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Tree species mixing can increase maximum stand density

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9

10 **Abstract:**

11 Mixed species stands are on the advance in Europe. They fulfil many functions better than
12 monocultures. Recent papers show mixed stands can have higher yields, but it remains open
13 whether mixed stands simply grow faster along the same self-thinning lines as pure stands, or
14 have higher maximum stand densities

15 We analysed the effect of species mixing on maximum density based on triplets of pure and
16 mixed stands at approximately maximum density. Most considered mixtures include Norway
17 spruce (*Picea abies*). We show that (i) in mixed stands maximum density is on average by
18 16.5% higher than in neighbouring pure stands, (ii) species mixtures with Norway spruce
19 exceed densities of pure stands by 8.8% on average. For individual species mixtures, we find
20 a significant density effect of +29.1% for Norway spruce mixed with European larch (*Larix*
21 *decidua*), and +35.9% for Scots pine (*Pinus sylvestris*) in association with European beech
22 (*Fagus sylvatica*).

23 No significant links with stand variables like age and mean tree size, and site fertility were
24 found.

The results indicate that species mixing substantially increases stand density indicating a higher carrying capacity caused by a higher supply and use-efficiency of resources. The implications for inventory, silviculture, and forest modelling are discussed.

Key words: maximum stand density; Assmann's yield level; transgressive overdensity; niche complementarity; canopy and root space filling

1 Introduction

The maximum stand density for a tree species on a given site is essential piece of information for assessing site productivity, modelling and predicting stand dynamics, and silvicultural regulation. While site productivity is often characterized by the site index, Assmann (1970, pp 165-172) showed that stands with equal site indexes can vary considerably in maximum stand density depending on the water and nutrients supply. For this phenomenon, he coined the term *yield level*. For example, assessing the yield level for a given site requires information about the maximum stand density, called the *natural stand density* by Assmann. Growth models such as yield tables (Assmann 1970, Assmann and Franz 1965), individual tree models (Pretzsch et al. 2002), or eco-physiological growth models (Grote and Pretzsch 2002) often base their predictions of stand density and mortality on species- and site-specific self-thinning lines that are intended to represent maximum stand density. Silvicultural guidelines such as stand density management diagrams (SDMD) often use maximum stand density as an upper boundary and reference line for regulating different density levels (Bégin et al. 2001, Sterba 1975, 1981, Weetman 2005).

For quantifying stand density, the number of trees per unit area (N, ha^{-1}) is ambiguous as the species of interest may differ in current mean tree size and growing area requirement. Stand

51 basal area (BA, m² ha⁻¹) is potentially more useful. However, Stand Density Index (SDI, ha⁻¹)
 52 is even more informative since it considers both tree number and size (as does basal area),
 53 but is additionally based on allometric theory (Pretzsch 2006, Pretzsch and Biber 2005,
 54 Reineke 1933). Reineke (1933) based SDI on the allometric relationship between a given
 55 number of trees per ha (N ha⁻¹) and the corresponding quadratic mean diameter in cm (d_q).

56 The standard equation for SDI is $SDI = N \times (25/d_q)^{-1.605}$ [1]

57 Recently Pretzsch and Schütze (2015) reported maximum SDI values in pure stands of
 58 Norway spruce (*Picea abies* (L.) H. KARST.), Scots pine (*Pinus silvestris* L.), Douglas-fir
 59 (*Pseudotsuga menziesii* (MIRB.) FRANCO) and European beech (*Fagus sylvatica* L.).
 60 According to their study, intra-specific variation depends mainly on site conditions, indicated
 61 by the site index. However, due to the lack of long-term observations in unmanaged and fully
 62 stocked stands, quantitative knowledge about maximum stand density is particularly poor for
 63 mixed-species stands.

64
 65 When information about stand growth and density of mixed species stands is missing, the
 66 standard approach is to derive it from pure stands by calculating the weighted mean of e.g.
 67 productivity, standing volume or stand density (Río et al. 2015). This is the usual procedure
 68 when forest management planning is based on yield table predictions (Kramer and Akça
 69 1995, Pretzsch et al. 2015a). However, many recently published works found that mixing
 70 may increase stand productivity (Forrester et al. 2006, Piotta 2008, Zhang et al. 2012) as well
 71 as stand density (Pretzsch et al. 2015b, see also Reyes-Hernandez and Comeau 2013).
 72 Several studies address the stand density issue in mixed stands from a conceptual or a
 73 methodological perspective. For quantifying stand density in mixed stands additional stand
 74 characteristics such as the skewness of the diameter distribution (Sterba and Monserud 1993)
 75 or specific wood density (Woodall et al. 2005) might be used.

76

Figure 1 shows a schematic representation of hypotheses of the effect of mixing on maximum stand density based on the $\ln(N)$ - $\ln(d_q)$ relationship. Note, that we show just the main part of the $\ln(N)$ - $\ln(d_q)$ line where its slope only varies slightly around $\alpha \cong -1.6$. This excludes the early development stages before a stand has fully closed and the very late stages with constant final yield (Körner 2002, Oliver and Larson 1996).

The dashed lines in Figure 1, a-c, represent the weighted mean of the maximum stand densities of the respective pure stands, i.e. the maximum stand density expected under the assumption that the mixed stand behaviour results from nothing more than a linear combination of the pure stands' dynamics. In this case, the $\ln(N)$ - $\ln(d_q)$ line observed in a mixed stand would be identical with the expected line, indicating the absence of any true mixing effect in the sense of Forrester and Pretzsch (2015).

Figure 1a assumes that mixing shifts the level of the maximum stand density above (+) or below (-) the expected level; this might be quantified by a modification of the intercept of the $\ln(N)$ - $\ln(d_q)$ line. For example, mixing species that are complementary in terms of light ecology can cause an increase (+), whereas a strong niche overlap may reduce the intercept (-). Figure 1b shows possible resulting patterns, when the positive or negative mixing effect on stand density is negligible in the early stand development phase but becomes more pronounced with proceeding stand development. An increasing positive density effect may result from progressing morphological adaptation to the inter-specific competition, accumulation of nutrient stocks or an enhanced water storage capacity. A continuous negative density effect might result e.g. from decreasing nutrient supply if both species contribute to soil acidification or podsolization (Heinsdorf 1999). Figure 1c shows a combination of both effects displayed in Figures 1a and 1b.

Any such deviation from the linear combination of the the pure stands (dashed line in Figure 1) means that the mixed stands can carry more (+) or fewer (-) trees of a given size per unit area. This would indicate emergent properties due to species mixing and a true mixing effect

with significant consequences for production ecology, prognosis, and silviculture. For the purpose of clarity we assumed straight $\ln(N)$ - $\ln(d_q)$ lines in Figure 1, however, this is not a pre-condition for such comparisons.

In this study we examined nine two-species mixtures, five of them including Norway spruce, by compiling a set of unthinned or just slightly thinned research plots in mixed and pure stands. This analysis aspires to answer the following questions:

- (i) Does the maximum density of mixed stands in general and the maximum density of mixtures including Norway spruce in particular differ from the weighted mean density of neighbouring pure stands?
- (ii) How does the relationship between maximum stand densities of mixed and pure stands depend on the ecological complementarity of the species assemblages?
- (iii) Does the relationship between maximum stand densities of mixed and pure stands depend on stand characteristics such as site conditions and stand development phase?

2 Material and Methods

2.1 Material

The study is based on research plot triplets each comprising two pure stands and one mixed stand, all even-aged and virtually mono-layered. The research plots which were used to compile the triplets come from two different sources. One is the network of long-term experimental plots in Southern Germany, the other is a set of temporary plots, most of them established by members of the COST Action FP1206 EuMIXFOR (see webpage www.mixedforests.eu). and The latter are spread over several European countries (Pretzsch et al. 2015b). Plot sizes range between 0.6 and 0.05 ha.

In order to understand the data structure and the statistical procedures described below, it is important to know that all research plots are organised in superordinate units, the so-called *trials*. All plots belonging to one trial are usually in close vicinity to each other and share the same local site and climate conditions. From all trials we selected only unthinned or slightly thinned plots in order to represent conditions at or close to maximum stand density. From the permanent plot network, which is under survey since 1870 (Pretzsch et al. 2014b), we selected 60 plots from 29 trials, comprising 217 surveys altogether (Table 1). As each plot in the network is completely documented since its establishment, selecting plots and surveys with approximately maximum stand density was a straightforward process.

The temporary plots amounted to 156 plots from 37 trials (Table 1). These trials are originally designed as plot triplets. 30 of these trials comprise 3 plots, 6 trials comprise 9 and 1 trial comprises 12 plots. Trials with more than 3 plots are designed as artificial time series with triplets at different stand ages. As these plots were surveyed only once, the number of available surveys (156) equals the number of plots. According to the management records all of these plots are located in stands which were not or only slightly thinned in the past decade.

When establishing them, selection criteria in the field were absence of stumps and presence of dead standing trees, both indicating approximate maximum stand density. In total, our data material incorporates 373 surveys from 216 plots from 66 trials (Table 1).

This collection of plots was the raw material to form the triplets which are the basis of the study at hand. As only in a few cases the permanent trials were pre-designed as triplets, we carefully checked the records in order to form triplets only from plots with comparable site conditions. This resulted in a set of 26 triplets from long-term plots (Table 2). As one such triplet can comprise more than one survey of the contributing research plots, we called these survey-specific combinations *builds*, which amounted to 87 for the permanent plots.

On the temporary plots there is usually only one build per triplet. However, in the case of the 7 trials representing artificial time series, we treated the whole time series like real time series

155 from long-term plots, thus defining each such time series as one triplet with several builds.
156 This procedure was more appropriate for the subsequent statistical evaluation (see below)
157 because the plots of such an artificial time series cannot be assumed to be perfectly
158 uncorrelated. It yielded 37 triplets with 52 from the temporary plots (Table 2). We formed 2
159 mixed triplets (with 2 builds) in addition; they are made up from temporary and permanent
160 plots. In total, the triplets amount to 65 with 141 builds altogether (Table 2).

161 Our data cover the coniferous tree species Norway spruce (*Picea abies* [L.] H. KARST.), silver
162 fir (*Abies alba* MILL.), Scots pine (*Pinus silvestris* L.), European larch (*Larix decidua* MILL.),
163 and Douglas-fir (*Pseudotsuga menziesii* [MIRB.] FRANCO), and the deciduous species
164 European beech (*Fagus sylvatica* L.), sessile oak (*Quercus petraea* [MATT.] LIEBL.), and
165 black alder (*Alnus glutinosa* [L.] GAERTN.).

166 The nine species combinations covered by our triplets are Norway spruce – silver fir (called
167 “spruce-fir” in the further text for better readability), Norway spruce – Scots pine (“spruce-
168 pine”), Norway spruce – European larch (“spruce-larch”), Norway-spruce – European beech
169 (“spruce-beech”), Norway spruce – black alder (“spruce-alder”), Scots pine – European beech
170 (“pine-beech”), European larch – European beech (“larch-beech”), European beech – sessile
171 oak (“beech-oak”), European beech – Douglas-fir (“beech-douglas”). Best represented are
172 spruce-beech with 15 triplets containing 52 builds, pine-beech (17 triplets, 17 builds), beech-
173 oak (5 triplets, 24 builds), and beech-douglas with 8 triplets and 19 builds (Table 3).

174 In general, as we were careful to form and only triplets with all plots having similar site
175 conditions, the total resulting number of 65 triplets was rather low. However, as such sets of
176 unthinned or just slightly thinned, fully stocked pure and mixed stands are rather rare to our
177 knowledge, we think they form a unique dataset for our questions of interest..

178 The triplets are concentrated in Southern Germany but also include other parts of Central
179 Europe. They range from -3.172° to 23.351° E-longitude, and from 41.895° to 56.153° N-
180 latitude. Their elevation range is 20 and 1715 m a.s.l., mean annual temperature ranges from

4.0 to 10.5 °C, and the annual precipitation amounts to 552-2400 mm a⁻¹, the length of the growing season, defined as the number of days per year with a mean temperature of 10° and more, is between 151-213 d a⁻¹ (Table 4). Table 4 also breaks this information down to the single species combinations where it becomes evident that the mixture pine-beech covers by far the widest geographic and climatic gradient. Most frequently, the soils are brown soils and para-brown soils originating from loess, loam, or sandy loam. The rather broad range of site conditions is also represented by the site index, according to appropriate yield tables from the compilation by Schober (1975). For the purpose of this study, we defined the site index as the mean stand height to be expected according to the yield table at an age of 80 years. For the pure stands, where the site index is not possibly influenced by mixing effects, its value ranges between 12.4 m in a European larch stand in the Alps and 52.9 m in a Douglas-fir stand on a fertile lowland site (Table 5). Stand ages cover a range between 25 and 214 years, stem numbers per ha, basal area, and standing volume in pure stands range from 58-5000 ha⁻¹, 8.0-113.7 m² ha⁻¹, and 35-2071 m³ ha⁻¹, respectively (Table 5). Note, that in Table 5, which displays this information for each species combination, standing volumes and other area-related stand characteristics for mixed stands refer to one hectare of the total mixed stand and not to each species' share of the area.

2.2 Methods

Although this study deals with two species mixtures, the following methods can be applied analogously to associations of an arbitrary number of species. As our method for quantifying stand density is based on the *SDI* which uses the tree number and quadratic mean diameter of each involved tree species, the methods are restricted to more or less even-aged cohorts. The reason being that the mean diameter is informative only for roughly unimodal diameter distributions.

Extending the SDI concept to mixed stands

As argued in the introduction, the most informative method for quantifying stand density is the Stand Density Index SDI as it considers both tree number and size and is based on allometric theory (Pretzsch 2006, Pretzsch and Biber 2005, Reineke 1933). However for making SDI-values of different species comparable, their specific growing area requirement must be taken into account. Consider two tree species, whose maximum stand densities ($SDIMAX_1, SDIMAX_2$) are known from observations of unmanaged, fully stocked pure stands. This information can be used to calculate equivalence coefficients

$$e_{2 \Rightarrow 1} = SDIMAX_1 / SDIMAX_2 \quad [2]$$

or

$$e_{1 \Rightarrow 2} = SDIMAX_2 / SDIMAX_1 \quad [3]$$

which allow for converting an SDI value of one species into the one of an arbitrarily chosen reference species. Assume we have observed SDI_1 in a stand of species 1. If species 2 is the reference species, the conversion into an equivalent SDI is straightforward:

$$SDI_{1 \Rightarrow 2} = SDI_1 \cdot e_{1 \Rightarrow 2} \quad [4].$$

Analogously, if species 1 is the reference species and we have measured SDI_2 in a stand of species 2, the conversion is

$$SDI_{2 \Rightarrow 1} = SDI_2 \cdot e_{2 \Rightarrow 1} \quad [5]$$

(Río et al. 2015). As our data cover fully stocked stands of nine different Central European tree species, we used the species specific median SDIMAX for calculating general equivalence coefficients which are presented in Table 6. Although we didn't need to use these generic coefficients in the study at hand (see below), we provide them here as they might be useful for some readers in their work. Species specific growing area requirements become

evident in this overview. For example almost all equivalence coefficients for converting Douglas-fir SDIs into other species are considerably below one, while they are very high for sessile oak, often even greater than 2 (Table 6).

Eliminating species specific growing space requirements from the SDI as shown above is not only a key to species-independent stand density comparisons, but also to calculating the area proportions of the different species in a mixed stand (Dimberger & Sterba 2014, Huber et al. 2014, Sterba et al. 2014). While the equivalence coefficients given in Table 6 are useful in this context if no pure stands at maximum density are available, our data allowed us an even more precise approach. As the analysis at hand is based on complete triplets in stands close to maximum density, we were able to calculate and to apply specific equivalence coefficients for each build of each triplet. Let, for a given build of such a triplet, $SDIMAX_{1,2}$ be the SDI of a mixed stand of species 1 and 2, converted to reference species 1. Consequently, if $SDIMAX_{1,(2)}$ and $SDIMAX_{(1),2}$ are the SDIs of species 1 and species 2, respectively, in the mixed stand, $SDIMAX_{1,2}$ results from

$$SDIMAX_{1,2} = SDIMAX_{1,(2)} + SDIMAX_{(1),2} \cdot SDIMAX_1 / SDIMAX_2 \quad [6]$$

with $SDIMAX_1$ and $SDIMAX_2$ being the species-specific SDIs from both pure stands from the same build in the same triplet. This enables us to calculate meaningful mixing proportions m_1 and m_2 for species 1 and species 2, respectively, in the mixed stand:

$$m_1 = SDIMAX_{1,(2)} / SDIMAX_{1,2} \quad [7]$$

$$m_2 = SDIMAX_{(1),2} \cdot SDIMAX_1 / SDIMAX_2 / SDIMAX_{1,2} \quad [8]$$

Obviously, choosing species 2 as the reference species would result in the same values for m_1 and m_2 .

These mixing proportions enable us to calculate $\hat{SDI}_{1,2}$, which is the mixed stand's SDI that would be expected if, biologically, the mixed stand's density would be a mere proportional combination, i.e. a weighted sum of both pure stand densities SDI_1 and SDI_2 :

$$\hat{SDI}_{1,2} = m_1 \times SDI_1 + m_2 \times SDI_2 \quad [9]$$

This expected $\hat{SDI}_{1,2}$ can be compared to the actual mixed stand's density $SDI_{1,2}$. If $SDI_{1,2}$ significantly deviates from $\hat{SDI}_{1,2}$, we identify the density effect as an emergent property of the mixture, whereby $SDI_{1,2} > \hat{SDI}_{1,2}$ and $SDI_{1,2} < \hat{SDI}_{1,2}$ indicate a density-increasing and a density-lowering mixture effect, respectively.

Quantifying site quality

A species-specific site index, which is the most straightforward measure of site quality, was obtained by applying appropriate yield tables from the compilation of Schober (1975). For the purpose of this study we defined the site index as the mean stand height at the age of 80 years given by the yield table as a function of the actual mean stand height and age. The reference age of 80 was chosen because, considering the whole data material, this required the least number of extrapolations beyond recorded stand ages.

This site index is a good integrative measure for comparing site quality as long as there is only one species involved. An interspecific comparison is problematic, because tree species differ considerably in their typical site-dependent age-height relationship. In order to overcome this difficulty, we designed a standardized site index $SISDT$ which is centered around a value of 1, which in turn should indicate typical site conditions for the species of interest. Values greater and smaller than 1 indicate better and inferior site conditions, respectively. For obtaining $SISDT$, we first calculated the species-wise median of the site

index at age 80 of each pure stand. Mixed stands were excluded, because due to mixing effects the explanatory power of the site index may be compromised. By dividing each actual site index by the corresponding species' median, we obtained $SISDT$. For expressing the site quality on the level of a given build of a given triplet, we took the average $SISDT$ of both pure stands.

Besides the site index and deduced information like $SISDT$, other more direct data about site conditions were available for all triplets. Most important were mean annual temperature T (°C) and precipitation P (mm/a) for which records of the last three decades were available.. This made it possible to calculate the aridity index M after de Martonne (1926) which results from

$$M = P / (T + 10) \quad [10].$$

The higher the Martonne index, the better the water supply for plant growth; the lower this index, the stronger the likelihood of drought. This index has been widely used in recent studies to describe the drought condition or aridity in a given region (Quan et al. 2013). As a recent study by Pretzsch et al. (2014a) shows, the length of the annual growing season LGS , defined as the number of days per year with a mean temperature $> 10^{\circ}\text{C}$, is another key driving force for forest growth. We were able to estimate LGS for each plot in each triplet using

$$LGS = 343.2 - 2.5268 \cdot \text{latitude} - 0.5312 \cdot \text{longitude} - 0.0402 \cdot \text{altitude} \quad [11]$$

(Rötzer and Chmielewski 2001) with latitude and longitude being northern latitude and eastern longitude in degrees, and altitude being the plot's elevation above sea level.

Statistical evaluation

All statistical evaluations in this paper ask for systematic density deviations between mixed and pure forest stands. All of them can be integrated into one general linear mixed regression model structure:

$$DENSR_{ij} = \beta_0 + \beta_1 \cdot X_{1ij} + \dots + \beta_{nij} \cdot X_{nij} + tr_i + pa_k + pa_{kl} + pb_p + pb_{pq} + m_s + m_{st} + \varepsilon_{ij} \quad [12]$$

DENSR is a variable that compares the actual density of a mixed stand in a triplet with the mixed stand density that would be expected from the mere combination of both pure stands. We calculated it as

$$DENSR = \frac{SDI_{1,2}}{\hat{SDI}_{1,2}} - 1 \quad [13].$$

DENSR can be meaningfully tested against zero, where a value greater or smaller than zero indicates a higher density in mixed stands or in pure stands, respectively. The variables $X_1, \dots, X_n$ are explanatory variables like site index, water supply, mean annual temperature, precipitation, length of the growing season, and de Martonne's aridity index, or indicators for a stand's development stage like age, height, and mean diameter. Thus, the variables $\beta_0, \beta_1, \dots, \beta_n$ are the fixed effects parameters. The indexes i and j represent a triplet and a build inside a triplet.

The random effect structure of the model is somewhat complicated because in order to account for the data structure having several builds inside many triplets. As each build inside a triplet represents another temporal realization of the superordinate triplet, we introduced a random effect on triplet level in order to cover the correlation among the builds inside a given triplet. This also accounts for the few triplets formed from artificial time series, where the builds cannot be assumed to be fully uncorrelated. In addition there are, in some rare cases, overlaps between different triplets, i.e. two triplets might share one of the contributing stands.

This possible correlation was taken into account by including random effects connected to the trials and plots contributing to a triplet. In detail, $tr_i \sim N(0, \tau_1^2)$, is the random effect on triplet level. Random effects concerning the first pure stand of a triplet are $pa_k \sim N(0, \tau_2^2)$ on trial level, and $pa_{kl} \sim N(0, \tau_3^2)$ on plot-in-trial level. Analogously, $pb_p \sim N(0, \tau_4^2)$ and $pb_{pq} \sim N(0, \tau_5^2)$ represent trial and plot-in-trial level for the second pure stand. Note that for all triplets covering a given species combination the pure stands of the same species were always coded as the first and the second pure stand, e.g. for the mixture of spruce and beech the pure spruce stands were always pure stand #1 and the pure beech stands were always pure stand #2. Finally, $m_s \sim N(0, \tau_6^2)$ and $m_{st} \sim N(0, \tau_7^2)$ represent trial and plot-in-trial level for a given triplet's mixed stand. The i.i.d residual errors are denoted as ε_{ij} .

When fitting the model, there was no case when the full set of these random effects needed to be kept. The decision about which random effects were omitted was made by AIC comparisons in every single case.

Note that for research questions i and ii, as formulated in the introduction, no explanatory variables X were included into the model. Thus, the estimate and the significance of the intercept β_0 tell us directly if a mixed stand effect can be statistically confirmed and how strong it is. E.g. $\beta_0 = 0.10$ and $\beta_0 = -0.15$ and would indicate an expectation of 10% higher and 15% lower stand density in mixed stands compared to pure stands, respectively.

For all evaluations we used the statistical software R (R Core Team 2015), especially the packages lme4 (Bates et al. 2014) and lmerTest (Kuznetsova et al. 2015). More details about mixed models can be taken from Zuur et al. (2009).

3 Results

353

354 Figure 2 shows for all species combinations (top left) and for the nine species assemblages
 355 separately how the observed *SDI* of the mixed stands (ordinate) deviates from the expected
 356 *SDI* (abscissa) that results from the area-proportion weighted *SDI*-sum of both pure stands in
 357 each triplet. The most frequent species association in our data is Norway spruce - European
 358 beech with $n = 52$, followed by the association European beech – sessile/pedunculate oak with
 359 $n = 24$ (see also Table 5). The mixtures spruce–alder ($n = 3$) and larch–beech ($n = 1$) are
 360 hardly represented in our data. Although they cannot be meaningfully analysed for
 361 themselves, we included them in our overarching analyses. For almost all mixtures the point
 362 cloud's center of gravity is located above the bisector line, i.e., it suggests that, on average,
 363 stand density tends to be higher in mixed compared with pure stands. Species with strong
 364 complementary in light ecology such as the combination of spruce-pine, spruce-larch, and
 365 pine-beech seem to result in higher over-density compared with combinations of ecologically
 366 more similar species.

367

368 Before we continue with describing the statistical results in detail we would like to point out
 369 that the fit results of each regression model (according to Equation 1) we present in this study
 370 are compiled in Table 7. From a technical point of view it is interesting to see that the random
 371 effects common to most models were connected with the mixed stand in each triplet on trial
 372 level and on plot level (random effects m_s and m_{st} in Equation 12). Only in a few cases do
 373 we observe noteworthy random variation with the first pure stand in a triplet (pa_k , pa_{kl} in
 374 Equation 12) at the triplet level itself (tr_i). In no case was the inclusion of random effects due
 375 to the second pure stand (pb_p , pb_{pq}) necessary.

376

3.1 Mixture effect on stand density in general and for species associations with Norway spruce

In order to test for significant *SDI* deviations in mixed from pure stands (research question i) we used the statistical model according to Equation 12 without including any explanatory variable *X*. Thus, the estimated value of the parameter β_0 represents the expected relative deviation *DENSR* (see Equation 13). If β_0 differs significantly from 0, we can assume a true species mixing effect on stand density at full stocking. Despite a large variance in *DENSR*, our analyses show that over all species associations there is a mean superiority of the mixed stands amounting to 16.5 % ($\beta_0 = 0.165$, $p < 0.001$, Figure 3 left, Table 7). Taking into account only the species associations containing Norway spruce, this superiority is at 8.8 % only, but still significant ($\beta_0 = 0.088$, $p < 0.05$, Figure 3 right, Table 7).

3.2 Mixture effect on stand density for single species associations

We also fitted the same model separately to the data for each single species association, except for larch-beech, where there was only one observation available. This analysis is related to research question ii. As can be taken from Figure 4, the relative density gain is always greater than zero (without considering larch-beech; note that the spruce-alder result comes from one triplet only); in the cases of spruce-larch and pine-beech it is significantly so with mixture-induced density gains of about 29 % and 36 % ($\beta_0 = 0.291$, $p < 0.01$, and $\beta_0 = 0.359$, $p < 0.001$, respectively, Table 7). Both significant effects are observed in species associations with a highly shade tolerant species (European beech) or an intermediately shade tolerant species (Norway spruce) mixed with a very light demanding species (European larch, Scots pine).

3.3 Mixture effect on density in connection with stand development and site quality

Although we examined several variables describing stand development stage (stand age, mean tree height, mean diameter, dominant height, dominant diameter) as predictor variables X in Equation 12, none of them showed even a weak significant effect on $DENSR$. Exemplary, we show the non-significant age-effect in Figure 5 (see also Table 7), where stand age as predictor variable was used untransformed for all species mixtures (left) and as its natural logarithm for all mixtures containing Norway spruce (right).

In the same way, we also couldn't detect any significant effect of site quality, regardless whether it was included as a climate variable (precipitation, temperature, aridity index, length of the growing season) or expressed through a site index. In Figure 6 (see also Table 7) we show this by example of a model which used the standardized site index $SDISTD$ (see methods section) for each build of a triplet.

4 Discussion

Species mixing as a cause for increased stand density

Many studies show that tree species mixing can significantly increase the stand productivity in terms of stem volume growth (Forrester et al. 2006, Piotta 2008, Pretzsch et al. 2010, 2013, 2015b, Zhang et al. 2012). In general, the stand volume growth results mainly from height growth (vertical component) and stand basal area growth (horizontal component), while changes of the stem form factor play a minor role as they occur rather slowly (Assmann 1970, p 165-167). Several studies provided evidence that mixing can significantly increase basal

area growth (Hein and Dhôte 2006, Pretzsch et al. 2015b). For the current state of knowledge about over-yielding in terms of basal area and volume growth in mixed-species stands of Norway spruce and Scots pine, that are also in the focus of this study, see the publication by Drössler et al. (in review) in this special issue.

Our findings show that mixing can also significantly increase the accumulation of remaining stand basal area, which means a reduction of mortality and increase of stand density (Figure 3, cf. Condés & Río 2015).

According to Pretzsch et al. (2015b), mixing hardly increases height growth or the site index; if one species in a mixed stand is inferior, its height growth may even decrease due to interspecific competition for light (Wiedemann 1951, p 131-133). Thus, while leaving the site index rather unaffected, species mixing can significantly increase stand basal area growth and stand density, which is equivalent with an increase of the yield level as defined by Assmann (1970, p 167).

Height growth and site index are primarily determined by *supra-regional* environmental conditions (Kahn 1994) like humidity, temperature, length of the growing season, which can hardly be influenced by mixing. Stand basal area growth, stand density and thereby yield level on different sites with the same site index, are mainly determined by the *local* supply, capture and use efficiency of water and nutrients. Following this line of thought, our results suggest that the local supply, capture and use efficiency of water and nutrients may be strongly modified by species mixing.

Other silvicultural measures such as spacing, thinning, or fertilization mostly accelerate growth but do not increase stand density, as they raise the turn-over, but not the stock of resources (Long et al. 2004). So, the stands develop faster but the tree numbers per unit area at a given mean diameter stay the same. Fertilization may only increase stand density if repeated so often, that the fertilizer is not simply absorbed by the faster growing trees, but can

sustain a higher stock and consequently a higher stand density. Species mixing seems to take effect like a continuous fertilization or irrigation.

Mixed stand density and niche complementary

Growth and yield on low growth sites is probably limited by water and nutrient supply, while growth on high growth sites is rather limited by light. Species assemblages with different and complementary structural and functional traits can induce a more complete use both above and below ground resources (Kelty 1992).

For the species mixtures with significant over-densities as identified before, Figure 7 illustrates this based on the mean diameter-tree number relationship in double logarithmic (left) and linear (right) representation. It can be seen as the empiric counterpart to Figure 1 in terms of how the displayed stem numbers and mean diameters are calculated. For the mixed stands, the stem number is simply the total number of trees per ha, and the mean diameter is the area share weighted mean of both species. For the monospecific stands, stem numbers and mean diameters result from applying the area shares of the corresponding mixed stand (i.e. from the same build in the same triplet) to the stem numbers and mean diameters and which results in a tree number and a mean diameter for a species combination without mixture effects on stand density. Throughout all species assemblages, the self-thinning line of the mixed stands (black) lies above the weighted mean self-thinning line of the two monocultures (grey). The level of the self-thinning line is raised by species mixing whereas the slope remains the same. This underpins that mixing can reduce tree mortality of the total stand so that their self-thinning line can be significantly higher as hypothesized in Figure 1a.

Complementarity in spatial or temporal niche occupation and exploitation may be relevant at the very beginning of stand development, and the role of the associated tree species may also change during the ongoing development. For example early-successional pioneer species may

be above late-succession species first, but below them in more advanced stages of stand development.

Four species included in this study, Scots pine, European larch, black alder, and sessile oak are light demanding and belong to the early-successional group. European beech and silver fir are shade tolerant late-succession species. Our analyses revealed a strong positive mixture effect for the species association pine-beech which is a classic combination of an early-successional and a late-successional species (Figure 4). For species assemblages with more similar ecological traits like beech-douglas and spruce-beech we cannot substantiate significant density effects due to mixing (Figure 4).

Norway spruce is somehow intermediate concerning growth dynamics, height dominance and shade tolerance. When mixed with light demanding, fast growing but early culminating species, Norway spruce often occupies the lower canopy space in the earlier phases of stand development but enters the upper canopy later. For one of these mixtures, spruce-larch, we can demonstrate a very pronounced positive density effect of mixture, whereas there is a weaker tendency for spruce-pine only, which cannot be corroborated statistically. When mixed with shade tolerant and late culminating species, Norway spruce may be ahead in the first part and be caught up by the admixed species in height growth in the second part. However, for both such mixtures, spruce-fir and spruce-beech, we cannot substantiate a significant density effect.

In both types of mixture (with early-successional and late-successional species) Norway spruce increases the vertical structure of the canopy space, either by extending it because of higher shade tolerance in the lower canopy space or by extending it due to faster height growth. Although this could only partly be shown on the level of single species associations, the combined analysis of all associations including Norway spruce reveals an effect which seems plausible given the considerations above: Species assemblages with Norway spruce tend towards positive mixture effects on density but mixtures with this species do not achieve

the high levels of over-density shown for combinations of other complementary species (Figure 3).

Niche complementary as described above is not limited to above ground space occupied by a forest stand. Species may also access below ground resources in a complementary way. For example, consider sandy soils impoverished by repeated cultivation of pure Scots pine or Norway spruce stands as described for instance by Heinsdorf (1999) and already Wiedemann (1923). Introducing European beech or other broadleaved species as additional species in such stands is believed to have positive effects on the litter decomposition (Augusto et al. 2002), humus type (Block 1997), as well as on soil penetration by roots, nutrient supply and water storage capacity (Rothe 1997). This may finally results in an increase in growth of mixed versus pure stands (Heinsdorf 1999, von Mammen et al. 2003). The stand-level combination of structurally and chemically contrasting litter types may, in the long term, improve fertility and resource storage capacity of soils (carbon, water and nutrients), perhaps mediated through stimulated bioturbation (Augusto et al. 2002, 2015, Heinsdorf 1999, Rothe and Binkley 2001).

Effect of site conditions and stand age

We expected that over-density would be higher on poor sites and become more distinct with increasing stand age. On poor sites, the benefit of niche complementary in terms of nutrient supply might be stronger than on rich sites. However, we found no significant relationship between site conditions and density effect. With progressing stand development, mixing effects on stand density may result from increasing morphological adaptations to the inter-specific environment and/or the above-mentioned continuous improvement of the soil fertility. However, we also found no significant change in over-density with progressing stand development (Figures 5, 6).

These results highlight the complexity of species interactions. Competition, complementarity, and facilitation depend on many factors such as stand developmental stage, stand density, and site conditions (Forrester 2014), and possibly also interactions among these factors that require further studies (Pretzsch et al. 2015b) .

Methodological considerations

This study is based on permanently and temporally established sets of fully stocked pure and neighbouring mixed-species stands that represent maximum or at least approximately maximum stand density. Such unthinned or just moderately thinned experiments with pure and mixed plots of comparable site conditions are essential for revealing any true effects of tree species mixing on the maximum stand density.

Studies based on long-term experiments regulated at different stand density levels below the maximum carrying capacity (e.g. Amoroso and Turnblom 2006, Forrester et al. 2006) provide valuable insight into the relationship between stand density and productivity (cf. Assmann 1970, pp 227-235, Pretzsch 2005, Zeide 2001, 2002). However, if mixed-species experiments do not include unthinned and fully stocked treatment variants, they cannot provide evidence of mixing effects on the carrying capacity. i.e. maximum stand density, because the sought-after effects are at least partly “thinned away”.

Studies based on forest inventory plots (Condés et al. 2013, Vallet and Pérot 2011) may cover a certain portion of fully stocked pure and mixed-species stands. However, if the stand history is unknown, it remains open which plots are really at maximum stand density. If pure and mixed stands differ in site conditions, site and mixing effects may be confounded. In addition, there might also be unknown provenance differences which add to the uncertainties.

Using unthinned and just slightly thinned plots of permanently or temporally established experiments, and ensuring comparable site conditions of the combined pure and mixed stands,

and knowing the history of the included stands we were able to exclude the most important confounding factors that might have impaired our results. Especially the maximum densities of the pure stands, which are of critical importance in this study, could be directly taken from each build of each triplet, ensuring avoidance of improper generalisations as far as possible. However, compiling the triplet collection used in this study, especially the post-hoc-triplets, required major effort, but still resulted in unbalanced representations among the different mixture types (cf. Figure 4). The range of site conditions, expressed through site indexes (cf. Table 5) is surprisingly broad, at least for the more common species combinations. Nevertheless, overall data supply of comparable pure and mixed stands at or near maximum stand density is only marginally satisfactory.

Consequences for research and forest practice

Long-term mixing experiments that include unthinned or just slightly thinned reference plots in mixed and pure stands as well as variants with different density reductions are of rather unique value. Future mixed-species trials should integrate such fully stocked and unmanaged plots as they can reveal the effect of mixing on maximum stand density and stand productivity. The maximum stand density on the fully stocked and unmanaged plots is a useful reference for keeping the thinned plots of such experiments on defined levels of relative density (e.g., 80, 50, 30 % of the maximum density). This can contribute to answering the essential question how any overyielding or underyielding of mixed-species stands compared with monocultures is modified by different thinning grades (Río et al. 2015).

In addition to the strengthening of the empirical basis, methodological approaches of quantifying stand density in homogeneous as well as in complex stands (Ducey and Knapp 2010; Ducey and Larson 2003), deriving the maximum stand density from experiments and inventory data (Río et al. 2015; Pretzsch et al. 2015b, Sterba 1975), and application of density

measures for regulating the stand density in experiments and forest practice (Bégin et al. 2001; Weetman 2005) are essential.

Growth models that use the concept of maximum stand density for predicting tree mortality should be complemented by mixture effects as revealed in this study in order to predict plausible stand densities.

Knowledge about any increase of maximum stand density by species mixing is relevant for developing useful silvicultural guidelines. If thinning guidelines for mixed stands simply adopt the target curves for stand basal area or tree number developed for pure stands, this may result in suboptimal stand densities and thereby losses in stand productivity.

5 Conclusions

While a series of recently published works quantified the enhancing effect of mixing on stand productivity, we show that mixing can also increase the maximum stand density compared with pure stands with similar site conditions and stand age. That means that mixed stands can carry more trees of a given size. The increase in maximum density compared with pure stands was significant for the full data set and for tree species combinations with complementary ecological traits, but not for more similar species. This finding suggests that especially in assemblages of complementary species the supply, capture, or use efficiency of resources is increased to such an extent that not only the growth rate but also the carrying capacity is continuously higher than in pure stands. The question, which particular resources become more efficiently used and how this depends on site conditions and stand age requires further research. The finding that neither site conditions nor stand age affected the increase in stand density needs further analyses on the grounds of a broader dataset in terms of site conditions and species combinations. Although the particular causes of over-density need further

clarification, their average of 16.5 % and species-dependent range from 8.8 up to 35.9 % calls for attention and consideration in stand inventories, experimental design, growth modelling, and silvicultural guidelines.

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Captions of figures and tables

Figure 1: Hypotheses on the effect of mixing on the maximum stand density in schematic representation based on the $\ln(N)$ - $\ln(dq)$ relationship. The broken line represents the weighted mean of the maximum stand densities of the respective pure stands, i.e. the maximum stand density expected under the assumption that the mixed stand behaviour is the linear combination of the pure stands. Compared with this expected maximum stand density the observed maximum density of the mixed stands may deviate in (a) the level of the $\ln(n)$ - $\ln(d)$ line, i. e., in its intercept, (b) the decline of density with increasing mean size, i. e., the slope of the $\ln(n)$ - $\ln(d)$ line, or (c) both the modification of intercept and slope on the $\ln(n)$ - $\ln(d)$ line.

Figure 2: Observed *SDI* in the mixed stands (*SDI mixed*) vs. expected *SDI* (*SDI mono*) from combining the monospecific (= pure) stands of a triplet. Each grey circle represents one build of a triplet. The black dots show the point clouds' centers of gravity. The grey lines indicate ratios of *SDI mixed* / *SDI mono* of (from top to bottom) 1.4, 1.0, and 0.7. The top left diagram shows all data, all other diagrams display single species combinations.

Figure 3: Boxplot of $DENSR = \frac{SDI_{1,2}}{\hat{SDI}_{1,2}} - 1$ for all species mixtures (left) and all species associations containing Norway spruce (right). In both cases, *DENSR* significantly deviates from 0, i.e. $\beta_0 = +0.165$ (***: $p < 0.001$) and $\beta_0 = +0.088$ (*: $p < 0.05$). Note that one outlier

close to $DENSR = 2$ (from the mixture beech-douglas) has been excluded from the display for the sake of a more appropriate scaling.

Figure 4: Boxplots of $DENSR = \frac{SDI_{1,2}}{\hat{SDI}_{1,2}} - 1$ for all species associations represented in our data. Numbers above the boxes indicate the expected deviation of $DENSR$ from zero. In the cases of spruce-larch and pine-beech these deviations are significant ($\beta_0 = +0.291$ **, $p < 0.01$; $\beta_0 = +0.359$ ***, $p < 0.001$). Note that one outlier close to $DENSR = 2$ (from the mixture beech-douglas) has been excluded from the display for the sake of a more appropriate scaling.

Figure 5: $DENSR = \frac{SDI_{1,2}}{\hat{SDI}_{1,2}} - 1$ plotted over stand age for all species associations (left) and all associations containing Norway spruce (right). Grey circles represent a build of a triplet, grey lines connect subsequent builds of one triplet. Black lines represent model predictions for $DENSR$ dependent on age, which are, however, not significant. Note that one outlier close to $DENSR = 2$ (from the mixture beech-douglas) has been excluded from the display in the left diagram for the sake of a more appropriate scaling.

Figure 6: $DENSR = \frac{SDI_{1,2}}{\hat{SDI}_{1,2}} - 1$ plotted over the standardized site index for all species associations (left) and all associations containing Norway spruce (right). Grey circles represent a build of a triplet, grey lines connect subsequent builds of one triplet. Black lines

represent model predictions for $DENSR$ dependent on age, which are, however, not significant. Note that one outlier close to $DENSR = 2$ (from the mixture beech-douglas) has been excluded from the display in the left diagram for the sake of a more appropriate scaling.

Figure 7: Self thinning in mixed and monospecific stands displayed for the species combinations where significant mixture effects were previously identified. For each build in each triplet we calculated a mean diameter d_q for the mixed and a combination of the two monospecific stands, by weighting the species specific diameters with the species' area shares of the mixed stand. In the same way, we obtained a stem number N per ha for the monospecific stands which represents a combination without mixture effects. The self thinning lines were obtained by fitting mixed linear $\log(N)$ - $\log(d_q)$ -models (random effect on triplet level); they show significant positive deviations of the mixed stands in the same order of magnitude as demonstrated before.

Table 1: Numbers of trials, plots and surveys which were used to compile triplets for the purpose of this study.

Table 2: Numbers of triplets and builds compiled from plots from different sources. The source "combined" means triplets and builds made up from both previously listed sources (permanent plot network, temporary plots).

Table 3: Number of triplets and builds for the investigated species associations. A triplet is a combination of three research plots (one mixed, two pure stands). A build is a combination of given surveys of these plots inside a triplet. Thus, a triplet contains at least one, typically more than one build.

Table 4: Overview of climate and location for all investigated species associations. The length of the growing season is defined as the number of days, where the mean daily temperature was at least 10°C.

Table 5: Stand characteristics grouped by investigated species associations. Note that the area-related stand parameters (stem number, basal area, volume, SDI) of the species in the mixed stands refer to the whole stand area, not to the species' share of the area. The site index was estimated by means of appropriate yield tables assembled by Schober (1975); for the purpose of this study, we defined it as the height of the tree with the quadratic mean diameter at stand age of 80 years from the yield table..

Table 6: Mean equivalence coefficients for converting the SDI from one species to the other. The matrix shows, for all eight tree species included in this study, the equivalence coefficients $e_{1 \Rightarrow 2} = \text{SDIMAX}_2 / \text{SDIMAX}_1$ for transforming the species-specific density of a species 1 (entry via the left column) to species 2 (read off via the upper line). A density of SDI= 900 in a Norway spruce stand is equivalent to a density of SDI = 567 in a European beech stand ($\text{SDI}_{\text{E.be.}} = \text{SDI}_{\text{N.sp.}} \times e_{1 \Rightarrow 2}$) with $e_{1 \Rightarrow 2} = 0.63$.

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969 Table 7: Fit results of all presented mixed linear models. The notation refers to Equation 12.

970 Significant fixed effect parameter estimates are printed in bold. Random effects with no entry

971 for their variance τ^2 were not included in the final model due to AIC comparisons or were not
972 meaningful due to the data structure.

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Figures:

Figure 1

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Figure 2

Figure 3

Figure 4

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Figure 5

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Figure 6

Figure 7

Tables

Table 1

Source	Trials	Plots	Surveys
Permanent Plot Network	29	60	217
Temporary Plots	37	156	156
Sum	66	216	373

Table 2

Source	Triplets	Builds
Permanent Plot Network	26	87
Temporary Plots	37	52
Combined	2	2
Sum	65	141

Table 3

	Spruce- Fir	Spruce- Pine	Spruce- Larch	Spruce- Beech	Spruce- Alder	Pine- Beech	Larch- Beech	Beech- Oak	Beech- Douglas	Sum
Triplets	3	7	8	15	1	17	1	5	8	65
Builds	8	7	10	52	3	17	1	24	19	141

Table 4

Species Association	Mean Annual Temperature [°]			Annual Precipitation [mm]			Height Above Sea Level [m]			Length of the Growing Season [d/a]			Longitude East [°]			Latitude North [°]			Exposition [°]			Slope [°]		
	min	mean	max	min	mean	max	min	mean	max	min	mean	max	min	mean	max	min	mean	max	min	mean	max	min	mean	max
Spruce-Fir	4	5.3	7.5	1170	1790	2400	650	1020	1280	165	176	190	10.144	11.078	11.720	47.398	47.665	47.941	0	90	180	0	10	15
Spruce-Pine	6.7	7.9	9.3	625	711	810	250	401	550	188	197	201	9.079	11.012	12.318	48.567	49.292	50.146	-	-	-	0	0	0
Spruce-Larch	5.5	7.3	10.4	552	917	1100	1245	1503	1715	151	157	167	10.779	12.686	13.639	46.590	46.928	47.097	45	90	180	22	24	26
Spruce-Beech	5.5	7.1	8.7	620	1018	1350	340	614	785	181	189	198	9.930	11.807	13.309	47.867	48.896	51.637	90	248	315	0	5	15
Spruce-Alder	8.4	8.4	8.4	1003	1003	1003	585	585	585	193	193	193	11.036	11.036	11.036	47.938	47.938	47.938	-	-	-	0	0	0
Pine-Beech	6	8.2	10.5	560	760	1175	20	325	1290	179	196	213	-3.172	12.992	23.351	41.895	50.236	56.153	0	80	315	0	4	20
Larch-Beech	6.5	7.3	7.7	900	1000	1200	380	405	435	194	195	196	9.441	9.834	10.519	49.852	50.002	50.197	0	135	225	7	10	12
Beech-Oak	7	7.4	8.5	690	936	1120	340	416	470	193	195	199	9.336	9.604	10.519	49.685	49.865	49.992	0	87	225	0	4	10
Beech-Douglas	7.5	8.3	9.4	651	826	927	330	473	588	192	195	198	6.743	9.871	11.909	48.121	49.179	50.173	125	125	125	0	2	12

Table 5

Species Association	Mixed / Mono	Species	Age [a]			Stem Number [1/ha]			Basal Area [m²/ha]			Volume [m³/ha]			Quadratic Mean Diameter [cm]			Height of the quad. mean diameter [m]			Site Index [m]			SDI [1/ha]		
			min	mean	max	min	mean	max	min	mean	max	min	mean	max	min	mean	max	min	mean	max	min	mean	max	min	mean	max
Spruce-Fir (3 triplets 8 builds)	mixed	Spruce	85	102	122	51	209	410	8.7	31.5	44.9	134	461	674	37.0	44.6	52.1	31.9	34.2	38.7	26.4	30.5	33.8	139	512	769
		Fir	113	123	134	75	179	352	15.0	24.6	38.9	202	346	557	36.4	43.9	55.7	27.7	31.7	36.6	19.4	23.0	26.2	247	406	662
	mono	Spruce	85	106	141	313	471	656	51.4	60.3	74.8	855	929	1118	33.9	41.8	50.5	31.6	35.0	38.8	25.2	31.0	33.9	824	1025	1221
		Fir	110	121	130	195	225	255	36.5	42.6	45.1	498	595	637	42.6	49.3	54.2	31.6	33.2	34.2	24.3	24.7	25.0	601	662	690
Spruce-Pine (7 triplets 7 builds)	mixed	Spruce	60	76	93	608	835	1338	23.0	29.1	38.7	216	341	521	17.6	21.5	26.9	18.4	22.3	26.7	17.9	23.4	27.8	524	627	769
		Pine	60	75	85	239	350	508	17.9	23.3	26.7	231	283	354	25.2	30.0	36.2	23.3	26.8	31.0	22.8	27.9	32.0	336	453	515
	mono	Spruce	60	74	93	635	885	1304	41.6	49.9	60.3	475	650	856	19.4	27.4	33.1	22.3	26.2	29.7	23.8	28.0	32.4	855	974	1098
		Pine	60	70	85	472	926	1558	38.4	45.9	60.3	397	519	721	25.6	29.1	33.7	22.4	25.6	29.2	25.2	27.6	32.6	737	1176	2230
Spruce-Larch (8 triplets 10 builds)	mixed	Spruce	64	100	232	212	644	989	7.9	23.4	36.7	46	230	491	11.8	23.0	46.9	8.0	17.4	29.9	10.6	16.0	23.5	216	485	709
		Larch	65	115	241	146	498	778	26.2	44.5	58.5	186	623	951	20.7	35.4	56.2	15.5	28.5	34.7	17.5	25.9	30.5	536	794	1004
	mono	Spruce	78	114	222	355	771	1908	38.2	51.3	61.9	239	695	935	16.0	31.8	47.1	13.2	25.5	29.4	12.4	21.6	25.8	904	961	1126
		Larch	60	110	213	356	817	1622	35.3	58.0	76.3	241	708	938	16.6	32.3	52.2	15.0	26.6	30.0	15.7	24.5	27.3	841	1073	1347
Spruce-Beech (15 triplets 52 builds)	mixed	Spruce	46	82	136	11	200	526	2.4	21.6	35.6	36	311	581	22.6	40.7	58.4	19.3	31.5	40.9	25.5	31.9	37.0	36	368	639
		Beech	50	91	136	122	340	937	5.3	36.5	49.0	39	236	509	15.0	26.9	49.3	15.9	25.9	35.3	16.1	24.1	32.7	133	327	658
	mono	Spruce	46	81	136	58	519	1287	14.4	43.4	63.2	218	629	1093	18.7	36.3	61.0	17.8	31.1	40.7	25.2	31.9	38.3	217	779	1128
		Beech	50	90	136	154	553	1325	22.2	29.5	50.4	178	420	716	15.6	28.6	53.5	16.8	26.4	38.6	18.6	25.0	33.1	374	577	1029
Spruce-Alder (1 triplet 3 builds)	mixed	Spruce	25	52	85	322	1129	2378	19.8	26.4	31.2	99	264	407	10.3	22.8	35.2	10.8	19.3	27.3	26.3	30.6	33.8	558	575	596
		Alder	27	52	85	407	955	1888	18.1	23.9	33.2	94	236	470	11.1	21.5	32.2	12.6	20.6	28.7	21.9	25.3	28.1	438	521	611
	mono	Spruce	28	51	80	1197	2532	5000	31.6	49.5	64.0	141	495	792	9.0	19.0	26.2	10.3	18.7	24.7	24.7	29.2	33.5	970	1131	1291
		Alder	33	54	85	498	1170	1594	32.5	44.9	55.3	254	483	607	17.0	26.4	34.9	17.1	22.5	26.7	25.3	27.0	29.5	851	1114	1632

Table 5 cont.

Species Association	Mixed / Mono	Species	Age [a]			Stem Number [1/ha]			Basal Area [m ² /ha]			Volume [m ³ /ha]			Quadratic Mean Diameter [cm]			Height of the quad. mean diameter [m]			Site Index [m]			SDI [1/ha]		
			min	mean	max	min	mean	max	min	mean	max	min	mean	max	min	mean	max	min	mean	max	min	mean	max	min	mean	max
Pine-Beech (17 triplets 17 builds)	mixed	Pine	39	74	149	50	425	1529	7.3	25.6	43.5	78	293	658	15.6	32.6	70.1	17.3	24.7	33.2	16.4	27.4	33.9	143	484	838
		Beech	39	74	149	125	611	1733	4.2	17.9	36.8	45	208	392	11.2	22.0	29.4	12.7	22.6	30.0	11.8	26.4	35.0	93	398	884
	mono	Pine	39	74	149	82	747	2054	8.3	35.5	53.6	97	383	671	16.8	29.2	45.5	16.0	24.0	33.9	14.7	26.7	33.3	155	713	1188
		Beech	39	74	149	220	962	2542	10.7	29.8	43.0	135	360	577	12.7	24.0	40.4	13.7	23.8	33.0	17.4	27.5	35.9	219	640	1034
Larch-Beech (1 triplet 1 build)	mixed	Larch	66	66	66	98	98	98	7.9	7.9	7.9	91	91	91	32.1	32.1	32.1	25.8	25.8	25.8	28.4	28.4	28.4	146	146	146
		Beech	66	66	66	293	293	293	15.4	15.4	15.4	182	182	182	25.9	25.9	25.9	23.2	23.2	23.2	27.3	27.3	27.3	310	310	310
	mono	Larch	55	55	55	498	498	498	38.7	38.7	38.7	549	549	549	31.4	31.4	31.4	30.7	30.7	30.7	37.2	37.2	37.2	718	718	718
		Beech	69	69	69	572	572	572	26.1	26.1	26.1	332	332	332	24.1	24.1	24.1	25.1	25.1	25.1	28.3	28.3	28.3	539	539	539
Beech-Oak (5 triplets 24 builds)	mixed	Beech	33	82	116	50	211	651	6.4	11.8	17.7	36	161	257	11.1	31.9	53.0	13.2	25.6	34.8	13.3	26.2	31.9	133	224	319
		Oak	33	82	116	86	276	983	6.2	12.2	27.2	33	158	365	9.2	27.0	42.4	11.5	24.5	32.2	21.5	24.7	27.5	139	246	524
	mono	Beech	33	82	135	128	352	660	9.8	25.5	35.3	68	385	661	14.0	33.3	51.6	15.4	28.2	35.9	18.7	29.1	35.1	260	469	586
		Oak	33	84	132	145	415	1178	8.8	21.3	31.3	47	283	482	10.4	28.8	42.2	11.9	25.0	32.5	21.9	24.9	27.8	254	415	562
Beech-Douglas (8 triplets 19 builds)	mixed	Beech	25	63	120	27	622	1755	4.1	17.2	40.3	18	220	485	7.8	22.6	43.4	7.5	23.3	33.9	15.7	31.2	40.4	65	372	900
		Douglas	25	63	120	35	385	1894	11.1	34.2	83.2	34	490	1184	9.1	50.4	83.2	8.4	33.3	48.6	30.4	41.2	52.0	221	573	1495
	mono	Beech	25	64	120	172	1079	3333	8.0	31.9	47.7	35	421	811	8.7	26.3	53.6	10.9	24.3	39.2	23.3	32.0	43.3	243	670	1146
		Douglas	25	65	120	182	660	2157	22.3	64.1	113.7	110	989	2071	11.5	43.0	74.0	11.8	33.7	50.5	30.7	41.1	52.9	620	1058	1665

Table 6

	Norway spruce	silver fir	Scots pine	European larch	European beech	sessile oak	Douglas-fir	black alder
Norway spruce	1.00	0.78	0.85	1.21	0.63	0.44	1.13	0.99
silver fir	1.29	1.00	1.09	1.56	0.81	0.56	1.45	1.27
Scots pine	1.18	0.92	1.00	1.43	0.74	0.51	1.33	1.16
European larch	0.83	0.64	0.70	1.00	0.52	0.36	0.93	0.82
European beech	1.60	1.24	1.35	1.93	1.00	0.70	1.80	1.58
sessile oak	2.29	1.78	1.94	2.77	1.43	1.00	2.58	2.26
Douglas-fir	0.89	0.69	0.75	1.07	0.56	0.39	1.00	0.88
black alder	1.01	0.79	0.86	1.23	0.63	0.44	1.14	1.00

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Table 7

Model	Fixed Effects					Random Effects						
	Fixed Effect Parameter	Predictor Variable X	Estimate	Std. Error	p	Triplet τ_1^2	First pure stand: Trial τ_2^2	First pure stand: Plot in Trial τ_3^2	Second pure stand: Trial τ_4^2	Second pure stand: Plot in Trial τ_5^2	Mixed stand: Trial τ_6^2	Mixed stand: Plot in Trial τ_7^2
All Mixtures #1 (n = 141)	β_0	-	0.1650	0.0429	0.0003	-	0.0000	0.0540	-	-	0.0321	0.0167
Spruce Mixtures #1 (n = 80)	β_0	-	0.0877	0.0390	0.0337	-	-	-	-	-	0.0195	0.0155
Spruce-Fir (n = 8)	β_0	-	0.0786	0.0738	0.4830	-	-	-	-	-	0.0093	-
Spruce-Pine (n = 7)	β_0	-	0.0889	0.0686	0.2430	-	-	-	-	-	-	-
Spruce-Larch (n = 10)	β_0	-	0.2908	0.0656	0.0028	0.0277	-	-	-	-	-	-
Spruce-Beech (n = 52)	β_0	-	0.0412	0.0639	0.5330	-	-	-	-	-	0.0156	-
Spruce-Alder (n = 3)	β_0	-	0.0446	0.1251	0.7560	-	-	-	-	-	-	-
Pine-Beech (n = 17)	β_0	-	0.3594	0.0606	0.0000	-	-	-	-	-	-	-
Beech-Oak (n = 24)	β_0	-	0.2085	0.1085	0.1320	0.0523	-	-	-	-	-	-
Beech-Douglas (n = 19)	β_0	-	0.1146	0.1500	0.4670	0.0920	-	-	-	-	-	-
All Mixtures #2 (n = 141)	β_0	-	0.1602	0.0637	0.0133	-	0.0000	0.0545	-	-	0.0322	0.0165
	β_1	Age [a]	0.0001	0.0006	0.9198							
Spruce Mixtures #2 (n = 80)	β_0	-	-0.3326	0.2696	0.2210						0.0168	0.0172
	β_1	ln(Age)	0.0964	0.0610	0.1180							
All Mixtures #3 (n = 141)	β_0	-	0.0489	0.1644	0.7670	-	0.0000	0.0573	-	-	0.0337	0.0160
	β_1	Standardized Site Index	0.1145	0.1564	0.4660							
Spruce Mixtures #3 (n = 80)	β_0	-	0.2237	0.1844	0.2320	-	-	-	-	-	0.0212	0.0137
	β_1	Standardized Site Index	-0.0047	0.0061	0.4500							