

Size-structure dynamics of mixed *versus* pure forest stands

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Abstract

Mixed species forests are presently on the advance and widely held to provide many ecosystem functions and services better than pure stands. Recent studies well explored species mixing effects at the individual tree or stand level. However, the link between individual and stand level which is represented by the size-structure dynamics of stands, is still hardly understood.

Aim of this study: The objective was to analyse how species mixing modifies the size-structure dynamics of mixed compared with pure forest stands.

Area of the study: The study was carried out in Southern Germany.

Material and methods: We selected 11 long-term experiments comprising 129 plots of un-thinned or just lightly thinned pure and mixed stands of European beech [*Fagus sylvatica* (L.)] and analysed their size structure dynamics.

Main results: Based on the Gini coefficient, skewness and kurtosis we show how mixing with Norway spruce [*Picea abies* (L.) Karst] and sessile oak [*Quercus petraea* (Matt.) Liebl.] modifies the size-structure dynamics of European beech. The size distribution of beech in mixture mostly lags behind the pure stand, is more size-asymmetric, and the mortality shifts from the smaller diameter classes further to the taller trees than in pure stands.

Research highlights: The revealed changes of the size-structure dynamics of beech in mixed *versus* pure stands result from a modification of both growth partitioning and self-thinning. We draw conclusions of the reduced size growth and size equality of beech in mixed *versus* pure stands for forest management planning and perspectives for forest research.

Key words: species selection effect; true mixing effect; morphological plasticity; size-distribution; growth partitioning between trees; mode of mortality; European beech [*Fagus sylvatica* (L.)]; Norway spruce [*Picea abies* (L.) Karst]; sessile oak [*Quercus petraea* (Matt.) Liebl.].

Introduction

Mixed species forests are presently on the advance as they are widely held to provide many ecosystem functions and services better than pure stands. Recent studies well explored species mixing effects at the individual tree level (Río *et al.*, 2014a,b; Webster & Lorimer, 2003) and at the stand level (Morin *et al.*, 2011; Piotto, 2007). However, the link between indi-

vidual and stand level, the way how species mixing modifies the growth partitioning between the trees in a stand and their size-structure dynamics, is still hardly understood.

Forest dynamics is often conceptualized at stand level by sum and mean values, at the collective level by tree size distributions, or at tree and organ level by the individuals' structure and growth. Each approach reveals special insights, not attainable at the levels abo-

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Abbreviations: D_1 , D_2 (diameter at breast height distribution of species 1 and 2 in a pure stand); $D_{1,2}$ (diameter at breast height distribution of species 1 and 2 in a mixed stand); $D_{1,(2)}$, $D_{1,(2)}$ (common diameter at breast height distribution of species 1 and 2 in the mixed stand); $\hat{D}_{1,2}$ (expected diameter at breast height distribution of the mixed stand as weighted mean of pure stands $\hat{D}_{1,2} = D_1 \times m_1 + D_2 \times m_2$); m_1 , m_2 (mixing proportion of species 1 and 2 in the mixed stand based on the species' portions of the above ground stand biomass); skew (skewness of a size distribution); kurt (kurtosis of a size distribution); GC (Gini coefficient); GC_v (Gini coefficient of tree volume); GC_{iv} (Gini coefficient of tree volume growth); $d_{removal}$ (mean diameter at breast height of the removal trees); d_{remain} (mean diameter at breast height of the remaining trees); d_{rel} (removal-ratio $d_{rel} = d_{removal}/d_{remain}$).

ve or below. This applies in particular for mixed forests stands, which were analyzed mostly at stand level (Morin *et al.*, 2011; Piotta, 2007; Pretzsch *et al.*, 2013) or individual tree level (Pretzsch, 2014; Río *et al.*, 2014; Webster and Lorimer, 2003) so far, but hardly regarding their size-structure dynamics in comparison with pure stands.

The development of the trees in a pure stand or a species in a community can be characterized by their tree size distribution, the growth distributions between the trees, and the mortality (Hara, 1993). In single-cohort pure stands the diameter distribution is narrow and right skewed in the early stage, and becomes more and more symmetric, Gaussian-shaped with progressing stand development (Prodan, 1951, pp: 129-130). Silvicultural treatment cuts mainly the left branch by thinning from below, the right branch by thinning from above, or simply reduces the level of the size distribution by systematic thinning, such as elimination of every n^{th} tree or tree row (Kramer, 1988, pp: 200-203). Shade tolerant species tend towards wider size distributions than light demanding species as a lower light compensation point allows better persistence of small trees in deep shade (Assmann, 1970, pp: 92-98).

Analyses of the state and development of the size distribution of mixed *versus* pure stands may contribute to both forest science and practice, *i.e.*, understanding and management of mixed species stands. The frequency distribution of the stem diameter or other tree characteristics indicate among others the role of each species in the respective community (Coomes & Allen, 2007; Nguyen *et al.*, 2012; Wenk *et al.*, 1990), the size hierarchy and competitive status of admixed species (Preuhsler, 1981; Westphal *et al.*, 2006; Zöhner, 1969), the effect of forest management (Murray & von Gadow, 1991), the heterogeneity of structures and habitats (Zhang *et al.*, 2013; Müller *et al.*, 2013; Pretzsch, 1998), and the assortment yield which determines the technical wood utilization (Buongiorno *et al.*, 1994; von Gadow, 1987; Haight *et al.*, 1985). The temporal change of the size distribution reveals the alien- and self-thinning effect in unmanaged stands (Enquist *et al.*, 2009; West *et al.*, 2009) and the combined effect of silvicultural interference and selective pressure in managed stands (Franz, 1965; Kramer, 1988).

The focus of this analysis is on beech and its interaction with admixed species such as Norway spruce and sessile oak. In Central Europe European beech has an overwhelming competition superiority compared to other native trees species, in particular in its

physiological optimum under mild climatic conditions and on fertile soils which are well supplied with water. On such sites European beech would probably cover more than 2/3 of the Central European forest area (Bohn *et al.*, 2003). However, since human influence on European forests, beech has been severely decimated by clearings for agricultural land or, during the last centuries, by replacing them in the forest by faster and straighter growing conifers such as spruce, fir, or pine species (Mantel, 1961). Presently, beech is strongly on the advance and becoming the pillar of close-to-nature forestry in the central European lowland, where it once dominated (Pretzsch *et al.*, 2010, 2013). There, its cultivation in mixed-species stands elucidates and recalls its high competitiveness. In the long term added species such as oak, pine, or spruce could hardly persist without being supported by tending or thinning.

Behind different size distributions in pure and neighbouring mixed stands may be a simple species 'selection effect' or a 'true mixing effect'. As we are mainly interested in the true mixing effect we use Fig. 1 to illustrate how to distinguish between both. Suppose the tree size distribution of species 1 and 2 in the pure stand are D_1 and D_2 , then the weighted mean of both distributions in case of a 50:50 mixture is $\hat{D}_{1,2}$ (left column from top to bottom). So, if the diameter distribution of a mixed stand of both species would resemble $\hat{D}_{1,2}$, it would of course differ from D_1 and D_2 , but it is simply the weighted mean of both. And as it simply results from the species selection it is called the "selection effect".

Any true mixing effects can be revealed by comparing D_1 of species 1 in the pure stand with the size distribution, $D_{1,(2)}$, of the same species in mixture (top row). In this model example the distribution of species 1 in the mixed stand is ahead of the pure stand but similar in shape. Size development of species 2, $D_{(1),2}$ in mixture is slower and its distribution is wider, more left shallow, and right-steep compared with its distribution D_2 in the pure stand (central row). For both comparisons the size distributions in mixture are scaled up to unit area of 1 hectare by the species' mixing portions (m_1 and m_2); in this example we assume a fifty-fifty mixture. The size superiority of $D_{1,(2)}$ over D_1 and their different shapes reveal true mixing effects.

A true mixing effect also becomes obvious at stand level by considerable differences between the expected distribution $\hat{D}_{1,2} = D_1 \times m_1 + D_2 \times m_2$ (weighted mean of pure stands) and the observed distribution of the mixed stand $D_{1,2}$ (bottom row).

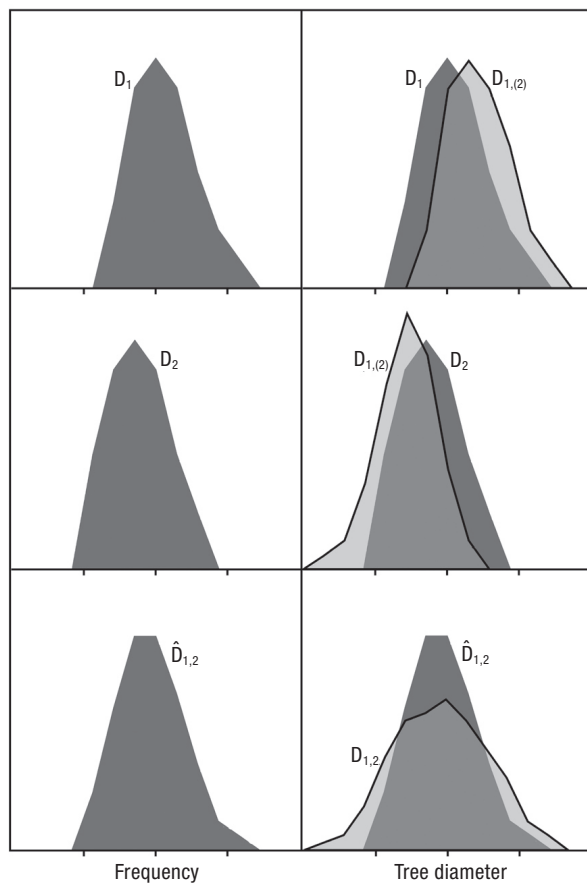


Figure 1. Schematic representation of the comparison between pure and mixed stands' tree diameter distribution and revelation of true mixing effects. At species level size distributions D_1 and D_2 of species in pure stands can be compared with the respective distributions $D_{1,(2)}$ and $D_{(1),2}$ in neighbouring mixed stands (top and centre row). For scrutiny of mixing effect at whole stand level the weighted mean of both pure stand distributions $\hat{D}_{1,2}$ can be compared with the observed whole stand distribution $D_{1,2}$ (bottom row). Differences between the reference distributions (black) and the observed size distribution (grey) indicate inter-specific interactions and true mixing effects.

So far, evidence of changes of the size-structure dynamics in mixed compared with pure stands is very limited as this requires long-term plots of equally treated pure and mixed stands in close neighbourhood. We use such data from pure and mixed plots of long-term experiments in South Germany, with some of them surveyed since more than 100 years, for scrutiny of differences at species level ($D_{1,(2)}$ vs. $D_{(1),2}$ vs. D_2). We analyse (i) how mixing modifies the species specific shape of the tree size-distribution, (ii) how mixing modifies the growth partitioning between the trees compared with the partitioning in neighbouring pure stands, and (iii) whether species mixing

modifies the mode of mortality in terms of size-distribution of the removed trees.

Material and methods

Material

As the focus was on effects of species mixing on the size-structure dynamics of European beech we included only fully stocked or at most moderately thinned stands, as they reflect the best the species specific behaviour. The study is based on more or less even-aged pure and mixed stands. As empirical basis we selected 11 long-term experiments in Germany in pure and mixed stands of European beech and sessile oak and European beech and Norway spruce (Table 1). The experiments MIT 101, ZWI 111, WIE 114, WAB 105 and WAB 106 cover only one stand development phase each. The age series NOR 811, FRE 813, SON 814, ROT 801, SWE 803, and KEH 804 cover pure and mixed stands at various stand development phases. Some of the in total 129 plots were excluded due to their small size, admixture of additional species, or damages by windthrow or bark beetle. Out of in total 129 plots we selected $n = 68$ pairs of beech in mixed and pure stands, $n = 41$ pairs of spruce, and 32 pairs of oak in mixed and pure stands. The dataset represents the growing conditions of a rather broad time span (1905-2012) range of stand ages (31-238 years) and mainly experiments from central and southeast of Germany. Table 1 summarizes basic characteristics of the plots, for more detailed information see Matyssek *et al.* (2012, pp: 243-271) and Pretzsch (2009), Pretzsch *et al.* (2010, 2013) who used the same experiments for analyzing mixing effects at tree and stand level.

Methods

Skewness, kurtosis and other measures for characterizing diameter distributions

For comparing the tree diameter distribution of mixed *versus* pure stands we use measures such as arithmetic mean diameter, minimum and maximum diameter, diameter range (max-min), and standard deviation of the breast height diameter. For analyzing any differences in the shape of the respective distributions we use the skewness

Table 1. Overview of the 11 long-term experiments and 129 plots included in this study. All listed experiments provide plots in pure as well as mixed stands and enable a comparison between the species performance in mixed *versus* pure stand at a given site

Experiments	Species	Plots	Survey		Age (years)	Coordinates		Site characteristics	
			First	Last		E long.	N lat.	Geology	Substrate
MIT 101	Spruce/beech	3	1934	1955	78	12.17	49.95	Basalt	Loam
ZWI 111	Spruce/beech	3	1954	2002	126	13.31	49.07	Gneiss	Loam
WIE 114	Spruce/beech	3	1950	2006	121	10.58	51.64	Schist	Sandy loam
NOR 811	Spruce/beech	15	1997	2008	47-126	11.53	50.35	Graywacke	Sandy loam
FRE 813	Spruce/beech	18	1994	2012	55-168	11.40	48.25	Tertiary	Loam
SON 814	Spruce/beech	24	2000	2011	62-142	10.46	47.52	Moraine	Loam
WAB 105	Oak/beech	3	1951	2007	105	9.87	49.71	Limestone	Loam
WAB 106	Oak/beech	3	1951	2007	116	9.86	49.68	Limestone	Loam
ROT 801	Oak/beech	18	1994	2009	47-238	9.26	49.57	Sandstone	Sand
SWE 803	Oak/beech	18	1995	2005	31-186	10.30	50.26	Keuper	Loam
KEH 804	Oak/beech	21	1996	2008	46-158	11.78	48.93	Marl	Loam

Species: spruce, Norway spruce; beech, European beech, oak, sessile oak; range of stand age: lowest stand age at the first survey and highest stand age at the last survey.

$$\text{skew} = \frac{\sum_{i=1}^n [(x_i - \bar{x})/s]^3}{n}$$

In case of symmetric distribution skew = 0. Suppose an observed diameter distribution is equipped with many small trees and a low number of tall ones it is left-steep (right shallow) and yields skew > 0. If the distribution is equipped with many tall trees but small are rare it is right-steep (left shallow). Skew is useful for characterizing the effect of any kind of thinnings (including self-thinning and alien-thinning in unmanaged stands) on the shape of the distribution.

Furthermore we calculated the kurtosis

$$\text{kurt} = \frac{\sum_{i=1}^n [(x_i - \bar{x})/s]^4}{n} - 3$$

which characterizes the degree of concentration of tree sizes around the mean. If the concentration resembles the Gaussian normal distribution, kurt = 0. Stronger concentrations around the mean (peaked shapes) are indicated by kurt > 0, lower concentrations (shallow shapes) yield kurt < 0. The kurtosis is appropriate for characterizing the degree of restriction of a species by intra- and inter-specific competition.

For the further evaluation it is important to notice that both skewness and kurtosis are invariant to linear transformation, *i.e.*, if the tree diameter distribution of a species occupying a certain portion of the mixed stand is scaled up to 1 ha, the skewness and kurtosis remain unchanged.

Coefficient by Gini and curve by Lorenz for characterizing the size and growth hierarchy

The coefficient by Gini and curve by Lorenz can be used for quantifying the size or growth hierarchy between the trees in forest stands (see de Camino, 1976; Kramer, 1988, p: 82). We use as a loan from economics the Gini coefficient, GC,

$$GC = \frac{\sum_{i=1}^n \sum_{j=1}^n |x_i - x_j|}{2n(n-1) \times \bar{x}}$$

for quantifying the relative distribution of tree volume (GC_v) and volume growth (GC_w), respectively, between the trees in mixed *versus* pure stands. Variables x_i and x_j denote size or growth (or other tree characteristics) for the i'th, respectively the j'th tree in the stand with i = 1...n trees. GC = 0.0 applies for a very homogeneous distribution of the respective tree variable, *e.g.* maximum equality of size or growth distribution. The higher GC, the stronger the inequality of size or growth between the trees (Fig. 2a,b). The curves of the cumulative distributions in Fig. 2b together with the sketched stands reflect the inequality of size which can cause also an inequality of growth.

Application to mixed and pure stands can reveal how mixing modifies the hierarchy between the trees in a population, *e.g.*, whether species mixing can favour the growth distribution towards small understory trees compared with pure stands. The Lorenz curve, known for analysing the inequality of income in hu-

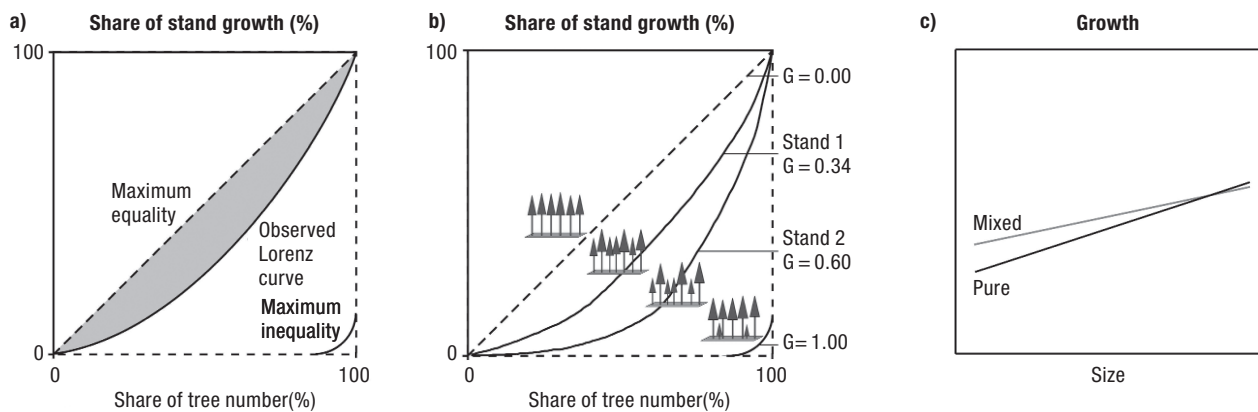


Figure 2. Schematic representation of the growth partitioning in forest stands. (a) Lorenz curve applied for quantifying the degree of equality respectively inequality of size and growth distribution in forest stands. (b) Equal growth distribution and resource partitioning between trees in rather mono-layered stands ($G = 0.00$), increasing inequality in heterogeneous stands (Stand 1, $G = 0.34$; Stand 2 $G = 0.60$), and strong inequality (G approaching 1.0). (c) size-growth relationship for characterizing the symmetry or asymmetry of competition. Here we hypothesize a more size-symmetric growth partitioning in a mixed stand (grey straight line) compared with a pure stand (black straight line).

man populations, can be used for visualizing the inequality of growth in forest stands. The larger the area between the bisector line (maximum equality) and the observed Lorenz curve, the stronger the inequality, and the higher GC. The GC is equivalent to the grey coloured area between the Lorenz curve and the bisector line (grey area in relation to the total area of the square) multiplied by 2 (see Fig. 2a).

Size-growth relationship for quantifying the size symmetry respectively asymmetry

Size growth plotted over size (Fig. 2c) reveals the inter-individual competition and growth partitioning between the trees in a stand (Schwinning & Weiner, 1998; Wichmann, 2001, 2002). A steeper slope indicates a stronger concentration of growth rates and resources on tall trees in the stand. Shallow size growth-size-relationships are assumed to prevail under limitation by below-ground resources (water and mineral nutrients), as they are mobile, diffuse quickly and are difficult to preempt by larger individuals. Strongly increasing size growth-size-relationships mean that larger individuals obtain a disproportionately higher share of resources and growth. This mode of growth-size relationship can be expected on high quality sites, where light is the limiting factor and pre-empted by the larger individuals (Weiner, 1990).

The growth-size slope might be suitable for indication of inter-individual growth allocation patterns and

their dependency on species mixture. In the model example (Fig. 2c) mixing strongly improves the growth of smaller trees, while the taller trees have just small benefits. The differences can be quantified by the intercept a and slope b resulting from fitting the relationship between diameter growth and diameter to a linear model.

Ratio between the diameter of the removal and total stand for characterizing the mode of mortality

Based on the mean tree diameter of the removal stand, d_{removal} , and the remaining stand, d_{remain} , the ratio $d_{\text{rel}} = d_{\text{removal}}/d_{\text{remain}}$ characterizes the size of the removal in relation to the remaining trees (Fig. 3). Notice, that latter is a schematic figure with simplified assumptions of the mean diameter of the remaining and removal trees and of the shape of the distributions. The higher the d_{rel} values the taller are the removed trees in relation to the remaining stand. Thinning from below or self-thinning befalls mainly small trees with $d_{\text{removal}} < d_{\text{remain}}$ and yields ratios of $d_{\text{rel}} < 1$. In case of a schematic thinning the mean size of the removal and remaining trees would be equal, and $d_{\text{rel}} = 1$ (range $d_{\text{rel}} = 0.9-1.1$). Thinning from above means tree elimination from the right side and yields $d_{\text{rel}} > 1$, e.g., selective thinning eliminates 1-2 of the strongest competitors of each future crop tree (range $d_{\text{rel}} = 0.8-1.2$). Comparison between a species d_{rel} in the mixed with the neighbouring pure stand may reveal how mixing superimposes the self-thinning process in the pure

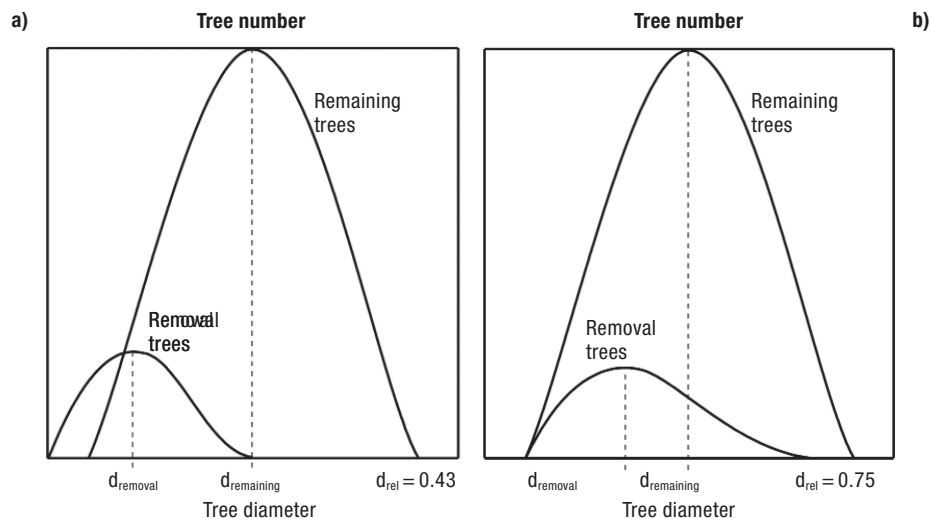


Figure 3. Schematic representation of changes of the removal-ratio $d_{\text{rel}} = d_{\text{removal}}/d_{\text{remaining}}$ by mixing. (a) restriction of the removals to the left side of the diameter distribution in the pure stand yields $d_{\text{rel}} = 0.43$ and (b) extension of the removals to the right side of the diameter distribution resulting in $d_{\text{rel}} = 0.75$.

stand which normally reduces the tree number from the left side of the tree size distribution.

Results

Table 2 gives an overview of the size-structure dynamics in mixed *versus* pure stands. While the scattergrams (Figs. 4-7) reflect the observed size-structure variables and correspond with the arithmetic means in columns “mixed” and “pure” in Table 2, the test for differences is based on the pair-wise ratios mixed/pure given in column “mixed/pure” of Table 2.

Notice, that in the columns “mixed” and “pure” we report the species specific arithmetic means of all n observations within the respective groups. In the column “mixed/pure”, in contrast, we report the mean of the ratio resulting from the pair-wise division of the characteristic of the mixed stand by the respective value of the neighbouring pure stand. The mean of the ratios is not necessarily equal to the ratio of the means. Pair-wise comparison is more informative and in the following used for testing any differences.

Effect of species mixing on tree size-distribution

A species’ frequency distribution in a mixed stand compared with the neighbouring pure stand reveals whether and how the species adapts to mixing by slowing down or accelerating growth (shifts of the mean

size), occupying the dominant or rather subdominant tree classes (changes of skewness), or getting decimated or decimating members of the same or alien species (change of kurtosis).

Fig. 4 reflects how the mean tree volume, v_{mean} , comes off in mixed *versus* pure stands for (a) beech and (b) spruce and oak. Observations (small symbols) close to the bisector line indicate similar behaviour in mixed and pure stands, while deviations indicate true mixing effects. Large symbols indicate mean values. The higher Gini coefficient for tree volume of beech in mixed stands compared with pure stands indicates a more unequal distribution of standing stock in favor of the tall trees (Fig. 5a). GC_v of spruce and oak remain rather unaffected by mixture (Fig. 5b).

Table 2 shows that the mean diameter, d_{mean} , as well as mean tree volume, v_{mean} , of beeches in mixture with spruce or oak are significantly ($p < 0.05$) smaller than in neighbouring pure stands. Norway spruce and sessile oak, in contrast, are about 12-30% ahead in mixed *versus* neighbouring pure stands. Neither skewness nor kurtosis are significantly modified by mixing.

Growth distribution between trees in mixed compared with pure stands

The mode of growth partitioning between the trees of different sizes in a stand determines its size-structure dynamics. For scrutiny whether mixed stands differ in

Table 2. Overview of the differences between mixed and pure stands in terms of size distribution, size-growth relationship, and mode of mortality. The columns “mixed” and “pure” report the species specific arithmetic means of all n observations within the respective groups. The column “mixed/pure”, in contrast, shows the mean of the ratio resulting from the pair-wise division of the characteristic of the mixed stand by the respective value of the neighbouring pure stand. Bold ratios indicate significant ($p < 0.05$) differences between the species behaviour in mixed *versus* pure stands

Variable	European beech			Norway spruce			Sessile oak		
	Mixed	Pure	Mixed/pure	Mixed	Pure	Mixed/pure	Mixed	Pure	Mixed/pure
n	68	68	68	41	41	41	32	32	32
d_{mean} (cm)	26.5	29.1	0.92 ± 0.08	37.2	33.2	1.12 ± 0.03	25.0	24.6	1.03 ± 0.05
v_{mean} (m ³)	0.89	1.05	0.82 ± 0.12	1.08	1.41	1.30 ± 0.08	0.62	0.59	1.13 ± 0.15
d_{min} (cm)	14.6	15.2	1.08 ± 0.14	25.8	21.0	1.27 ± 0.11	17.7	17.0	1.07 ± 0.07
d_{max} (cm)	49.0	43.6	0.96 ± 0.07	49.4	46.4	1.07 ± 0.04	35.9	33.7	1.08 ± 0.06
s_d (cm)	74.7	79.3	1.05 ± 0.10	73.6	64.5	1.17 ± 0.09	46.5	41.5	1.13 ± 0.13
skew	0.362	0.099	0.35 ± 1.35	0.086	0.114	2.44 ± 4.61	0.57	0.33	4.31 ± 2.67
kurt	-0.017	0.144	-3.82 ± 5.06	-0.283	-0.284	1.30 ± 1.33	0.31	-0.25	-12.02 ± 19.78
GC_v	0.18	0.16	1.27 ± 0.15	0.12	0.11	1.11 ± 0.18	0.79	0.47	1.40 ± 0.46
GC_{iv}	0.44	0.39	1.17 ± 0.11	0.35	0.34	1.06 ± 0.16	0.46	0.37	1.17 ± 0.15
a	-0.27	-0.65	0.74 ± 1.10	-2.10	-2.22	0.51 ± 1.00	-0.64	-1.18	-0.65 ± 3.16
b	0.024	0.014	2.02 ± 0.96	1.04	0.02	1.04 ± 0.22	1.28	0.02	1.29 ± 0.78
d_{rel} (cm cm ⁻¹)	0.82	0.73	1.20 ± 0.09	0.75	0.74	1.03 ± 0.10	0.78	0.79	1.0 ± 0.08

Number of stands analyzed, n; arithmetic mean diameter, d_{mean} ; arithmetic mean tree volume, v_{mean} ; minimum and maximum tree diameter, d_{min} respectively d_{max} ; standard deviation of tree diameter, s_d ; skewness and kurtosis of tree diameter distribution, skew respectively kurt; Gini coefficient of tree volume, GC_v ; Gini coefficient of tree volume increment GC_{iv} ; intercept and slope of the id-d-relationship, a respectively b; mode of mortality, $d_{\text{rel}} = d_{\text{removal}}/d_{\text{remaining}}$.

the mode of growth partitioning we use the Gini coefficient for tree volume growth, GC_{iv} , and the intercept a and slope b of the id-d-relationship fitted to a linear model.

Fig. 6 shows the coefficient of Gini, GC_{iv} , for the distribution of tree volume growth in mixed *versus* pure stands for (a) beech and (b) spruce and oak. In ca-

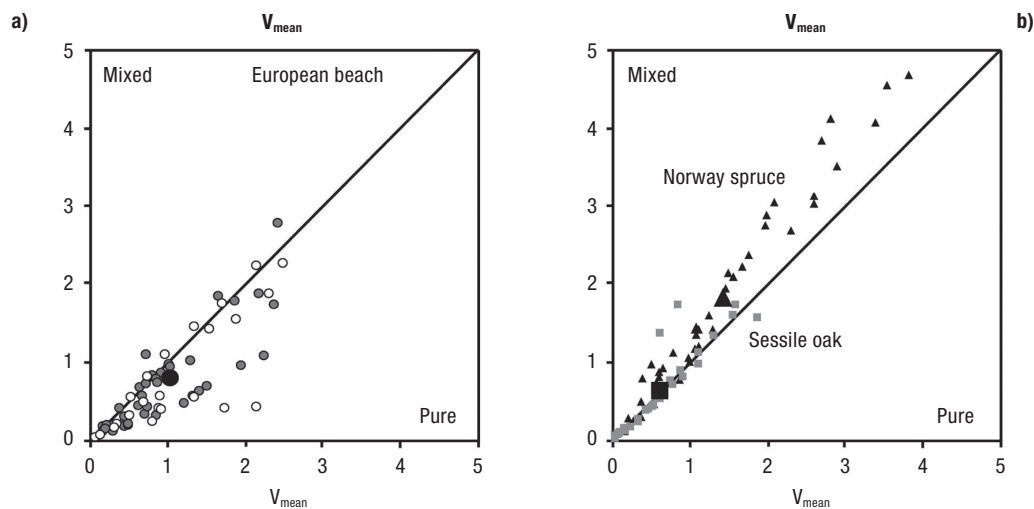


Figure 4. Mean tree volume, v_{mean} , in mixed *versus* pure stands for (a) beech and (b) oak and spruce. Observations close to the bisector line indicate similar behaviour for mixed and pure stands, while deviations indicate true mixing effects. (a) Response of beech to admixture of oak is represented by empty circles, its response to spruce by filled circles. The large black circle indicates the mean relationship for beech in mixed *versus* pure stands. (b) Response of oak to the admixture of beech is represented by rectangles and the response of spruce to beech by triangles. The large black rectangle and triangles indicates the mean relationship for oak respectively spruce in mixed *versus* pure stands.

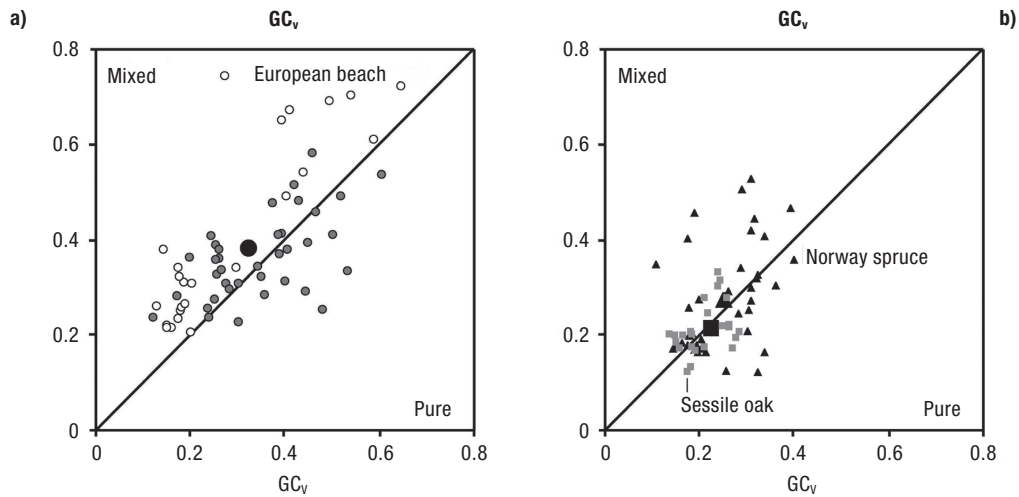


Figure 5. Coefficient of Gini, GC_v , for the distribution of tree volume in mixed *versus* pure stands for (a) beech and (b) oak and spruce. Observations close to the bisector line indicate similar behaviour for mixed and pure stands, while deviations indicate true mixing effects. (a) Response of beech to admixture of oak is represented by empty circles, its response to spruce by filled circles. The large black circle indicates the mean relationship for beech in mixed *versus* pure stands. (b) Response of oak to the admixture of beech is represented by rectangles and the response of spruce to beech by triangles. The large black rectangle and triangles indicates the mean relationship for oak respectively spruce in mixed *versus* pure stands.

se of beech the mean GC_{iv} values lie often above the bisector line, while the corresponding values for spruce and oak remain rather unmodified by mixing.

Table 2 reflects, that both the Gini coefficient and slope of the id-d-relationship indicate a significant increa-

se of the size-asymmetry in mixed *versus* pure stands for beech, *i.e.* an increase of the size hierarchy in mixed compared with pure stands. Except the GC_{iv} value of sessile oak the other species are not significantly modified in their size-structure dynamics by the admixture of beech.

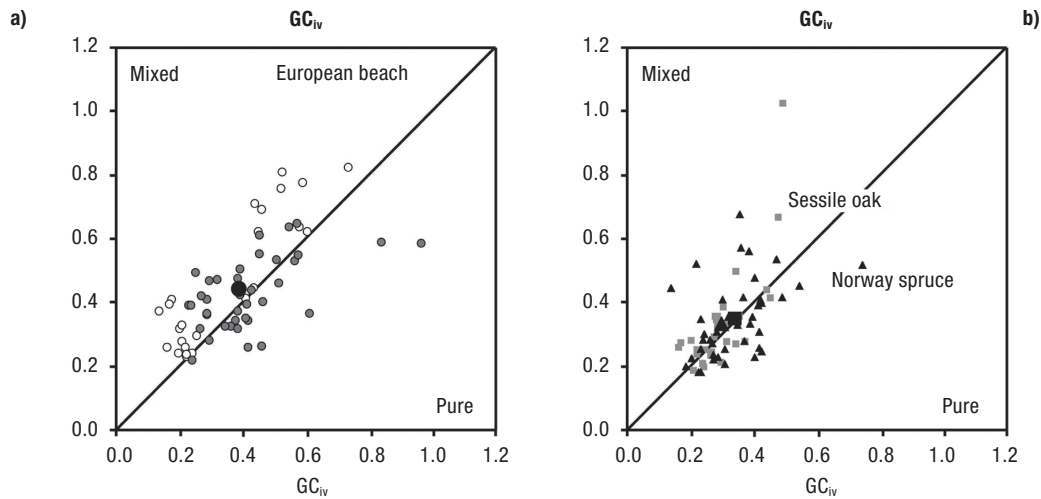


Figure 6. Coefficient of Gini, GC_{iv} , for the distribution of tree volume growth in mixed *versus* pure stands for (a) beech and (b) oak and spruce. Observations close to the bisector line indicate similar behaviour for mixed and pure stands, while deviations indicate true mixing effects. (a) Response of beech to admixture of oak is represented by empty circles, its response to spruce by filled circles. The large black circle indicates the mean relationship for beech in mixed *versus* pure stands. (b) Response of oak to the admixture of beech is represented by rectangles and the response of spruce to beech by triangles. The large black rectangle and triangles indicates the mean relationship for oak respectively spruce in mixed *versus* pure stands.

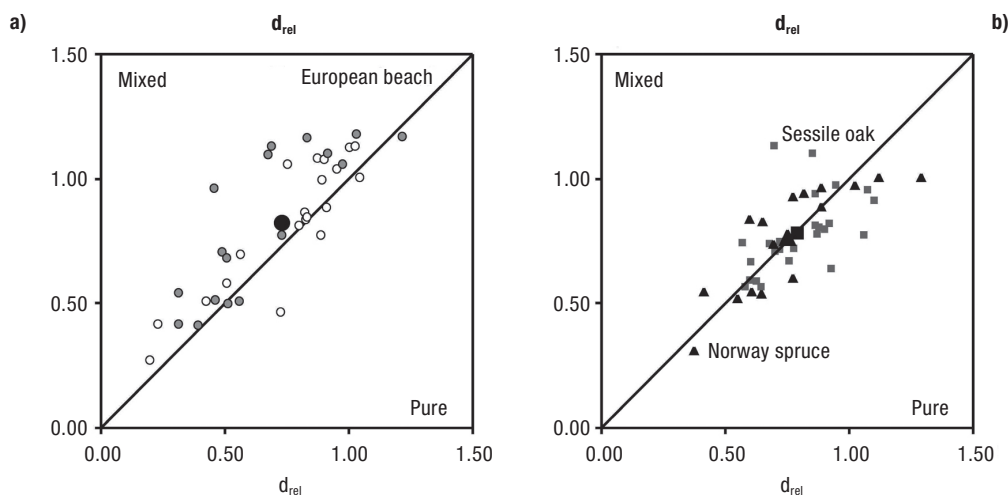


Figure 7. Ratio between the diameter of the removal and remaining stand, d_{rel} , for mixed *versus* pure stands for (a) beech and (b) oak and spruce. Observations close to the bisector line indicate similar behaviour for mixed and pure stands, while deviations indicate true mixing effects. (a) Response of beech to admixture of oak is represented by empty circles, its response to spruce by filled circles. The large black circle indicates the mean relationship for beech in mixed *versus* pure stands. (b) Response of oak to the admixture of beech is represented by rectangles and the response of spruce to beech by triangles. The large black rectangle and triangles indicates the mean relationship for oak respectively spruce in mixed *versus* pure stands.

Mode of tree mortality in mixed versus pure stands

The significantly higher ratio d_{rel} of beech in mixture compared with monocultures (Table 2, Fig. 7a) indicates that the associated tree species exert an alien-thinning effect from above. The mean d_{rel} ratio of the removal beeches in the mixed stand is about 10% higher ($d_{rel} \cong 0.83$ *versus* $d_{rel} \cong 0.73$) than in monoculture, *i.e.*, mortality reaches wider into the right branch of the tree size distribution in mixed stands compared with pure stands. In the analysed even-aged mixed stands Norway spruce and Sessile oak are ahead in size growth (Fig. 4b) and obviously able to slow down the growth and reduce the number of beeches during early stand development.

In contrast, the d_{rel} of Norway spruce and Sessile oak is not significantly modified by mixing (Fig. 7b). As shown in Fig. 4a the mean tree size growth of Norway spruce and Sessile oak can be fostered by mixing. However, the presence of beech does not significantly modify the removal-ratio of Norway spruce and Sessile oak. Their d_{rel} values indicate a thinning-from-below effect which is rather equal in mixed and pure stands ($d_{rel} \cong 0.75$). Table 2 underlines that significantly ($p < 0.05$) exceeds 1.0 and indicates the mortality shifts from the smaller diameter classes further to the taller trees in mixed stands.

Discussion

Studies of mixing effects at stand level, *e.g.*, analyses of over- and underyielding at the species or stand level on the basis of sum values (productivity, standing stock) or mean tree attributes (mean tree diameter or volume) may reveal the relevance of mixing effects in terms of stand productivity gains, but not evidence of the underlying reactions (Pretzsch *et al.*, 2010, 2013). They do not reveal, *e.g.*, whether modified stand density, growth partitioning in favour of higher or lower size classes, or a combination of both is behind effects found at stand level.

In contrast, studying of mixing effects at the individual tree level may deliver valuable insight how trees change their crown allometry (Dieler & Pretzsch, 2013), growth (Webster & Lorimer, 2003), and root-shoot-relationship (Schmid & Kazda, 2001) in mixed *versus* pure stands. However, the relevance of such findings for any productivity gains at species or stand level remains mostly unclear as the effects are rarely up-scaled from individual level to unit area. Up-scaling from individual tree level to the species or stand level has to take into account how general the observed reactions at organ or tree level are (variation between trees of different sizes) and how often the individual trees occur (frequency of the trees in different size classes).

Research into the size-structure dynamics can link findings at individual tree and stand level and thus contribute to tracing effects of species mixing, thinning, fertilization from tree to stand level (Hara, 1993; Webster & Lorimer, 2003). Tracing mixing effects from stand level to individual tree level via analyses of size-structure dynamics concerns also forest practice. It makes a big difference regarding assortment yield, whether a species increases the productivity by higher survival, growth of many small but non-merchantable trees or by growth distribution in favour of more valuable tall trees by both alien-thinning and growth acceleration. By taking into account both the modification of the frequency distribution (tree number per size class) and the growth-size relationship (growth rate depending on size) it becomes possible to reveal whether mixing modifies the size distribution, the growth rate at given sizes, or both. The size-structure approach may solve the apparently contradictory findings that mixing may strongly affect the growth of dominant trees in mixed compared to pure stands but hardly changes the stand productivity in total.

Changes of the frequency distribution or negative mixing reactions of smaller trees may counteract or even cancel the reactions observed at the subset of dominant trees. Behind a neutral effect of productivity at stand level, in contrast, may be hidden a higher density of smaller trees which have a lower growth rate so that the mixed stand may come off equal to the pure stand but may differ considerably in size-structure (Binkley *et al.*, 2006). Size-structure dynamics reveals on the one hand the reaction at tree level for trees of different sizes (quality of the mixing effect) and on the other hand the frequency of such individuals in mixed *versus* pure stands (quantity of the effect); both together (product of change of growth and frequency of such changes) yields the mixing effect at stand level.

The focus of this study is on the behavior of beech in mixed compared with pure stands. European beech is a late-successional species which would finally dominate on many sites in Central Europe as it can endure strong competition by other species in the early state of stand development (Ellenberg and Leuschner, 2010, p: 102, 288). Its behaviour during the rotation of 100-120 years, which is much shorter than its natural lifespan of 300-500 years, is relevant for both ecological and forest management. On most sites growth of beech is, especially in the early phase of stand development, much slower than spruce or oak so that

beech temporarily falls behind when mixed with them (Mitscherlich, 1970, pp: 98 and 115-122). Our study reflects this by the smaller mean size of beech in mixed stands.

Based on the relationship between cumulative tree growth and cumulative tree mass Binkley (2004) and Binkley *et al.* (2006) distinguish the following four phases growth dominance in stand development: In Phase 1 of the stand development, when open-grown trees have only little competition, the cumulative growth can be proportional to the cumulative mass and thus $GC = 0$ (see Fig. 2b). In Phase 2, when larger trees get more dominant and suppress the growth of smaller neighbours, the cumulative growth increases progressively with cumulative mass and thus $GC > 1.0$ (see Fig. 2b). The Gini coefficients GC_v and GC_{iv} of our experimental plots are mostly considerably lower than 1.0 and indicate that according to Binkley (2004) they are in Phase 2 of growth dominance in stand development. With increasing stand age a declining growth dominance of larger trees may cause a return to a proportional relationship between cumulative tree growth and cumulative tree mass (Phase 3) or even a reverse growth dominance (Phase 4) when smaller trees get superior to taller trees (Binkley, 2004).

The equality of the size distribution between the trees in a stand is increased by thinning from below and reduced by thinning from above (Kramer, 1988, p: 82). Growing in community with spruce and oak obviously increases the inequality of beech comparable with the effect of thinning-from above. Behind this tendency of beech towards inequality is the growth allocation in favour of taller trees, reflected by coefficient GC_{iv} and the id-d-relationship which are significantly higher in mixed *versus* pure stands. Because of the much more advanced concentration of growth on the taller stand members, the mean diameter of the removed beeches in relation the remaining ones is higher in mixed *versus* pure stands. This is the result of a stronger self- and alien-thinning effect and considered as one component of the "biological automation" in complex *versus* homogeneous stands (*e.g.*, Knoke, 2009), in addition to natural regeneration and mechanical stability. Norway spruce and sessile oak are often ahead in size growth in the early and middle phase of stand development but show no significant changes regarding the parameters of the size-growth relationship, GC_v and GC_{iv} .

Its high shade tolerance and crown plasticity (Dieler & Pretzsch, 2013) nevertheless enables beech

to persist and often finally dominate the admixed species in the late phase of stand development. However, in order to achieve economically usable stem dimensions in reasonable rotation times, beech needs strong competition release by active thinning from above in order to compensate its size inferiority to neighbouring species in the early stand development phase (Wiedemann, 1951, p: 146).

Fig. 8 summarizes in a schematic representation the accelerated forward shift of the size of Norway spruce and sessile oak in mixture (species 1) as well as their slowing down effect on beech (species 2). In the analyzed temperate forests, where mainly light is limiting individual tree growth, the effect of mixing on size-structure dynamics can be conceptualized as shown in Fig. 8. In most cases one of the two even-aged species is ahead of the other regarding size development (in Figure 8 species 1 is ahead of species 2). We speculate that the leading species is often more light demanding and quicker in growth, while the slower species is often more shade tolerant. Then mixing can modify the size distribution compared with pure stands by accelerating the growth of dominant trees, *e.g.*, by triggering their above ground growth in order to keep a given hierarchical status (Kennel, 1965). Species 2 which is behind the size growth of species 1 may cause a thinning-from-below effect on species 1 by out-

competing smaller population members of species 1. In contrast, species 1 may reduce species 2 similar to a thinning-from-above effect.

So far, we analyzed the size-structure dynamics in order to better understand mixed-species stand development compare with pure stands. For forest practice the modification of the frequency distribution by mixing towards taller trees of the leading species (Norway spruce, sessile oak) and less small-sized and more uniform individuals in case of the beech may cause an improvement of the assortment yield, even when productivity at stand level may remain unchanged. Further comparison of the frequency distribution of species in mixed and pure stands may be extended to proxies of wood quality such as ratios of h/d or cd/d which may decrease and cl/h , which may increase wood quality (tree height, h ; tree diameter, d , crown diameter, cd ; crown length, cl). Frequency distributions of latter proxy variables of tree wood quality enable an integrated view on the effect of species mixing on both quality (quality aspects such as distortion, knottiness, wood density, stiffness, and strength) and quantity effect (number of trees with respective qualities) of the produced wood and potential wood products.

Conclusions

The size distribution of beech in mixture mostly lags behind the pure stand, is more size-asymmetric, and the mortality shifts from the smaller diameter classes further to the taller trees than in pure stands. In contrast, the mixing effect of beech on the size size-structure dynamics of spruce and oak is much less pronounced. In this study the community of mixed tree species was conceptualized by its size-structure dynamics. As the species' roles in a given mixture becomes most obvious in unmanaged stands where silvicultural operations do not superimpose natural dynamics we included just unmanaged or moderately thinned stands into this study. We showed how the size distribution, the growth distributions between the trees, and their mortality in mixed stands differs from the respective patterns and processes in pure stands. The analysis yielded promising results, though based on a rather limited number of available pure and mixed stands. Future application to a broader set of triplets covering different species combinations, stand density levels and site conditions may lead to a refined understanding of how mixing modifies the size-structure dynamics.

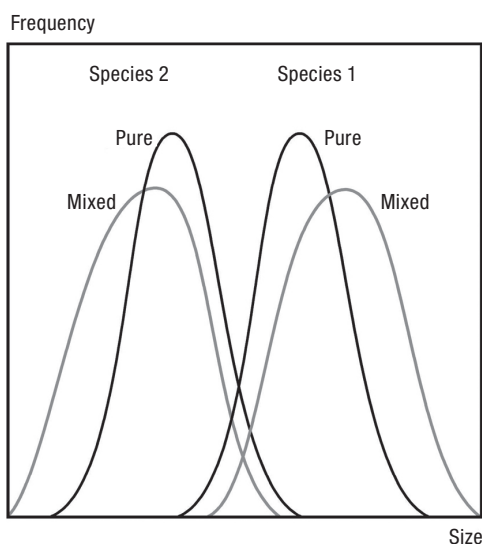


Figure 8. Schematic representation how the species' tree size density distribution in a two-species mixed stand (grey lines) can differ from the size distribution in neighboring pure stands (black lines). In the mixed stand the accelerated forward shift of the size distribution of species 1 (right) can slow down and modify the shape of the size distribution of species 2 (left).

Classical measures such as skewness, kurtosis, standard deviation hardly provided further insight into mixing effects as they probably are too insensitive for characterizing shape modifications. Further studies should use more data material and more detailed methods. Analyzing the diameter distribution by its percentiles or by the parameters of the Weibull distribution (Bailey & Dell, 1973; Zutter *et al.*, 1986) may contribute to further analyses of mixing effects. Both broader data and more appropriate quantification of the size-structure may enable even better insight into the effect of species mixing on the frequency distribution at species level, their interplay, and the resulting frequency distribution at stand level.

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