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Mixing effects on Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karst.) productivity along a climatic gradient across Europe

Ricardo Ruiz-Peinado [a,b,*], Hans Pretzsch [c], Magnus Löf [d], Michael Heym [c], Kamil Bielak [e], Jorge Aldea [d], Ignacio Barbeito [d,f], Gediminas Brazaitis [g], Lars Drössler [h], Kšištof Godvod [g], Aksel Granhus [i], Stig-Olof Holm [j], Aris Jansons [k], Ekaterina Makrickienė [g], Marek Metslaid [l], Sandra Metslaid [l], Arne Nothdurft [m], Ditlev Otto Juel Reventlow [n], Roman Sitko [o], Gintarė Stankevičienė [g], Miren del Río [a,b]

[a] *Spanish Institute for Agriculture and Food Research and Technology (INIA), Forest Research Center (CIFOR), Spain*
[b] *Sustainable Forestry Management Research Institute UVa-INIA (iuFOR), Spain*
[c] *Chair for Forest Growth and Yield Science, TUM School of Life Sciences, Technical University of Munich, Germany*
[d] *Swedish University of Agricultural Sciences (SLU), Sweden*
[e] *Warsaw University of Life Sciences (SGGW), Poland*
[f] *Université de Lorraine, AgroParisTech, INRAE, UMR Silva, Nancy, France*
[g] *Vytautas Magnus University, Institute of Forest Biology and Silviculture, Lithuania*
[h] *Ilia State University (ISU), Georgia*
[i] *Norwegian Institute of Bioeconomy Research (NIBIO), Norway*
[j] *Umeå University (UMU), Sweden*
[k] *Latvian State Forest Research Institute (SILAVA), Latvia*
[l] *Estonian University of Life Sciences (EMU), Estonia*
[m] *University of Natural Resources and Life Sciences (BOKU), Austria*
[n] *Department of Geosciences and Natural Resource Management, University of Copenhagen (UCPH), Denmark*
[o] *Technical University in Zvolen (TUZVO), Slovakia*

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ABSTRACT

Mixed-species stands have been found to be more productive than would be expected from the performance of their component species in monocultures due to facilitation and complementarity between species, although these interactions depend on the combination of species present. Our study focuses on monospecific and mixed-species stands of Scots pine and Norway spruce using 20 triplets established in nine countries along a climatic gradient across Europe. Differences in mean tree and stand characteristics, productivity and stand structure were assessed. Basal area increment in mixed stands was 8% higher than expected while volume increment was only 2% greater. Scots pine trees growing in mixed-species stands showed 11% larger quadratic mean diameter, 7% larger dominant diameter, 17% higher basal area and 25% higher stand volume than trees growing in monospecific stands. Norway spruce showed only a non-significant tendency to lower mean values of diameters, heights, basal area, as well standing volume in mixtures than monocultures. Stand structure indices differed between mixed stands and monocultures of Scots pine showing a greater stratification in mixed-species stands. Furthermore, the studied morphological traits showed little variability for trees growing in monospecific stands, except for diameter at breast height, crown length and crown length ratio. For trees growing in mixed stands, all the morphological traits of the trees were identified as different. Some of these morphological traits were

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[*] Corresponding author.

E-mail addresses: ruizpein@inia.es (R. Ruiz-Peinado), hans.pretzsch@tum.de (H. Pretzsch), magnus.lof@slu.se (M. Löf), michael.heym@tum.de (M. Heym), kamil.bielak@wl.sggw.pl (K. Bielak), jorge.aldea@slu.se (J. Aldea), ignacio.barbeito@slu.se (I. Barbeito), gediminas.brazaitis@vdu.lt (G. Brazaitis), lars.drossler@iliauni.edu.ge (L. Drössler), ksistof.godvod@vdu.lt (K. Godvod), aksel.granhus@nibio.no (A. Granhus), stig-olof.holm@umu.se (S.-O. Holm), aris.jansons@silava.lv (A. Jansons), ekaterina.makrickiene@vdu.lt (E. Makrickienė), marek.metslaid@emu.ee (M. Metslaid), sandra.metslaid@emu.ee (S. Metslaid), arne.nothdurft@boku.ac.at (A. Nothdurft), dire@ign.ku.dk (D. Otto Juel Reventlow), roman.sitko@tuzvo.sk (R. Sitko), gintare.stankeviciene@vdu.lt (G. Stankevičienė), delrio@inia.es (M. del Río).

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associated with relative productivity. Nevertheless, relative productivity in mixed-species stands was not related to site conditions.

1. Introduction

In the context of climate change, it has been shown that mixed-species forests can be more resistant and resilient to disturbances compared to monocultures (Bauhus et al., 2017a). This reflects different growth patterns of species along with other mechanisms such as niche complementarity and facilitation (Jactel et al., 2017). Thus, forests with higher species richness may display greater productivity, as revealed at various scales, e.g. Mediterranean forests (Vilà et al., 2007), temperate and boreal forests (Paquette and Messier, 2011), as well as through a worldwide meta-analysis (Liang et al., 2016). Productivity has also been found to be more temporally stable in mixed-species forests (Aussenac et al., 2017; del Río et al., 2017). This higher and more stable productivity suggests that mixed-species forests can be capable of sequestering and storing more carbon than monospecific forests (Ruiz-Benito et al., 2014; Poorter et al., 2015; Liu et al., 2018). Mixed forests can provide a wider range of ecosystem services than monospecific forests (Gamfeldt et al., 2013; Bauhus et al., 2017b).

Almost 70% of the forest land in Europe is covered by stands containing two or more species (Forest Europe, 2015, p. 135). Different studies have reported that overyielding, i.e. greater productivity in mixture than that of the weighted mean productivity of the corresponding monospecific stands, is usually observed in mixed stands (e.g., Liang et al., 2016; Pretzsch and Forrester, 2017). Higher productivity is expected in mixtures of complementary species, mainly due to the differences in their functional traits. Individual species exploit available site resources differently, so the effects of mixing species on productivity could also change along spatial and temporal gradients of climatic conditions and resource availability (Forrester, 2014). Moreover, other stand features such as age, density, or structure can also modify mixed-forest productivity (Condés et al., 2013; Lu et al., 2016; Pretzsch and Schütze, 2016).

Investigations of the effects of environmental gradients upon overyielding have been inconclusive, with different findings being reported according to species composition (Toïgo et al., 2015). In a meta-analysis, Jactel et al. (2018) found that overyielding increased with precipitation, as the effects of complementarity could be expressed when water requirements were met. Similarly, better climatic or site conditions were beneficial to species complementarity in some species compositions, leading to increased overyielding (Forrester et al., 2013; Pretzsch et al., 2020a; 2020b). However, other studies have reported greater overyielding under harsher conditions (Pretzsch et al., 2010; Bielak et al., 2014; Toïgo et al., 2015), in accordance with the stress-gradient hypothesis (Bertness and Callaway, 1994). In some cases, overyielding was not directly related to site conditions (Pretzsch et al., 2013a; 2013b; Pretzsch et al., 2015; Mina et al., 2018). Therefore, to identify the effect of environmental conditions on productivity of a given mixture, analyses must be conducted along a broad ecological gradient.

Variation in canopy and size structure was also reported to affect productivity (Pretzsch and Schütze, 2016; Williams et al., 2017; Torresan et al., 2020). In this regard, overyielding in mixtures may be related to improved light interception and light-use efficiency due to complementary crown plasticity and space occupation (Pretzsch and Schütze, 2016; Thurm and Pretzsch, 2016; Riofrío et al., 2017). A difference in shade tolerance between species, which affects competition for light and leads to variation in horizontal and vertical canopy structure, can therefore have an important impact on stand productivity (Williams et al., 2017; Toïgo et al., 2018). In a mixed stand, each species can occupy different ranges of the size distribution, resulting in horizontal or vertical stratification, which can in turn influence stand productivity (Barbeito et al., 2017; Torresan et al., 2020). Although species traits are important in determining the vertical stratification of species, it can also be significantly modified by other factors such as site conditions, stand density or disturbances (del Río et al., 2016).

Norway spruce (*Picea abies* (Karst.) L.) and Scots pine (*Pinus sylvestris* L.) cover large areas of Europe with Norway spruce accounting for more than 30 million ha (Jansen et al., 2017) and Scots pine 28 million ha (Houston Durrant et al., 2016). These two species have a considerable economic importance for the wood market in Europe. Mixtures of these species are estimated to cover more than 20% of the combined growing area (Wellhausen et al., 2017) and certain advantages over monocultures have been identified in terms of ecosystem service provision (Biber et al., 2015; Felton et al., 2016). Scots pine is a light-demanding species with a wide crown and deep rooting habit, often found in both dry and wet oligotrophic sites. In contrast, Norway spruce is a shade tolerant species with a slim crown and shallow root profile and mainly grows in moist mesotrophic locations (Bielak et al., 2014; Wellhausen et al., 2017). Thus, in accordance with the niche complementary hypothesis, although both species are evergreen conifers, their growth could be enhanced in mixtures due to differences in resource capture and use. In this case, a more complex canopy structure (canopy packing and vertical profile) in mixtures could lead to positive effects on productivity (Williams et al., 2017). Pretzsch (2014) found that crown expansion in mixtures can be greater resulting in denser canopies and higher stand density. Although Scots pine and Norway spruce are considered to be species with low crown plasticity (Pretzsch, 2014), the differences in light requirements of the two species could modify crown development. Previous studies have also reported productivity benefits for mixtures of species with similar traits, such as pine mixtures (Riofrío et al., 2017) or mixtures of various coniferous species in Central Europe in the meta-analysis by Pretzsch and Forrester (2017).

A number of studies have focused on Scots pine and Norway spruce mixtures in Europe, although most of them have been conducted at a regional level. Pukkala et al. (1994) using a modelling approach found that volume increment can be 10–15% higher in mixtures in Finland. Pretzsch and Forrester (2017) found mean overyielding of 21% in Germany, while a study of long-term experiments in Poland by Bielak et al. (2014) revealed higher productivity in mixed forests and also pointed to greater overyielding under harsh climatic conditions. Similarly, Mason and Connolly (2014) found higher productivity in mixtures than in monocultures at young ages in Britain, and similar results were observed by Jonsson et al. (2019) in term of biomass production in Sweden. However, Lindén and Agestam (2003) and Holmström et al. (2018) reported only small benefits in terms of productivity for mixed stands in Sweden. Drössler et al. (2018) compared the performance of this mixture using data from existing experiments in Northern and Central Europe, which differ in certain methodological aspects and their results for productivity indicated general overyielding although there was a large variation between sites and a negative influence of latitude and young stand age.

In order to obtain a better understanding of factors influencing the performance of this economically important mixture, we established 20 new experimental sites (triplets) across northern and central Europe where Scots pine and Norway spruce were growing in monocultures and mixed-species stands. A protocol was adopted to create common and consistent datasets that allowed tree and stand productivity to be estimated, as well as describing horizontal and vertical stand structure. The productivity approach was similar to that adopted by other recent studies (e.g., Pretzsch et al., 2010; Pretzsch et al., 2015; Riofrío et al., 2017; Pretzsch et al., 2020a; 2020b). The main objectives were to identify any overyielding by comparing the mixed stands with neighboring monospecific stands, and test the influence of structure on productivity. Specifically, we pose the following research questions:

i. Do mixed stands of Scots pine and Norway spruce differ from monocultures in terms of mean tree dimension, stand structure and stand state variables?
ii. Is the productivity of mixed stands similar to the weighted mean productivity of neighboring monospecific stands?
iii. Do site conditions influence the effects of mixing on productivity?
iv. Does the structure of the mixed-species stands affect productivity?

2. Material and methods

2.1. Study area

A triplet approach was used to study the mixture effect in Norway spruce and Scots pine (Pretzsch et al., 2015; Pretzsch et al., 2020a; 2020b). Twenty Scots pine-Norway spruce triplets were established covering the majority of both species' distribution range within Europe including Norway, Sweden, Denmark, Germany, Lithuania, Estonia, Latvia, Poland and Slovakia (Fig. 1). Each triplet consisted of three plots representing species growing in monospecific stands and one plot with both species growing in mixture, so the total number of plots in this study was 60. The plot size varied from 0.025 – 0.326 ha. Plots in each triplet were located in close proximity (<1 km) to ensure as far as possible that site conditions and management history were similar. Plots were established in stands located between 30 m a.s.l. and 860 m a.s.l. Mean annual temperature ranged between 3.0 and 8.9 °C and annual precipitation between 614 and 963 mm (data for the period 1988–2017). An overview of the location and climatic variables of the triplets are presented in Table S1.

All plots were more or less even-aged, fully stocked and had not been thinned for at least the last 8–10 years to better represent maximum stand density. Plots both in monocultures and mixed stands were selected with similar ages and occasional presence of single admixed additional species. Buffer areas around the plots were demarcated to avoid edge effects or effects of mixing with other tree species.

2.2. Data

Plots were inventoried in order to estimate common dendrometric state variables both at tree and stand level. The position of all living trees within the plots with diameter greater than 7 cm was recorded and species identified. Diameter at breast height (*dbh*) was measured for all living trees as well as standing dead trees. When any stump was found, stump diameter (diameter at base height) was recorded and time of tree

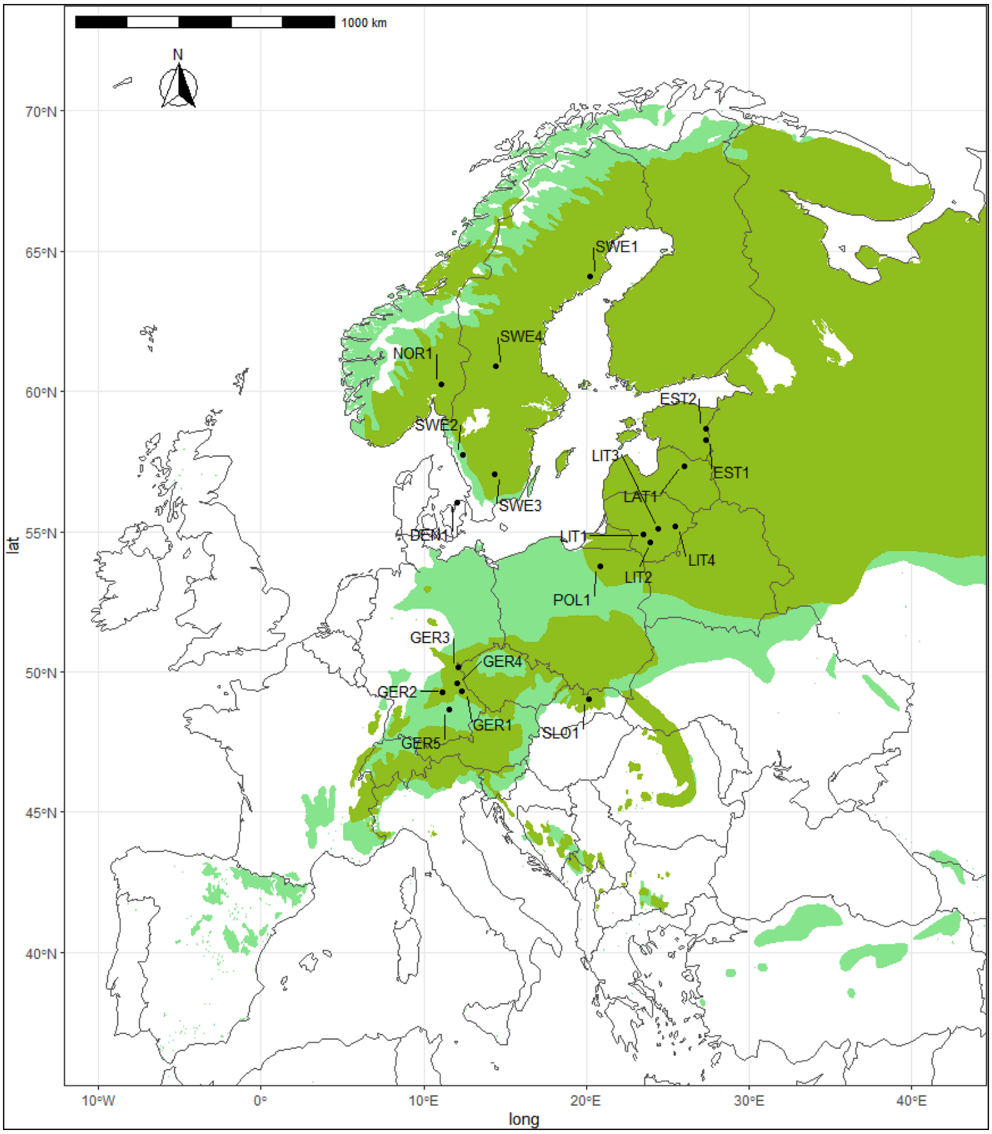

Fig. 1. Distribution map of the Scots pine and Norway spruce triplets and the joint distribution area of Scots pine (light green) and Norway spruce in Europe (dark green) (from EUFORGEN data). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

death was estimated. For a subsample of trees, stump diameters and *dbh* were also recorded. Therefore, *dbh* of occurring stumps can be predicted based on this observed relationship.

For diameter reconstruction, 20 dominant trees (thickest trees) and 10 additional trees distributed randomly across the rest of the diameter range per plot and species were selected for increment core sampling. Two cores were taken from the north and east directions at breast height on each tree, attempting to reach the pith. Cores were prepared, sanded and annual ring widths were measured with a digital positioning table. Standard dendrochronological methodologies were used including cross-dating and synchronization techniques (Fritts, 1976; Cook and Kairiukstis, 1990).

At least 30 trees per plot and species (cored trees) were selected for tree height (*h*) and height to living crown base (*hcb*) measurements. Crown radii in the four cardinal directions were recorded for all living trees inside the plot, as well as for trees outside the plot with partially overlapped crowns with the plot area.

To calculate the main stand characteristics and perform diameter and height reconstruction we followed the approach described by Heym et al. (2017; 2018). The main stand variables (by species and total) were calculated directly from the survey data: quadratic mean tree diameter (d_q), diameter of the 100 largest trees per hectare (d_o), height of the tree with the quadratic mean tree diameter (h_q), dominant height (h_o), number of trees per hectare (*N*), stand density index (SDI), stand basal area (*BA*) and standing volume over bark (*V*) per hectare using *dbh*, height and species-specific form factors (Franz et al., 1973). Mean stand characteristics are shown in Table 1.

To calculate the mean periodic stand basal area increment (IBA) and mean periodic stand volume increment (IV) for the previous 5-year period, the stand characteristics had to be reconstructed based on tree data. This included also the reconstruction of dead trees during last 5 years by using estimates of the year of death. Annual ring widths were used for diameter reconstruction of the cored trees. For non-cored trees and dead trees, a plot- and species-specific allometric regression between *dbh* and the mean periodic diameter increment was fitted to obtain diameter increments for the period. Height reconstruction was performed using yield tables (Wiedemann (1943) for Scots pine and Wiedemann (1936/42) for Norway spruce) and individual tree heights were calculated using different height curve systems (Kennel, 1972; Franz et al., 1973). All details on the applied diameter and height reconstruction methods can be found in Heym et al. (2017; 2018).

2.3. *Quantification of mixing effects*

Species proportions in mixed plots were calculated according to the approach described by Dirnberger and Sterba (2014) and Sterba et al. (2014) based on the Reineke stand density index (SDI) (Reineke, 1933), along the same lines as presented in Pretzsch et al. (2015; 2020a; 2020b). Differences in potential stand density between species were controlled by using an equivalent coefficient computed for each triplet by the ratio between SDI of Scots pine (SDI_{pi}) and SDI of Norway spruce (SDI_{sp}) growing in monospecific stands ($e_{pi} = SDI_{pi}/SDI_{sp}$), where *pi* is Scots pine and *sp* is Norway spruce. This coefficient related the growing space requirements of one species to those of the other species. Thus, the mixing proportion was calculated as:

$$m_{pi,(sp)} = \frac{SDI_{pi,(sp)}}{SDI_{pi,(sp)} + SDI_{(pi),sp} \bullet e_{pi}}$$

where $m_{pi,(sp)}$ is the mixing proportion of Scots pine in relation to Norway spruce; $SDI_{pi,(sp)}$ is the SDI of the Scots pine growing in mixture; $SDI_{(pi),sp}$ is the SDI of Norway spruce growing in mixture and e_{pi} is the ratio of SDI_{pi} and SDI_{sp} growing in monocultures.

Basal area increment (IBA) and volume increment (IV) in the 5-year period prior to the survey were analyzed as proxies of stand productivity. Although IBA is less correlated to productivity than IV, it has the advantage that it can be easily estimated from field measurements, avoiding potential biases derived from using common form factors and yield tables in IV reconstruction (see 2.2). The observed productivity of the mixed-species stands was termed $P_{pi,sp}$ and is the sum of the combined productivity in the mixture of Scots pine $P_{pi,(sp)}$ and Norway spruce $P_{(pi),sp}$. Expected productivity was calculated as the weighted mean of the monospecific stands as $\widehat{P}_{pi,sp} = P_{pi} \bullet m_{pi} + P_{sp} \bullet m_{sp}$ by the observed productivities in monospecific stands (P_{pi}, P_{sp}) and the corresponding mixing proportions. Overyielding at stand level, i.e. positive mixing effects on productivity, would be indicated by observed productivity higher than expected productivity ($P_{pi,sp} > \widehat{P}_{pi,sp}$) (Table 2). Transgressive overyielding is when the observed productivity in the mixed stand is higher than the maximum productivity observed in either monospecific stand. Underyielding and degressive underyielding can be

Table 2
Characterization of the mixing effects on productivity.

Type	Mixing effect	Stand level	Species level	
Productivity	Overyielding	$P_{pi,sp} > \widehat{P}_{pi,sp}$	$P_{pi,(sp)} > P_{pi}$	$P_{(pi),sp} > P_{sp}$
	Underyielding	$P_{pi,sp} > \widehat{P}_{pi,sp}$	$P_{pi,(sp)} < P_{pi}$	$P_{(pi),sp} < P_{sp}$
	Transgressive overyielding	$P_{pi,sp} >$ max (P_{pi}, P_{sp})		
	Degressive underyielding	$P_{pi,sp} <$ min (P_{pi}, P_{sp})		
Relative productivity	Overyielding	$P_{pi,sp} / \widehat{P}_{pi,sp} > 1$	$P_{pi,(sp)} / P_{pi} > 1$	$P_{(pi),sp} / P_{sp} > 1$
	Underyielding	$P_{pi,sp} / \widehat{P}_{pi,sp} < 1$	$P_{pi,(sp)} / P_{pi} < 1$	$P_{(pi),sp} / P_{sp} < 1$

pi is Scots pine; *sp* is Norway spruce; $P_{pi,sp}$ is the observed productivity in mixed stands; $\widehat{P}_{pi,sp}$ is the expected productivity in mixed stands; P_{pi} and P_{sp} are the observed productivities in monospecific stands.

Table 1
Mean stand characteristics and ranges (min–max) for the triplets included in the study by mixed and monospecific stands.

Type	Species	n	Stand age (years)	N (trees ha^{-1})	d_q (cm)	h_q (m)	BA (m^2 ha^{-1})	IBA (m^2 ha^{-1} $year^{-1}$)	V (m^3 ha^{-1})	IV (m^3 ha^{-1} $year^{-1}$)	Mixing proportion
Mixture	Sc. pine + N. spruce	20	60	1007			41.64	0.87	460.1	15.0	
			41–93	363–1517			20.05–63.90	0.46–1.46	178.1–873.8	6.2–26.1	
	Scots pine		60	370	27.3	24.1	20.81	0.37	232.8	6.5	0.46
			41–85	123–718	20.7–36.2	16.6–30.9	7.88–31.93	0.19–0.55	72.4–353.1	2.9–10.5	0.23–0.67
	N. spruce		61	637	22.4	22.5	20.83	0.50	227.3	8.6	0.54
			45–93	170–1093	16.3–30.6	14.8–29.6	8.84–38.74	0.25–1.02	62.3–520.7	3.2–17.2	0.33–0.77
Monospecific	Scots pine	20	58	948	24.8	23.6	40.04	0.79	425.5	13.4	1.00
			45–78	355–1577	17.9–29.5	17.9–30.4	20.31–60.26	0.30–1.31	185.2–713.6	4.9–25.3	
	N. spruce	20	61	984	24.5	23.5	42.22	0.86	493.4	16.6	1.00
			45–93	470–1744	17.6–34.0	17.5–29.4	20.48–63.43	0.51–1.46	202.0–866.8	8.7–36.1	

n: number of plots, *N*: number of trees per hectare, d_q: mean quadratic diameter, h_q: quadratic mean height, *BA*: stand basal area, *IBA*: mean periodic stand basal area growth, *V*: standing volume, *IV*: periodic annual volume growth also detected in the triplets when $P_{pi,sp} < \widehat{P}_{pi,sp}$ and $P_{pi,sp} < \min(P_{pi}, P_{sp})$, respectively. To upscale the productivity of given species in mixture to one hectare and thus be able to compare directly with respective monocultures productivity and calculate relative productivity at species level, the observed production in mixed ($pp_{pi,(sp)}$, $pp_{(pi),sp}$) was divided by the respective species mixing proportion ($P_{pi,(sp)} = pp_{pi,(sp)}/m_{pi}$ and $P_{(pi),sp} = pp_{(pi),sp}/m_{sp}$). At species level, a positive effect can be identified when the productivity in the mixed stand exceeds observed productivity in the monoculture ($P_{pi,(sp)} > P_{pi}$ or $P_{(pi),sp} > P_{sp}$).

Finally, we refer to relative productivity at the stand level where we divided the observed productivity by the expected one ($RP_{pi,sp} = P_{pi,sp}/\widehat{P}_{pi,sp}$). We also estimated the species-specific relative productivity when the productivity of the given species in mixed stand was divided by corresponding productivity of monospecific stand, i.e. ($RP_{pi,(sp)} = P_{pi,(sp)}/P_{pi}$) for Scots pine and ($RP_{(pi),sp} = P_{(pi),sp}/P_{spi}$) in case of Norway spruce. Furthermore, we also compared the relative productivity at stand level of the mixed-species stand with the relative productivity of Scots pine ($R_{pi}P_{pi,sp} = RP_{pi,sp}/RP_{pi,(sp)}$) and Norway spruce ($R_{sp}P_{pi,sp} = RP_{pi,sp}/RP_{(pi),sp}$) (Table 2).

2.4. Characterizing canopy and size structure

Several indices, described below and summarized in Table 3, were calculated in order to describe stand stocking and size structure, tree morphology, and horizontal and vertical species stratification.

Beyond stand density and stand density index (*SDI*), the relative sum of crown projection area (*RCPA*) was calculated. Crown projection area (*cpa*) of each tree was calculated using the quadratic mean radius from the four crown measurements and the sum for all trees gave the cumulative crown projection area (*CPA*). *RCPA* is the ratio between cumulative crown projection area and the stand area; $RCPA = 1.0$ when the *CPA* and the stand area are equal.

Table 3
Variables applied in the study for the canopy and size structure characterization.

Characteristics	Index	Acronym	Interpretation
Stocking	stand density	*N*	Number of trees per area
	stand density index	*SDI*	Relative density that informs about stand competition
Canopy packing	crown projection area	*cpa*	Horizontal projection of crown area
	Relative sum of crown projection area	*RCPA*	$RCPA = 1$; both *cpa* and stand area are equal $RCPA > 1$ there are overlapping of crown more than the stand área $RCPA < 1$ *cpa* is not covering all the stand area
Size structure	ranges (*dbh*, height, volume)	*range*	Dispersion of the values in the data
	Gini index	*G*	$G_i = 0.0$; all trees are equal in size G_i increasing to 1 the more inequality exists among trees
Vertical structure	species profile index	*A*	$A = 0$; Monospecific and monolayer stand The higher the index the more equal the presence of species in different height zones of the stand
Species stratification	variables ratio for the different species growing in mixtures	X_{pi} / X_{sp}	Comparison of the variables by species in the mixed stand
Tree allometry	slenderness	*h/d ratio*	Higher values indicate greater height growth vs diameter
	crown ratio	*cl/h*	Proportion of live crown in trees
	crown diameter vs diameter	*cpa/d*	Ratio indicates how much larger is the crown width than *dbh*
	crown projection area vs basal area	*cpa/ba*	Ratio indicates how much larger is the crown area than stem basal area

To describe the size distribution and heterogeneity in mixed and monospecific stands, several statistics were used (del Río et al., 2016; Torresan et al., 2020). Ranges of *dbh*, *h* and volume were used to to show the spread of the size distribution. The Gini coefficient was used to quantify the heterogeneity of tree diameter (G_{dbh}), height (G_h), tree basal area (G_{ba}) and tree volume (G_v) in mixed stands and monocultures. For this index, a value of 0.0 indicated that all trees were equal in size and the higher the value (towards the maximum of 1) the greater the size inequality among the trees.

The vertical species profile index (*A index*) was used to quantify the vertical stand structure and indicates the presence of different species in different height zones of the stand. The higher the index the more equal the presence of species in all the different height zones of the stand, while 0 values indicate completely monospecific and monolayer stand (Pretzsch, 1998).

Furthermore, we estimated the ratio of the main mean tree variables between the two species in mixtures to characterize the size stratification of the two species. Hence, we calculated the ratio between the mean *dbh* of Scots pine and mean *dbh* of Norway spruce growing in mixtures; the ratio between mean *h* for both species in mixtures; the ratio for the mean *cl* of both species in mixtures; and the ratio for the mean *cpa* of both species in mixed-species stands.

Individual morphological traits were characterized to identify differences between tree allometry in mixed and monospecific stands. We calculated for each tree the crown length (*cl*) by subtracting crown base height (*hcb*) from tree height (*h*). The following size ratios were calculated for each tree and averaged for every plot and species: slenderness (*h/d* ratio), crown ratio (*cl/h*), crown diameter-diameter (*cd/d*), and crown projection area-tree basal area (*cpa/ba*). A higher *h/d* ratio indicates a greater height growth in relation to diameter growth and slenderness. The larger crown ratio indicates the importance of crown length in tree height. Crown diameter-diameter and crown projection area-stem basal area ratio indicate how many times larger the crown width or area is than the stem diameter or stem basal area. Large intraspecific variations of the ratios within a population indicate crown plasticity and potential to acclimate to a given growing space in the canopy (Assmann, 1970).

2.5. Statistical analysis

To better evaluate the variables in mixed-species stands and monospecific stands, ratios between variables (those observed/expected or mixed/monocultures) were calculated to compare them in a relative manner. These ratios were centered to zero (value of the ratio minus 1) so that any deviation from this value indicates better performance of mixtures vs monocultures if the value is positive and the opposite if the value is negative.

The analysis aimed at identifying differences between mixed-species and monospecific stands was conducted by applying linear mixed-effects models, considering random effects of country as a proxy for biogeographical zones and of location nested to country (triplet group level for those triplets located in the vicinity) in order to consider any spatial correlation at these levels. All analyses were conducted in R version 3.5.1 (R Core Team, 2018) using package ‘nlme’ (Pinheiro et al., 2018).

The model structure for the analysis was:

$$\frac{Variable_{mix,i,j,k}}{Variable_{mono,i,j,k}} - 1 = a + b_i + b_{i,j} + \in_{i,j,k}$$

where *variable mix* indicates the studied variable growing in mixed-species stand; *variable mono* indicates the studied variable growing in monoculture; *a* is the intercept and indicates whether the ratio is greater or lower than 0; *b* shows the random effect on the levels; $\in$ is the independent error; indices *i*, *j*, and *k* represent country, triplet group level and triplet.

In order to determine the influence of site conditions or stand structure on the productivity of mixed-species stands versus monocultures, the inclusion of other variables in the previous model was tested. The model structure was:

$$\frac{Variable_{mix,i,j,k}}{Variable_{mono,i,j,k}} - 1 = a + b_i + b_{i,j} + X_{i,j,k} + \in_{i,j,k}$$

where *X* indicates other variables of interest to include in the analysis. To quantify the site conditions we used the site index of the two species and local climate variables (Table S1). The site index (*SI*) was calculated as the height at the age of 100 years using the quadratic mean height (h_q) in yield tables (Wiedemann, 1936/42; 1943). Among the climate variables, mean annual temperature, annual precipitation and the de Martonne index were tested. The aridity index by de Martonne (*dMI*) (de Martonne, 1926) was calculated for each triplet from annual mean temperature (*T*) and annual precipitation (*P*) ($dMI = P/(T + 10)$). Climatic data for each triplet were obtained from the nearest meteorological station and were based on the annual records for the 30 years 1988–2017. Finally, the previously defined structural variables or ratios between mean tree variables (*dbh*, *h*, *cl*, *cpa*) of the two species growing in mixtures (Table 3) were also considered.

3. Results

3.1. Mixing reactions

At the stand level, tree density per hectare (*N ratio*) was 6% higher in the mixed stands than the weighted mean of the monospecific stands but the differences were not statistically significant (Table 4). A similar non-significant pattern was observed for *BA* (+2%) and *V* (+2%).

At the species level, there were no significant differences in quadratic mean height and dominant height of Scots pine when comparing mixtures with monocultures. However, significant differences were detected for quadratic mean diameter (+11%) and dominant diameter (+7%) (Table 4). In contrast, the slenderness ratios for Scots pine were lower in mixtures than monocultures (h_q/d_q: −8%, h_o/d_o: −4%). On the other hand, we found no significant differences when comparing the dimensions of Norway spruce trees grown in mixture with those in monocultures. Mean stand density was lower (-11%) in mixtures than expected for Scots pine and higher for Norway spruce (+21%), although the latter was not statistically significant. *BA* (+17%) and *V* (+25%) for Scots pine were significantly increased in mixture. For Norway spruce, no significant effects were detected.

Basal area increment (*IBA*) at stand and species level was always higher than expected for both species (Table 4), although a significant effect was only detected at stand level (+7%). Stem volume increment (*IV*) at stand level showed slight overyielding (+2%) but with no statistical significance. At species level, opposite tendencies were detected for Scots pine (overyielding) and Norway spruce (slight underyielding), although no statistically significant differences were found.

The comparison of the *IV* productivity of Scots pine and Norway spruce in the mixed stands in relation to their monocultures showed overyielding at the stand level in 55% of the cases (points were above the decreasing line) (Fig. 2a). 35% of the cases were in quarter I which suggested that both species benefit in the mixture. 25% of cases fell into quarter III, indicating detriment to both species. 40% of cases were in quarters II or IV which indicated that one species benefits at the expense of the other species. In these two quarters, in 30% of the total cases the beneficiary was Scots pine and in 10% of cases the beneficiary was Norway spruce. Transgressive overyielding was detected in 35% of the mixed-species stands and degressive underyielding in 15% (mixed-species stands productivity were lower than the minimum of both monospecific stands). Those triplets showing transgressive overyielding were highlighted in red on Fig. 2a and b and those displaying degressive overyielding were shown as empty circles.

Concerning *IBA* (Fig. 2b), overyielding was observed in 70% of the cases. Considering all cases, 25% were showing gains for both species (quarter I) and 20% losses (quarter III), while the remaining 55% revealed benefits from one species against the other.

Fig. 3 shows the relative productivity (*IV*) of the mixture at stand level ($P_{pi,sp}/\widehat{P}_{pi,sp}$) in comparison to the relative productivity at both species level ($P_{pi,(sp)}/P_{pi}$ and $P_{(pi),sp}/P_{sp}$) (Figure Supplementary 1 for IBA). At the species level the relative productivity (IV) of Scots pine was higher than that of Norway spruce in most of the studied cases, although differences between species reduced as overyielding at stand level increased.

3.2. Effect of site conditions on productivity

No significant effects were observed when including site variables such as *SI*, *dMI*, *T* or *P* in the models at species and stand level (Table S2). The inclusion of age as covariate did not show any significant improvement of the statistical characteristics of the models.

3.3. Structure

Tree number and *SDI* values showed large variation with lower mean values in monospecific stands than in mixtures; however differences

Table 4

Results of the linear mixed model analysis for the stand level relationships between observed (*obs*) vs expected (exp) mixed stand values, and the species-specific level comparison for given tree species in mixed (*m*) and monospecific (*p*) stands.

Stand variables	($Mixed_{obs}$ / $Mixed_{exp}$) −1 Estimate	SE (±)	p value	(Scots $pine_m$ / Scots $pine_p$) −1 Estimate	SE (±)	p value	(Norway $spruce_m$ / Norway $spruce_p$) −1 Estimate	SE (±)	p value
N (trees ha^{-1})	0.0627	0.0690	0.3873	**−0.1084**	**0.0459**	**0.0424***	0.2134	0.0981	0.0577
d_q (cm)				**0.1144**	**0.0255**	**0.0015****	−0.0699	0.0416	0.1277
d_o (cm)				**0.0671**	**0.0253**	**0.0267***	−0.0187	0.0290	0.5346
h_q (m)				0.0292	0.0253	0.2771	−0.03764	0.0237	0.1477
h_o (m)				0.0240	0.0235	0.3337	−0.0175	0.0199	0.4017
h_q/d_q				**−0.0773**	**0.0152**	**0.0004****	0.0479	0.0279	0.1209
H_o/d_o				**−0.0398**	**0.0165**	**0.0397***	0.0124	0.0241	0.6183
BA (m^2 ha^{-1})	0.0184	0.0225	0.4243	**0.1721**	**0.0738**	**0.0446***	−0.0441	0.0448	0.3508
V (m^3 ha-1)	0.0165	0.0365	0.6619	**0.2465**	**0.0985**	**0.0338***	−0.0881	0.0575	0.1600
IBA (m^2 ha^{-1} $year^{-1}$)	**0.0754**	**0.0337**	**0.0383***	0.0705	0.0518	0.2064	0.1085	0.0587	0.0979
IV (m^3 ha^{-1} $year^{-1}$)	0.0196	0.0273	0.4809	0.1001	0.0478	0.0657	−0.0022	0.0531	0.9666

N: number of trees per hectare, d_q: mean quadratic diameter, d_o: dominant diameter, h_q: quadratic mean height, h_o: dominant height, h_q/d_q: ratio of the quadratic mean height and mean quadratic diameter, H_o/d_o: ratio of the dominant height and dominant diameter, *BA*: stand basal area, *IBA*: mean periodic stand basal area growth, *V*: standing volume, *IV*: periodic annual volume growth, *SE*: standard error. Significance levels for comparison: ** p-value < 0.01, * pvalue < 0.05 (estimates that are statistically significant are given in bold type).

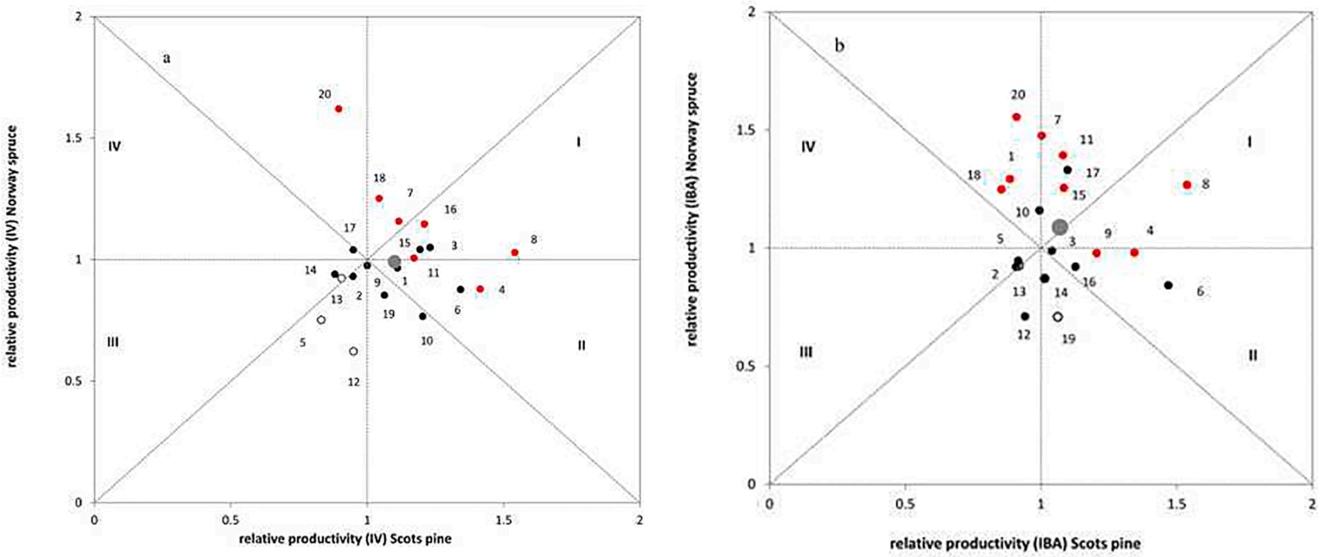

Fig. 2. Relative productivity, IV (a) and IBA (b), for Scots pine and Norway spruce in mixed stands compared with respective monospecific stands. Points in quarter I underlines that both species contribute to the overyielding of the mixed-stands, while quarter II and IV indicate the gain of one species is at the expense of the other one, respectively an advantage of Scots pine over Norway spruce or *vice versa*. The large grey point is showing the mean mixing effect on basal area/volume increment. Red points highlight transgressive overyielding, empty points degressive underyielding. Numbers refer to triplet location (see table S1). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

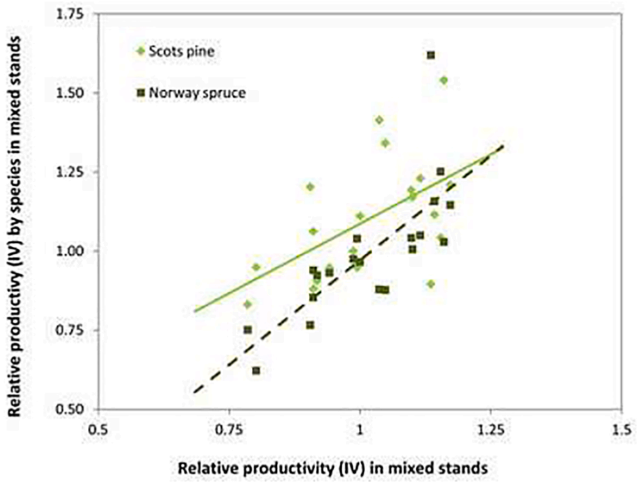

Fig. 3. Relative productivity (IV) at stand level ($RP_{pi,sp} = P_{pi,sp} / \widehat{P}_{pi,sp}$, x-axis) and by species ($RP_{pi,(sp)} = P_{pi,(sp)} / P_{pi}$ for Scots pine or $RP_{(pi),sp} = P_{(pi),sp} / P_{spi}$ for Norway spruce, y-axis) in mixed stands.

obtained were not statistically significant as mean values were very similar (Table 5). *RCPA* was 54% higher (statistically significant) in mixed stands than in Scots pine monospecific stands and 23% higher (not statistically significant) than in Norway spruce monospecific stands.

The range for *dbh* and *h* showed significant differences between mixed stands and monocultures of both species (Table 5). Nevertheless, the distribution range for *v*, the Gini coefficient for the *dbh* (G_{dbh}), tree basal area (G_{ba}) and volume (G_v) revealed significantly higher variation in mixed stands compared with Scots pine monocultures. Positive and significant differences were detected in the vertical profiles of both species (*A index*) in favour of mixtures over both monocultures.

Vertical structuring analysed through tree morphological variation showed that Scots pine showed lower slenderness (*h/d*) and Norway spruce had larger crown lengths in mixed stands compared to monocultures, both differences being statistically significant (Table 6). Significant differences were also detected in mean *dbh* between mixed stands and monocultures for Scots pine and tree height for Norway spruce (Table 6). Comparison of both species growing in mixed stands showed that *dbh* was larger for Scots pine than for Norway spruce (Figure Supplementary 2) as well as in monospecific stands, being both statistically significant. The comparison of mean tree height revealed than Scots pine was higher in mixtures and monocultures but differences were not significant. For Norway spruce, a statistically significant reduction in height was detected in mixed stands since Scots pine was taller than Norway spruce in mixtures. The mean height of Scots pine growing in mixed stands was greater than that of Norway spruce in all stands except for one triplet, and Scots pine height was also greater than that of Norway spruce in 75% of the cases growing in monospecific stands (Figure Supplementary 3). In the case of crown length (Figure Supplementary 4), crowns were significantly longer for Norway spruce than for Scots pine in mixtures and in monocultures. Scots pine crown projection area in mixtures was statistically larger than that of Norway spruce, although for monospecific stands the differences were not significant (Figure Supplementary 5). Slenderness (*h/d*) was found to be higher for Norway spruce than for Scots pine growing in mixtures, with statistically significant differences. Crown ratio (*cl/h*) was found to be higher and statistically significant for Norway spruce in comparison to Scots pine growing in mixtures, with significant differences. The same pattern was observed for the crown projection area to stem diameter relationship and crown projection area to stem basal area. Differences were statistically significant, with larger values for Norway spruce growing in mixed-species stands.

3.4. *Effects of structure on productivity*

The structural variables explaining the size stratification between species growing in mixtures were those found to significantly impact productivity (see Table 7 and Fig. 4). The ratios for mean *dbh*, *h* and *cl* for both species growing in mixtures were found to be significant at species level (Table 7). At the stand level, no significant differences were detected of structure in productivity.

At the species level, in the case of Scots pine, an increase in the relative productivity was identified with the mean height ratio for *BAI* and *IV* (Table 7, Figure Supplementary 6 and Supplementary 7). For

Table 5

Minimum, arithmetic mean and maximum values for structural measurements in monospecific stands of Scots pine and Norway spruce and mixed stands of these species. Last two columns are showing the mean and standard error of the ratio resulting from the pair-wise division of the characteristics of the mixed-species stands and the respective value of the monocultures (ratio −1) and if significant differences were detected between mixed and monocultures of Scots pine and Norway spruce respectively.

Stand structure indices	Mono Scots pine			Mono Norway spruce			Mixed			Mixed vs Scots pine mono		Mixed vs Norway spruce mono	
	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max	Mean	SE (±)	Mean	SE (±)
Stand and canopy density													
N	355	948	1577	470	985	1744	363	1007	1517	0.07	0.07	0.04	0.23
SDI	415	919	1802	459	910	1310	417	923	1388	0.02	0.03	0.02	0.05
RCPA	0.37	0.86	1.55	0.61	1.02	1.52	0.63	1.29	2.38	**0.54****	**0.12**	0.23	0.11
Size structure													
$range_{dbh}$	14.80	19.79	26.90	17.10	26.58	38.50	25.00	32.34	42.10	**0.69*****	**0.09**	**0.25***	**0.08**
$range_h$	3.2	9.6	20.6	7.6	16.1	21.7	11.9	19.8	25.9	**1.52****	**0.36**	**0.36***	**0.15**
$range_v$	0.44	1.25	4.34	0.55	1.47	3.25	0.85	1.61	3.08	**0.47***	**0.20**	0.23	0.14
G_{dbh}	0.07	0.16	0.29	0.12	0.17	0.24	0.11	0.20	0.27	**0.32***	**0.11**	0.18	0.09
G_h	0.02	0.09	0.22	0.04	0.10	0.17	0.04	0.12	0.19	1.00	0.37	0.32	0.20
G_{ba}	0.14	0.29	0.49	0.23	0.31	0.43	0.20	0.35	0.46	**0.30***	**0.10**	0.15	0.07
G_V	0.16	0.35	0.58	0.27	0.37	0.52	0.23	0.42	0.55	**0.31***	**0.11**	0.14	0.08
Vertical structuring													
A	0.10	0.67	1.25	0.64	0.88	1.32	1.08	1.36	1.68	**2.83****	**0.80**	**0.58*****	**0.06**

N: number of tree per ha; *SDI*: stand density index; *RCPA*: relative crown projection area in the stand (%); G_i: Gini coefficient for diameter (*dbh*), height (h), basal area (ba) and volume (v); *A*: species profile index for vertical structuring; *SE*: standard error. Significance levels for comparison of mixed-species stand versus monocultures: *** p-value < 0.001, ** p-value < 0.01, *p-value < 0.05 (estimates that are statistically significant are given in bold type).

Norway spruce, a negative effect was observed for IV when the mean *dbh* ratio was included in the model (Figure Supplementary 8). The same pattern of reduction was reported for *IBA* and *IV* as the difference between *cl* for pine and spruce reduces (ratio increasing) (Figure Supplementary 9 and Supplementary figure 10). Fig. 4 shows the evolution of the *IV* relative productivity (Figure Supplementary 11, Supplementary 12, Supplementary 13 and Supplementary 14 for *IBA*) in relation to the ratios for *dbh*, *h*, *cl* and *cpa* of the two species growing in mixed-species stands. The ratios for *h*, *cl* and *cpa* of the two species show opposite tendencies; as one species increases the other decreases.

4. Discussion

We detected limited mixing effects on Scots pine and Norway spruce productivity on triplets across Europe. Although our results indicated that tree and stand structures in mixtures of Scots pine and Norway spruce differed from those of monospecific stands, mixed stands were characterized by only slightly better volume growth but significantly higher basal area increment.

Stand productivity was slightly influenced by the canopy structure, vertical structuring and size distribution pattern. However, these parameters were found to be very different for Scots pine trees growing in mixed species stands compared to Scots pine in monocultures. By contrast, in Norway spruce the only parameters to differ between mixtures and monocultures were the *dbh* and *height* size ranges as well as vertical structuring. Mixing species resulted in differences in all the studied morphological traits between species. However, only a slight influence on stand productivity was identified.

The observed *IBA* in mixture was significantly higher (7.5%) than expected, although significant overyielding was not observed for *IV* (2%). These results contrast with previous findings on Scots pine-Norway spruce mixtures which point to general overyielding (*IV*) of about 10–15% in Finland (Pukkala et al., 1994) or 40% in Poland (Bielak et al., 2014) and England (Brown, 1992; Mason and Connolly, 2014). However, our results are in line with the slight overyielding reported by Pretzsch and Forrester (2017) and Wellhausen et al. (2017) in Germany, and other studies which did not find significant overyielding (Lindén and Agestam, 2003; Drössler et al., 2018; Holmström et al., 2018). However, it is important to note that the *BAI* estimation was carried out using a more precise approach than *IV*, as the diameter increment reconstruction was based on increment core measurements while height reconstruction was done using yield tables. Moreover, common species-specific form factors were used for tree volume calculations. The use of common yield tables and form factors for all sites was a proxy to standardize the comparisons between triplets, as this information was not always available. Although the yield tables employed were developed

Table 6

Observed morphological variation of trees growing in monospecific stands and mixed stands and ratios for comparison between species or stand types (ratio −1).

Tree morphological variation	Scots pine mono		Norway spruce mono		Scots pine mono vs Norway spruce mono		Scots pine mixed		Norway spruce mixed		Scots pine mixed vs Scots pine mono		Norway spruce mixed vs Norway spruce mono		Scots pine mixed vs Norway spruce mixed	
	Mean	SE (±)	Mean	SE (±)	Mean	SE (±)	Mean	SE (±)	Mean	SE (±)	Mean	SE (±)	Mean	SE (±)	Mean	SE (±)
dbh	25.08	0.81	22.79	0.99	**0.11***	**0.05**	27.06	0.76	19.62	0.85	**0.09****	**0.02**	−0.12	0.05	**0.39*****	**0.07**
h	23.37	0.72	22.04	0.81	0.06	0.04	23.92	0.74	19.34	0.67	0.03	0.02	**−0.10***	**0.04**	**0.22****	**0.05**
cl	7.54	0.27	10.55	0.45	**−0.27*****	**0.03**	7.64	0.27	10.91	0.58	0.02	0.03	0.04	0.06	**−0.28*****	**0.04**
cpa	12.62	1.05	11.49	0.91	0.16	0.11	13.55	1.06	10.90	0.81	0.13	0.08	−0.01	0.07	**0.24*****	**0.04**
h/d	0.96	0.02	1.01	0.02	−0.04	0.02	0.92	0.02	1.03	0.03	**−0.05****	**0.01**	0.01	0.02	**−0.10*****	**0.01**
cl/h	0.32	0.01	0.48	0.02	**−0.31*****	**0.03**	0.32	0.02	0.56	0.03	−0.00	0.03	**0.18*****	**0.04**	**−0.41*****	**0.04**
cd/d	0.48	0.03	0.49	0.03	−0.01	0.08	0.48	0.03	0.56	0.04	0.03	0.06	0.13	0.06	**−0.15****	**0.05**
cd^2/d^2	1.13	0.15	1.13	0.11	0.15	0.19	1.12	0.12	1.52	0.78	0.14	0.14	0.31	0.16	**−0.23***	**0.07**

dbh: mean tree diameter at the breast height (cm), *h*: mean total tree height (m), *cl*: mean crown length (m), *cpa*: mean crown projection area per tree (m^2), *h/d*: height vs. diameter relationship (slenderness), *cl/h*: crown length vs height relationship (crown ratio), *cd/d*: crown radii vs stem diameter relationship, cd^2/d^2: crown projection area vs. basal area relationship, *SE*: standard error. Significance levels for variables of both species growing in mixed-species stands: *** p-value < 0.001, ** p-value < 0.01, *p-value < 0.05 (estimates that are statistically significant are given in bold type)

Table 7
Linear models of the relative productivity (IBA and IV in mixed species vs monospecific stands) at the stand and species level as function of changes in structural attributes in mixed stands.

		Structure variable	Intercept			Slope		
			Estimate	SE (±)	p-value	Estimate	SE (±)	p-value
Relative productivity stand level	IBA	$dbhmean_{pi}/dbhmean_{sp}$	1.382	0.272	<0.001	−0.257	0.217	0.251
	IV	$dbhmean_{pi}/dbhmean_{sp}$	1.338	0.218	<0.001	−0.259	0.174	0.155
	IBA	$Hmean_{pi}/Hmean_{sp}$	0.707	0.196	0.002	0.270	0.148	0.084
	IV	$Hmean_{pi}/Hmean_{sp}$	0.901	0.173	0.0001	0.087	0.130	0.513
	IBA	cl_{pi}/cl_{sp}	1.203	0.192	<0.001	−0.195	0.261	0.464
	IV	cl_{pi}/cl_{sp}	1.233	0.151	<0.001	−0.300	0.206	0.163
Relative productivity Scots pine	IBA	$dbhmean_{pi}/dbhmean_{sp}$	1.193	0.368	0.004	−0.099	0.294	0.739
	IV	$dbhmean_{pi}/dbhmean_{sp}$	1.227	0.368	0.004	−0.102	0.294	0.731
	IBA	$Hmean_{pi}/Hmean_{sp}$	0.328	0.217	0.147	**0.564**	**0.163**	**0.003****
	IV	$Hmean_{pi}/Hmean_{sp}$	0.424	0.229	0.080	**0.514**	**0.172**	**0.008****
	IBA	cl_{pi}/cl_{sp}	0.796	0.247	0.005	0.377	0.336	0.277
	IV	cl_{pi}/cl_{sp}	1.030	0.255	0.001	0.096	0.347	0.785
Relative productivity Norway spruce	IBA	$dbhmean_{pi}/dbhmean_{sp}$	1.706	0.461	0.002	−0.496	0.369	0.195
	IV	$dbhmean_{pi}/dbhmean_{sp}$	**1.767**	**0.360**	**<0.001**	**−0.624**	**0.288**	**0.044***
	IBA	$Hmean_{pi}/Hmean_{sp}$	1.067	0.367	0.009	0.017	0.276	0.952
	IV	$Hmean_{pi}/Hmean_{sp}$	1.298	0.298	<0.001	−0.233	0.224	0.312
	IBA	cl_{pi}/cl_{sp}	**1.717**	**0.299**	**<0.001**	**−0.867**	**0.408**	**0.047***
	IV	cl_{pi}/cl_{sp}	**1.596**	**0.240**	**<0.001**	**−0.835**	**0.326**	**0.020***

IBA: periodic annual basal area increment ($m^2\ ha^{-1}\ year^{-1}$), *IV*: periodic annual volume increment ($m^3\ ha^{-1}\ year^{-1}$), $dbhmean_{pi}/dbhmean_{sp}$: ratio of the mean diameter of Scots pine and Norway spruce growing in mixed-species stands, $Hmean_{pi}/Hmean_{sp}$: ratio of the mean height of Scots pine and Norway spruce growing in mixed-species stands, cl_{pi}/cl_{sp}: ratio of the mean crown length of Scots pine and Norway spruce growing in mixed-species stands, *SE*: standard error. Significance levels for parameters: ** p-value < 0.01, * pvalue < 0.05 (estimates that are statistically significant are given in bold type when slope also was).

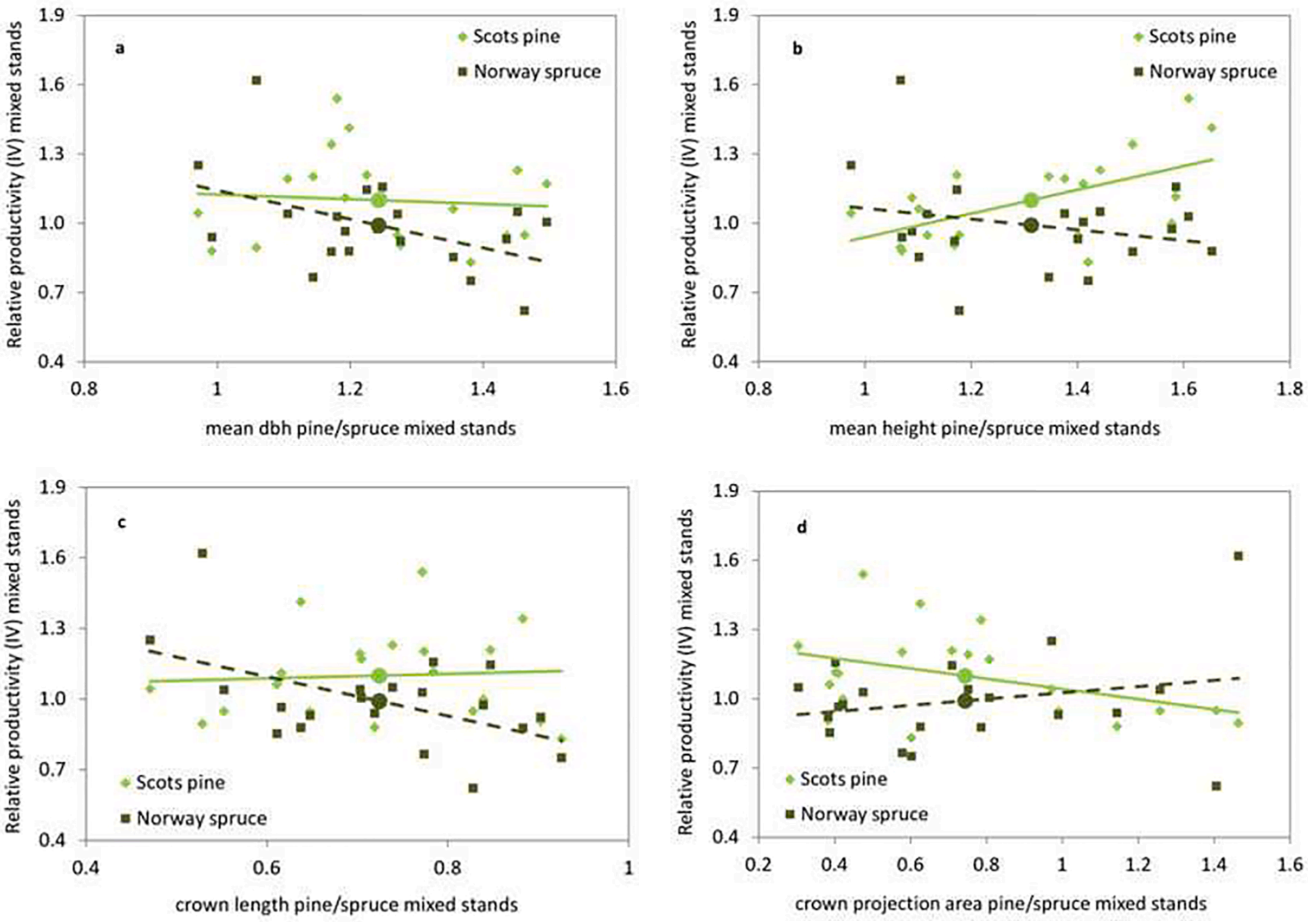

Fig. 4. Relative productivity (IV) by species in the mixed stands related with structural attributes: (a) mean dbh ratio pine/spruce in mixed stands; (b) mean height ratio pine/spruce in mixed stands; (c) crown length ratio pine/spruce in mixed stands; (d) crown projection area ratio pine/spruce in mixed stands. Dotted and dashed lines refer to Scots pine and Norway spruce, respectively. Big dot is showing the mean value.

from long-term plots established at the end of the 19th century in an wide area of Central Europe (from south to north of Germany and Poland), this approach may however increase uncertainty of *IV* results, as tree height and form depend on site conditions, stand density, and species composition (Forrester et al., 2017; del Río et al., 2019). As this regard, a sensitivity analysis using different form factors and yield tables would provide relevant information about the impact of this uncertainty on overyielding results.

Observations in monocultures and mixed-species stands were restricted to stands between 50 and 90 years old in this study, which for those species represent the stem exclusion phase. The rather narrow age range may also compromise the identification of robust trends as the effects and dynamics of species growing in mixtures may not be constant over time (Pretzsch, 2009; Forrester, 2014). At this development stage, spruce is starting to enter the crown space of pine, thus increasing the occupation of the canopy space. This may be associated with the more rapid growth pattern of Scots pine in the young development stages in comparison with Norway spruce, although the opposite tendency may occur in the mature stages, particularly at richer sites, which may result in a productivity increase in mixed stands (Bielak et al., 2014; Wellhausen et al., 2017). Our results based on (at average) 60 years old mixed and monospecific stands, when Scots pine is taller than spruce, are in line with this pattern. Another challenge in this study was that fully stocked stands were sometimes difficult to find as the usual management in most of the Norway spruce and also in some of the Scots pine stands involves regular thinning. Although the studied stands had not been thinned in the last 8–10 years and showed fully stocked conditions, they may represent managed stands which can be below the maximum stand density, as many of them could have been repeatedly thinned in the past. This could influence the estimate of species proportion and therefore affect overyielding results, especially in relation to species relative productivities (Sterba et al., 2014). Moreover, stand density reduction by thinning can weaken spruce-pine species interactions (Houtmeyers and Brunner, 2020), which might result in lower overyielding and therefore trigger some underestimation of overyielding in our study.

Overyielding at stand level showed no relationship with mean annual climate values or site index. One possible reason is that only mean annual climate values were considered in the analysis, while stand growth could be better explained by incorporating soil information and/or using more complex climate indices or some seasonal climatic conditions. For instance, Aldea et al. (2020) identified some effects of seasonal climate values on the tree growth of Scots pine and Norway spruce mixtures with data coming from the same triplets. Regarding other site conditions, Drössler et al. (2018) reported a significant negative effect of latitude on productivity, with pine monocultures having higher growth in northern sites and Norway spruce monocultures having greater productivity in southern sites than mixed-species stands, while mixtures performed better in Central Europe. The lack of any relationship between overyielding and climatic factors or site indices in this study confirms that there is not a common pattern of overyielding variation with site conditions, but may depend on limiting factors and species composition (Forrester, 2014; Pretzsch and Forrester, 2017, pp 183-186).

Complementarity in mixtures of tree species may be associated with changes in the stand structure that improve the capture or use efficiency of resources (Forrester et al., 2013; Riofrío et al., 2017). Lower overyielding or no effect at all may be expected as a general tendency when mixtures comprise species with similar light requirements, rooting profiles or other ecological traits, in comparison with mixtures of species which differ more from each other (Pretzsch and Forrester, 2017). Accordingly, in different pine mixtures neutral effects or even underyielding were found (Aguirre et al., 2018), although other conifer mixtures suggest that even small differences between species can result in overyielding. Forrester et al. (2013) and Toïgo et al. (2015) reported that in mixed stands of Norway spruce and silver fir (*Abies alba* Mill.) both species benefited, although this effect depended on site conditions (expressed by climate and site index, respectively). Riofrío et al. (2017) found overyielding in mixtures of Scots pine-maritime pine (*Pinus pinaster* Ait.) although maritime pine was found to benefit more in terms of volume increment. However, even where there is a neutral effect, one species may be benefited and the other hindered. Based on the results obtained, pine benefited more than Norway spruce, with higher mean stand values of d_q, d_o, *BA* and *V*, and lower slenderness (*h*/*d* ratio) in mixtures than in monocultures, as well as higher *IBA* and *IV* although these were not statistically significant. Norway spruce was not significantly influenced by mixture although this species presented lower mean values of d_q, d_o, h_q, h_o, *BA* and *V* in mixtures than monocultures.

Stand structure and forest dynamics are strongly interdependent (Pretzsch, 2009). This relationship is especially relevant in mixed forests, where tree species morphology adapts to coexisting species and modifies tree growth (Pretzsch, 2014). Our results indicated a significant change in tree allometry for both species, with Scots pine being sturdier in mixed stands, whereas spruce trees are smaller and have larger crowns. These changes result in a slight stratification between species, leading to greater canopy cover (Table 5) with Scots pine occupying the upper layer in most of the sites (Figure Supplementary 3). In some mixtures, overyielding was related to vertical structuring and species stratification (Riofrío et al., 2017; Lu et al., 2018), as different species occupy the canopy layer more effectively and light use efficiency is improved (Forrester et al., 2006). In the studied mixture, there was greater productivity of Scots pine in mixture since this species was favored by its faster early height growth compared to Norway spruce. Currently vertical stratification between the two species can be observed in mixture, although this is reducing as the growth of the spruce increases (Table 7). However, pronounced vertical structure stratification may have a negative effect on Norway spruce, resulting in similar crown lengths of the two species. Species mixing did not result in an increase in density, as reported for other mixtures with a certain degree of stratification (Pretzsch et al., 2015). This suggests that the smaller size of the spruce trees in mixtures is not compensated by a larger number of trees and greater canopy packing in comparison to monospecific stands of Norway spruce.

A more diverse stand structure has been associated with certain benefits in forest functioning, such as greater stability against biotic (Jactel et al., 2017) and abiotic disturbances (Martín-Alcón et al., 2010; Griess and Knoke, 2011), an increase in habitat diversity (e.g., Signorell et al., 2010; Gao et al., 2014), or greater aesthetic value (Schütz, 2002). Norway spruce is among the most susceptible European tree species to storm damage (Gardiner et al., 2010; Wallentin and Nilsson, 2014). The stand structure of Scots pine and Norway spruce in mixtures in comparison to monospecific stands may increase their stability against wind and snow damage as a result of changes in tree allometry and vertical structuring. The lower slenderness of Scots pine and the larger crown ratio of the Norway spruce in mixtures might favor their individual stability, which in turn could increase stand stability (Gardiner et al., 2010). The stratification and greater vertical occupancy of space may help to reduce both wind speed and the amount of snow that piles up on the crowns (del Río et al., 1997; Martín-Alcón et al., 2010).

Mixtures of Norway spruce and Scots pine offer a good alternative to the corresponding monocultures, providing several benefits and no important disadvantages, although various uncertainties have yet to be addressed (Felton et al., 2016). Both species have high economic importance, supplying a large proportion of timber in Europe. Recall that transgressive overyielding can occur despite that one of the species exhibit lower production in the mixture compared to in the monoculture. In addition, their monocultures are subject to increasing risks such as extreme climatic events (Chapin et al., 2007; Albrecht et al., 2012; Zang et al., 2012), pest and pathogen outbreaks (Lindén and Vollbrecht, 2002; Hlásny and Turčáni, 2013; Felton et al., 2016), etc. Although we found that transgressive overyielding occurs in only 35% of the sites, other benefits associated with mixing species can occur. Yield losses due to disturbances could be less frequent in mixtures than in monocultures due to their elastic response and great resilience (Pretzsch, 2009, Bauhus et al., 2017a). The two species seem to respond to extreme drought through different mechanisms; Norway spruce being more limited by high temperatures while water supply may be more important in the case of Scots pine (Kunert, 2020). Similarly, they show different degrees of vulnerability to other increasing abiotic risks (late frost, storms, fires) and are affected by different biotic agents (Wellhausen et al., 2017, and references therein). The more stratified and therefore more stable stand structures found in mixtures in our study, as well as the positive effect expected when mixing two species with different vulnerabilities (Yachi and Loreau, 1999), point to greater stability and resilience in mixed compared with monospecific stands under the scenarios of future global change.

5. Conclusions

The results showed that mixed-species stands of Scots pine and Norway spruce, at the average age of 60 years, did not show significantly higher volume productivity than corresponding monospecific stands and thus mixing effects of both species is nearly neutral and limited to the positive basal area increment. Nevertheless, transgressive overyielding was detected in 35% of the cases, showing that these mixtures can also display an interesting complementary effect.

Scots pine and Norway spruce mixtures present a more complex stand structure than monocultures of the two species. Mixing results in a vertical species stratification that may lead to better light use, Scots pine being the main beneficiary. Moreover, tree allometry changes between mixed and monospecific stands for both species, with higher stratification likely increasing stability at both tree and stand level. These potential benefits of mixed Scots pine and Norway spruce stands should be considered in forest management, and are especially relevant taking into account the broad current and potential distribution of this mixture under global climate change in Europe.

CRediT authorship contribution statement

Ricardo Ruiz-Peinado: Conceptualization, Methodology, Formal analysis, Writing - original draft. **Hans Pretzsch:** Data curation, Methodology, Writing - review & editing. **Magnus Löf:** Data curation, Writing - review & editing. **Michael Heym:** Data curation, Formal analysis, Writing - review & editing. **Kamil Bielak:** Data curation, Writing - review & editing. **Jorge Aldea:** Data curation, Writing - review & editing. **Ignacio Barbeito:** Data curation, Writing - review & editing. **Gediminas Brazaitis:** Data curation, Writing - review & editing. **Lars Drössler:** Data curation, Writing - review & editing. **Kšištof Godvod:** Data curation, Writing - review & editing. **Aksel Granhus:** Data curation, Writing - review & editing. **Stig-Olof Holm:** Data curation, Writing - review & editing. **Aris Jansons:** Data curation, Writing - review & editing. **Ekaterina Makrickienė:** Data curation, Writing - review & editing. **Marek Metslaid:** Data curation, Writing - review & editing. **Sandra Metslaid:** Data curation, Writing - review & editing. **Arne Nothdurft:** Data curation, Writing - review & editing. **Ditlev Otto Juel Reventlow:** Data curation, Writing - review & editing. **Roman Sitko:** Data curation, Writing - review & editing. **Gintarė Stankevičienė:** Data curation, Writing - review & editing. **Miren del Río:** Conceptualization, Methodology, Writing - original draft.

Declaration of Competing Interest

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

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Appendix A. Supplementary material

Figure S1. Relative productivity (*IBA*) at stand level ($RP_{pi,sp}= P_{pi,sp} / \widehat{P}_{pi,sp}$, x-axis) and by species ($RP_{pi,(sp)}= P_{pi,(sp)} / P_{pi}$ for Scots pine or $RP_{(pi),sp}= P_{(pi),sp} / P_{sp}$ for Norway spruce, y-axis) in mixed-species stands. Figure S2. Mean *dbh*, Figure S3. Mean tree height, Figure S4. Mean crown length (*cl*), MeM and Figure S5. Mean crown projection area (*cpa*) for Scots pine and Norway spruce growing in mixed-species stands (diamonds, blue) and monocultures (squares, red). Dashed line is showing the 1:1 line to illustrated equal characteristics for both species. Figure S6. Relative productivity (*IBA*) for the mixed stands related with structural attributes (mean height). Figure S7. *IV* relative productivity for the mixed stands related with mean height. Figure S8. *IV* relative productivity for the mixed stands related with mean *dbh*. Figure S9. *IBA* relative productivity for the mixed stands related with crown length. Figure S10. *IV* relative productivity for the mixed stands related with crown length. Figure S11. *IBA* relative productivity by species in the mixed stands related with structural attributes for mean dbh ratio pine/spruce in mixed stands. Figure S12. For the mean height ratio pine/spruce in mixed stands; Figure S13. For the crown length ratio pine/spruce in mixed stands. Figure S14. For the crown projection area ratio pine/spruce in mixed stands. Dotted and dashed lines refer to Scots pine and Norway spruce, respectively. Big dot is showing the mean value. Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.118834.

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