Facilitation and competition reduction in tree species mixtures in Central Europe: Consequences for growth modeling and forest management

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ARTICLE INFO

Keywords: Facilitation, Competition, Competition reduction, Canopy density, Niche complementarity, Individual tree model, Growth modifier

ABSTRACT

That tree species mixing may strongly affect tree structure and tree growth is so far hardly considered in tree and stand models. Hence, for a better understanding and design of mixed species stands, the inter-specific facilitation and competition needs better representation in individual tree models. Here, we show for the five most common tree species combinations in Central Europe that mixing causes facilitation and competition reduction in mixed stands and how such effects can be implemented in individual tree stem diameter growth models.

This study was based on 62 long-term experimental plots belonging to 10 chronosequences in Germany with repeated spatially explicit stand inventories from 1991 to 2016. They covered monospecific and mixed species stands of Norway spruce (Picea abies [L.] KARST.), Scots pine (Pinus sylvestris L.), European beech (Fagus sylvatica L.), sessile oak (Quercus petraea [MATT.] LIEBL.), European ash (Fraxinus excelsior L.), and sycomore maple (Acer pseudoplatanus L.). The study represented medium and high qualitative site conditions, fully stocked, or only moderately thinned stands of 22–238 years of age, and the mixing patterns ranged from individual-tree to cluster-mixtures.

Based on spatially explicit measurements, we quantified for each tree the intra- or interspecific neighborhood, local stand density, and growth. We applied mixed models to analyze how inter-specific neighborhood modified tree growth.

First, we showed that the inter-specific neighborhood can increase tree growth significantly beyond the level of open-grown trees in intra-specific neighborhoods (net facilitation). The potential growth rates of the fastest growing trees in mixed stands were 14–78% higher compared to monospecific stands matched for size, crown, and site index. The mixing effect differed between species combinations. Second, we provided evidence that mixing on average reduced competition by 16%, and that this effect increased with the mixing proportion. In four out of the five species combinations we observed a competition reduction of both associated tree species (mutualistic relationship). Third, for the mixtures of Norway spruce/European beech and sessile oak/European beech that covered a broader range of site conditions, we found a mainly positive modulation of facilitation and competition depending on site conditions.

We discussed the potential causes for the observed facilitation and competition reduction, their implementation in tree growth models, and the relevance of the findings for the design and management of mixed-species stands.

1. Introduction

The widely-used individual tree models for forest stands represent a bottom-up approach, which starts with the individuals of a system, ends at the stand level, and aims to understand and predict how a stand’s properties emerge from the interaction between its trees (Weiskittel et al., 2011; Grimm 1999). The core of most of these models is a potential-modifier algorithm (Burkhart and Tomé 2012; Biging and Dobbertin 1995; Moore 1989; Botkin et al., 1972). The potential-modifier approach is based on the potential tree growth expected without competition, and this potential growth is modified according to the current competition by neighbors. The prediction of growth and mortality of all individuals, the ingrowth of regeneration, and the consideration of management interventions enables a
simulation of the stand dynamics in 1- or 5-year increments or other time intervals. Previous literature provides excellent overviews of such models (Weiskittel et al., 2011), their evaluation (Mette et al., 2009), and their application in science (Grimm, 1999) and forest management (Hilmers et al., 2020; Weiskittel et al., 2016; Pretzsch et al., 2002).

Since their introduction, individual tree growth models have greatly facilitated insights into the patterns and processes in forest ecosystems (Grimm 1999; Shugart 1984; Shugart and West, 1981). However, their impact on forest management was initially low due to the scarce information on initialization and parameterization, the limited computing power available for their application, and their limited added value for the mass-oriented forestry with homogeneous monocultures that was dominating in the past. Then, the following five trends substantially promoted the application of individual tree growth models in forest management and planning over the last decades.

First, individual tree-based forest experiments, forest inventories, and remote sensing techniques strongly improved the database for analyzing and modeling individual tree growth (Nagel et al., 2012). Second, computing capacity rapidly increased, allowing for individual tree-based scenario analyses at the regional, national, or even global level, using microcomputers. Third, many forests have been transformed from homogeneous to more heterogeneous stands (del Rio et al., 2016; Reventlow et al., 2021; Pommerening and Murphy, 2004). Whereas monocultures may be abstracted by mean characteristics or frequency distribution models, multi-layered mixed-species stands are better modeled using individual tree approaches (Coates et al., 2013). Fourth, the paradigm shift from mass-oriented forestry to multipurpose approaches has been accompanied by spatially explicit individual tree models. The latter enable the prediction of structural heterogeneity, wood quality, micro-habitats, and even recreational and esthetic values (Pretzsch et al., 2006). Fifth, the individual tree approach aligns well with many innovative prescriptions to silviculturally steer complex forest stands (Bravo et al., 2019).

These five trends have resulted in a boom in the development and use of individual tree models in forest management. Examples of this development include the models HEUREKA (Wikström et al., 2011), BWINpro by Nagel et al., (2006), PROGNAUS (Ledermann 2004; Sterba and Monserud, 1997), and SILVA (Pretzsch et al., 2002; 2008). In view of the establishment and silvicultural steering of even more heterogeneous mixed forest stands, most existing individual tree models appear as an oversimplification, as they often neglect species interactions (Pretzsch et al., 2015). This study aims to contribute to the adaptation of existing individual tree models to the needs of forest science and practice. We address an improved integration of tree species mixing effects, in particular the effects of inter-specific facilitation and competition reduction.

Fig. 1 visualizes the basic relationship of the potential-modifier approach commonly used in individual tree growth models. The potential-modifier approach is competition-based and assumes that the rate of tree size growth peaks when trees grow open, solitarily, and with no or only little competition. The growth rate of open-grown trees is assumed to be the potential growth and set to 1.0 in Fig. 1. The absolute level of the potential growth is certainly depending, among others, on the tree species, the respective site conditions, and the crown size.

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Overview of main measurements variables and metrics used in this study.

<table>
<thead>
<tr>
<th>Variables’ and metrics’ names</th>
<th>Abbreviation</th>
<th>Explanation and Indication</th>
</tr>
</thead>
<tbody>
<tr>
<td>(i) Tree level variables</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stem diameter</td>
<td>d</td>
<td>Indication of tree present size</td>
</tr>
<tr>
<td>Tree height</td>
<td>h</td>
<td>Determination of radius for competition analysis</td>
</tr>
<tr>
<td>Height to crown base, to lowest branch</td>
<td>hcb</td>
<td>Indication of bole length, used for visualization</td>
</tr>
<tr>
<td>Crown radius</td>
<td>r</td>
<td>( r = \sqrt{r_1^2 + r_2^2 + \ldots + r_n^2} / n ), for visualization</td>
</tr>
<tr>
<td>Crown length</td>
<td>cl</td>
<td>( cl = h - hcb ), used for visualization</td>
</tr>
<tr>
<td>Search radius for Neighbor analysis</td>
<td>sr</td>
<td>( sr = 0.25 \times h ), for analyzing</td>
</tr>
<tr>
<td>Annual stem diameter increment</td>
<td>id</td>
<td>Periodical diameter increment/period length</td>
</tr>
<tr>
<td>Local competition index</td>
<td>SDL</td>
<td>Local SDL in circle calculated without center tree</td>
</tr>
<tr>
<td>Binary variable indicating monospecific vs. mixed on circle</td>
<td>mfactor</td>
<td>( m = 0 ), i.e. mixing proportion &lt; 10%</td>
</tr>
<tr>
<td>Mixing proportion in the reference circle around a tree</td>
<td>mportion</td>
<td>( m = 0 ), i.e. monospecific stand, 0.1, 0.2, mixing proportions based on standardized SDL</td>
</tr>
<tr>
<td>(ii) Stand level Variables</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stand age</td>
<td>age</td>
<td>Read off from historical stand documentation or increment cores</td>
</tr>
<tr>
<td>Quadratic mean stem diameter</td>
<td>dq</td>
<td>Calculated species-overarching</td>
</tr>
<tr>
<td>Mean height</td>
<td>hq</td>
<td>Height of the tree with the quadratic mean stem diameter</td>
</tr>
<tr>
<td>Standing stem volume</td>
<td>V</td>
<td>Merchandable volume &gt; 7 cm at the smaller end</td>
</tr>
<tr>
<td>Stand stem volume growth</td>
<td>IV</td>
<td>Periodical mean annual stem volume growth</td>
</tr>
<tr>
<td>Site index</td>
<td>SI</td>
<td>Site index based on hq at age 100 and the yield tables cited at the beginning of section “2.3 Descriptive data evaluation”</td>
</tr>
</tbody>
</table>

However, most models assume that any competition, quantified, e.g., by competition indices or local stand density (Grams et al., 2021; Pretzsch et al., 2015; Burkhart and Tomé, 2012; Biging and Dobbertin, 1995) reduces the tree growth. In models the potential growth rate is modified by multiplier mod, which decreases exponentially with increasing competition or local stand density. In Fig. 1 the decreasing curve represents the modifier function. The tree growth results from \( id = \frac{dq \times \text{pot}}{\text{pot} + \text{mod}} \). The fact that neighbors (especially of other species) can facilitate growth, e.g., by atmospheric nitrogen-fixation, hydraulic lift, or nutrient upward transport from deeper soil layers, is known from scattered experiments, but rarely considered in individual tree simulation models so far.

Most available individual tree models have been parametrized using data from solitary trees in order to derive the potential growth rate (Hasenauer, 1997). They used mainly trees in monospecific stands to parametrize the modifier function (Hasenauer et al., 2006; Pretzsch et al., 2002). The application of such models to mixed stands will produce useful results only if trees behave similarly in inter- as in intra-specific neighborhoods. However, recent studies stress that mixed-species stands can be by 2–59% more productive than monospecific stands (Rui-Peirano et al., 2021, Steckel et al., 2019, Jactel et al., 2018) and that their maximum stand density can be by 5–25% higher (Thurm and Pretzsch, 2021; Pretzsch and del Rio, 2020; Pretzsch and Biber, 2016; Binkley, 1984). Hence, it is possible to increase forest diversity by tree species mixing with a potential increase in tree growth compared to monospecific stands (Chamagne et al., 2017). Obviously, when growing together, some tree species can facilitate each other. The effect can be similar to a fertilization. One or both species may grow more due to inter-specific facilitation (Forrester, 2014; Pretzsch et al., 2013; Kelty, 1992). Additionally, there may be a competition reduction when different species are mixed, leading to higher packing density. This may be caused by morphological complementarity and spatial niche separation (Pretzsch, 2014; von Felten and Schmid, 2008) or by temporal asynchrony (del Rio et al., 2017; Jucker et al., 2015). Both may result in a reduction of the inter-specific competition (Metz et al., 2020; Forrester, 2017; Pretzsch, 2017; Pretzsch, 2022). Such effects of tree species mixing should be considered.
to better model, understand, and design mixed species stands. Because of their advantageous functioning and provisioning of ecosystem services (Dieler et al., 2017), especially under changing environmental conditions (del Río et al., 2017; Jucker et al., 2014), mixed stands are presently on the rise; and suitable models, guidelines, and training plots are essential for their promotion (Coll et al., 2018).

A more detailed understanding of how an interspecific-neighborhood can facilitate tree growth and raise the potential growth rate (similarly to fertilization, but without the respective costs) may improve the nature-based design of resource-efficient forest ecosystems. Quantifying how mixing may modify tree growth efficiency is a pertinent issue in view of the increasing spread and relevance of mixed stands. Monitoring, inventories, and sampling should consider the spatial neighborhood to appropriately interpret the recorded tree growth. Models should be adapted to mixed species stands. Silvicultural prescriptions based on monospecific stands may be misleading when applied to mixed-species stands. For instance, they may neglect that mixed stands enable increased growth rates even when growing at higher stand densities. Consequently, they may prescribe overly strong stand density reductions and thereby undercut maximum stand productivity.

Here, we used a unique dataset of mono- and mixed-species growth conditions to quantify the effects of mixing on both the modification of the potential growth rate and the reduction of competition in inter-versus intra-specific neighborhoods. To address these questions we posed the following hypotheses:

H I: Inter-specific neighborhood can increase tree growth significantly above the level of open-grown trees in intra-specific neighborhoods. The potential growth rate in mixed stands can be higher compared to monospecific stands that are matched for size, crown, and site index.

H II: Tree species mixing can reduce competition. This competition reduction increases with the mixing proportion.

H III: Facilitation and competition reduction are modulated by site conditions. Facilitation and competition increase with the quality of the respective sites.

2. Material and methods

2.1. The study plots

The study based on 10 chronosequences (see example in Fig. 2) with altogether 62 long-term plots in Southern Germany with repeated stand inventories. The plots were established in the 1990ies in 18–238 years old stands. They cover the main tree species in Central Europe in intra- and interspecific neighborhood throughout the whole rotation. The plots represent the most common medium and high quality site conditions (Table 1), fully to moderately thinned stands, and mixture patterns reaching from individual-tree to cluster-mixtures. Since their establishment and first survey the chronosequences were remeasured up to 5 times. In this way the original chronosequences have become real time series of long-term survey and cover for all considered mixtures an age span of a whole rotation. The surveys cover the tree and stand growth in the time period 1991–2016.

The three-dimensional visualization of the age series FRE 813 in Fig. 2 was based on the inventory of the tree co-ordinates and species identity first recorded in 1991 and the measurements of the stem diameters, tree heights, crown sizes surveyed in autumn 1994. The plots size increases from the young to the old stands (see 20 m scale at the bottom of each plot) in order to cover representative sections of the representative stand development phases. For the sake of simplicity, we visualized the crown diameters calculated as the quadratic mean of the eight crown radius measurements.

Table 2 gives an overview of the main measurement variables and
Table 3. Overview of the age 10 series with 62 plots included in this study. The number of measurements refers to the number of measured tree attributes such as stem diameters, stem coordinates, or crown characteristics at the first survey.

<table>
<thead>
<tr>
<th>Age</th>
<th>Site index</th>
<th>Site name</th>
<th>Species</th>
<th>Age from</th>
<th>Number of trees measured h</th>
<th>Number of trees measured x, y</th>
<th>Total number of crowns</th>
<th>Number of trees measured at each survey</th>
<th>Number of trees measured hcb</th>
<th>Number of trees measured h</th>
<th>Number of trees measured x, y</th>
</tr>
</thead>
<tbody>
<tr>
<td>35.1</td>
<td>Freising</td>
<td>N. sp., E. be.</td>
<td>35.1</td>
<td>37-168</td>
<td>0.48</td>
<td>1994</td>
<td>2012</td>
<td>4</td>
<td>7939</td>
<td>2498</td>
<td>2725</td>
</tr>
<tr>
<td>37.4</td>
<td>Schnepfau</td>
<td>N. sp., E. be.</td>
<td>37.4</td>
<td>39-142</td>
<td>0.48</td>
<td>1991</td>
<td>2011</td>
<td>5</td>
<td>7527</td>
<td>4204</td>
<td>3358</td>
</tr>
<tr>
<td>36.1</td>
<td>Northeim</td>
<td>N. sp., E. be.</td>
<td>36.1</td>
<td>36-126</td>
<td>0.44</td>
<td>1997</td>
<td>2008</td>
<td>2</td>
<td>3474</td>
<td>1494</td>
<td>1796</td>
</tr>
<tr>
<td>37.7</td>
<td>Kolleheim</td>
<td>s. oak, E. be.</td>
<td>37.7</td>
<td>17-165</td>
<td>0.65</td>
<td>1996</td>
<td>2005</td>
<td>4</td>
<td>14587</td>
<td>7843</td>
<td>2743</td>
</tr>
<tr>
<td>26.6</td>
<td>Rottenbuch</td>
<td>s. oak, E. be.</td>
<td>26.6</td>
<td>32-238</td>
<td>0.56</td>
<td>1994</td>
<td>2009</td>
<td>3</td>
<td>11252</td>
<td>9429</td>
<td>4129</td>
</tr>
<tr>
<td>31.5</td>
<td>Schwaig</td>
<td>s. pl., E. be.</td>
<td>31.5</td>
<td>21-186</td>
<td>0.46</td>
<td>1996</td>
<td>2005</td>
<td>2</td>
<td>8174</td>
<td>6874</td>
<td>1426</td>
</tr>
<tr>
<td>32.0</td>
<td>Giesing</td>
<td>s. pl., E. be.</td>
<td>32.0</td>
<td>18-214</td>
<td>0.35</td>
<td>1996</td>
<td>2010</td>
<td>3</td>
<td>7923</td>
<td>1877</td>
<td>1319</td>
</tr>
<tr>
<td>31.5</td>
<td>Amberg</td>
<td>s. pl., E. be.</td>
<td>31.5</td>
<td>26-136</td>
<td>0.14</td>
<td>1991</td>
<td>2016</td>
<td>5</td>
<td>5142</td>
<td>1869</td>
<td>1942</td>
</tr>
<tr>
<td>32.0</td>
<td>Noesring</td>
<td>s. pl., N. sp.</td>
<td>32.0</td>
<td>26-136</td>
<td>0.41</td>
<td>1997</td>
<td>2014</td>
<td>3</td>
<td>11343</td>
<td>4902</td>
<td>5135</td>
</tr>
<tr>
<td>30.0</td>
<td>Arendon</td>
<td>E. map., E. ash</td>
<td>30.0</td>
<td>20-94</td>
<td>0.26</td>
<td>1998</td>
<td>2004</td>
<td>3</td>
<td>5559</td>
<td>2664</td>
<td>1486</td>
</tr>
</tbody>
</table>

For characterization of the site productivity we used the site index. For the site-indexing we applied the yield tables (moderate thinning) for Norway spruce by Wiedemann (1936/42), for Scots pine by Wiedemann (1943), for European beech by Schober (1967, 1975), sessile oak by Jüttner (1955), European ash by Volquards (1958) and sycamore maple by Nagel (1986).

2.3. Descriptive data evaluation

2.3.1. Stand level evaluation

To give an overview of the included chronosequences, we first evaluated them at the stand level using standard procedures (Biber, 2013, Pretzsch 2009, Johann, 1993). The reported stand-level data was derived from the diameter and height records, as well as from the removal of trees. The results encompassed the quadratic mean tree diameter, stand volume, and volume growth (see stand variables in Table 2 and Overview of the tree and stand characteristics of the Results section).

For characterization of the site productivity we used the $hq$ values and stand ages on the plots to derived the $hq$ at stand age 100 as site index. For the site-indexing we applied the yield tables (moderate thinning) for Norway spruce by Wiedemann (1936/42), for Scots pine by Wiedemann (1943), for European beech by Schober (1967, 1975), sessile oak by Jüttner (1955), European ash by Volquards (1958) and sycamore maple by Nagel (1986).

2.3.2. Tree level evaluation

Tree height estimation: As boundary and search radius $sr$ for the neighborhood analyses (Fig. 3b) we used the quarter of the individual tree height of every tree. However, in the course of the repeated surveys the tree diameters were measured completely, the tree heights only randomly. For estimation of the individual tree height, $h$, depending on the stem diameter and tree age we parameterized the model

$$ln(h) = a_0 + a_1 \times ln(d) + a_2 \times ln(age) + a_3 \times ln(d) \times ln(age)$$

for each species on each of the 10 age series separately. For model parameters see Supplement Table 1.

The tree heights were also used for stem volume estimation in dependence on tree diameter, tree height, and form factor. For considering the stem form we used the approach by Franz et al., (1973) with the stem form equations and coefficients published by Pretzsch (2002, p. 170).

Neighborhood analyses within sample circles: To analyze the individual trees’ competition indices, we used the concept of the stand density index (SDI) (Reineke 1933). For this purpose we defined around each tree an influence zone by a circle with search radius $sr = 0.25 \times h$ (see Fig. 3b). This study and a preliminary study by Pretzsch and Schütze (2021) showed that this circle size resulted in the highest correlations between the characteristics of stand structure and growth. All trees within the circle except the center tree were used to calculate the local density $n$ on circle area $a$. $N = 10.000 / a \times n$ was the respective tree number upscaled to one hectare. For the $n$ trees, we calculated the quadratic mean stem diameter $d_n$; based on $N$ and $d_n$ we then calculated the local density $SD = N / (25 \times d_n)^a$ around each individual tree. In the constructed circles, there were, on average, 8–9 trees and at least 5–6 most impactful neighbors (Prodan, 1968a, b). The local SDI was calculated using species-specific allometric exponents derived by Pretzsch and Biber (2005). They were applied for the component metrics used in this study. From each tree on the 62 plots we recorded the species identity, measured the $x$-, and $y$-stem coordinates at the first survey and all stem diameters at each of the up to 5 surveys (Fig. 3a, Table 3). Tree height, $h$ and height to the crown base, $hcb$, were sampled (>30 trees per species, sampled over the whole range of stem diameters) at each survey.

The stand age was read off from the historical documentation of the stand establishment. If such documents were not available we derived the tree age by tree-ring counting on increment cores sampled at the foot of the trunks of three trees of each species per plot. Stand ages were assumed to be identical with mean tree age in case of natural regenerated stands. In planted stands, stand age were assumed to be mean tree age minus three years to take into account the usual age of plants coming from the nursery.
species in intra- and interspecific neighborhood, as general allometric exponents for mixed stands were not yet available. Note that the latter exponents \( \alpha \) were derived on A-grade and unthinned plots of long-term experiments in South Germany that are located in the same area as the age series of this study. They deviate from the species-overarching exponent of \(-1.605\), as proposed by Reineke (1933), are species-specific and representative for South Germany. The resulting local density index SDI was distant-dependent and easy to interpret. To standardize the density we applied the equivalence factors by Pretzsch and Biber (2016). These factors for the main tree species assemblages are shown in Supplementary Table 2.

**Edge correction:** Before calculating the local SDI values and mixing proportions for neighborhood analysis, we established a toroidal shift of the plot to all eight directions of the plot periphery for edge bias compensation (Radtke and Burkhart 1998; Pomerening and Stoyan 2006; Pretzsch, 2009). We use the plot SON 814/2 at the survey in autumn 2011 for visualization of this method in Supplementary Figure 4. Using the toroidal shift, we extended the same mixing patterns and distances between trees in all eight directions and avoided any over-estimation of density, as it could result from other techniques (Radtke and Burkhart, 1998).

**Mixing proportions:** The trees sampled in the circle were also used to calculate local mixing proportions. The mixing proportions \( m_{\text{portion}} \) should reflect the area proportions of two or more species in the observed mixed stands (Pretzsch and del Río, 2020; Dirnberger et al., 2017). Tree number, basal area, or volume proportions are only appropriate for this purpose if the mixed species have similar growing area requirements (Pretzsch et al., 2017). Tree species can vary per se in the observed mixed stands (Pretzsch and del Río, 2020; Dirnberger et al., 2017). Tree number, basal area, or volume proportions are only appropriate for this purpose if the mixed species have similar growing area requirements (Pretzsch et al., 2017). Tree species can vary per se in the observed mixed stands (Pretzsch and del Río, 2020; Dirnberger et al., 2017).

The following mixed linear model revealed the mean effect of inter- versus intra-specific neighborhood after elimination of all relevant co-determining effects (see last paragraph of this section for a comprehensive explanation of the notation and assumptions used for testing HI, II, and III):

\[
\ln(id) = a_0 + a_1 \times \text{mfactor}_i + a_2 \times \ln(d_i) + a_3 \times \ln(c_i) + a_4 \times \ln(SDI_i) + a_5 \times \ln(SI_i) + b_i + \epsilon_i
\]  

Eq. (2) represented the full model if all variables would be included. Depending on the respective species-specific relationships it was simplified. We eliminated those variables that were not significant (i.e., \( p > 0.05 \)) and did not lower the AIC value.

The model Eq. (2) with \( \text{mfactor} \) being the binary 0/1 variable addressed the effect of monospecific (\( \text{mfactor} = 0 \)) or mixed stand condition (\( \text{mfactor} = 1 \)). The back transformed version, e.g., \( y = e^{a_0 + a_1 \times \text{mfactor}} \) showed that the dummy variable \( \text{mfactor} \) results in \( e^0 = 1 \) in case of monoculture and \( e^1 \) in case of mixed stands. This means that \( e^0 \) directly reveals any multiplicative effects of mixing on the dependent variables. Suppose \( a_1 = 0.25 \), the mixing effect on the target variable would be \( e^{0.25} = 1.284 \) and the effect size would be 28.4%. This helps to easily interpret the biological meaning of the respective coefficients of \( \text{mfactor} \) in model 2.

### 2.4. Statistical models for hypotheses testing

#### 2.4.1 Inter-specific neighborhood can facilitate tree growth (H I)

For scrutiny whether maximum stem diameter growth rates, at parity of competition, can be increased in inter-specific compared with intra-specific neighborhood we used the individual trees’ annual stem diameter growth, the local competition SDI, and the mixing proportions within the respective circles (Fig. 3b). The data was grouped in trees from monospecific and mixed circles. We then sorted the trees into classes of increasing local SDI values from SDI = 0–100, 100–200, …, 1800–2000 trees per hectare. For each SDI-class we used the 10% fastest growing trees and calculated the mean and standard error of their stem diameter growth. In this way we could find out whether the best growing trees in the mixed group grow better than in the monospecific group. The species-specific id-SDI relationships were visualized for each mixture in total but also for each ages series separately. Any exceedance of the tree growth in mixed neighborhood above the respective growth in monospecific neighborhood provided evidence for facilitation.

The detailed statistical analysis of facilitation by inter-specific neighborhood was also based on the 10% fastest growing trees on each plot and in each group (mono and mixed). By using only the respective 10% fastest growing trees, we addressed the potential growth. In this way we eliminated growth reductions by genetically determined low growth, crown size and shape effects (e.g., crown transparency and leaf losses), detrimental silvicultural treatment in the longer past (e.g., narrow spacing, abrupt and strong competition release), or abiotic (e.g., drought, frost) and biotic (e.g., bark beetle, fungal infestation) damages. This approach is suitable for addressing whether ceteris paribus the potential tree growth rates in inter-specific neighborhood can exceed those in intra-specific conditions indicating facilitation (H I).

The following mixed linear model revealed the mean effect of inter-versus intra-specific neighborhood after elimination of all relevant co-determining effects (see last paragraph of this section for a comprehensive explanation of the notation and assumptions used for testing HI, II, and III):

\[
\ln(id) = a_0 + a_1 \times \text{mfactor}_i + a_2 \times \ln(d_i) + a_3 \times \ln(c_i) + a_4 \times \ln(SDI_i) + a_5 \times \ln(SI_i) + b_i + \epsilon_i
\]  

This model was fitted for each species using the whole dataset, i.e., using all data including the 10% fastest growing trees.

#### 2.4.2 Tree species mixing reduces the competition and the competition reduction increases with the mixing proportion (H II)

For testing this hypothesis model 3 was formulated as follows:

\[
\ln(id) = a_0 + a_1 \times \ln(d_i) + a_2 \times \ln(\text{age}_i) + a_3 \times \ln(SDI_i) + a_4 \times \ln(\text{portion}_i) + +a_5 \times \ln(SI_i) \times \ln(\text{portion}_i) + b_i + \epsilon_i
\]  

This model was fitted for each species using the whole dataset, i.e., using all data including the 10% fastest growing trees.
conditions (H III): The plots of the mixture of Norway spruce and European beech and of sessile oak and European beech covered a sufficiently wide range of site conditions for analyzing any interaction between mixing and site index on growth. We first analyzed the interaction between mixing and site index on the growth of the 10% fastest growing trees by model 4.

\[
\ln(id) = a_0 + a_1 \times mfactor_i + a_2 \times \ln(SI_{ik}) + a_3 \times mfactor_i \times \ln(SI_{ik}) + b_i + \epsilon_{ik}
\]  

(4)

Using the same model, we further analyzed the interaction between mixing and site index based on the full dataset for the mixtures of Norway spruce and European beech and of sessile oak and European beech.

“For testing H I–H III we applied linear mixed models”. The dependent variable was the mean annual stem diameter growth, id. The independent variables were individual tree diameter, d, tree age, local SDI, the binary variable mfactor (0/1 for mono/mixed), mixing proportion, mportion, and site index, SI. In all equations, the indexes i and k represented the kth observation of the ith tree. The fixed effects were covered by the parameters \(a_0-a_n\). With the random effect \(b_i \sim N(0, \tau^2)\)

![Fig. 4. Annual stem diameter growth (mean±se) of the 10% fastest growing trees plotted over local SDI in mixed (green) compared with monospecific stands (red). The broken horizontal line reflects the mean growth rate of the 10% fastest growing trees in monospecific neighborhood under sparsely stocked conditions (SDI = 250–500 ha\(^{-1}\)) as reference. For the graphs we pooled all trees of the respective species combinations. (a and b) Norway spruce and European beech (FRE 813, SON 814, NOR 811), (c and d) sessile oak and European beech (KEH 804, ROT 801, SWE 803), (e and f) Scots pine and European beech (GEI 832, AMB 833), (g and h) Scots pine and Norway spruce (NEU 841), (i and j) European ash and syc. maple (ARN 851). For separate evaluation of each of the 10 age series of this study see Supplement Figs. 1–3.
we cover the correlation between the single observations on tree level. In preliminary model formulations we also worked with random effects on plot level, i.e., one additional nesting level. As this caused confounding effects with the fixed effect, we constrained ourselves to the simpler random effect structure of Eqs. (2)–(4). With \( e_u \) we denote the independently and identically distributed errors (\( e_u \sim N(0, \sigma^2) \)).

For all calculations we used the statistical software R 3.6.3 (R Core Team, 2019); for fitting the mixed linear models explained above, we in particular used the libraries nlme (Pinheiro et al., 2018) and lme4 (Bates et al., 2015).

### 3. Results

#### 3.1. Overview of the tree and stand characteristics

The mixtures were represented by young to old stands with an age range of 15–238 years (Supplementary Table 3). The mean diameter ranged from 7.8 to 51.5 cm. The standing volume was the highest (1774 m\(^3\) ha\(^{-1}\)) in mature stands of Norway spruce and European beech. The annual stem volume growth was the highest (36.2 m\(^3\) ha\(^{-1}\) yr\(^{-1}\)) in the stands with Norway spruce and European beech and Scots pine and European beech. For further information see Supplementary Table 3.

The models could be based on \( n = 1112-6233 \) observations per

### Table 4

Statistical characteristics of models 2.1–2.8 for testing H 1. The equation numbers refer to the models introduced in section 2.5 Statistical models for hypotheses testing. For reasons of space the table reports only the fixed effect variables of the respective models. The factor \( e^{e_u} \) (in bold letters) reflects the ratio between the potential growth in inter- versus intra-specific environment. For further variable explanation see Table 2. Model 2.1 \( \ln(id) = a_0 + a_1 \times \text{mfactor} + a_2 \times \ln(id) + a_3 \times \ln(cr) + a_4 \times \ln(SI) \), Model 2.2 \( \ln(id) = a_0 + a_1 \times \text{mfactor} + a_3 \times \ln(cr) + a_4 \times \ln(SDIF) + a_5 \times \ln(SI) \), Model 2.3 \( \ln(id) = a_0 + a_1 \times \text{mfactor} + a_2 \times \ln(id) + a_3 \times \ln(cr) + a_5 \times \ln(SI) \), Model 2.4 \( \ln(id) = a_0 + a_1 \times \text{mfactor} + a_2 \times \ln(id) + a_5 \times \ln(SI) \), Model 2.5 \( \ln(id) = a_0 + a_1 \times \text{mfactor} + a_3 \times \ln(id) + a_4 \times \ln(cr) + a_5 \times \ln(SI) \), Model 2.6 \( \ln(id) = a_0 + a_1 \times \text{mfactor} + a_2 \times \ln(id) + a_3 \times \ln(cr) + a_5 \times \ln(SI) \), Model 2.7 \( \ln(id) = a_0 + a_1 \times \text{mfactor} + a_2 \times \ln(id) + a_4 \times \ln(cr) + a_5 \times \ln(SI) \), Model 2.8 \( \ln(id) = a_0 + a_1 \times \text{mfactor} + a_2 \times \ln(id) + a_3 \times \ln(cr) + a_5 \times \ln(SI) \).

<table>
<thead>
<tr>
<th>Group</th>
<th>Model</th>
<th>n</th>
<th>( \sigma_0 )</th>
<th>( \sigma_0 ) p-value</th>
<th>( a_1 )</th>
<th>Factor ( e^{e_u} )</th>
<th>( a_2 )</th>
<th>( \sigma_0 )</th>
<th>( \sigma_0 ) p-value</th>
<th>( a_3 )</th>
<th>( \sigma_0 )</th>
<th>( \sigma_0 ) p-value</th>
<th>( a_4 )</th>
<th>( \sigma_0 )</th>
<th>( \sigma_0 ) p-value</th>
<th>( a_5 )</th>
<th>( \sigma_0 )</th>
<th>( \sigma_0 ) p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>N. sp., (E. be.)</td>
<td>2.1</td>
<td>134</td>
<td>-3.55</td>
<td>1.26</td>
<td>0.006</td>
<td>0.13</td>
<td>1.14</td>
<td>0.05</td>
<td>0.004</td>
<td>-0.47</td>
<td>0.06</td>
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<td>0.11</td>
<td>0.011</td>
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<td>&lt;0.001</td>
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<td>0.11</td>
<td>&lt;0.001</td>
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<td>1.39</td>
<td>0.08</td>
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<td>-0.21</td>
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<td>1.78</td>
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<td>&lt;0.001</td>
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</table>

![Fig. 5](image_url) Potential stem diameter growth in mixed- compared with monospecific neighborhood plotted over crown ratio. The inscribed factors reflect the relative growth superiority of mixed- versus monospecific conditions (see regression results in Table 4). (a and b) Norway spruce in mixture with European and Scots pine, respectively. (c and d) European beech in mixture with Norway spruce and Scots pine, respectively.
species and species combination (Supplementary Table 4). The annual stem diameter growth rates ranged from 0.01 to 1.48 cm yr\(^{-1}\), and the diameters from 9.28 to 103.40 cm. The crown diameters ranged from 0.18 to 15.58 m and the crown ratios from 0.05 to 0.94 m/m. The data covered low local competition of SDI = 2.64 but also very dense stand parts with SDI = 4487.49 trees per hectare. Compared to the usually reported stand related SDI values of 500–2000 trees per hectare (Pretzsch, 2019; Sterba, 1981) the local SDI’s can become low as well as very high as they refer to the local density within the search radius sr. The site index related to the quadratic mean height at age 100 and based on the yield tables quoted in the section Descriptive data evaluation. The SI ranged between 20 - 43 m at age 100. The mixing proportions cover the whole range between monospecific conditions of one to the other species. Especially the wide range of diameters, local densities, mixing proportions, and site indices made the data suitable for testing of H-I-H III. For further information see Supplementary Table 4.

3.2. Facilitation and increase of potential growth rate in inter- versus intra-specific environment (H I)

Fig. 4 shows that the annual stem diameter growth of the 10% fastest growing trees in inter-specific neighborhood (green) can significantly exceed the growth rates under monospecific conditions at parity of stand density. The horizontal broken lines indicate the growth rate of the 10% fastest growing trees in monospecific neighborhood for trees with competition of SDI = 250–500 trees. In mixed stands (green curves) the growth rates exceed this level by up to 40%. The finding that the potential growth is superior in mixed environment provides evidence of inter-specific net facilitation. In seven out of 10 cases this net facilitation occurs mainly under low competition. For detailed information about the stem diameters of the 10% fastest growing trees see Supplementary Table 5.

For Fig. 4 we pooled all trees of all chronosequences of the same species assemblage. For separate visualization of each of the ten chronosequences of this study see Supplement Figs. 1–3. In summary out of 10 species assemblages provided evidence of net facilitation and increased potential growth rates in mixed compared with monospecific environment.

For further statistical analysis of any facilitation effects by inter-specific neighborhood on the potential growth rate of trees we used again the fastest 10% of trees without and with interspecific neighborhood. Table 4 reflects that in all 10 cases the growth in the inter-specific group was significantly higher than in the intra-specific group at least at the level \(p < 0.05\). The superiority ranged between a plus of 14% in case of Norway spruce in European beech or sessile oak in European beech. The superiority amounted to plus 74 and 78% in case of Norway spruce when growing in Scots pine or sycamore maple growing mixed with European ash. In most cases the crown ratio had and additional positive influence. In some cases also the other considered variables such as d, SDI, and SI had an additional effect. This covariance analyses of the potential stem diameter growth in inter- versus intra-specific neighbor- hood (factor m) based on model 2. The model included the covari- ables stem diameter, crown ratio, local SDI, and site index in case that they were significant at least at the level \(p < 0.05\) and that they increased the AIC criteria of the regression compared with the basic model (id = f (factor)). This variable selection resulted in the model variants 2.1–2.8 presented in Table 4.

Fig. 5 visualizes the results for four selected tree species combinations where the potential growth was 14–78% higher in mixed-compared with monospecific neighborhood (factor = 1.14–1.78). In three out of the shown four cases the crown ratio had an additional positive effect on the growth rate. Fig. 5 corroborates that any benefit of mixing depends on both the species identity of the basis species and the neighbors. Figs. 5, a and b show that the potential growth rate of Norway spruce benefitted moderately when mixed with European beech (14%) but much stronger when mixed with Scots pine (74%). Fig. 5, c and d show a plus of 38% for European beech when mixed with Norway spruce and a plus of 69% when mixed with Scots pine. Note that the mentioned severities refer to growth rates of the 10% best growing trees in both groups (mixed versus mono) after elimination of any additional effects of d, cr, SDI, SI. Thus the 14–78% plus reflects mainly the effect of facilitation of the different neighboring tree species in low density environment and at parity of other modulating factors such as d, SI. This means that competition and density effects were as far as possible eliminated by only selecting the fastest growing trees per plot and group and by elimination of any other size or density related group differences.

Table 5

<table>
<thead>
<tr>
<th>Group</th>
<th>( a_4 )</th>
<th>std (( a_4 ))</th>
<th>p-value</th>
<th>( a_5 )</th>
<th>std (( a_5 ))</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>N. sp., (E. be.)</td>
<td>1.38</td>
<td>0.36</td>
<td>&lt;0.001</td>
<td>0.39</td>
<td>0.05</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>(N. sp.), E. be.</td>
<td>1.12</td>
<td>0.33</td>
<td>&lt;0.001</td>
<td>1.22</td>
<td>0.04</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>S. oak, (E. be.)</td>
<td>0.91</td>
<td>0.19</td>
<td>&lt;0.001</td>
<td>0.91</td>
<td>0.19</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>(s. oak), E. be.</td>
<td>0.36</td>
<td>0.08</td>
<td>&lt;0.001</td>
<td>0.36</td>
<td>0.08</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>S. pine, (E. be.)</td>
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<td>0.23</td>
<td>0.041</td>
<td>0.47</td>
<td>0.23</td>
<td>0.041</td>
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<tr>
<td>(S. pine), E. be.</td>
<td>0.36</td>
<td>0.08</td>
<td>&lt;0.001</td>
<td>0.36</td>
<td>0.08</td>
<td>&lt;0.001</td>
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<td>&lt;0.001</td>
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<td>(S. pine), N. sp.</td>
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<td>&lt;0.001</td>
<td>2.26</td>
<td>0.39</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

3.3. Density dependent competition reduction (H II)

When testing H II based on model 3 we found in nine out of ten cases an increase of stem diameter growth with increasing admixture proportion (Table 5). For Norway spruce when mixed with European beech we found a neutral effect of admixture; there was no significant facilitation. In most species assemblages both tree species benefitted from the mixture (see, e.g., Fig. 6, c and d). In the mixture of Norway spruce and European beech only the latter benefitted (Fig. 6, a and b). There were no cases were one species benefitted at the expense of the other species, i.e., that an increase of one was coupled with a loss of the other. In all
mixtures the growth of European beech strongly benefitted from living in mixture (Fig. 6, b, d, f). In most of the cases the benefit of growing in mixture was present under low density but even increased with local stand density from SDI = 500–2500 trees per hectare.

<table>
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<tr>
<th>Group</th>
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<th>p-value</th>
<th>a5</th>
<th>std</th>
<th>p-value</th>
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<td>0.80</td>
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<td>0.60</td>
<td>0.008</td>
<td>0.29</td>
<td>0.09</td>
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</tr>
<tr>
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<td>1.73</td>
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<td>0.08</td>
<td>&lt; 0.001</td>
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<td>0.23</td>
<td>0.630</td>
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</table>

3.4. Inter-specific facilitation and competition depending on site conditions (H III)

Any dependency of inter-specific facilitation on site conditions was first tested for the collective of the 10% fastest growing trees per group and plot by model 4. Any dependencies of the mixing effects on the site conditions were analyzed only for the mixtures of Norway spruce/European beech and sessile oak/European beech. For the other species the range of the site conditions was too narrow for analogous analyses.

We found a significantly positive effect of inter-specific neighborhood on growth, however, this on average positive effect remained constant along the whole site gradient. In none of the cases there was a significant interaction between site conditions and mixing effect (see coefficients a3 in Table 6). Fig. 7 visualizes that in both mixtures the fastest growing trees benefited from living in mixture. However, the benefit did not change along the site gradient (SI = 20–40 m mean height at age 100) covered by this study.

An analogous analysis based on model 4 was done based on the whole dataset in order to reveal any modulation of the competition reduction by site quality. For the competition reduction we found a tendency of increase with site quality that was close to significant for the mixture of Norway spruce and European beech (see Table 7 and Fig. 8). For European beech when growing in association with oak we found a significant (p < 0.002) increase of competition reduction with increasing site quality cases (see last row in Table 7 and Fig. 7d). In summary in all cases diameter growth was higher in mixed compared with monospecific stands, in case of beech in oak the superiority increased slightly with improving site quality.

4. Discussion

4.1. A consolidated view of facilitation and competition effects on growth

Analyzing, understanding, modeling, and prognosticating monocultures often entails a thorough consideration of the effects of competition between neighboring plants (Larocque et al., 2013; Namibi and Sands, 1993), but hardly of the facilitation or reduction of competition by neighbors (Maestre et al., 2005; Bruno et al., 2003; Vandermeer, 1992). The results of this study provide evidence that the assumption of maximum growth under solitary conditions and of an exponential growth reduction through increased competition and density (as shown in Fig. 1) is an over-simplification. In particular, we show that tree growth can be increased beyond solitary growth (by 14–78%) through an inter-specific neighborhood under moderate density (Fig. 5 and Table 4).

We analyzed the feedback spatial stand structure → facilitation and competition → tree growth and its dependency on site conditions (e.g., site index) and silvicultural interventions (e.g., stand density, mixing proportion) (Fig. 9). By modeling the effects of different stand characteristic on individual tree growth we showed that tree growth can be promoted or reduced (facilitation versus competition) by intra- and interspecific neighborhood. Models 1–3 showed for different species combinations how the facilitation and competition is modulated by site conditions and stand density.

Our results suggest that the growth-competition relationship is unimodal, as represent by the bold curve in Fig. 10a. Facilitation and competition act simultaneously (Pretzsch, 2017; Vandermeer, 1992). They are difficult to disentangle, and the measured growth reaction represents the net effect of the interaction between facilitation and competition (thin and broken lines, respectively, in Fig. 10a). In Fig. 10a the tree growth in solitary conditions is used as a reference (1.0-line) and indicates that the trajectory of the measured growth may result from the interplay between facilitation and competition. This pattern may apply even in some monospecific populations, especially under harsh conditions (Callaway and Walker 1997; Canham et al., 1994, 2004). We also found that an inter-specific neighborhood can increase the facilitation, and reduce the competition, so that the net effect on growth becomes more positive (see Fig. 10b, vertical and horizontal arrows).

Fig. 10b indicates the shift of the tree growth-density relationship due to a facilitation (e.g., tapping of nutrients in deep soil layers which are favorable for species 1) or a reduction in competition (e.g., by spatial or temporal niche complementarity). Further, the inter-specific neighborhood may cause a widening of the density range with net facilitation (horizontal arrow). This may cause a narrowing of the range where net competition has the upper hand. Figs. 4 and 5 showed such a facilitation of trees in mixed stands. In several cases trees with moderate density grew even faster in an inter-specific neighborhood than trees with low competition in monospecific stands.

Fig. 10a shows that net facilitation may dominate at low densities, and that net competition may predominate in denser stands. The reason may be, that around widely spaced trees, the negative effect of competition on growth may be still low enough to be compensated or even overcompensated for by the positive effect of facilitation. When stand density further increases, the growth reduction cannot be balanced out as easily by facilitation and may cause net competition. Although not easy to detect and to disentangle from competition, facilitation may also play a role in closed forest stands with high stand density.

The study further showed that facilitation and competition reduction may depend on environmental conditions (Gonzales de Andres et al., 2018). They may become stronger in high quality sites. This means that the stand density range with a net facilitation effect and an increase of tree growth is extended towards higher stand densities (see horizontal arrow in Fig. 10c). Finally, this study showed a strong facilitation and competition reduction through inter-specific conditions. However, this facilitation was site-invariant (Fig. 7, Table 6). The competition reduction increased only slightly with improving site quality (Fig. 6, Table 7).

4.2. Causes of facilitation and reduction of competition in an inter-specific neighborhood

Comparing the 10% fastest growing trees in a mixed- versus monospecific neighborhood (Fig. 5, Table 4) showed a 14–78% increase in growth in mixed stands. This result remained consistent across different neighboring tree species in low density environments and at parity of other modulating factors, such as d and SI. The finding that stem diameter was not always significant in the models may be attributed to the fact that other tree dimensions such as crown ratio or age overtopped d in correlation with growth. The finding that the 10% fastest growing trees of several species were superior means that they had a higher growth rate when surrounded with other species, than when growing
widely spaced and open. We furthermore found a competition reduction of 16% on average (ranging from −1% - +36%) calculated for a local SDI value of 1000 ha$^{-1}$, quadratic mean diameter of 25 cm, stand age of 30 years, and a mixing proportion of 50:50 for each pair of species (Fig. 5, Table 5).

How can a higher growth in inter-specific mixtures compared to growth without neighbors be explained, i.e., how is it possible that the positive effect of a neighbors is higher than the negative effect? What may be the main causes underlying the demonstrated competition reduction under high density conditions? The measured net effects of density and distance of neighboring trees on tree growth allowed us the following speculations about the potential mechanisms underpinning the revealed mixing effects.

**Norway spruce and European beech:** Many studies showed that the negative effects of soil compaction (Wiedemann, 1923), acidification (Pallant and Rihac, 1990), and nutrient depletion (Kaarakka et al., 2014) through Norway spruce monocultures can be mitigated by many species admixtures, and especially by European beech (Rothe and Binkley, 2001; Rothe, 1997; Wiedemann, 1942). The latter can facilitate the growing conditions of Norway spruce by increasing the temperature (especially in early spring) by improving litter decomposition, and nutrient cycling and turnover (Pretzsch et al., 2020, 2010; Goisser et al., 2016; Rothe et al. 2002, 2003). Furthermore, beech can benefit from Norway spruce through its higher leaf area, resulting in higher eutrophic deposition filtering (Alveteg et al., 1998; Cannell et al., 1998; van Dijk and Roelofs, 1988). An advantage and competition reductions for both species may be their crown shape complementarity, i.e., the △-shaped Norway spruce (bottom heavy) versus ▽-shaped European beech (top

![Fig. 6.](image-url)
heavy) crowns enable a higher canopy packing density (Barbeito et al., 2017; Jucker et al., 2015; Pretzsch, 2014). Complementarity in shape may, across all mixtures, reduce mechanical abrasion and crown shyness (Hajek et al., 2015; Fish et al., 2006; Meng et al., 2006). It may also cause higher canopy packing density, stand density (Thurm and Pretzsch, 2021), and stand leaf area (Pretzsch and Schütze, 2021; Peng et al., 2017). In this way complementarity in shape may result in overyielding (Williams et al., 2017). In addition, physiological asynchrony of tree species may be beneficial for their growth (Pretzsch, 2005; Rötzer et al., 2017; Schober, 1950/51). For instance, Norway spruce may benefit of a reduced competition for water in early spring when European beech is still leafless and lives from the reserves of the previous year. During this period, photosynthesis and growth of spruce may further profit from higher temperatures and light supply until beech sprouts in April/May.

**Sessile oak and European beech:** In mixture with oak, beech may be facilitated by hydraulic lift. This has been observed in particular on dry sites with deeply extending root systems, which release water at night into surface-near soil horizons of low water potential (Caldwell et al., 1998; Prieto et al., 2012). Sessile oak may benefit from beech by the improvement of soil activity, decomposition, and nutrient turnover (Jonard et al., 2008). Competition reduction may promote European beech when admixed to all species that are less shade tolerant (e.g., oak).

**Scots pine and European beech:** Especially on poor sites, Scots pine can be facilitated by the substantial nutrient input from European beech-induced litter translocation and the improved decomposition and turnover of the mixed litter (Vest et al. 2021). This can improve the water storage and have a particularly positive effect on the mineral nutrient supply. European beech can have a beneficial effect on pine, primarily through stimulation of the bio-element turnover, and by improving the nutrition of pine. In comparison to pine, beech litter has a higher Ca, Mg and K content, as well as a lower C/N ratio (Augusto et al., 2002). Moreover, activity of soil fauna and microflora is higher in beech than in conifer stands, resulting in a higher litter decomposition rate (Augusto et al., 2002; Wiedemann, 1942), reduced acidity, and a better humus type (Block et al., 1997).

**Scots pine and Norway spruce:** Both species complement each other in light ecology, crown and root shape, and in behavior under drought (Ruiz-Peinado et al., 2021; Wellhausen et al., 2017). Competition reduction may result from the fact that pine is light demanding, round-crowned, deep-rooted, and less drought sensitive, whereas spruce is shade-tolerant, slim-crowned, shallow-rooted, and strongly isohydric.

**Table 6**

<table>
<thead>
<tr>
<th>Group</th>
<th>n</th>
<th>$a_0$</th>
<th>std ($a_0$)</th>
<th>p-value</th>
<th>$a_1$</th>
<th>std ($a_1$)</th>
<th>p-value</th>
<th>$a_2$</th>
<th>std ($a_2$)</th>
<th>p-value</th>
<th>$a_3$</th>
<th>std ($a_3$)</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>N. sp., (E. be.)</td>
<td>134</td>
<td>3.40</td>
<td>2.06</td>
<td>0.101</td>
<td>−0.02</td>
<td>3.028</td>
<td>0.095</td>
<td>0.80</td>
<td>0.58</td>
<td>0.167</td>
<td>0.02</td>
<td>0.86</td>
<td>0.978</td>
</tr>
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<td>(N. sp.), E. be.</td>
<td>135</td>
<td>1.95</td>
<td>4.38</td>
<td>0.675</td>
<td>−6.89</td>
<td>4.54</td>
<td>0.135</td>
<td>−0.87</td>
<td>1.31</td>
<td>0.509</td>
<td>2.12</td>
<td>0.11</td>
<td>0.18</td>
</tr>
<tr>
<td>s. oak, (E. be.)</td>
<td>106</td>
<td>−3.98</td>
<td>1.71</td>
<td>0.022</td>
<td>−0.87</td>
<td>1.79</td>
<td>0.627</td>
<td>0.98</td>
<td>0.52</td>
<td>0.064</td>
<td>0.28</td>
<td>0.55</td>
<td>0.616</td>
</tr>
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<td>(s. oak), E. be.</td>
<td>247</td>
<td>−2.07</td>
<td>0.48</td>
<td>&lt;0.001</td>
<td>1.11</td>
<td>0.55</td>
<td>0.046</td>
<td>0.25</td>
<td>0.15</td>
<td>0.109</td>
<td>−0.11</td>
<td>0.18</td>
<td>0.510</td>
</tr>
</tbody>
</table>

Fig. 6. (continued).
This species combination creates high biodiversity in the soil, high nutrient turnover, and a suppression of other competing species (e.g., European beech) in its stand (Ellenberg and Leuchner, 2010, pp. 297–303, Frech, 2006). These effects may facilitate both component species in such mixtures.

This brief literature review of the most likely mixing effects within the five analyzed species combinations suggests a differentiation between (i) density invariant, far-range effects, such as far reaching root systems, mycorrhiza (Nickel et al., 2018) and other root-associated microbial networks (Steidinger et al., 2019). To this category of effects also belong the slowing-down of wind speed, avoidance of storm-breakage, shading and avoidance of sunburn, provision of barriers against spread of insects, suppression of forest floor vegetation and competing weeds, and protection against snow slides or browsing by different neighboring tree species. A second category of effects may be (ii) density-driven close-range mixing effects, such as mechanical abrasion, crown shyness, and pre-emption of water and light by neighbors of a different tree species.

Our results show that density invariant/far-range effects may cause facilitation and growth increase at low stand density. Low density conditions are often created in contemporary forest management through edges, strong thinning, opening for natural regeneration, or by natural disturbances. They generate the potential of considerable facilitation of tree growth. This may not raise the stand-related productivity above the level of closed stands, but can reduce the losses brought about by density reduction. This is in line with the finding by Thurm and Pretzsch (2021) that the stand density-productivity relationship has a broader plateau in mixed compared with monospecific stands. In mixed stands the plateau of the stand density-productivity relationship may reach further into both the low-density and also high-density range.

The percentage of diameter growth increase caused by reduction of competition (16% on average, ranging from −1% to +36%) is in line with the magnitude of overyielding reported for the respective mixtures in fully stocked stands (see introduction). This indicates that the overyielding in fully stocked stands may be driven mainly by close-range effects. It may result from competition reduction and increased density, resulting in an advantageous productivity. This is in line with Thurm and Pretzsch (2021), who recently showed that density can be raised by tree species mixing, and that overyielding in mixed stands can peak at

**Fig. 7.** Effect of site conditions in terms of site index (SI = 20–40 m at age 100) on the facilitation of stem diameter growth of the 10% fastest growing trees in both groups on each plot. The parallel lines indicate a site-invariant facilitation for both species and species assemblages. Results based on Model 4, see Table 6.

**Table 7**

Statistical characteristics of Models 4 for analyzing H III based on the growth of all trees. The equation numbers refer to the models introduced in Section 2.5. For reasons of space the table reports only the fixed effect variables of the respective models. For variable explanation see Table 2. \( \ln(id) = a_0 + a_1 \times mfactor_i + a_2 \times \ln(SI_{ik}) + a_3 \times mfactor_i \times \ln(SI_{ik}) \).

<table>
<thead>
<tr>
<th>Group</th>
<th>n</th>
<th>( a_0 )</th>
<th>std ((a_0))</th>
<th>p-value</th>
<th>( a_1 )</th>
<th>std ((a_1))</th>
<th>p-value</th>
<th>( a_2 )</th>
<th>std ((a_2))</th>
<th>p-value</th>
<th>( a_3 )</th>
<th>std ((a_3))</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>N. sp., (E. be.)</td>
<td>11,017</td>
<td>−5.00</td>
<td>0.39</td>
<td>&lt; 0.001</td>
<td>−0.62</td>
<td>0.47</td>
<td>0.194</td>
<td>1.08</td>
<td>0.11</td>
<td>&lt; 0.001</td>
<td>0.18</td>
<td>0.13</td>
<td>0.173</td>
</tr>
<tr>
<td>(N. sp.), E. be.</td>
<td>6549</td>
<td>−2.05</td>
<td>0.40</td>
<td>&lt; 0.001</td>
<td>−0.74</td>
<td>0.46</td>
<td>0.111</td>
<td>0.23</td>
<td>0.12</td>
<td>0.046</td>
<td>0.23</td>
<td>0.14</td>
<td>0.101</td>
</tr>
<tr>
<td>s. oak, (E. be.)</td>
<td>7945</td>
<td>3.72</td>
<td>0.50</td>
<td>&lt; 0.001</td>
<td>−0.20</td>
<td>0.51</td>
<td>0.701</td>
<td>0.72</td>
<td>0.15</td>
<td>&lt; 0.001</td>
<td>0.07</td>
<td>0.16</td>
<td>0.662</td>
</tr>
<tr>
<td>(s. oak), E. be.</td>
<td>19,650</td>
<td>1.24</td>
<td>0.12</td>
<td>&lt; 0.001</td>
<td>−0.39</td>
<td>0.13</td>
<td>0.003</td>
<td>−0.05</td>
<td>0.04</td>
<td>&lt; 0.195</td>
<td>0.13</td>
<td>0.04</td>
<td>0.002</td>
</tr>
</tbody>
</table>

(From Drössler et al., 2018, p.3).

**European ash and sycamore maple:** This species combination creates high biodiversity in the soil, high nutrient turnover, and a suppression of other competing species (e.g., European beech) in its stand (Ellenberg and Leuchner, 2010, pp. 297–303, Frech, 2006). These effects may facilitate both component species in such mixtures.
maximum density.

4.3. Consequences of the facilitation and competition reduction for individual tree modeling

The potential-modifier approach for individual tree growth modeling splits the prediction of the size growth (e.g., stem diameter growth) into two components (Pretzsch et al., 2019; Weiskittel et al., 2016). The first is the estimation of the potential tree growth rate, i.e., the expected growth without competition that mainly depends on the tree and site characteristics. The second component is the modifier that reduces the potential growth rate depending on the competition and density in the tree’s neighborhood.

Our results suggest that in contrast to the common assumptions made in many individual tree models, the tree stem growth may not peak under monospecific open-grown conditions, but rather in mixed-species environments and at moderate stand density. Thus, the potential-modifier function may not exponentially decrease, but rather grow

Fig. 8. Modulation of the competition reduction by tree species mixing shown for site index levels SI = 20...40 (d, age, and SDI kept at a constant level). The results are based on model 4 and visualized for (a) Norway spruce when mixed with European beech, (b) European beech when mixed with Norway spruce, (c) sessile oak when mixed with European beech, and (d) European beech mixed with sessile oak.

Fig. 9. The models 1–3 of this study analyze the feedback spatial stand structure → facilitation and competition → tree growth and its modulation by site conditions and stand density.
unimodal with modifier values above 1.0 at moderate density in mixtures. In contrast to the declining modifier function shown in Fig. 1, the modifier function in mixed stands may be bell shaped, as shown in Fig. 10. Further research considering other tree species, species combinations, site conditions, and stand structures is required to substantiate these assumptions.

Relevant for modeling are the mostly positive interactions between mixing proportion and local competition that we found in this study. Positive interactions between tree species were also found by Rebola-Lichtenberg et al., (2021), Cavard et al., (2011) or Forrest et al., (2011). However, our results indicate that the competition reduction through an inter-specific neighborhood is even stronger in denser stands. We also found a slight positive interaction effect of site index and mixing proportion on growth of European beech when mixed with

The presented findings may aid the further development of models (Hilmers et al., 2020; Mason et al., 2018; Hanewinkel and Pretzsch, 2000). The presented findings may aid the further development of individual tree models.

4.4. Consequences of the results for forest management

This study aimed to answer several of the ten highest-ranked questions regarding mixed-forests that Coll et al., (2018, Table 1) identified by interviewing 168 managers from European countries. Specifically, the study addressed which species combinations are beneficial (question #4), how the productivity of mixtures differs from that in monospecific stands (#5), and which positive and negative effects mixtures can have (#6 and #7).

This study substantiated that, at parity of tree size and stand density, trees in the most common species combinations in Central Europe grew faster than in monospecific stands in the considered time period 1991–2016. This superior wood production of trees in mixed stands adds to their well-known advantages in biodiversity (Dieler et al., 2017; Felton et al., 2010), stability (Hilmers et al., 2020; Knoke et al., 2008), and recreation (Edwards et al., 2012; Pukkala et al., 1988) services. In forest management, facilitation effects are, so far, specifically used in terms of nurse crop against frost damage (Pommerening and Murphy, 2004), and in the admixture of atmospheric nitrogen fixing tree species, such as Alnus, Robinia, or Acacia (Binkley, 2003; Carl et al., 2018; Forrester et al., 2006). It is also well known that trees growing in group structures in the alpine zone compete for light but their neighbours also protect them against snow and wind, so that they frequently benefit from being associated and grow more than solitary trees. Forest management makes use of such a permanent facilitation by planting trees in groups or clusters known as “Rotten” in the alpine zone (Ströbel, 1995) and “Nester” in the lowlands (Saha et al., 2012).

The results of this study quantified the facilitation in inter-specific neighborhood. It showed that facilitation can improve tree growth in common mixed species forests in both widely spaced stands by far-range facilitation effects and in dense stands by near-distance competition reduction effects. Both effects are relevant for silviculture. Facilitation, even at low density conditions, enables the production of large and long-lived forest products with lower expenses in terms of stand stock and mass productivity at the stand level. This means an advantageous growth at low-density, as commonly observed in selective or future crop thinning systems for individual tree size growth acceleration (Schober, 1988a and b; Abetz, 1975; Schädelin, 1942). Competition reduction enables an increase in stand density, mass production, and climate change mitigation through higher carbon storage. The competition reduction observed here enables the maximization of mass production at high density stand management in mixed stands (Zeller et al., 2021; de Prado et al., 2020; Pretzsch, 2020, 2022; Assmann, 1970).

Silvicultural management mainly entails the modification of spatial design and interference into stand structure. The distinction between (i) density invariant, far-range effects and (ii) density-driven close-range operating mechanisms may be a step forward for future spatially explicit tree and stand modeling approaches and experiments, as well as for a more goal-oriented silvicultural design and stand establishment. Thus, silvicultural measures are suitable for the regulation of density-driven close-range mixing effects.

Both facilitation and competition reduction can result in higher
growth per unit area, and be exploited by low or high stand density, respectively. The reported effects apply to all analyzed species and sites. To implement these findings, they should be integrated into silvicultural guidelines for mixed species stands, as claimed by Coll et al., (2018) and proposed by Mason et al., (2018) and Pretzsch and Zenner (2017).

CRediT authorship contribution statement

Hans Pretzsch: Conceptualization, Data curation, Writing – original draft, Writing – review & editing.

Declaration of Competing Interest

The author declares that he has no conflict of interest.

Acknowledgements

Thanks are due to Brian D. Fath for inviting me to this contribution to the Jorgensen Reviews and Research series of the journal Ecological Modelling.

Supplementary materials


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