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Density regulation of mixed and mono-specific forest stands as a continuum: a new concept based on species-specific coefficients for density equivalence and density modification

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A wealth of recent research has improved our understanding of the structure, growth and yield of mixed-species stands. However, appropriate quantitative concepts for their silvicultural regulation remain scarce. Due to the species-specific stand densities, growing area requirements and potential over-density, the density and mixing regulation in mixed stands is much more intricate than in monospecific stands.
Here, we introduce the species-specific coefficients: density equivalence coefficients (DEC), for density equivalence; and density modification coefficient (DMC), for density modification in mixed species stands. DEC is suitable for the conversion of the stand density and growing area requirement of one species into that of another species. DMC estimates the modification of maximum stand density by tree species mixing using as reference the maximum stand density of one of the species.
First, we introduce the theoretical concept of these coefficients. Second, we derive the mean values of these coefficients based on long-term experiments using different mixtures of European beech. Third, we apply DEC and DMC for flexible regulation of the stand density and mixing proportion. Thus, silvicultural regulation of monospecific stands and mixed-species stands forms a continuum, where monospecific stands represent an extreme case of mixed-species stands. Lastly, we discuss the advantages and limitations of these concepts. Future directions comprise the inclusion of additional species, their integration in guidelines and simulation models, and their establishment for the quantitative regulation of experimental plots and the practical implementation in forest stands.

Introduction

A wealth of recent studies has analyzed mixed-species stands and their advantages. Nonetheless, in contrast to monocultures, quantitative silvicultural prescriptions for the establishment and successful regulation of mixed-species stands remain scarce. Research on mixed-species stands include, for instance, the monographs by Bravo-Oviedo *et al.* (2018), Pretzsch *et al.* (2017) and Scherer-Lorenzen *et al.* (2005); the meta-analyses and big data analyses by Jactel *et al.* (2018), Liang *et al.* (2016) and Piotto (2008); and the modelling studies by Morin *et al.* (2011), Gonzalez *et al.* (2017) and Rötzer *et al.* (2009). These bodies of work provide information on crown allometry, stand density and structural-functional complementarity, which may contribute to the development of quantitative silvicultural prescriptions for the analysis and management of mixed species stands. Such quantitative silvicultural prescriptions may subsequently promote the transition from the analysis to the design of mixed-species stands and their increased implementation and successful regulation.

The regulation of stand density and individual growing space forms the basis of silvicultural interventions. For monocultures, species-specific stands reference curves for stand basal area (BA) (Assmann, 1970), tree number per hectare (Abetz, 1975, Long, 1985, Newton, 1997) or species-specific minimum distances (Johann, 1982) are available.

A well-established approach is to derive the natural, site-specific maximum stand density, e.g. the maximum BA, tree number or stand density index (SDI) (Assmann, 1970; Franz, 1965; Reineke, 1933; Sterba, 1981; Sterba and Monserud, 1993) and to use it as a reference. Based on this ceiling density (100 per cent), various trajectories of density reduction can be unambiguously defined, controlled and prescribed for scientific or practical purposes (Assmann, 1970; Döbbeler and Spellmann, 2002; Long, 1985). As the maximum stand density and growing space requirements are species-specific, ceiling density curves need to be derived separately for each species (Newton, 1997; Pretzsch and Biber, 2005, 2016; Wördehoff *et al.*, 2014). Moreover, evidence suggests that the maximum stand density for a given species can vary based on site conditions (Condés *et al.*, 2017).

There are various ways to extend the concept of maximum stand density for monospecific to mixed stands (see del Río *et al.*, 2018, pp. 31–35), which require several considerations and adaptations (Assmann, 1954). For instance, the level and slope of the maximum density lines are species-specific (Curtis, 1982; del Río *et al.*, 2016; Zeide, 1985). The level of the maximum density can, for example, be modified through tighter canopy packing in mixed compared with monospecific stands (Ducey and Knapp, 2010; Pretzsch, 2014, 2019; Pretzsch and Biber, 2016), resulting in over-density, i.e. greater stand density in mixed than in monospecific stands. Moreover, the ratios of the species-specific density and the growing space requirements or the over-density of mixed *vs* monospecific stands can vary with progressing stand development and size relationship of the mixed tree species (Ducey and Knapp, 2010; Sterba and Monserud, 1993).

The present paper develops the theory and tests empirically a method for the density regulation of mixed and monospecific forest stands as a continuum. Monospecific and mixed-species stands of beech are chosen as examples as they are of increasing importance in Central Europe; nonetheless, we also outline how our methods may be extended to other species mixtures.

First, we derive species-specific coefficients for density equivalence which will allow the standardization of different species' density and growing space requirements onto a common 'scale'. Second, we introduce species-specific coefficients for density modification which predict the modification of the maximum stand density through tree species mixing. Third, we apply these new coefficients in algorithms for the density regulation of mixed- and monospecific stands. Finally, we discuss the relevance of this new method for defined density regulation to long-term experiments, the integration in stand growth models and forest management guidelines.

Theoretical derivation of the density equivalence coefficient and the density modification coefficient

In the following section, we develop the species-specific coefficients DEC, for density equivalence, and density modification coefficient (DMC), for density modification in mixed stands. These may be useful for the empirical analysis of mixed-species stands and their density and mixing regulation based on the maximum stand density concept. Furthermore, we introduce density level factors (Th) which help to reduce the maximum stand density to a chosen level.

Maximum stand density and density regulation in monospecific stands

The potential or maximal carrying capacity for a specific species growing in monospecific stands is commonly described through the self-thinning line or maximum size-density relationship. This relationship is based on an expression proposed by Reineke (1933), which relates the number of trees per hectare in fully stocked stands, N, to the quadratic mean diameter, d_q, through the expression $N = a \times d_q^{-1.605}$. Since then, numerous studies have found that the exponent of this expression may vary from $b = -1.605$, suggesting it is species-specific (e.g. Pretzsch and Biber, 2005). Consequently, this equation expresses the allometric relationship between the tree size and the species growing space requirement for a given species. To restrict the complexity in the following derivation of density coefficients, we will first omit other extensions of this relationship, e.g. considering the variation of a and b parameters based on site conditions (e.g. Condés *et al.*, 2017; Hynynen, 1993).

In Figure 1a, we present the self-thinning lines $N_1 = a_1 \times {d_{q1}}^{b_1}$ and $N_2 = a_2 \times {d_{q2}}^{b_2}$, which denote the maximum stand density or ceiling density of species 1 and 2, respectively, given certain conditions (see Figure 1a). Their levels can be characterized by the SDI; e.g. for species 1, $\mathrm{SDI}_1 = a_1 \times 25^{b_1}$. These self-thinning lines can be used as a reference, i.e. the natural density, when choosing a density reduction (Long, 1985). For instance, a multiplication by level = 0.6 yields the thinning line for stands permanently kept at 40 per cent below the maximum density. A common pattern includes strong density reductions in young stands (level = 0.5–0.6) followed by increasing densities (level = 0.8–0.9) later in the rotation. For practical applications, the maximum and target curve can be displayed in graphs with N *vs* d_q (Newton, 1997) (Figure 1a). While the tree number, N, can sometimes be plotted over mean height, h, the principle holds (Abetz, 1975; Klädtke *et al.*, 2012). It is also common to show the maximum stand BA BA_1 depending on d_q. This expression can be derived by multiplying both sides of the self-thinning line by ${d_{q_1}}^2/4 \times \pi/10\ 000$, resulting in $\mathrm{BA}_1 = a_1 \times d_{q1}^{b_1} \times d_{q1}^2/4 \times \pi/1000 = a_1^{'} \times d_{q1}^{b_1+2}$. Given that b-values typically range from −1.4 to −1.8, the exponent of $\mathrm{BA}_1 = a_1^{'} \times d_{q1}^{b_1+2}$ lies between 0.2 and 0.6, which indicates an under-proportional increase of the maximum BA with increasing diameter (Figure 1b). The BA for the thinning line can be derived analogously.

As the mean growing area, $\overline{g}_1$, of a tree in the species 1 stand is the reciprocal of the tree number $\overline{g}_1 = 10\ 000/N_1$, the self-thinning line also reflects the species-specific increase of the tree growing area requirement with increasing tree diameter $\overline{g}_1 = 10\ 000/a_1 \times {d_{q_1}}^{b_1}$. Note that b_1 ranges between −1.4 and −1.8 and indicates an over-proportional increase of growing area with increasing diameter (Figure 1c).

Density equivalence coefficient

The self-thinning line of a species reflects its specific allometry, i.e. its structural trait for tolerating and competing with other species (Zeide, 1985). Suppose species 2 follows $N_2 = a_2 \times {d_{q_1}}^{b_2}$ with a_2 and b_2 values being different from species 1, $N_1 = a_1 \times {d_{q1}}^{b_1}$, the coefficient

$$\mathrm{DEC} = N_1/N_2 = a_1/a_2 \times {d_{q1}}^{b_1-b_2} \qquad 1$$

expresses the stand density and growing area requirement of one species in relation to the other for equal stem diameters. As they

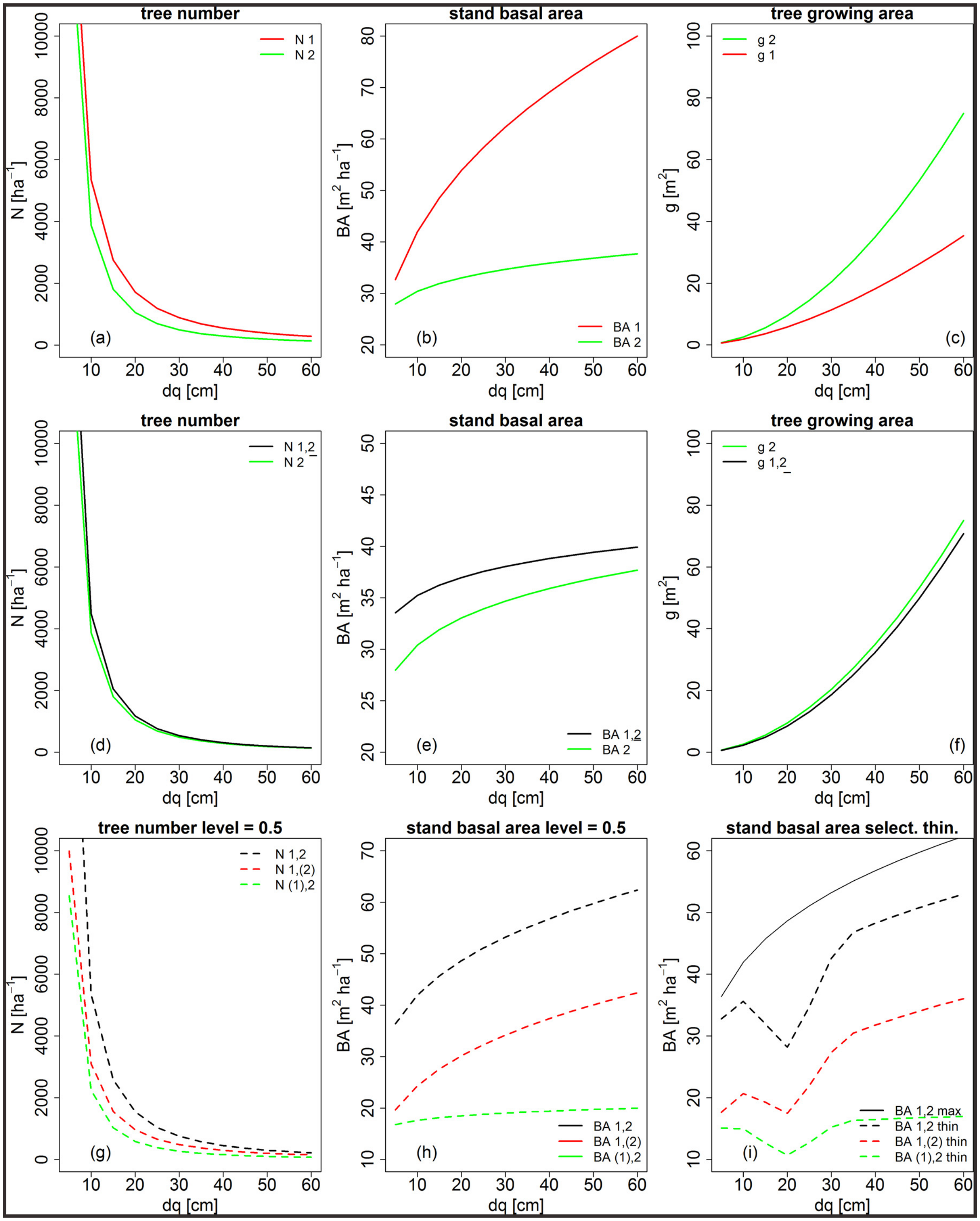

Figure 1 Transition from the maximum stand density line of a common standard tree species to the density regulation curves for two-species mixed stands. For clarity, we assume equal mean tree diameter for species 1 and 2. (a–c) Ceiling curves for the tree number, *N*, stand BA and mean tree growing area $\bar{g}$ of species 1 and 2. Species 2 is selected as the standard species. (d–f) Adjustment of species 2 curves through DMC to account for stand density modification through mixing of tree species. (g–h) derivation of *N* and BA of the mixed stand of species 1 and 2 from the adjusted standard curve, assuming an area-related mixture of 0.5:0.5. (i) Stand density reduction of both species with strong selective thinning and density reduction to Th = 0.5 in the young stand; followed by a reconvergence to the maximum density line with progressing stand development.

Table 1 Abbreviation and subscripts.

Abbreviation	Description
N	Number of trees per hectare
dq	Quadratic mean diameter
BA	Basal area
g	Tree growing area
SDI	Stand density index
m_N	Species proportion of tree numbers by hectare
m_A	Species proportion by area
sp	Species
X_1, X_2	Characteristic X of species 1 and species 2 in monospecific stands
$X_{1,(2)}$, $X_{(1),2}$	Characteristic X of species 1 and species 2 in mixed stands
$X_{1,2}$	Characteristic X of mixed stand
$X_{1,\underline{2}}$	Characteristic X of mixed stand standardized to species 2
DEC	Density equivalence coefficient
DMC	Density modification coefficient
Th	Density reduction factor (by thinning)

can be used to convert the density or growing area requirement of one species into that of the other, they are called density equivalence coefficients (DEC). The DEC value is also called $\mathbf{DEC_{sp_2 \to sp_1}}$, because it is used later to convert the tree number of species 2 to that of species 1 through multiplication with $\mathbf{DEC_{sp_2 \to sp_1}}$. Once DEC values have been derived for different species, they can be used for the standardization of density or growing area requirements into a common scale (Pretzsch, 2019a, p. 404–408; Pretzsch, 2019b).

For example, if for species 1 and species 2 the DEC is $DEC_{sp2 \to sp1} = 2$, we can then apply the DEC to compare a mixed and monospecific stand density as follows: suppose the monospecific stand of species 2 has a stem number $N_2 = 600$ trees ha^{-1} and the mixed stand consists of $N_{1,2} = 900$ trees ha^{-1}, with $N_{1,(2)} = 600$ trees ha^{-1}of species 1 and another $N_{(1),2} = 300$ of species 2 ($N_{1,2} = N_{1,(2)} + N_{(1),2}$). Then, a standardization of the tree number of the mixed stand to the standard of species 2 yields $\mathbf{N_{1,\underline{2}} = 600/DEC_{sp2 \to sp1} + 300 = 600}$ trees ha^{-1}. This shows that, due to the lower space requirements of species 1, even though it contains more trees, the mixed stand possesses the same density as the monospecific stand. Standardization of a variable to the level of species 2 is indicated by underlining the subscripted number, e.g. $X_{1,\underline{2}}$ (Table 1). This standardization is achieved through the use of DEC $_{sp2 \to sp1}$. Note that DEC $_{sp1 \to sp2} = 1/$DEC $_{sp2 \to sp1}$.

Until now, we have assumed equal quadratic mean diameters for both species ($d_{q_1} = d_{q_2}$). Indeed, the diameters of species in mixed stands are often similar in the early stages of stand development and then diverge with increasing age. The following expression of the DEC accounts for this size difference between species, using the species-specific mean diameters $\mathbf{d_{q_{1,(2)}}}$ and $\mathbf{d_{q_{(1),2}}}$ in the mixed stand:

$$\mathrm{DEC}_{sp_2 \to sp_1} = a_1/a_2 \times d_{q1,(2)}{}^{b_1} \times d_{q(1),2}{}^{-b_2}. \quad (2)$$

Thus, using DEC, we can convert a given maximum stand density of a given standard species (species 2 in our example) into that of any species composition, provided that the respective DEC values are known. The number of the standard species is simply expanded to the various species by multiplying it with respective$\mathbf{DEC_{sp_2 \to sp_1}}$ value.

Coefficients for density modification in mixed compared with monospecific stands (DMC)

Above, we have mentioned that tree species mixing can contribute to higher canopy packing and stand density (Jucker *et al.*, 2015; Morin, 2015; Pretzsch and Biber, 2016). In the following section, this effect is captured through the DMC. The DMC is computed as the quotient of the maximum stand density of mixed stands divided by that of monospecific stands, derived from respective self-thinning lines.

If the mean tree diameters of the two species are equal, the expression of DMC is the following:

$$\mathrm{DMC} = \left(N_{1,(2)}/\mathrm{DEC}_{sp_2 \to sp_1} + N_{(1),2}\right)/N_2. \quad (3)$$

Then, DMC values should be based on fully stocked stands with maximum stand density.

The development and application of the DMC follow the same principle as that introduced for the DEC. Once derived from mixed and monospecific stands at given sites (see section 2.2), the DMC can be used to scale the tree number-mean diameter or BA-mean diameter relationship of monospecific stands to the level of mixed stands. As the mixing may modify the maximum stand density disparately in different stand development phases, the DMC can be derived also depending on the quadratic mean tree diameters.

Potential of DEC and DMC for generic stand density and mixing regulation

We will begin with the maximum stand density line $\mathbf{N_2 = a_2 \times d_{q2}{}^{b_2}}$ of a given standard species (Figure 1a). This may, for instance, be European beech (*Fagus sylvatica* L.), which is a common forest tree in Central Europe. In the following, we will refer to it as species 2 and use it in our practical example (see section 'Practical application for stand density regulation'). This N_2-d_{q2} curve, or the BA$_2$-d_{q2} curve (Figure 1b) introduced in the last section, can be used as the maximum density for density reduction and regulation.

Using DEC, the maximum density curve of species 1 can be standardized to the reference, which is species 2. This allows us to estimate the stand density in mixed stands as $N_{1,(2)}$/DEC $_{sp2 \to sp1} + N_{(1),2}$ and to use the maximum density curve of species 2 $\mathbf{N_2 = a_2 \times d_{q2}{}^{b_2}}$ as a reference. Using DMC, the reference curve $\mathbf{N_2 = a_2 \times d_{q2}{}^{b_2}}$ can subsequently be used to derive the maximum density curves for mixed species stands (species 1 and 2) by multiplying $\mathbf{N_2}$ values with DMC coefficients ($\mathbf{N_{1,\underline{2}} = N_2 \times DMC_{1,2}}$). This can be approximated using the mean $\mathbf{DMC_{1,2}}$ value. A more accurate result can be achieved by multiplying $\mathbf{N_2}$ values with diameter-dependent $\mathbf{DMC} = f\left(\overline{d}_{q_{1,2}}\right)$ values, which consider

Table 2 Derivation of tree number by species in mixed stands from $N_{1,\underline{2}}$ for a given species proportion. See details of derivation in online Supplementary data.

Species proportion of numbers of trees (m_{N1}, m_{N2}, where $m_{N1}+m_{N2}=1$)

$N_{1,(2)} = N_{1,\underline{2}} \times \left(1/\mathrm{DEC}_{sp_2\rightarrow sp_1} + 1/m_{N_1}\text{-}1\right)^{-1}$

$N_{(1),2} = N_{1,\underline{2}} \times \left(1/\left(\mathrm{DEC}_{sp_2\rightarrow sp_1} \times m_{N_2}\right) - 1/\mathrm{DEC}_{sp_2\rightarrow sp_1} + 1\right)^{-1}$

$N_{1,2} = N_{1,\underline{2}} \times \left(\left(1/\mathrm{DEC}_{sp_2\rightarrow sp_1} + 1/m_{N_1}\text{-}1\right)^{-1} + \left(1/\left(\mathrm{DEC}_{sp_2\rightarrow sp_1} \times m_{N_2}\right) - 1/\mathrm{DEC}_{sp_2\rightarrow sp_1} + 1\right)^{-1}\right)$

Species proportion by area (m_{A1}, m_{A2}, where $m_{A1}+m_{A2}=1$)

$N_{1,(2)} = N_{1,\underline{2}} \times m_{A_1} \times \mathrm{DEC}_{sp_2\rightarrow sp_1}$

$N_{(1),2} = N_{1,\underline{2}} \times m_{A_2}$

$N_{1,2} = N_{1,\underline{2}} \times \left(m_{A_1} \times \mathrm{DEC}_{sp_2\rightarrow sp_1} + m_{A_2}\right)$

stand development-dependent changes in density (Figure 1d). From them, the corresponding stand BA and mean tree growing space $g_{1,2}$ can be calculated (Figure 1f,e).

Both approaches yield an adjusted maximum density line for the tree number $N_{1,\underline{2}}$ based on the standard species, which can be used for further calculations (Figure 1d). Specifically, the $N_{1,\underline{2}}$ maximum reference values can be used to derive the tree numbers of species 1 and 2 in mixed stands given a specific proportion of tree numbers (m_{N_1}, m_{N_2}) or proportions by areas (m_{A1}, m_{A2}) as presented in Table 2. In the first option, the equation provides the absolute numbers of trees per hectare for both species and a desired proportion of a number of mixed trees (e.g. 0.5:0.5 regarding the tree number). In contrast, the second equations provide the absolute numbers of trees per hectare for both species for a desired proportion by areas (e.g. 0.5 ha stocked with species 1 and 0.5 ha with species 2). For more information on the derivation of equations in Table 2, refer to the online Supplementary data.

In Figure 1g,h, we began with the adjusted standard curve in Figure 1d and calculated the numbers of trees (Figure 1g) and stand BAs (Figure 1h) of the mixed stand of species 1 and 2, assuming an area-related mixture of 0.5:0.5.

We have now calculated the tree numbers depending on the mean tree diameter for different mixing proportions at maximum stand density, i.e. in fully stocked stands. These can now be used to determine the stand density reduction, for instance by reducing the density to 60 per cent of the maximum. In this specific case, $N_{1,(2)}$, $N_{(1),2}$ and $N_{1,2}$ total numbers are multiplied by level$=0.6$. However, a more common approach is to reduce the density first and then allow it to near the maximum stand density again in later stages of the stand development (Figure 1i). For this purpose, the density level can be defined using either the mean diameter of both species or that of each species separately (see examples in subsection 'Considering differences between mean tree size of the mixed species').

Empirical evidence

Maximum stand density levels and coefficients for density equivalence, DEC

In order to obtain stable DEC values, we computed maximum N-d_q relationships for five primary tree species in Central Europe: Norway spruce (*Picea abies* (L.) Karst), Scots pine (*Pinus sylvestris* L.), Douglas-fir (*Pseudotsuga menziesii* (Mirb) Franco), European beech L. and sessile oak (*Quercus petraea* (Matt) Liebl). These were parameterized using 64 long-term thinning experiments combining 328 plots and 2627 surveys beginning in 1870 (see Supplementary Table 1–5). Together, they represent the range of growing conditions in Central Europe. Each includes fully stocked un-thinned reference plots that are important for indicating the maximum stand density (see Figure 2).

We used the 95 per cent quantile regression to derive the maximum stand density lines and respective intercepts and slopes for each species. Figure 2 displays the observations and quantile regressions lines. The lines differ between the species with relatively low and steep lines for European beech and Scots pine, and higher and shallower slopes in the cases of Norway spruce and Douglas-fir (Table 3). Level aa indicates the size and the slope *b*, the expansion of the respective species with progressing stand development. Consequently, they represent crucial species-specific structural traits to compete in populations.

We use the model $\ln(N) = aa + b \times \ln(d_q)$ and the 95 per cent quantile for parameterization (Pinheiro *et al.*, 2017). We name the intercept aa to distinguish it from $a = e^{aa}$ in the de-logarithmic formulation $N = a \times {d_q}^b$ used elsewhere in this paper.

These coefficients can be used to compute DEC (Eq. 1) as shown in Table 3 for two species compositions. The descending diagonal represents DEC values given equal diameters of both species. In the case of Norway spruce and European beech (Table 2, above), the lines indicate that, for equal diameters of both species, Norway spruce is packed 27 to 86 per cent more densely than European beech, which results consequently in greater stand BA. This advantage in density increases with progressing stand development. In mature stands, Norway spruce possesses nearly twice as many trees as European beech per hectare; in line with this, the growing space of a mature beech would suffice for almost two spruces.

For Scots pine and European beech (Table 4, above), the densities and changes of shape with increasing size growth differ less. Scots pine displays lower tree numbers than European beech at the beginning, but, with increasing diameter, the densities and growing space of both species converge.

The right upper corners of the matrix show DEC values when Norway spruce respectively Scots pine have the greater growth and the bottom left corner when European beech has the lead in diameter growth. DEC values and their dependency on the species-specific stem diameters d_{q1} and d_{q2} will be used to adjust different tree species to the same scale level and to upscale from a standard scale to different species and species combinations.

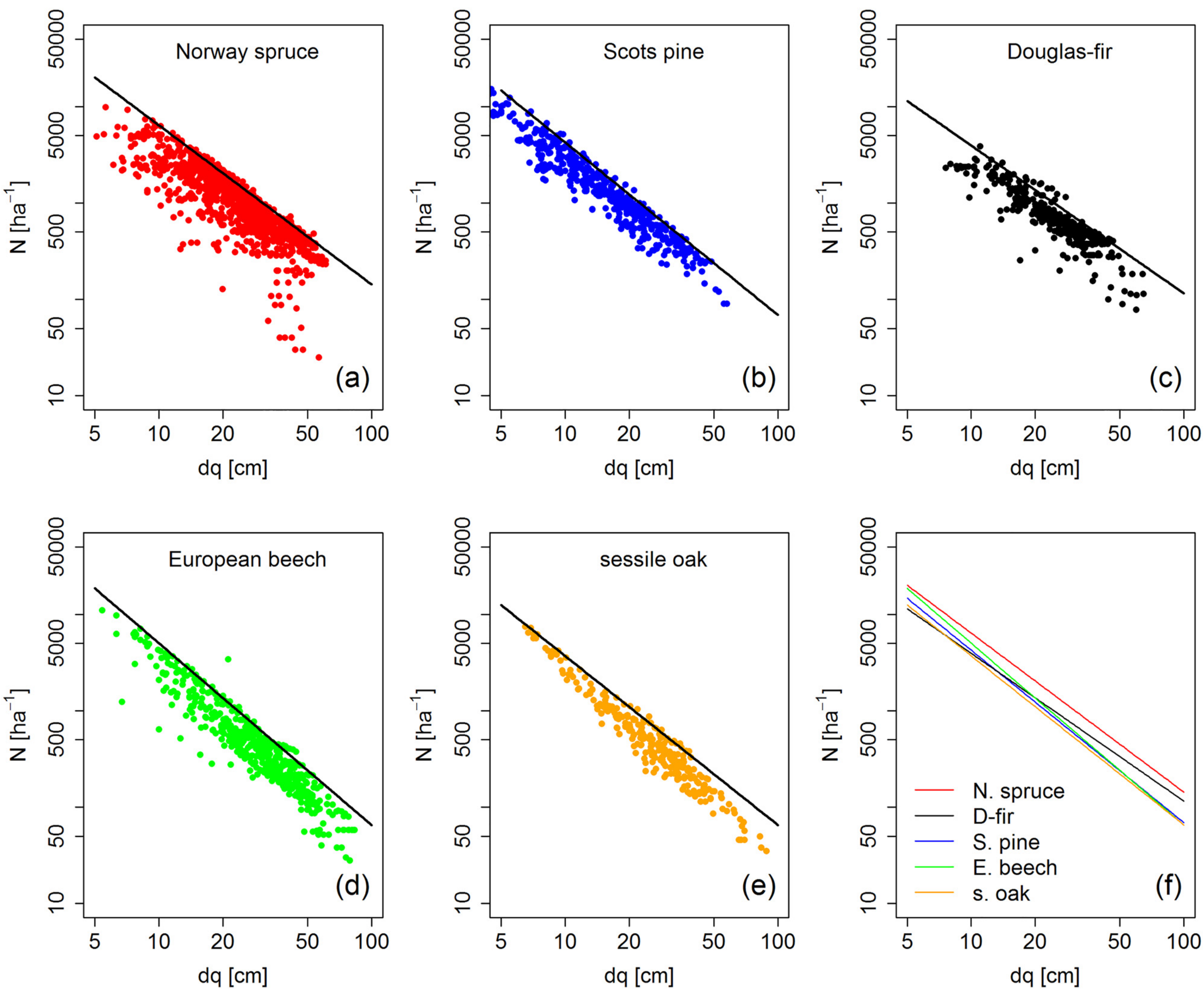

Figure 2 Maximum stand density lines N-d_q derived for (a) Norway spruce, (b) Scots pine, (c) Douglas-fir, (d) European beech and (e) sessile oak based on measurements in long-term experiments in Central Europe. (f) Maximum N-d_q lines for all five species compared with each other.

Table 3 Results of the 95 per cent quantile regressions $\ln(N) = aa + b \times \ln(d_q)$ for Norway spruce, Scots pine, Douglas-fir, European beech and sessile oak (see Figure 2).

Model	Species	*n*	aa	std (aa)	*P*-value	b	std (b)	*P*-value
1	N. spruce	1074	12.560	0.075	0.001	−1.650	0.023	0.001
1	S. pine	436	12.473	0.084	0.001	−1.789	0.034	0.001
1	D-fir	375	11.811	0.208	0.001	−1.534	0.060	0.001
1	E. beech	482	12.865	0.104	0.001	−1.887	0.041	0.001
1	s. oak	260	12.254	0.054	0.001	−1.753	0.021	0.001

Density modification in mixed-species compared with monospecific stands and coefficients DMC

To account for alterations induced by tree species mixing, the maximum stand density of the monospecific stand is modified through DMC. This coefficient is derived for different tree species mixtures. We also attempted to model DMC depending on quadratic mean tree diameter and mixing proportions to account for any changes associated with progressing stand development and proportion of tree species; however, the available data were too scarce to draw informed and confident conclusions.

To calculate empirically the DMC values (Table 5), we used data from experimental plots and temporary triplets available and published for the mixtures Norway spruce/European beech

Table 4 Diameter-dependent DEC for species combinations of Norway spruce and European beech ($\mathbf{DEC}_{E.b\rightarrow N.sp}$, above) and Scots pine and European beech ($\mathbf{DEC}_{E.b\rightarrow S.p}$, below). The bold numbers in italics represent the Density Equivalence Coefficients in case of equal tree diameters of both considered tree species.

d_q	d_q Norway spruce					
E. beech	10	20	25	30	40	50
10	***1.27***	0.41	0.28	0.21	0.13	0.09
20	4.70	***1.50***	1.04	0.77	0.48	0.33
25	7.16	2.28	***1.58***	1.17	0.73	0.50
30	10.10	3.22	2.23	***1.65***	1.03	0.71
40	17.39	5.54	3.83	2.84	***1.76***	1.22
50	26.49	8.44	5.84	4.32	2.69	***1.86***
d_q	d_q Scots pine					
E. beech	10	20	25	30	40	50
10	***0.85***	0.24	0.16	0.12	0.07	0.05
20	3.13	***0.91***	0.61	0.44	0.26	0.18
25	4.77	1.38	***0.93***	0.67	0.40	0.27
30	6.72	1.95	1.31	***0.94***	0.56	0.38
40	11.57	3.35	2.25	1.62	***0.97***	0.65
50	17.63	5.10	3.42	2.47	1.48	***0.99***

Table 5 Mean ratios of mixed *vs* monospecific stand density, DMC, for species combinations represented by data and analyzed so far.

species combination	N. spruce E. beech	s. oak E. beech	S. pine E. beech	Douglas-fir E. beech	S. pine s. oak
n	178	254	32	18	36
mean	1.020	1.257	1.130	1.281	1.137
SE	0.015	0.046	0.054	0.141	0.040

(Pretzsch *et al*., 2010), Scots pine/European beech (Heym *et al*., 2017; Pretzsch *et al*., 2015), Douglas-fir/European beech (Thurm *et al*., 2016; Thurm and Pretzsch, 2016), sessile oak/European beech (Pretzsch *et al*., 2013) and Scots pine and sessile/common oak (Pretzsch *et al*., 2019). All setups include the two respective tree species in monocultures and mixed-species stands and represent fully stocked, un-thinned stands close to maximum stand density.

For each of these triplet sets of two monospecific and one mixed-species stand, we calculated DMC (Eq. 3) assuming that their values of the SDI (Reineke, 1933) represent the maximum density for $dq = 25$ cm. So using the species-specific allometric exponents in Table 3, we calculated $\mathbf{DMC} = \mathbf{SDI}_{1,(2)}/\mathbf{DEC}_{sp_2\rightarrow sp_1} + \mathbf{SDI}_{(1),2}/\mathbf{SDI}_2$. The resulting mean DMC values were used for the example applications in next section.

Practical application for stand density regulation

Effect of tree species combination

Site-specific maximum N-d_q relationships, e.g. for European beech, can be used to derive maximum density curves for different tree species mixtures. For instance, we begin with an N-d_q relationship of beech with $\mathrm{SDI} = 600$, where $\mathbf{600} = \boldsymbol{a} \times 25^{-1.8867}$, i.e. $\boldsymbol{a} = 600/25^{-1.8867} = 260\ 369$, and $N_{\mathrm{E.be}} = 260\ 369 \times \boldsymbol{dq}_{\mathrm{E.be}}{}^{-1.8867}$ (Figure 3a). The corresponding BA-d_q curve is shown in Figure 3b.

For mixed stands of Norway spruce and European beech, and Scots pine and European beech, the area-related proportion of 0.75:0.25 (conifers: beech) is very common in forest practice. Figure 3d–f shows that the equivalent tree numbers and stand BAs for the mixture of Norway spruce and European beech considerably exceed the respective values of beech monocultures. Figure 3g–i shows that the differences in the case of mixed stands of Scots pine and European beech are that the DEC is lower, but that the DMC is higher (see Table 5). In the figures, we assumed that the two species have equal quadratic mean diameters.

The horizontal lines in Figure 3a,c,e show that, for a stand with a 25-cm mean diameter, the total tree number is 600 ha^{-1} in the case of the European beech monoculture (lower broken line) and 878 ha^{-1} in the mixture of Norway spruce and European beech (upper solid line), whereas the respective tree numbers of the Scots pine and European beech mixture is 702 ha^{-1} and lies in between (medium dotted line). The respective values are 772 ha^{-1} for the mixture of Douglas-fir and European beech and 547 ha^{-1} for sessile oak and European beech.

The respective stand BAs shown in Figure 3b,d,famount to 29.5 $\mathrm{m}^2\ \mathrm{ha}^{-1}$ for European beech, 43.1 $\mathrm{m}^2\ \mathrm{ha}^{-1}$ for Norway spruce/European beech and 34.5 $\mathrm{m}^2\ \mathrm{ha}^{-1}$ for Scots pine and European beech. The respective stand BAs for equivalent mixtures of Douglas-fir and sessile oak would be 37.9 and 26.8 $\mathrm{m}^2\ \mathrm{ha}^{-1}$, respectively.

Thus, maximum stand density lines for the combination of any species can be derived and used as a reference for the assess-

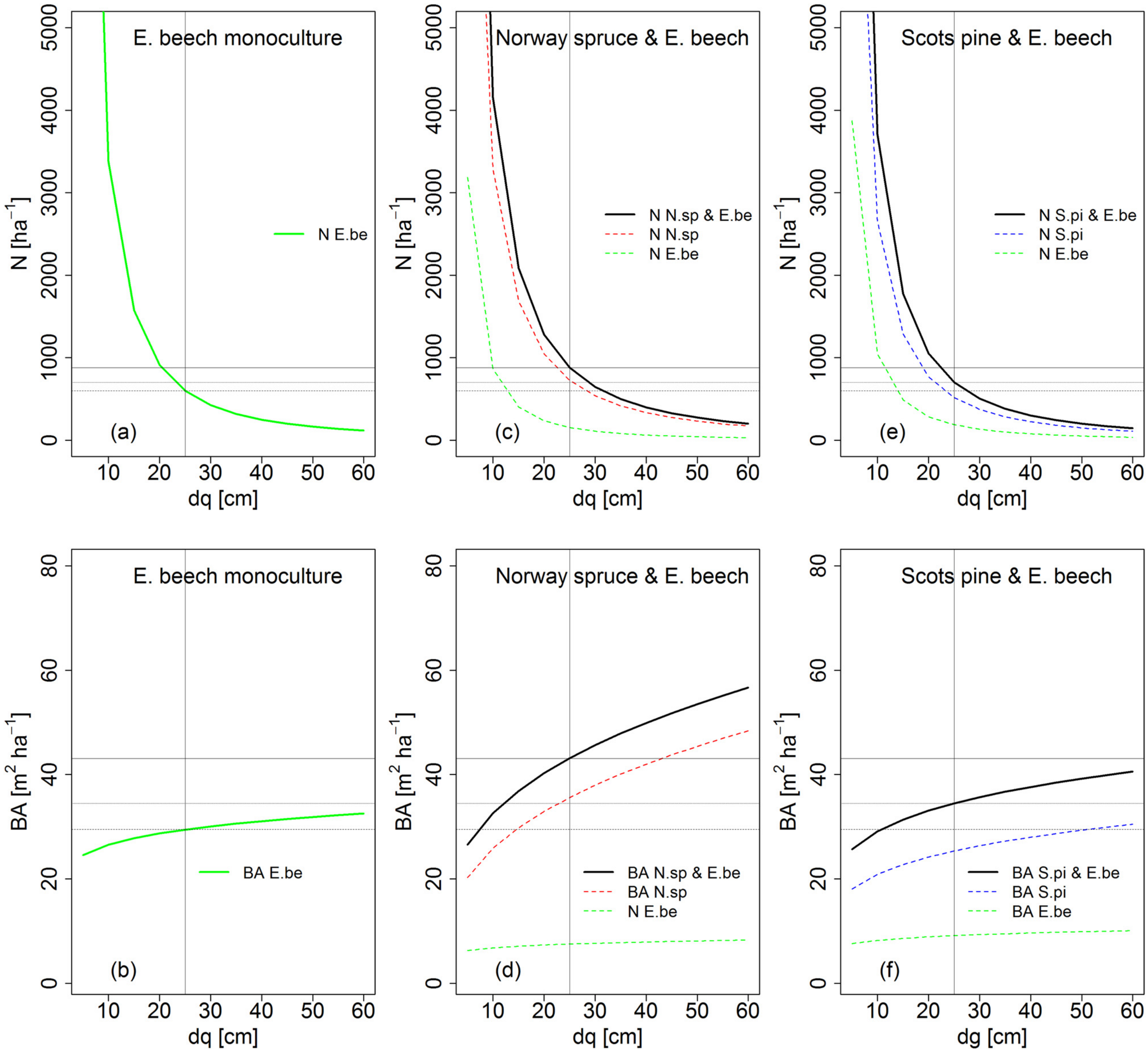

Figure 3 Derivation of the maximum tree numbers and stand BAs for mixed-species stands of Norway spruce (N.sp), European beech (E.be), Scots pine (S.pi) and European beech based on the coefficients DEC and DMC, assuming equal quadratic mean diameters for both species. (a–c) tree number and stand BA plotted over mean tree diameter for a monospecific stand of European beech with SDI = 600. (d–f) Equivalent tree numbers and stand BAs for a mixed stand of Norway spruce and European beech with an area-related mixing proportion 0.75:0.25 (N.sp: E.be). (g–i) Equivalent tree numbers and stand BAs for a mixed stand of Scots pine and European beech with an area-related mixing proportion 0.75:0.25 (S.pi: E.be).

ment of the relative density, for developing treatment variants for experimental plots or for modelling guideline development for forest practice.

The differences between area-related and tree number-related mixing proportions

The definition of the mixing proportion strongly affects the tree numbers and stand BAs of the species and the stand as a whole. Figure 4 shows this for the stand BA; the BA closely correlates with the standing volume and is most relevant for the management planning and fixing of the annual cut. The differences between area-related mixing proportions (a–c) and tree number-related mixing proportions (d–f) are shown for Norway spruce and European beech, Scots pine and European beech, and sessile oak and European beech (from top to bottom), assuming equal quadratic mean diameters for the two species. Using equations in Table 2 and the coefficients provided in section ‘Empirical evidences’, we calculated the respective mixing proportions of 0.5 (Norway spruce, Scots pinei, sessile oak, respectively): 0.5 (European beech).

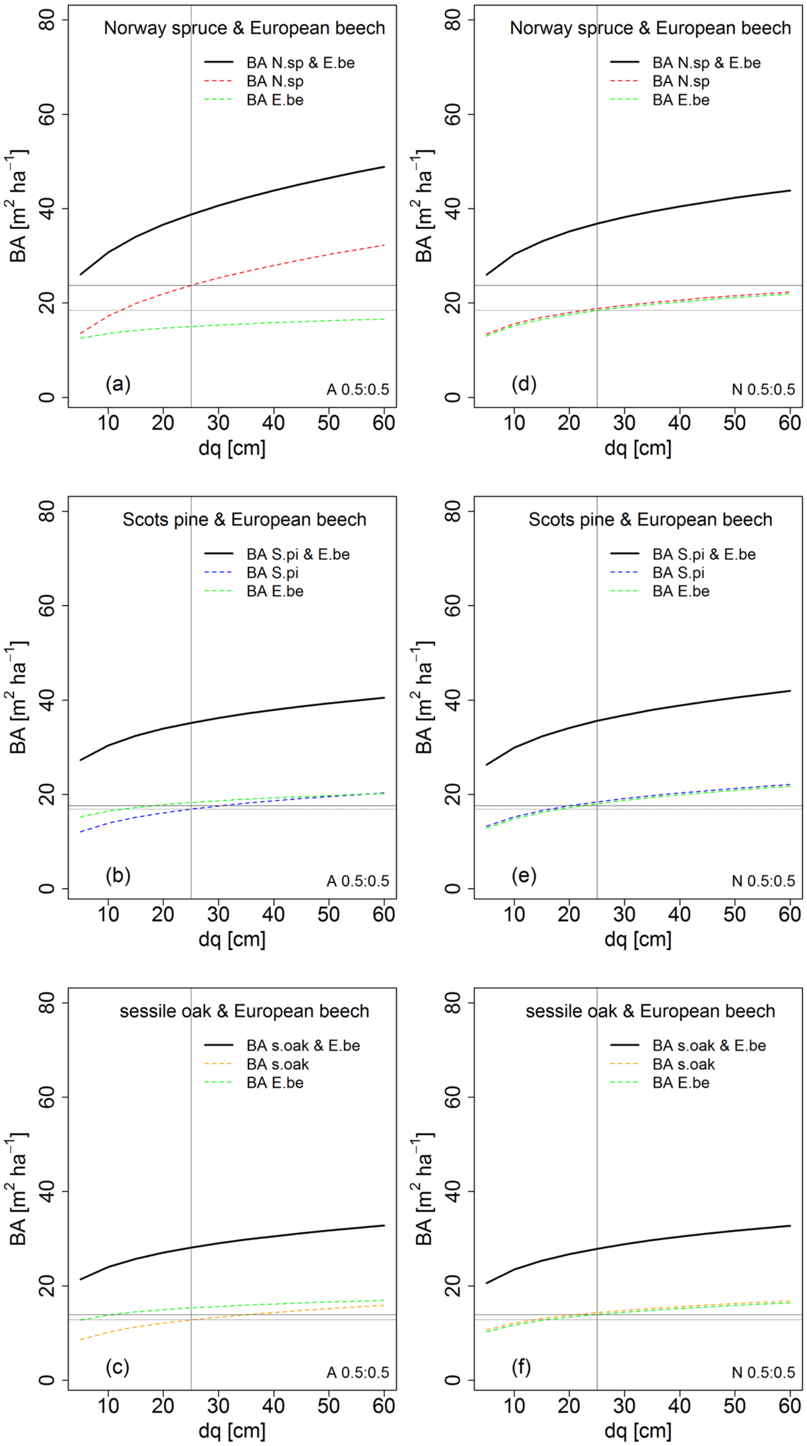

Figure 4 The differences between (a–c) area-related mixing proportions and (d–f) tree number-related mixing proportions shown for mixing proportions of 0.5:0.5 for Norway spruce and European beech, Scots pine and European beech, and sessile oak and European beech (from top to bottom). In this example, we assumed equal quadratic mean diameters for the two species. The horizontal lines indicate the different levels of the BA of Norway spruce, Scots pine and sessile oak depending on the definition of the mixing proportion.

In the case of area-related mixing proportions, the BA of Norway spruce per hectare reaches a high level as this species, with its high packing density, is assigned to 50 per cent of the area (Figure 4a). The upper horizontal line indicates a BA of 23.7 m^2 ha^{-1} for Norway spruce for stands with a mean diameter of 25 cm. Accordingly, the BA of European beech is low as it is assigned to only 50 per cent of the area and possesses only approximately half of the packing density compared with spruce.

In the case of tree number-related mixing proportions, the BA of Norway spruce decreases in favour of European beech (Figure 4d). The lower horizontal line indicates a BA of only 18.4 m^2 ha^{-1} for Norway spruce for stands with a mean diameter of 25 cm.

The mixture of Scots pine and European beech (Figure 4b,e) is less affected by the definition of the mixing proportion as both species have similar densities and space requirements. Here, the area-related definition results in a BA of 16.9 m^2 ha^{-1} (upper horizontal line); the tree number-related definition results in a BA of 17.6 m^2 ha^{-1} for Scots pine in stands with a mean diameter of 25 cm.

As sessile oak is equal to European beech regarding space requirements, their relationship in terms of this mixture is similar (Figure 4c,f). Specifically, the area-related definition results in a BA of 12.8 m^2 ha^{-1} for sessile oak and a tree number-related mixing of 13.9 m^2 ha^{-1}.

Note that, in Figure 4 from top to bottom, the total level of maximum BA decreases from 38.8 to 28.1 m^2 ha^{-1} and from 36.8 to 27.9 m^2 ha^{-1} for area- and tree number-related mixing proportions, respectively (for stands with 25-cm mean diameter). This is due to the increasing space requirements from Norway spruce to Scots pine and sessile oak. If the species-specific densities and growing area requirements of the mixed species are similar, both definitions of mixing proportion have the same effect on both species. If one species requires less space (e.g. Norway spruce) than the other (e.g. European beech), the BA of the first species is increased by the area-related, and decreased by the tree number-related, definition. The area-related mixing proportion assigns a defined growing area and living space to each species; a tree number-related mixing proportion, on the other hand, provides a target tree number, BA or standing volume.

Considering differences between mean tree size of the mixed species

In mixed stands, the mean diameter of one species usually exceeds that of the other(s). For instance, in mixed stands of Norway spruce and European beech, the mean diameter of spruce is usually around 50 per cent greater than the diameter of beech (Pretzsch *et al.*, 2010). Therefore, in the following, we assume that $\boldsymbol{d_{qN.sp}} = \mathbf{1.5} \times \boldsymbol{d_{qE.be}}$. As an example, we further assume an area-related mixing proportion of 0.5:0.5. We begin with the N-d_q reference relationship of E. beech with SDI = 600 ($\boldsymbol{N_{E.be}} = \mathbf{260\ 369} \times \boldsymbol{dq_{E.be}}^{-1.8867}$). Stem numbers are then multiplied by DMC to account for the density increase through mixing (see Figure 5a,e). Next, we apply equations from Table 2 to obtain the respective tree numbers for Norway spruce and European beech in the mixed stand (Figure 5b–d). Based on the tree numbers, the corresponding stand BAs can be calculated (Figure 5f–h). As the mean tree diameters of Norway spruce and European beech differ, we apply the diameter-dependent DEC using $\mathbf{DEC_{sp_2 \rightarrow sp_1}} = \boldsymbol{a_1/a_2} \times \boldsymbol{d_{q1}}^{\boldsymbol{b_1}} \times \boldsymbol{d_{q2}}^{\boldsymbol{-b_2}}$, as shown in Table 4 (above).

Figure 5 displays the results. For the specified conditions, we obtain the tree numbers and stand BAs for maximum stand density as a guide for the specific ceiling density and as the basis for density regulation and reduction. If the species differ in mean diameter, we use species-specific N-d_q and BA-d_q diagrams for Norway spruce (Figure 5b,f) and European beech (Figure 5c,g). In the summary graphs (d and h), the tree numbers and BAs are shown depending on the mean diameter of European beech and summarized.

As Norway spruce is ahead in size growth, the total tree number is about 30 per cent lower and the BA 10 per cent higher. The upper horizontal line in Figure 5e,h indicates the stand BA (for a mean tree diameter of 50 cm) when Norway spruce is ahead (51.1 m^2 ha^{-1}); the lower line indicates the stand BA (46.4 m^2 ha^{-1}) when both species have equal mean tree diameters.

Regulating the stand density by Th

The introduced coefficients DEC and DMC can be applied both to quantify the stand density and to derive the maximum stand density level as a guideline when quantitatively scheduling the regulation of stand density. The density level can be modified at the stand level; this modification can be performed across species or separately for each species.

Figure 6 displays these options using the example of a growing area-related mixture of Norway spruce and European beech (0.75:0.25), assuming the same preconditions as those outlined in Figure 3. In the first simulated thinning scenario (Figure 6a), we show guideline curves for a constant stand density reduction to Th = 0.8 of the maximum stand density; this corresponds to a continuous moderate thinning of both tree species. Note that the relative density reduction for both species is the same; but, due to the high DEC values of Norway spruce, the absolute stand density reduction for this species is stronger than that for European beech.

The second simulated scenario represents a selective thinning of both species with a density reduction to Th = 0.5 for stands with a mean diameter of d_q = 25 cm (Figure 6b). Following this, the density rises again. For this density regulation option, we defined the Th regime using a vector with specified density levels, ranging from the young to the mature stand (0–60 cm), in 5-cm (diameter) increments.

To promote European beech, a stand level density reduction can be achieved simply by removing Norway spruces (Figure 6c). Here, Norway spruce is reduced even more strongly than in thinning scenario (b) and the BA level of European beech is maintained. This gradually increases the mixing proportion of European beech beyond 25 per cent.

Finally, Th can be expressed as a function of the mean stand diameter (Figure 6d). This example of density regulation aims at a stabilization, natural regeneration and preparation of the stand for conversion to an uneven-aged stand structure. Beginning in a stand development phase with a mean stem diameter of d_q = 25 cm, the initially high density is gradually reduced to Th = 0.5 (based on Th = 1.033–009 × d_q).

Regulating the density at the stand level and/or at the species level allows for a general density regulation but also the promotion of one tree species by reducing the density and mixing proportion of the other.

Hence, if, for a given mixed stand, we know the number of trees and the quadratic mean diameters of the two species, we

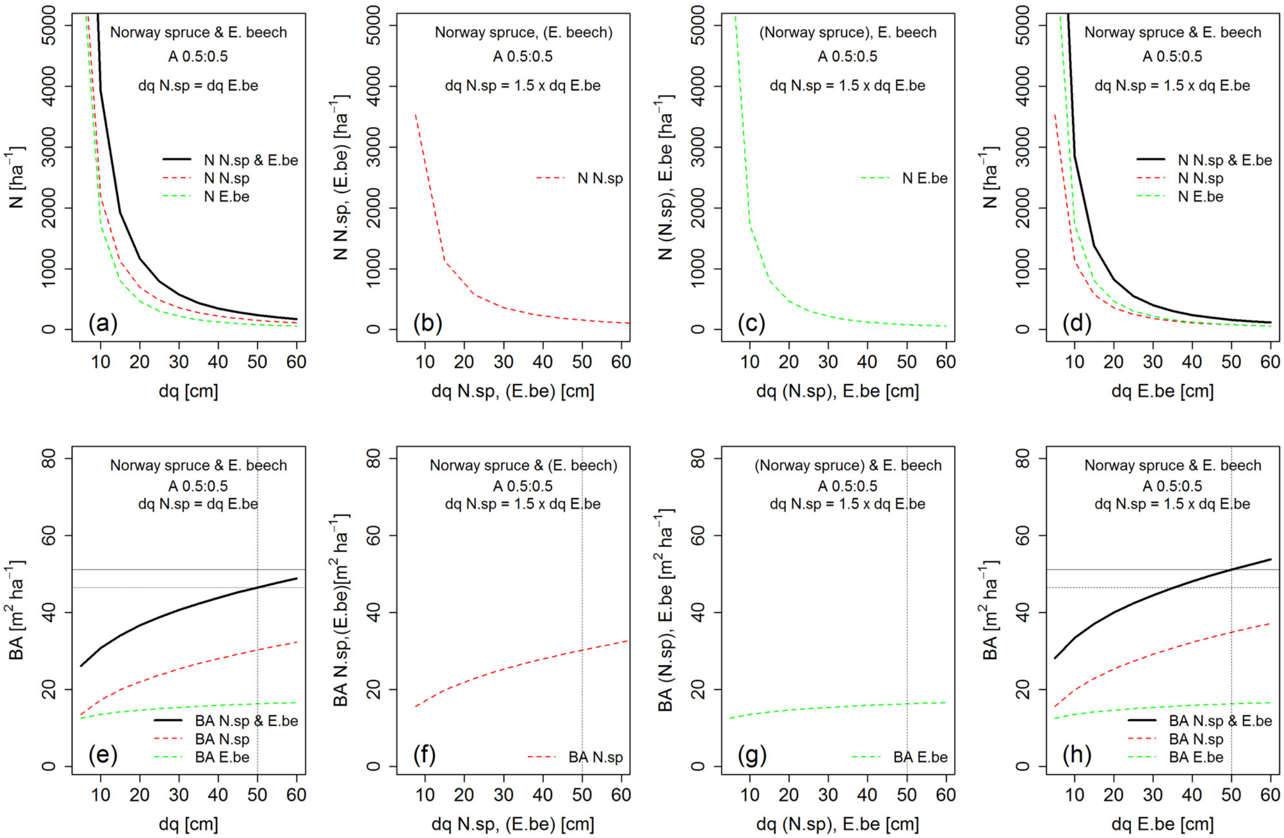

Figure 5 Effects of differences in the mean tree diameter of the admixed species on their (a–d) maximum tree number and (e–h) maximum BA development over mean tree diameter. (a and e) the N-d_q and BA-d_q relationships for Norway spruce/European beech mixed stands assuming equal mean tree diameters. (b–d) and (f–h) show how the N-d_q and BA-d_q relationships, respectively, are modified if Norway spruce is ahead in size growth ($d_{q\mathrm{N.sp}} = 1.5 \times d_{q\mathrm{E.be}}$) in the mixture.

can estimate the density level and the stand density in relation to its maximum level using the size-dependent DEC and DMC. The Th value can be used in forest management as a density index to compare stands, define silvicultural treatments, or quantify silvicultural options in stand simulators when developing silvicultural guidelines.

Discussion

In our theoretical derivation of the use of DEC and DMC in regulating stand density in mixed stands (section 2), we included mean DEC and DMC values for the purpose of simplification; this explains the size-dependence observed later. However, both coefficients may vary based on different factors (not only including species size) for a given species and can be altered by the methods used to fit maximum density curves.

The species-specific self-thinning lines $N = a \times d_q{}^b$ indicate the structural traits of essential species (Zeide, 1985); the intercept a expresses their level of density and growing space requirement and the slope b indicates the change of the density and growing space requirement with progressing size development. We derived a and b using 95 per cent quantile regression; thus, we obtained a and b values for maximum stand density conditions for all analyzed species eliminating the effects of density reductions through disturbances on the plots. Both a and b are crucial for the spatial niche complementarity, competition and density in mixed stands. The intercept indicates the mean difference in stand density and can be used to identify mean DEC values. The slope indicates that a species may start out with a slim crown and low space requirements and then expanding and demand more space (e.g. European beech with steep slope b); others may begin with broad crowns, but display low crowns and demands for space later (e.g. Norway spruce with more shallow slope b). Large differences in slopes suggest a need for size-dependent DECs. Moreover, the greater slopes differ, the higher the potential for structural diversity, complementarity and increase in packing density in a mixture (Barbeito *et al.*, 2017; Bayer *et al.*, 2013; Metz *et al.*, 2013).

The slope b of the self-thinning line is specific to species rather than sites. Its level, expressed by intercept a, indicates the local SDI (Sterba, 1981; Zeide, 2004) and yield level (Assmann, 1970; Franz, 1965). However, different studies report that not only the intercept depends on site conditions but also the slope may vary with site index or site climate (Weiskittel *et al.*, 2009; Condés *et al.*, 2017). Therefore, here, we selected experiments for our analyses that displayed similar medium-to-good site quality under temperate growing conditions. The monospecific

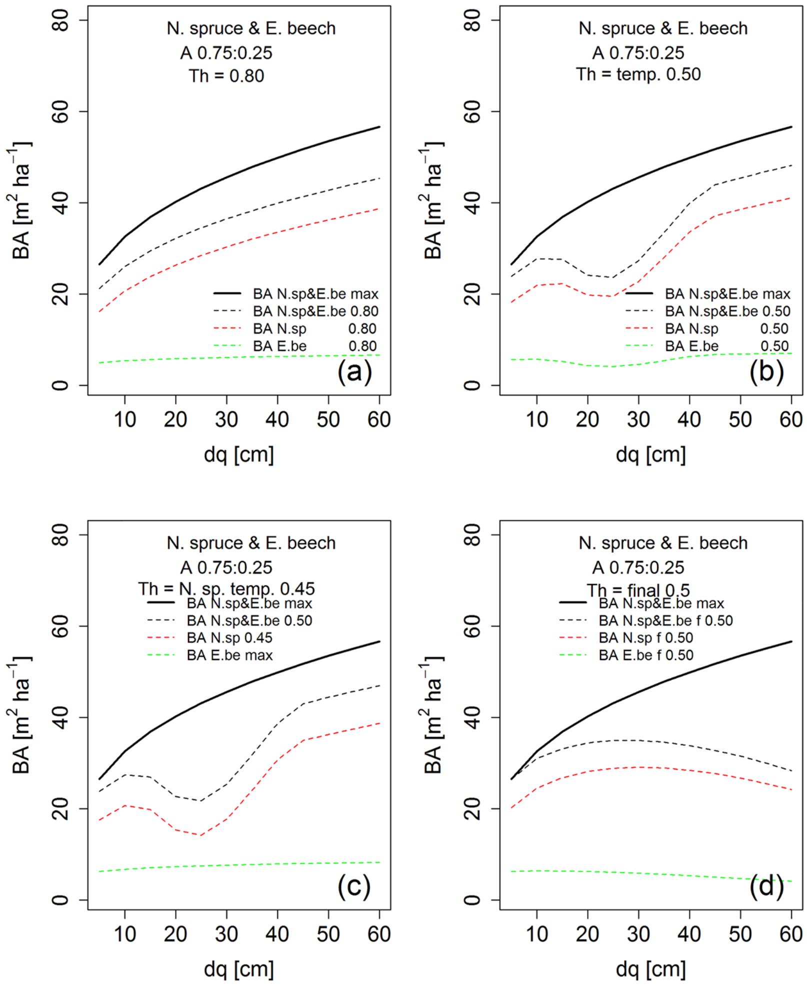

Figure 6 Maximum stand BA line (upper black solid line) for a growing area-related 0.75:025 mixture of Norway spruce und European beech in different simulated thinning scenarios (broken lines below). (a) permanent density level reduction of both species to Th = 0.8. (b) temporary density reduction of both species to Th = 0.5, followed by reconvergence to the maximum level. (c) similar stand density reduction as in scenario (b), but with reducing Norway spruce in favour of European beech. (d) high density followed by an early gradual reduction to Th = 0.5 for stabilization, natural regeneration and preparation of conversion to uneven-aged structure.

and mixed species stands included displayed similar site conditions and were suitable for developing and testing our concept. In the future, the relationship between species and maximum density might be formulated e.g. depending on climate variables, resulting in climate-dependent DECs (Aguirre *et al.*, 2018; Condés *et al.*, 2017); this will aid the sensitivity to site differences and help generalize our approach.

To adjust the density of mixed compared with monospecific stands, we can apply either mean DMC values or a size-dependent (mean diameter) relationship (both are species specific). If we use the DMC for approximately even-aged and mono-layered stands, the mean diameters of both species remain similar and the common mean diameter is suitable for predicting the change of DMC with progressing stand development. Here, the distinction between monospecific stands and mixed stands is discrete; if the admixture is >25 per cent (in BA), we apply DMC. In future, more refined versions, the DMC values may be dependent on the species sizes and mixing proportion in the continuum from monospecific to mixed stand density. At the present time, however, the data for a modelling of DMC based on diameter and mixing proportion are too limited. Some previous studies have developed maximum stand density relationships directly for monospecific and mixed stands by including species proportions in the equation to account for possible over- or under-density in mixed stands (Woodall *et al.*, 2005; Reyes-Hernandez *et al.*, 2013). However, this approach requires a large sample of plots in monospecific and mixed stands under similar site conditions, which are unavailable for most mixtures. Similar to species maximum density relationships and DEC, maximum density in mixed stands and DMC may also vary with environmental conditions. For instance, over-yielding is more frequent in humid conditions (Jactel *et al.*, 2018). Nonetheless, in a study of temperate European mixtures, Pretzsch and Biber (2016) did not observe any site effects on over-density.

At the centre of our approach, it lies the idea that growth and density regulation of monospecific and mixed-species stands should be understood and formulated as a continuum. The differences between plantations with clones, mono-specific stands with low or high genetic diversity, even-aged and uneven-aged mixed species stands are gradual.

Consequently, their growth and density regulation should be formulated in a generic way, so that e.g. the monospecific stand represents a borderline case of mixed-species stands. Coefficients such as DEC, DMC or the relative productivity RP and relative density RD (Pretzsch *et al.*, 2015) of mixed *vs* monospecific stands pave the way for such an approach. Specifically, they utilize our comprehensive knowledge of the structure and growth of monospecific stands and expand it through coefficients that express gradual, but not principle, differences between both.

The DEC and DMC coefficients introduced above are useful for the analysis of mixed-species stands. The DEC relation between two species, and its change with progressing stand development, indicates their temporal-structural complementarity. The more different a and b, and therefore DEC values are, the higher the potential of niche complementarity and over-density compared with monospecific stands. The DMC coefficients may be used for further analyses of the over-density of mixed stands and its dependency on age and site conditions. An important advantage of our approach is that the use of DEC and DMC permits practical simplifications based on the available data. This includes, for instance, the estimation of density coefficients considering (or not) the species size, the climate and/or species proportion effects.

Reducing stand density through Th is a useful concept for density regulation and a first step towards developing silvicultural guidelines. However, information on the stand density-growth relationship and thinning growth responses in mixed stands remains scarce (Pretzsch, 2005; Bauhus *et al.*, 2017, pp. 473–478). Thus, further research on these topics is needed to identify the most suitable Th for each mixture.

However, the main contribution is that our coefficients permit a quantitative density and mixing regulation for mixed-species stands following the maximum stand density concept. This will be useful for the definition of treatment variants on long-term experiments consisting of plots with mixed and pure stands as reference. Density regulation will be particularly powerful after its implementation in stand simulators. Thus, our concept can be applied for density regulation in forest planning and for the development of silvicultural recipes that are urgently needed for translating mixed-species approaches from analysis to practice. In the context of climate change, this will be crucial, given that mixed forest stands may thus increase stand resilience to biotic and abiotic risks and temporal stability of productivity (del Río *et al.*, 2017; Jactel *et al.*, 2017; Jucker *et al.*, 2014; Pretzsch *et al.*, 2013). Reducing stand density is considered an adaptive management strategy to reduce stand vulnerability to extreme drought events (Sohn *et al.*, 2016). This has also been confirmed in some mixed stands (Aldea *et al.*, 2017; Navarro-Cerrillo *et al.*, 2016). Hence, our approach can support the development of management options for risk reduction and stand resilience.

Conclusions and future directions

To provide DEC values for various species combinations, 95 per cent quantile density relationships ($N_n = f(d_{qn})$, DEC $= f(N_1, N_2, d_{q1}, d_{q2})$) and their species-specific intercepts a_n and slopes b_n will be derived from un-thinned long-term experiments or, where necessary, from forest inventory plots. The additional parameterization of the dependency of DMC on the quadratic mean diameter and the mixing proportion of the stand (DMC $= f(d_{q1,2}, m_{1,2})$ will focus on species combinations that include one primary species suitable as a standard species; this may be European beech in the temperate, Norway spruce in the alpine and boreal or Scots pine in the transition to Mediterranean zone. The resulting DEC and DMC relationships will be validated for analyzing, modelling and regulating stand dynamics. An expansion of the concept encompassing the analysis and generic regulation of heterogeneous two species-mixtures and multi-species selection forests, difficult to model and manage until now, is currently underway.

Supplementary data

Supplementary data are available at *Forestry* online.

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Conflict of interest statement

All authors declare that they have no conflict interest.

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Authors’ contributions

H.P. developed the idea, initiated the study, leaded the evaluation and wrote the manuscript. M.d.R. further developed the idea, supported the evaluation and wrote the manuscript.

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