences in young spruce development across pure and mixed stands. Our specific research questions were: Did the early development of spruce differ in recently established pure and mixed species forest in terms of (Q1) tree-level age-size relationship, (Q2) tree-level recent growth, and (Q3) stand-level mean size? In all cases, we considered both tree diameter and height.

Materials and methods

Study area

A total of 44 stands with 97 plots was surveyed (Figure 1, Table 1). We searched within various companies and organization databases for stands fulfilling our desired criteria in Southern and Central Finland. All potential stands had to be field checked before being included in the study. Only a few stands corresponded to our needs, so we were constrained in stand selection, especially for the species mixtures. Once we reached an acceptable sample size, we stopped the survey.

Pure spruce stands (16) were selected in accordance with the following criteria: (i) a stand area of at least two hectares; (ii) a development class from sapling stand (average dominant height from 1.3 to 7 m) to young stand class (average diameter from 8 to 16 cm); (iii) an establishment method: planted spruce seedlings; (iv) properly managed, that is, juvenile stand management practices were conducted, but first commercial thinning was not yet conducted. These data were not previously presented.

For mixed spruce stands with either pine (9 stands) or birch (19 stands), the following additional criteria were also considered: (i) the proportion of pine or birch mixture of at least 20% and 15% respectively; (ii) the mean height difference between spruce and birch of at most three meters (spruce–birch stands only); (iii) the establishment method: pine either naturally regenerated or seeded (spruce–pine stands), birch naturally regenerated (spruce–birch stands); and (iv) without full species segregation. For spruce–pine stands, it was evident from the past management decisions that they were purposefully established as mixtures during the regeneration phase. For spruce–birch stands, they were originally regenerated for spruce alone, but for unknown reasons, the birch was not removed during juvenile stand management. Refer to Bianchi et al. (2021), Huuskonen et al. (2022), and Männistö et al. (2024) for further details on the admixture datasets. Unfortunately, the sampled trees in the spruce-pine dataset were approximately half than in the other datasets.

Regarding soil preparation, mounding was performed in more than half the stands (23), superficial methods (disc trenching or patch scarification) in more than one-third (16), while undetermined methods were performed in the rest (5). Juvenile stand management activities included early cleaning (EC) or pre-commercial thinning (PCT). EC is needed in newly regenerated stands to control the competition of abundant fast-growing broadleaves, which is typically done when conifers reach one meter in height. PCT is needed to control the stand's overall structure and density, which is usually done (depending on tree species) when the height reaches 3–6 m by thinning the stand to a density of 1600–2200 stems per hectare. At least one juvenile stand management operation was performed (either EC or PCT) in half the stands (22), while both were performed in the other half (22).

Data collection

In the spruce–pine dataset, three circular plots with an area of 300 m^2 were established in each stand, while in the other datasets, two circular plots with an area of 500 m^2 were established. In all cases, plot locations were planned based on office maps, depending on stand shape, and were finalized in the field to keep them at least 25 m from the edges. For the admixture datasets, if plots showed less mixture than desired for the secondary species, they were horizontally displaced to the north and then followed the other cardinal directions until the above criteria were met. This method was used due to the need to study actual mixtures with local neighbors where the two species had developed together.

In each plot, soil cores were taken in a cross-shaped pattern centered on the plot center with a steel auger (diameter: 58 mm), seven in spruce–pine stands, and ten in spruce–birch and pure stands. The soil sample depth was also recorded. The organic layer and mineral soil were separated, and all the replicates were combined in plastic bags to form

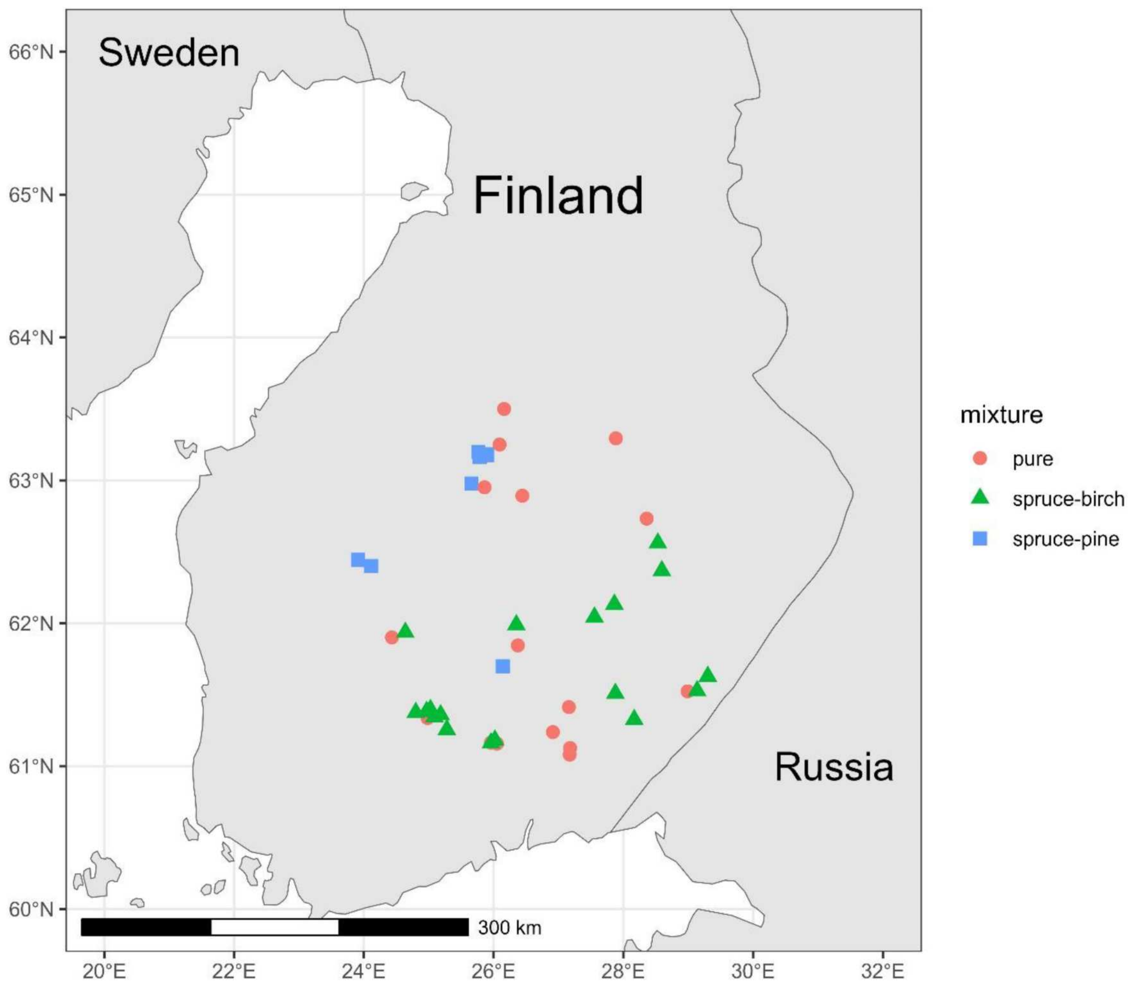

Figure 1. Location of study sites.

one composite sample for each layer. The sample was brought to the laboratory and stored at 2°C–3°C before analysis. Total carbon (C) and nitrogen (N) concentrations were assessed separately for the organic and mineral layers from air-dried samples by the Dumas method, using a Leco elemental analyzer (Leco Corporation, USA). The ratio between the carbon and nitrogen content (C:N) was then calculated for both layers. Note that the smaller values of this ratio signal higher mineralization rates and generally higher soil fertility (i.e. more nitrogen is present). Soil texture was also defined in the laboratory for each composite sample. The vegetation type was also recorded, varying from Vaccinium type (VT), suggesting low-fertility and dryish conditions, to Myrtillus type (MT), suggesting medium-fertility and fresh conditions, and to Oxalis-Myrtillus type (OMT), herb-rich sites suggesting high fertility (Cajander 1949; Tonteri et al. 1990). We retrieved temperature sum values (accumulated daily temperature over 5°C) for the 1980–2010 period from climatic data for all the locations that were retrieved from the web portal ClimateDT (Marchi et al. 2024).

In the sapling class stands and young stand class, trees higher than 0.5 and 1.3 m were measured respectively. Where

Table 1. Characteristics of stands. When multiple values are shown, they display the minimum, mean ± standard deviation, and maximum values.

	Pure	Spruce–birch	Spruce–pine
no. Stands (no. Plots)	16 (32)	19 (38)	9 (27)
no. Sample trees	267	296	132
Stand age (years)	20 ± 5 (13–29)	17 ± 6 (8–29)	14 ± 6 (8–26)
Temperature sum (dd)	1318 ± 87 (1174–1430)	1306 ± 58 (1270–1466)	1,298 ± 69 (1,164–1328)
Carbon:nitrogen ratio in humus layer	27.5 ± 3.5 (21.7–33.7)	25.1 ± 3.3 (19.7–30.5)	31.1 ± 3.6 (24.2–35.9)
Dominant height (m)	10.6 ± 2.4 (6.7–14.3)	10.9 ± 4.5 (3.2–16.5)	6.4 ± 3.2 (4.1–13.5)
Stems (ha^{-1})	1750 ± 362 (1560–2890)	2090 ± 756 (910–3920)	2278 ± 272.4 (2000–2889)
Spruce % (stems)	0.89 ± 0.1 (0.66–1.00)	0.60 ± 0.1 (0.47–0.67)	0.65 ± 0.1 (0.48–0.74)
Basal area (m^2 ha^{-1})	16.5 ± 6.8 (7.0–30.5)	12.9 ± 8.9 (0.9–24.9)	7.8 ± 8.6 (1.72–27.3)
Spruce % (basal area)	0.93 ± 0.1 (0.70–1.00)	0.63 ± 0.1 (0.46–0.91)	0.59 ± 0.2 (0.43–0.95)
Birch % (basal area)	0.02 ± 0.1 (0.00–0.24)	0.27 ± 0.1 (0.05–0.38)	0.00 ± 0.0 (0.00–0.05)
Pine % (basal area)	0.02 ± 0 (0.00–0.21)	0.03 ± 0.0 (0.00–0.27)	0.40 ± 0.0 (0.05–0.57)

The percentage of species presence is evaluated for basal area.

PCT was not yet carried out, only future crop trees were measured (around 3,000 stems per hectare). Spruce crop trees were selected as those assumed to reach merchantable stem size at the time of the first commercial thinning. The criterion for crop tree varied according to the management history of the stand and local neighborhood characteristics. After PCT, we consider all trees future crop trees. For the measured trees, the location, diameter at breast height – that is, 1.3 m from base (dbh, in cm) – and the height of each tree was measured (in m). Heights were measured with a 10 cm accuracy using Vertex IV (Haglöf 2007). At plot level, we calculated the basal-area weighted mean diameter and basal-area weighted mean height (also called Lorey's height) for the spruce component only. We also calculated the presence of spruce, pine, and birch as a percentage of the plot basal area. Thanks to the tree location, we could verify the mingling index for spruce trees, defined as the proportion of trees not belonging to the same species among the five nearest neighbors: each non-spruce tree would contribute 0.20 toward this index. Across all mixed species stands, the index resulted in 0.37 ± 0.10, meaning each spruce tree had on average of around two trees of a different species in their local neighborhood.

On each plot, five and eight spruce sample trees were selected (if no PCT was carried out, only among the crop trees) respectively in the spruce–pine and the other datasets (the differences were due to the different size and number of plots per stand). The selection was based on the individual tree basal area distribution by species on each plot. The distributions were split into five or four classes of equal range respectively in the spruce–pine and the other datasets. For the former, one tree was sampled from each class, while two were sampled in the latter. Only good-quality single-stem trees were considered sample trees, with a final subjective choice by the field crew. The annual past height and diameter growth were measured in the sample trees. Each sample tree was felled, and core increment samples at stump height (0.1 m) and breast height (1.3 m) were collected. The past underbark diameter growth and total age of the trees were measured by means of the annual ring increment (considering each distance between successive rings as one-year growth). Ring widths were measured using WinDENDRO™ (Regent Instruments Canada Inc. 2009) after digital scanning. Past annual height growth was assessed by identifying whorls on the stem (considering each distance between successive whorls as one-year growth). Eventually, a few sample trees were discarded when outlier values were identified, especially when the tree was considered to have advanced regeneration established much earlier than recorded stand regeneration.

Statistical analyses

All analyses were run using R Statistical Software (R Core Team 2023). First, we investigated if there were differences in site quality between admixtures. Using the dataset as categorical predictors, we investigated plot-level differences in C:N and temperature sum using linear models, and in vegetation type using an ordered logistic regression (a regression method extended from the logistic model but used for ordinal-dependent variables) from the *MASS* package (Ripley et al. 2013).

The dynamics of the spruce age–size relationships in different admixtures (Q1) were analyzed using a Bertalanffy–Richards type growth model (Salas-Eljatib et al. 2021; Huuskonen et al. 2022). Analyses were conducted using the age–size data from stump height diameters and the heights of the sample trees. Instead of breast height diameter, the stump height diameter was analyzed to cover the full development. The following model was used to predict the diameter at stump height and the height of the individual trees at a given age, using the *nlme* package (Pinheiro et al. 2020):

$$\mathrm{y}_{\mathrm{ijt}} = \beta_1 \{ 1 - \exp(-\beta_2 \cdot \mathrm{age}_{\mathrm{ijt}}) \}^{\beta_3} + \mathrm{age}_{\mathrm{ijt}},$$

where y_{ijt} is the underbark diameter at stump height (cm) or tree height (m) of tree *i* on plot *j* at time *t*; age is the tree age (years) of tree *i* on plot *j* at time *t*; parameter β_1 indicates the asymptotic maximum size of the growth curve, and β_2 and β_3 determine the inflection points. The parameters β_1 and β_2 were linearly dependent on various site and stand characteristics used as covariates, as in the following structure:

$$\beta_n = \sum_{1}^{k} \beta_{nk} \cdot \mathrm{cov}_k$$

The covariates tested were: C:N; soil texture; soil depth; temperature sum; vegetation type class; the basal area percentage of the three species (spruce %, pine %, and birch %); admixture as dummy variable (either spruce–birch or spruce–pine set to 1).

Due to the hierarchical structure of the data, we considered β_1 as a nested random effect of trees within plots. A further nested effect at stand level was found either to cause problems for convergence or not significantly decrease AIC (see later).

The differences in the recent tree-level growth across admixtures (Q2) were analyzed by fitting Generalized Linear Mixed Effects (GLMM) models using the *lme4* package (Bates et al. 2015), using a Gaussian family and log link. As a response variable, we considered the total growth of the last three years respectively for the basal area (preliminary results indicated better fit than for dbh), estimated by the values of tree rings at breast height; and height, calculated from the same stem analyses as above. As potential covariates, we tested the corresponding size (dbh or height) at the start of the growth period, total basal area, and the same site and stand characteristics previously mentioned for Q1. Correlation between predictors was checked with the function *vif* from *car* package (Fox and Weisberg 2019). Due to the data's hierarchical structure, we added a random intercept effect at plot level.

Differences in the spruce–component mean size (Q3) were analyzed considering basal-area weighted mean diameter and basal-area weighted mean height as variables of interest. We first tried using a Bertalanffy–Richards age–growth model. Given the problems in converging, we then used Generalized Additive Mixed Models (GAMM) using the *gamm4* package (Wood and Scheipl 2020), setting stand age as a smooth term (i.e. modeling the predictor response as a flexible spline). As potential linear covariates, we tested the same site and stand characteristics previously mentioned for Q1. Due to the data's hierarchical structure, we added a random intercept effect at plot level.

In all the research questions, we selected the final models according to lower AIC values (models with differences within two points were considered equal) and sound biological plausibility.

Results

Site quality

Compared to pure spruce stands, spruce–birch and spruce–pine stands were located on sites more and less fertile respectively (Figure 2). Regarding C:N, spruce–pine stands had significantly higher values than pure stands (organic and mineral layers, $p<0.0001$), while spruce–birch had lower values than pure stands (organic layer only, $p<0.0001$). Regarding the vegetation type, spruce–birch had significantly better odds of being located on higher fertility sites ($p = 0.0187$), while there were no differences between pure and spruce–pine stands ($p = 0.3757$). C:N was significantly lower going from VT to MT to OMT (results not shown). The temperature sum significantly decreased from spruce–birch to pure stands ($p = 0.0106$), and from pure to spruce–pine stands ($p = 0.0063$); the temperature sum decreased from south to north (Figure 1). We were therefore careful to account for site quality confounding effects when analyzing the data.

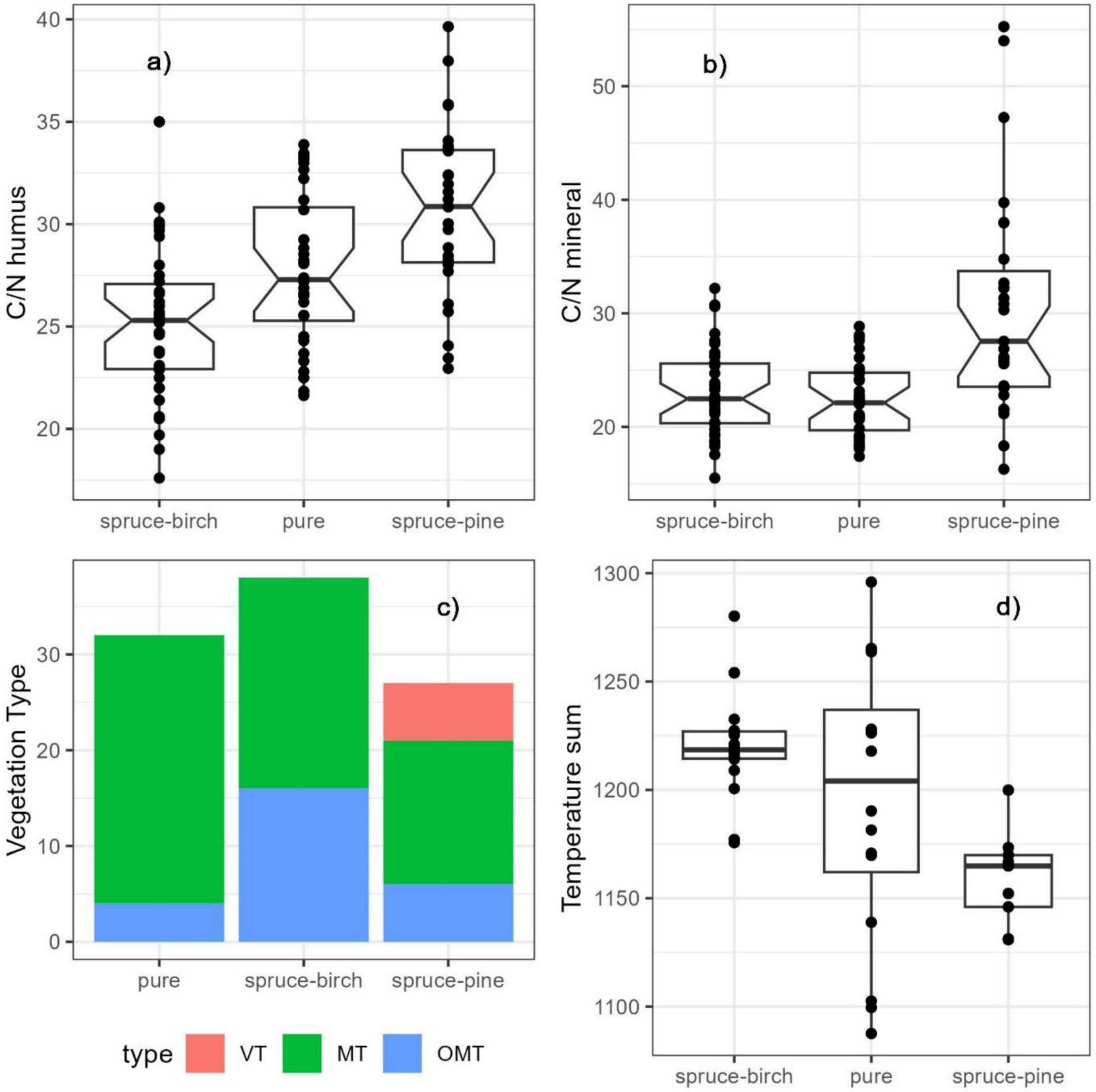

Figure 2. Distribution of variables describing site quality across datasets: (a) & (b) carbon nitrogen ratio values respectively for humus and mineral layer (plot-level average of all samples), (c) stand-level distribution of vegetation types, Vaccinium type (VT), Myrtillus type (MT), and Oxalis-Myrtillus type (OMT); (d) stand-level values of accumulated degree-days over 5°C.

Table 2. Summaries of the age–size relationship models.

Model	Variable	Value	Std.Error	*p*-value
Diameter at stump height	*Fixed effect*			
	β_1	39.3499	2.6495	<0.0001
	β_1 [C:N organic]	−0.3693	0.0976	0.0002
	β_1 [pine %]	−16.2225	2.4342	<0.0001
	β_2	0.0609	0.0010	<0.0001
	β_2 [pine %]	−0.0876	0.0069	<0.0001
	β_3	2.0751	0.0156	<0.0001
	Random effect	*St.dev*		
	Plot	2.3776		
	Tree	7.6460		
	Residual	0.3777		
Height	*Fixed effects*			
	β_1 [log(temp.sum)]	4.3763	0.4596	<0.0001
	β_1 [C:N organic]	−0.4381	0.1051	<0.0001
	β_2	0.0448	0.0031	<0.0001
	β_3	1.6007	0.0402	<0.0001
	Random effect	*St.dev*		
	Plot	4.2995		
	Residual	1.2492		

Q1: Tree-level age–size relationships

Spruce trees in admixture with pine had slightly lower growth than in the other datasets, both pure and spruce–birch stands (Table 2). This was indicated by the significant inclusion of the pine % as a negative coefficient for the asymptote β_1. However, its negative sign in the inflection point β_2 had a counteracting positive effect on growth, although it was much lower in absolute terms. To describe site quality, only the C:N of the organic layer had a significant result. The residuals were homogenously distributed (Figure 3(a)). The resulting modeled diameter development was very similar to the observed one (Figure 4), until the age of 20–25 years, after which growth seemed to be underestimated and overestimated respectively for spruce–pine and other datasets. Around that age, the observed data seem to be converging, and we need to highlight that the 99th percentile of the data fell below the age of 26.

Regarding height development, we found no significant difference between pure and mixed species stands (Table 2). Height development was positively affected by

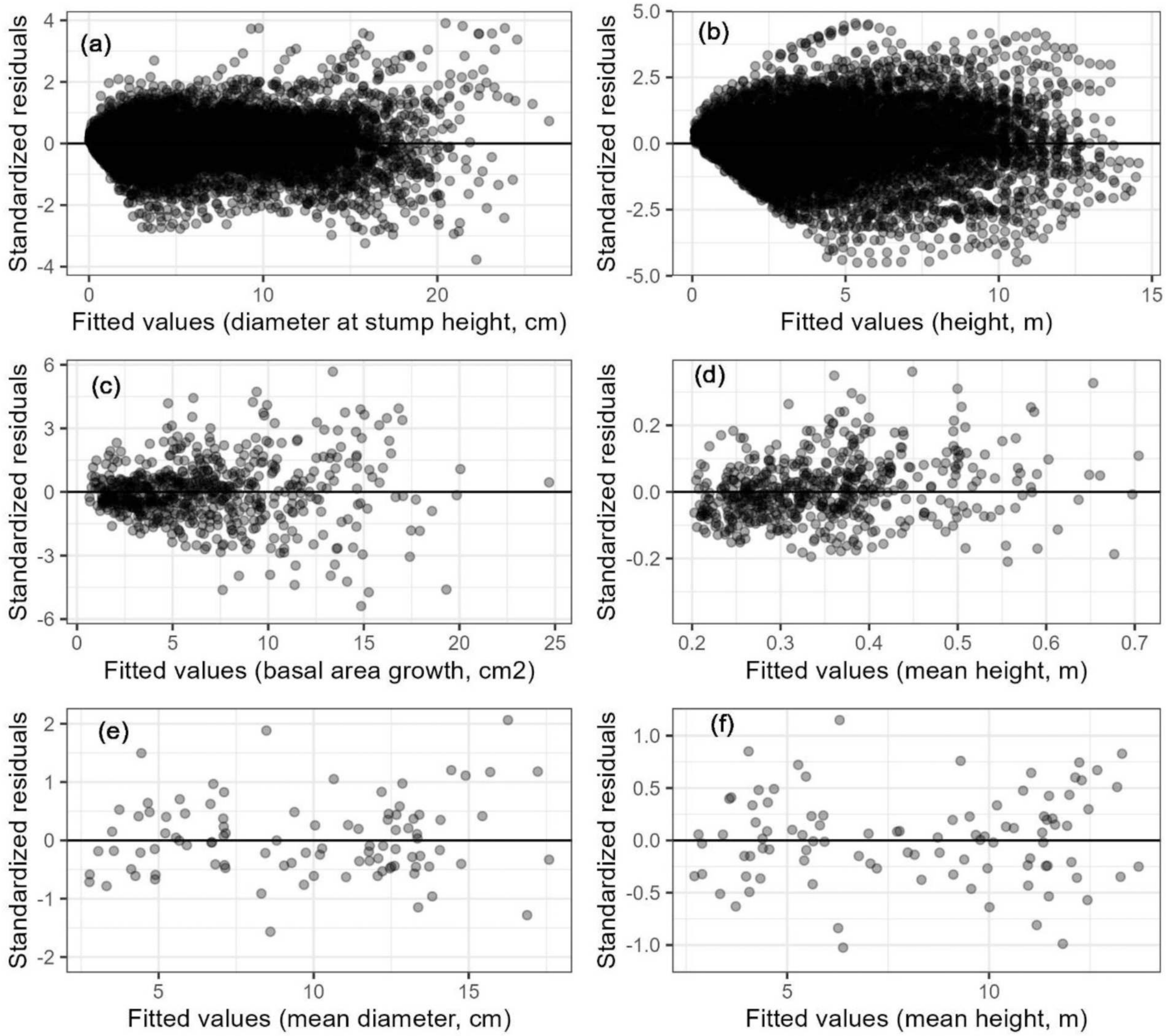

Figure 3. Standardized residual distribution versus fitted values, for all models, considering both fixed and random effects. Age–size relationship for (a) diameter and (b) height; recent growth for (c) basal area and (d) height; stand-level mean size for (e) diameter and (f) height.

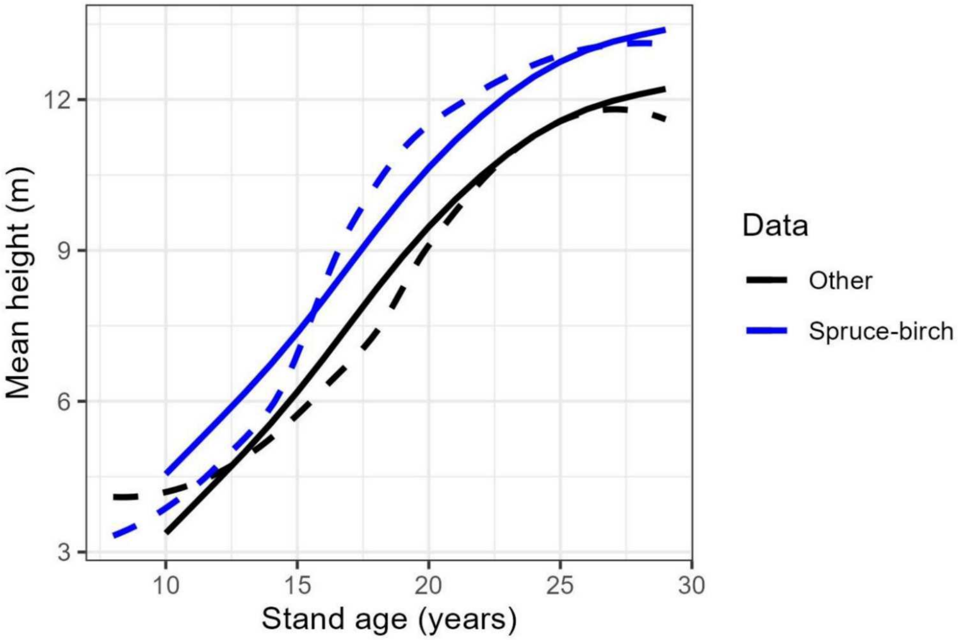

Figure 4. Development of diameter at stump height as function of age for different datasets: continuous line, simulated development given mean site conditions (age–size model predictions); dashed lines, observed development (locally weighted smoothing of observed points).

the temperature sum and negatively by C:N in the organic layer. Including a random effect at tree level caused convergence problems, so it was excluded. The residuals were homogenously distributed (Figure 3(b)), although with some artifacts still visible due to the data's longitudinal nature.

Q2: Tree-level recent growth

We found no significant difference in recent growth between pure and mixed species stands, either for basal area or height (Table 3). Basal area was positively affected by tree diameter at the start of the growth period, with a sigmoid shape due to the inclusion of the two terms. Additionally, it was negatively affected by decreasing site quality, namely, VT type and higher C:N in the organic layer (Table 3) and by stand density (total basal area). The recent height growth model did not have any significant predictor except for the size before growth. The residuals were homogenously distributed in both cases (Figure 3(c and d)).

Q3: Stand-level mean size

At stand level, we found significant higher values of achieved basal-area weighted mean height in spruce–birch stands compared to the other datasets (indicated by a positive dummy variable, Table 4). The mean height models indicated the average size in spruce–birch to be almost one meter higher than in the other datasets, on average fitting the observations very well (Figure 5). For mean diameter, there were no differences across datasets. In both cases, the only significant site predictor was C:N, and the residuals were homogenously distributed (Figure 3(e and f)).

Table 3. Summaries of the recent growth models.

Model	Variable	Value	Std.Error	*p*-value
Basal area	*Fixed effects*			
	(Intercept)	4.3146	0.4055	<0.0001
	dbh	−0.1625	0.0208	<0.0001
	sqrt(dbh)	1.9385	0.1356	<0.0001
	C:N organic	−0.0602	0.0079	<0.0001
	VT	−0.3974	0.1746	0.0228
	log(BAtot + 1)	−0.5625	0.0501	<0.0001
	Random effects	*St.dev*		
	Plot	0.4088		
	Residual	1.4805		
Height	*Fixed effects*			
	(Intercept)	−1.4101	0.0636	<0.0001
	height	0.0347	0.0074	<0.0001
	Random effects	*St.dev*		
	Plot	0.2062		
	Residual	0.1059		

Table 4. Summaries of the stand-level mean size models.

Model	Variable	Value	Std.Error	*p*-value
Basal-area weighted mean diameter	*Fixed effects*			
	(Intercept)	14.0627	0.9868	<0.0001
	C:N organic	−0.1588	0.0352	<0.0001
	Random effects	*St.dev*		
	Stand	0.9932		
	Residual	0.8593		
	Smooth terms	*edf*		
	Stand age	3.430		<0.0001
Basal-area weighted mean height	*Fixed effects*			
	(Intercept)	10.6184	0.7577	<0.0001
	C:N organic	−0.1053	0.0255	0.0001
	Spruce–birch stands	0.9265	0.3112	0.0037
	Random effects	*St.dev*		
	Stand	0.8572		
	Residual	0.5648		
	Smooth terms	*edf*		
	Stand age	3.369		<0.0001

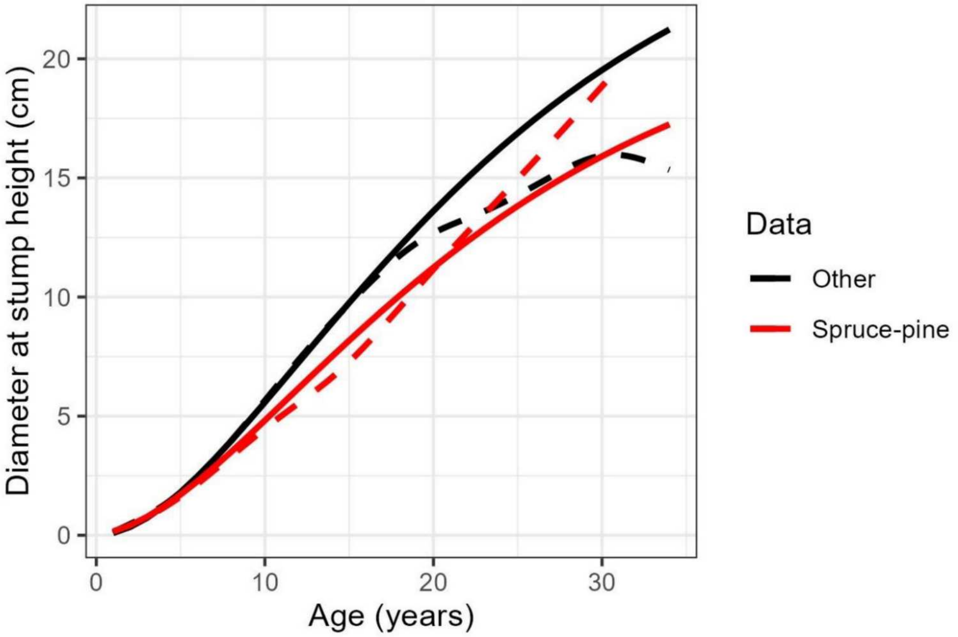

Figure 5. Basal-area weighted mean height (Lorey's height) as a function of stand age for spruce–birch data compared to spruce–pine and pure spruce (labeled "others"): continuous line, simulated development given mean site conditions (model predictions); dashed lines, observed development (Loess smoother).

Discussion

We investigated spruce development in recently established and well-managed pure and mixed species stands, checking different tree- and stand-level dynamics, to obtain an overall picture of the situation. For spruce growing in spruce–pine mixtures, we found a negative significant effect in pure stands. In the age–diameter model, there was a slower growth of spruce with a higher presence of pine. However, both the recent basal area growth and achieved stand-level mean diameter of spruce were not significantly affected by the presence of pine; and no effect was seen at all for height. Naturally regenerating pine has faster early growth than spruce, so spruce growing in mixtures is expected to suffer more from competition than in pure stands (Koivisto 1959). This was the case in Jonsson (2001) for stands direct seeded in the 1950s, where a generally lower growth in mid-rotation spruce growing with pine mixtures was found than in pure spruce, albeit resulting in a non-significant lower mean diameter (Holmström et al. 2018) as in our results. In our data, the early lower spruce growth in a mixture with pine seems to have already been overcome, and spruce was currently developing as fast as in pure stands.

Yet for spruce–birch mixtures, we found the only positive significant mixture effect compared to pure stands. For mean spruce height, the model indicated higher values in spruce–birch than in the other datasets. However, both the age–height relationship and recent height growth were not significantly affected by mixture. No effect was seen at all for diameter. Using the same data, Männistö et al. (2024) found slightly lower growth in spruce growing in the birch than in the pine dataset. The negative effects of a birch overstory on spruce (growth suppression, increased mortality, and release stress) were considered relatively small by Valkonen and Valsta (2001). The inclusion of birch in spruce stands was found in other cases to promote the spruce nutrient balance (Thelin et al. 2002), although without resulting in faster growth than in pure stands. In some cases, under increasing pressure for light availability, trees may have more sustained growth for height than for diameter (Bebre et al. 2021; Lee et al. 2021). Our data, however, do not represent all spruce-birch stands in Finland. At this stage, our focus was to explore the potential for optimal outcomes where spruce and birch grow in nearly the same layer. Once this potential is demonstrated, further research will be necessary to develop silvicultural guidelines for achieving this result.

The tree-level age–size and stand-level mean size models may have been affected by the restricted age range used. Especially for the Bertalanffy-Richard models, the lack of real maximum values may have affected the asymptotic estimations (Huuskonen et al. 2022). However, growth models for spruce generally show a lower inter-specific competition effect from both pine and birch than in intra-competition (e.g. Pukkala et al. 2013; Bianchi et al. 2023). This further justifies the notion that if spruce is aided in closing the initial gap in early development, there may be no long-lasting growth loss for the spruce component in mixed stands compared to pure stands.

Another possible explanation for the few differences between datasets could be the intensive silvicultural management applied. The timely early cleaning and pre-commercial thinning may have been successful in decreasing the competition between trees, both inter- and intra-specific. Spruce trees may thus have been able to fully express their growth potential in all stands.

When investigating differences between young spruce growing in different admixtures (pure, spruce–birch, and spruce–pine), we found significant differences in site quality between datasets. The higher and lower fertility in spruce–birch and spruce–pine stands respectively was probably the result of the corresponding site requirements of the secondary species. As this bias may have affected the analyses, we addressed it through the careful inclusion of site quality parameters such as the traditional temperature sum and vegetation type used in various national forest growth models (e.g. Hynynen et al. 2014). We also tested more advanced soil characteristics such as the carbon-to-nitrogen ratio (C:N), soil texture, and soil depth. The C:N of the organic layer especially resulted as significant in almost all models (5 out 6), with higher values (indicating lower presence of nitrogen and hence lower fertility) corresponding to lower growth. We wish to highlight that C:N values in the mineral soil were correlated with the humus layer. Nitrogen is an important plant nutrient, and especially in boreal forests, tree growth may be limited by a low supply of soil nitrogen (e.g. Tamm 1991). C:N values were significantly correlated with the fertility scale of the ground vegetation type classes observed (i.e. the vegetation types considered more fertile had lower values); indeed, they mostly superseded their use as predictors. Such a correlation was not found in Häkkinen et al. (2010), showing that there was still no accepted explanation between the differences in ground vegetation composition and productivity (Högberg et al. 2017). C:N has been found to be correlated with individual tree locations and forest species composition, but often in a two-way interaction in which it is difficult to determine cause and effect (Häkkinen et al. 2010; Ross et al. 2011). Unexpectedly, the temperature sum was significant only in one model, perhaps due to the relatively limited range of values. We acknowledge that although we accounted for site characteristics in our analyses, the results still point to lower and higher spruce growth according to the average site fertility of the datasets. We do not consider those differences conclusive and the highlight of our study, while comparing spruce growth in pure and mixed species stands.

In conclusion, having accounted for possible confounding effects due to differences in site fertility, we observed no negative effects in the early development of spruce trees in mixed stands that had recently been established and managed compared to pure stands. Modern regeneration material and methods and juvenile stand management activities seem to have helped spruce trees to resist the competition of typically faster-growing species such as pine and birch and reach the same growth rate as in pure stands.

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Disclosure statement

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Authors' contributions

Conceptualization (SH, JM), data curation (LM, SH, JM), data analysis (SB, LM, JM, SH), original draft preparation (SB), writing (SB, LM, SH, JM), project administration (SH). All authors have read and agreed to the published version of the manuscript.

Declaration of openness of research materials, data, and code

Data available on request from the corresponding author.

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