Oak often needs to be promoted in mixed beech-oak stands – the structural processes behind competition and silvicultural management in mixed stands of European beech and sessile oak

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Introduction
The European beech (Fagus Sylvatica L.) and the sessile oak (Quercus petraea [Matt.] Liebl.) are two of the most prevalent broad-leaved tree species in Central Europe and they occur mostly in Central Europe, ranging from the north of Spain up to southern Scandinavia (Bolte et al. 2007). As soon as the canopy is closed in mixed stands of oak and beech, there is only a low amount of light penetration (Emborg 1998). The shade-tolerant European beech saplings therefore seem to out-compete the light-demanding sessile oak saplings in mixed stands in all light conditions (Ligot et al. 2013). The morphological plasticity of European beech additionally allows a restriction or even penetration of the crowns of neighbouring oak trees. On most sites, European beech also reaches much higher maximum tree heights and diameters than sessile oak, and consequently overgrows and impedes sessile oak severely. A warmer and drier climate can reduce the height growth of beech (Bontemps et al. 2012). Sessile oak, on the contrary, is expected to adapt better to a warmer and drier climate than European beech (Rubio-Cuadrado et al. 2018), which will therefore modify the competitive relationship between the two species.

Silvicultural management can modify the forest structure and interactions between tree species, and can foster not only wood production but also other ecosystem goods and services beyond the additional effects of mixing (Ammer 2008). However, specific silvicultural guidelines for mixed-species stands are often lacking. Experience in the field of silviculture shows that the cultivation of oak in mixed stands requires a considerate management in order to establish and maintain beneficial forest structures to support the regeneration and development of oak (Von Lüpke 1998), e.g., through thinning. The production of high quality oak wood and the need for silvicultural intervention are therefore often in conflict with conservation interest groups, aiming at an increase in unmanaged forest area (Frech 2006).

Despite the potential interspecific competition and the need for frequent management interventions, mixed-species stands have in many cases shown benefits compared to pure forest stands (Gamfeldt et al. 2013). These benefits mostly result from a functional diversity (Mensah et al. 2018) and include a general reduction in the risk of mortality, higher stability, above-ground carbon storage (Mensah et al. 2018), and productivity (Liang et al. 2016). One reason for the superior growth in beech-oak stands may be the hydraulic lift of water (Pretzsch et al. 2013). European beech also shows a higher number of fine roots compared to sessile oak (Leuschner et al. 2001),

Forest ecosystems nowadays provide multiple ecosystem goods and services at a time and throughout all development phases. Species mixing is considered an effective measure to gain benefits beyond purely additive effects. However, the complex structural processes behind interspecific competition and temporal and spatial facilitative effects through mixing are still far from being understood and predictable. In particular the mixture of European beech (Fagus Sylvatica L.) and sessile oak (Quercus petraea [Matt.] Liebl.) is gaining even more importance due to the fact that forests from these species are considered more tolerant to climatic effects and are expected to expand their natural range to the north due to global warming. The 30 long-term experimental plots analysed in this study reveal the structural processes in mixed beech-oak stands based on data at the tree and stand level. Using spatial and non-spatial structural indices, we can show an increasing dominance of beech over oak in unmanaged stands and the effectiveness of thinning operations to support oak. Those processes are representative for other light-demanding tree species in mixtures with shade-tolerant species. Improving the knowledge on the structural processes in mixed-species stands is particularly relevant when trying to modify forest structure in order to adapt forest management to shifting environmental conditions and the increasing demand for ecosystem services.

Keywords: Ecosystem Services and Functions, Facilitation and Competition, Mixing Regulation, Silvicultural Prescriptions, Spatial Distribution, Stand Development, Structural Complexity, Thinning

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which may result in a more efficient use of below-ground resources. A more efficient vertical and horizontal exploitation of space due to the different needs in light intensities may be an additional reason for overyielding.

As stand structure plays an important role in the effective and sustainable management of mixed forest stands, it may be specifically modified with the aim of supporting certain ecosystem functions. By thinning from above, for example, structural heterogeneity can be increased compared to thinning from below, which can make stands more homogeneous (Pretzsch 1998). The structural heterogeneity of a stand can then enhance stand productivity (Danesu et al. 2016), diminish it (Bourdier et al. 2016) or both. The structural effect may be positive or negative, depending on the site conditions and on the development phase of the forest stand (Zeller & Pretzsch 2019). In addition, enhanced forest biodiversity and stand structural complexity are assumed to be positively related (Zellweger et al. 2015), which in turn can positively influence stand productivity. In order to modify and benefit from these structural effects, effective silvicultural management has to consider not only species-mixing and changes in environmental conditions, but also the initial stand structures and how they are modified over time by species identity and management (Mizuaga et al. 2010).

By analysing 30 long-term experimental forest plots of European beech and sessile oak in southern Germany, the aim of this study is to demonstrate the structural processes behind facilitation, competition and silvicultural management in mixed beech and oak stands over time. The experimental plots (between 0.2 and 1 hectare in size) were subjected to different intensities and oak stands over time. The experimental plots were located close to Waldbrunn, Burgsinn, Illertissen, Lohr-West, Elmstein-Nord, Rohrbrunn, Rothenbuch, Schweinfurt, and Kelheim. On the plots, the mean annual temperature ranges from 7 to 8.5 °C, the annual precipitation is between 660 and 1150 mm and elevation is between 270 and 555 m a.s.l. Several measurements of long-term experimental plots were carried out in the time between 1927 and 2017. Since this study deals with spatial analyses, which require the coordinates of all trees, and since this study deals with spatial analyses, which require the coordinates of all trees, the aggregation index (Clark & Evans 1954) and the Pielou index (Pielou 1959) refers to the distances between the reference trees and the random points

### Materials and methods

#### Study area

For the current study, we used inventory data of long-term experimental plots dominated by sessile oak and European beech, which are all located in Bavaria, Germany, and have similar climatic conditions. The water and nutrient supply is favourable for both species. Additional species occurring in small numbers were European hornbeam (Carpinus betulus), birch (Betula pendula and Betula pubescens), lime (Tilia platyphyllos and Tilia cordata) and European Larch (Larix decidua). The experimental plots are located close to Waldbrunn, Burgsinn, Illertissen, Lohr-West, Elmstein-Nord, Rohrbrunn, Rothenbuch, Schweinfurt, and Kelheim. On the plots, the mean annual temperature ranges from 7 to 8.5 °C, the annual precipitation is between 660 and 1150 mm and elevation is between 270 and 555 m a.s.l. Several measurements of long-term experimental plots were carried out in the time between 1927 and 2017. Since this study deals with spatial analyses, which require the coordinates of all trees, and since this study deals with spatial analyses, which require the coordinates of all trees, the aggregation index (Clark & Evans 1954) and the Pielou index (Pielou 1959) refer to the distances between the reference trees and the random points

#### Stand structure quantification

A set of structural indices – describing the plots according to the intensity and spatial arrangements of the trees, the size distribution, and species intermingling – were selected for further analyses (Tab. S1 in Supplementary material). Either the structural measures were simple non-spatial measures of stand properties, which are often available in almost all forest inventories, or spatial quantifications of a central tree (reference tree) related to its neighbourhood. The spatial indices account for one or four nearest neighbours of each reference tree. Depending on the algorithm of the structural indices, the calculated values were at trees, species or plot level.

Indices 1-4 in Tab. S1 are non-spatial measures of stand properties, which are simple to assess, and can be used for more complex assessments. The quadratic mean diameter at breast height of trees (D₄) was representative of the trees’ dimensions, whereas the stand basal area (BA), the number of trees per hectare (N) and the Reineke stand density index (SDI – Reineke 1933), describe stand density. SDI sets the allometric relationship between N and D₄ and estimates the expected number of trees at a quadratic mean diameter of 25 cm.

Indices 5-7 (Tab. S1 in Supplementary material) explore the horizontal distribution pattern of trees within the study plots. The contagion index (Con), also known as the uniform angle index, counts for the four neighbours (Hui & Von Gadow 2002) whereas the aggregation index (Clark & Evans 1954) and the Pielou index (Pielou 1959) refer to the distances between the reference trees and the random points

### Tab. 1 – The initial stand characteristics (mean ± standard error) of the study plots in total and for the two main species. (N): number of trees (ha⁻¹); (D₄): quadratic mean diameter of trees at breast height (cm); (BA): basal area (m²·ha⁻¹); (H): height of the trees (m); (CRP, CRR): mean crown projection (m) and crown radius (m) of trees within a plot, respectively. “Managed” and “Unmanaged” refer to plots with and without thinning practices, respectively.

<table>
<thead>
<tr>
<th>Plot</th>
<th>Species</th>
<th>N</th>
<th>D₄</th>
<th>BA</th>
<th>H</th>
<th>CRP</th>
<th>CRR</th>
</tr>
</thead>
<tbody>
<tr>
<td>Unmanaged</td>
<td>European beech</td>
<td>739 ± 98</td>
<td>17.88 ± 1.57</td>
<td>12.69 ± 0.86</td>
<td>18.18 ± 1.00</td>
<td>32.89 ± 3.28</td>
<td>3.01 ± 0.15</td>
</tr>
<tr>
<td>Unmanaged</td>
<td>Sessile oak</td>
<td>449 ± 120</td>
<td>36.34 ± 3.55</td>
<td>20.61 ± 1.42</td>
<td>26.58 ± 1.16</td>
<td>36.56 ± 6.69</td>
<td>3.03 ± 0.28</td>
</tr>
<tr>
<td>Unmanaged</td>
<td>Total</td>
<td>1232 ± 177</td>
<td>23.65 ± 1.90</td>
<td>34.36 ± 1.14</td>
<td>21.65 ± 1.01</td>
<td>31.92 ± 3.63</td>
<td>2.91 ± 0.18</td>
</tr>
<tr>
<td>Managed</td>
<td>European beech</td>
<td>684 ± 95</td>
<td>18.24 ± 1.40</td>
<td>12.28 ± 0.79</td>
<td>18.44 ± 0.95</td>
<td>33.71 ± 2.96</td>
<td>3.07 ± 0.14</td>
</tr>
<tr>
<td>Managed</td>
<td>Sessile oak</td>
<td>414 ± 119</td>
<td>37.48 ± 3.54</td>
<td>20.37 ± 1.21</td>
<td>26.67 ± 1.16</td>
<td>38.34 ± 6.61</td>
<td>3.12 ± 0.28</td>
</tr>
<tr>
<td>Managed</td>
<td>Total</td>
<td>1144 ± 173</td>
<td>24.61 ± 1.97</td>
<td>33.38 ± 1.11</td>
<td>21.85 ± 1.00</td>
<td>33.24 ± 3.48</td>
<td>2.99 ± 0.18</td>
</tr>
</tbody>
</table>
from the first nearest tree, respectively.

We assessed the difference in stem diameters at breast height by another five indices, of which two are spatial (indices 8-9) and one is non-spatial (index 10). The diameter differentiation index (DiF – Füldner 1995) and diameter dominance index (Dom – Von Gadov & Hui 2002) count for the four nearest neighbours and quantify the diameter differentiation and the dominance status of a reference tree, respectively. Finally, the diameter heterogeneity of trees within a stand is evaluated by diameter variation (Dvar – Pretzsch 2009), where the higher Dvar indicates the higher diameter variation.

The spatial structure of species mixture was described by species mingling (Füldner 1995) and species segregation (Pielou 1977) (indices 11-12 – Tab. S1 in Supplementary material). The mingling index (Minling) quantifies the proportion of four nearest neighbours of a species other than that of the reference tree, whereas the segregation index (Seg) accounts for all pairs of reference trees and their first nearest neighbours within a stand and describes the intermingling of two species or species groups.

**Competition quantification**

Additional to the structural indices, we quantified the spatial competition amongst the neighbouring trees applying the competition index introduced by Hegyi (1974 – eqn. 1). The intention was to examine the importance of species identity, stand density and tree dimensions in stand dynamics and structure, by using a single index. To do so, the competition load from oak (Clow) and beech (Clbw) neighbouring trees on each reference tree was separately quantified and summed up, to obtain a value for the competition forced by each species within a stand (eqn. 1):

\[
\sum_{e=1}^{s_c} \left( \frac{d_{j,e}}{d_{j,r}} \right)_{\text{Seg}}
\]

To test whether a neighbouring tree j of any diameter (dj) is an active competitor for reference tree i with any diameter (di), we controlled the distance between them (r). Based on the crown overlap method (Alemadg 1978), we set a critical distance as the sum of the reference tree’s potential crown radius (Cr) and the neighbouring tree’s potential crown radius (Cr) and assumed trees i and j were actively interacting when r < Cr + Cr. Since the crown radius was not available for all trees within a plot, the non-linear allometric relationship between the potential crown projection (crp) and the diameter at breast height of trees with a crown measurement was employed (Pretzsch 1992 – eqn. 2):

\[
\ln(\text{crp}) = a_i + b_i \ln(d_i)
\]

The potential crown projection model was derived for tree species of the Bavarian region, which made the use of the model plausible. In order to estimate the parameters ai and bi for both species in the beech-oak mixture we used the nonlinear least squares regression and the trees with measured crowns from empirical data. For further analyses, we then used estimated crown projection area for all trees.

The edge effect correction

The immediate neighbours for trees standing near the monitoring plot borders may stand outside the plots, and there may be no information available about them. Among the different methods developed for avoiding the biased statistical estimations due to the edge effect, a combination of border method or buffer zone (Ripley 1981) and reflection method (Radtke & Burkhart 1998) was applied. For indices counting the first nearest neighbour, a buffer zone was set to exclude the reference trees, where their distance to the plot borders were shorter than their distance to their first nearest neighbours (Pretzsch 2009). However, those trees could serve as the nearest neighbours for other reference trees. This method ensures the removal of all border errors for the mentioned indices quantifications. The reflection method results in periodic neighbourhood situations that do not naturally exist, when applied to rectangular inventory plots (Diggle 2003). However, in order to avoid losing many reference trees, as might happen when using the border method, we used the reflection method when quantifying the indices accounting for more than one nearest neighbour.

The status of natural mortality and thinning throughout stand development

In a preliminary analysis, we checked the height development of sessile oak and European beech reference (central) trees both in managed and unmanaged stands. Since the heights of all reference trees were not recorded, individual tree heights were estimated by the uniform height curve system that was first created for the European beech and then parameterised for other species (Franz et al. 1973) in Bavaria, Germany (eqn. 3):

\[
h = 1.34 \left( \frac{d}{b_i + h_i + d_i} \right)^{0.66}
\]

where h is the individual tree height, estimated as a function of a tree’s diameter at breast height, d. We derived the parameters b1, b2 and b3, utilising the trees with measured height on the plots.

The effect of natural mortality and thinning on stand structure

In order to examine the changes in stand structure due to natural mortality and thinning practices, we computed the structural and competition indices for three phases. This was performed for all existing trees, in managed and unmanaged plots, prior to any natural mortality and thinning practices (phase 1); after drop-outs due to natural mortality in managed and unmanaged plots (phase 2); and for the remaining trees after natural mortality and thinning practices, in managed plots (phase 3). We calculated the differences in the indices presented in Tab. S1 (Supplementary material), for the three aforementioned phases, as dmort (phase 2 – phase 1) and dthinn (phase 3 – phase 2). In the next step, we quantified the mortality rate and thinning intensity as the ratio of the removed basal area of plots (BAremoved, m² ha⁻¹) to the total basal area of plots (BA, m² ha⁻¹), due to natural mortality and thinning, respectively (eqn. 4). We also defined the mortality and thinning mode by the relative diameter of the remaining trees (Dremaining, cm) following the natural mortality and thinning, respectively, to the quadratic mean diameter of the plots (D, cm) prior to mortality or thinning (eqn. 5).

Eventually, we assessed the effect of mortality and thinning as follows:

\[
\text{intensity} = 100 \frac{BA_{removed}}{BA}
\]

\[
\text{mode} = \frac{D_{remaining}}{D}
\]

We quantified the values of intensity and mode both for mortality (between phase 1 and phase 2) and thinning practices (between phase 2 and phase 3). In this context, the intensity can take values between 0 and 100% depending on the removed basal area (m² ha⁻¹). Mode values equal to 1 show that mortality and thinning were equally distributed among trees of any diameter. Mode values smaller than 1 refer to the mortality of larger than average diameter trees and thinning from above. Mode values larger than 1 refer to the mortality of smaller than average diameter trees and thinning from below.

The statistical analyses

In order to check the effect of natural mortality and thinning practices on structural indices, we used the generalised additive mixed effects model (GAMM). The GAMM can appropriately address the unequal number of reference trees on the different inventory plots, and other unknown differences between the plots and potential correlations of residuals within the plots (Fahrmeir & Jung 2001 – eqn. 6):

\[y_i = a + f_1(x_{i1}) + \ldots + f_p(x_{ip}) + \epsilon_i\]

where y is a function of x independent variables, with unknown and possibly non-linear effects, b represents a vector of random effects, ε is the remaining errors and a is the model’s intercept to be estimated, and f1, ..., fp are nonlinear smoothing functions.

We first fitted the model for the mortality analyses and then for evaluating the thin-
ning effects. We set Δmor and Δthin as response variables, intensity and mode (of mortality and thinning) as predictor variables and trees within plots and measurements as a random vector to cover any unknown variability of different study plots. We assessed the significant effect of tree mortality and thinning practices on the structural indices (p-values < 0.05) and the direction of changes (positive / negative).

Using the GAMM, we also tested the relationship between the mortality rate and thinning intensity, the relationship between intensity and mode of both mortality and thinning for European beech and sessile oak trees, and the changes in intensity and mode of both mortality and thinning during the stand development (expressed by stand age).

Furthermore, we used a GAMM to assess the tendency of changes in the height development of trees, as related to natural mortality and thinning practices. The smooth curves deduced from the model show how the natural mortality and thinning influenced the height of beech and oak trees in unmanaged and managed stands. We conducted the analysis once for all trees in the mixed stands and once for beech and oak separately. In our regression analyses, in order to find influential outliers, we calculated the studentized residuals. If an observation had a studentized residual larger than 3 (in absolute value) we counted it as an outlier and excluded it from our predictor variables sets.

We repeated the regression analyses, and if the exclusion of the possible outliers did not significantly change the results, we put those omitted observations back into the regression calculations.

data preparation, indices calculations and analyses were carried out in R statistical software ver. 3.5.0 (R Core Team 2018). We used the “mgcv” package to fit the generalised additive mixed effects models, and the “ggplot2” package combined with “ggpubr” package to visualise the results.

Results

Natural mortality and thinning

Fig. 1a illustrates a negative correlation between the mortality rates and thinning intensities on the study plots at a 95% confidence interval; however, the correlation was only significant for oak trees (p-value < 0.05). Fig. 1b shows the positive correlation between the mortality mode and mortality rate for both species, explaining that the increase in mortality rate results in a significant increase in drop-out of trees of smaller than the average size (p-value < 0.001). Fig. 1c shows the statistically significant (p-value < 0.001) negative relationship between the thinning mode and intensity for beech, where the high intensity thinning removed medium-sized to large trees. The trend was statistically significant (p-value < 0.001) but in the opposite direction for oak trees, whereby mostly small trees were thinned out while maintaining a higher number of large trees.

We also detected significant changes (p-value < 0.05) in mortality rate / thinning intensity and mortality mode / thinning mode related to stand age, at the plot and at species level. As illustrated in Fig. 2a, the mortality rate of oak was almost similar to the mortality rate of the entire plot, whereas a much lower mortality rate was detected for beech, which could be due to senescence at older ages. Fig. 2b shows that the high mortality in oak was mostly...
related to the drop-out of small oak trees of below-average diameter. The mortality rate of smaller oak trees decreased up to a age of around average size or larger, or to the death of small trees in stands older than 60 years (Fig. 2b).

Fig. 2a shows that the thinning intensity was a lot higher for beech compared to oak, as the curve of thinning intensity for beech was similar to the thinning intensity of the entire stand. Fig. 2b shows that mostly smaller than average oak trees (thinning mode > 1) and larger than average beech trees (thinning mode < 1) were thinned. Thus, the high thinning intensity of beech tree is due to the removal of many large beech trees.

Effects of natural mortality and thinning on structure and competition

We presented a general overview of the quantified structural and competition indices in Tab. 2. The effect of natural mortality and thinning on stand structure is shown in Fig. 1. Tab. 3 shows the relation of natural mortality and thinning by indices divided into four groups: indices counting for (i) tree size distribution, (ii) stand density and horizontal distribution patterns, (iii) species intermingling and for (iv) competition.

Tree size distribution

The intensity and the mode of mortality and thinning had a significant effect on the size distribution of trees within the study plots (Tab. 3). The removal of rather large beech trees, in the case of low mortality rates (Fig. 1b) and high thinning intensities (Fig. 1c) reduced the quadratic mean diameter ($D_3$) of beech. In the case of higher mortality rates, the death of small beech trees increased the $D_3$ of beech. In oak trees, the quadratic mean diameter increased with a rising both in mortality rate and thinning intensity. This can be explained through the mortality and thinning of smaller oak trees (Fig. 1c). The basal area (BA) of both species was reduced due to removal of oak and beech trees through natural mortality and thinning practices.

The dominance status of trees (DOM) due to natural mortality changed significantly for the two studied species (Tab. 3). Sessile oak showed a higher mortality rate than beech (Fig. 1b), which resulted in the death of many small oak trees, and consequently increased the dominance of larger oak trees over their direct neighbours. In managed stands, a larger number of small oak (also beech) trees were thinned out in high-intensity thinning practices for oak (about 20-25 %, see Fig. 1c). This increased

Tab. 2 - The quantified structural and competition indices for the studied plots in total and for the two main species. The means are given in plain text, and standard deviations in italics. The meaning of each acronym is reported in Tab. S1 (Supplementary material).

<table>
<thead>
<tr>
<th>Data</th>
<th>Species</th>
<th>N</th>
<th>$D_1$</th>
<th>BA</th>
<th>SDI</th>
<th>Con</th>
<th>Agg</th>
<th>I$_P$</th>
<th>I$_D$</th>
<th>D$_{av}$</th>
<th>Ming</th>
<th>Seg</th>
<th>$C_{beech}$</th>
<th>$C_{oak}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>phase1</td>
<td>Total</td>
<td>1042</td>
<td>270.6</td>
<td>34.3</td>
<td>714.0</td>
<td>0.56</td>
<td>0.99</td>
<td>1.03</td>
<td>0.47</td>
<td>0.52</td>
<td>56.84</td>
<td>0.41</td>
<td>-0.16</td>
<td>1011.6</td>
</tr>
<tr>
<td></td>
<td>Beech</td>
<td>670</td>
<td>201.6</td>
<td>13.6</td>
<td>309.2</td>
<td>0.56</td>
<td>0.96</td>
<td>1.04</td>
<td>0.45</td>
<td>0.39</td>
<td>51.41</td>
<td>0.34</td>
<td>-0.15</td>
<td>861.2</td>
</tr>
<tr>
<td></td>
<td>Oak</td>
<td>464</td>
<td>154.0</td>
<td>6.3</td>
<td>163.1</td>
<td>0.33</td>
<td>0.12</td>
<td>0.22</td>
<td>0.11</td>
<td>0.14</td>
<td>10.05</td>
<td>0.19</td>
<td>0.30</td>
<td>305.1</td>
</tr>
<tr>
<td>phase2</td>
<td>Total</td>
<td>952</td>
<td>274.3</td>
<td>33.6</td>
<td>692.5</td>
<td>0.59</td>
<td>0.93</td>
<td>1.03</td>
<td>0.46</td>
<td>0.52</td>
<td>55.36</td>
<td>0.42</td>
<td>-0.17</td>
<td>877.6</td>
</tr>
<tr>
<td></td>
<td>Beech</td>
<td>625</td>
<td>204.5</td>
<td>13.4</td>
<td>302.3</td>
<td>0.56</td>
<td>0.96</td>
<td>1.05</td>
<td>0.45</td>
<td>0.38</td>
<td>50.21</td>
<td>0.34</td>
<td>-0.16</td>
<td>757.5</td>
</tr>
<tr>
<td></td>
<td>Oak</td>
<td>401</td>
<td>159.1</td>
<td>21.3</td>
<td>398.1</td>
<td>0.55</td>
<td>1.04</td>
<td>1.00</td>
<td>0.50</td>
<td>0.82</td>
<td>19.62</td>
<td>0.69</td>
<td>-0.20</td>
<td>146.3</td>
</tr>
<tr>
<td>phase3</td>
<td>Total</td>
<td>892</td>
<td>274.3</td>
<td>30.5</td>
<td>630.7</td>
<td>0.56</td>
<td>1.00</td>
<td>1.02</td>
<td>0.46</td>
<td>0.52</td>
<td>55.69</td>
<td>0.41</td>
<td>-0.16</td>
<td>793.7</td>
</tr>
<tr>
<td></td>
<td>Beech</td>
<td>599</td>
<td>199.0</td>
<td>12.3</td>
<td>278.4</td>
<td>0.56</td>
<td>0.96</td>
<td>1.02</td>
<td>0.45</td>
<td>0.38</td>
<td>49.84</td>
<td>0.34</td>
<td>-0.15</td>
<td>695.6</td>
</tr>
<tr>
<td></td>
<td>Oak</td>
<td>393</td>
<td>361.1</td>
<td>19.8</td>
<td>373.0</td>
<td>0.55</td>
<td>1.05</td>
<td>0.99</td>
<td>0.49</td>
<td>0.81</td>
<td>19.67</td>
<td>0.66</td>
<td>-0.20</td>
<td>139.9</td>
</tr>
</tbody>
</table>

Tab. 3 - Summary analyses of the effect of natural mortality (intensity and mode) and thinning practices (intensity and mode) on the stand structure. (sp*): significant difference between Oak and Beech species ($p$-value $<0.05$); the direction of relationship is shown with + and -, showing positive and negative correlation, respectively and the first +/- sign is for Beech species and the last is for Oak. The meaning of each structural and competition acronym is reported in Tab. S1 (Supplementary material).
the probability of larger remaining trees occurring in close proximity to reference oak trees, and caused a reduction in the dominance of oak.

The diameter differentiation of trees (Dif) reflects that an increased rate and mode of mortality led to a rise in the homogeneity of the diameters of oak and beech trees. In the case of a high mortality rate and mode (Fig. 1b), a higher number of small trees dropped out, and consequently the difference in diameter between the measured reference trees and their neighbours decreased. In managed stands, the thinning of rather large beech trees (thinning mode < 1) and small oak trees (thinning mode > 1), increased the difference in the diameter of beech trees and decreased it for oak.

The non-spatial measure of diameter variation (Odiff) showed that an increasing mortality rate lowered the diameter variation for beech and oak trees through the drop-out of suppressed trees or through releasing target trees of disturbing neighbours (higher value of Agg and smaller values of I). The beech trees exhibited a slight tendency towards clumping, in the case of a high thinning intensity, high mortality rate and thinning of large trees. Many small oak trees died out in the stands with high mortality rates (> 8.3%), which resulted in a lower density and higher regularity (see higher Agg and lower I, in Tab. 2). During the thinning phase, the mean distances to the immediate neighbours decreased through the elimination of a high number of large beech trees standing large distances from their nearest neighbours.

Tree species intermingling

In the third group of indices, Ming accounted for four nearest neighbours and revealed that oak trees appeared mostly in mixed groups. An increasing mortality rate increased the mixture level of the remaining oak trees. On the other hand, we realized lower degrees of species mingling among beech trees. An increase in the mortality rate, mostly due to the drop-out of oak trees, even decreased the species intermingling of beech central trees and their surrounding oak trees. The positive correlation between the mortality mode and mingling in beech trees showed that large surviving beech trees tend to be more intermingled with oak trees compared to small beech trees. Thinning practices countered by removing more beech trees and increasing the relative share of oak within the stand, resulted in a drop in the mingling level of oak trees and an increase in the mingling level of beech trees (Tab. 3).

Accounting only for the closest neighbour (Seg), we found an increased segregation for both species in the case of high mortality rates and high thinning intensities. This can be explained by a lower number of mixed oak-beech pairs, potentially due to the death of many oak trees in the case of high mortality rates (> 8.3%). Those lessened the chance of beech trees having an oak tree as a direct neighbour. Another reason was the thinning of many large beech trees, which increased the chance for oak central trees to have other oak trees as neighbours. However, the remaining presence of large beech and oak trees after natural mortality decreased species segregation, and the thinning mode demonstrated no significant effect on the Seg values of either species (Tab. 3).

Tree competition

An examination of the competitive status of beech and oak trees (CCh and CCo) showed that the competition posed by beech vis-à-vis oak trees declined during the mortality phase, which might be explained by the mortality of suppressed oak trees suffering from a high competition load imposed by the neighbouring beech trees. Thinning practices reduced the competition induced by oak and beech through releasing the reference trees and eliminating the competing neighbours of both species.

Regarding the competition influences of beech on oak, we also compared the height development of oak and beech trees in unmanaged and managed plots, with different thinning intensities. As illustrated in Fig. 3, oak appeared to be dominant in height compared to beech; however, in unmanaged plots older than 150 years of age, beech dominated oak in terms of height. Oak trees were more dominant in height within managed stands where thinning practices favoured oak trees by thinning large beech trees, as shown in Fig. 2b.

Discussion

In our study, the structural processes in mixed beech-oak stands became visible in different structural traits. The analysis of tree-size distribution, spatial distribution, and competition at individual tree and stand level in unmanaged and managed plots demonstrates the clear dominance of European beech, and how the interspecific competition can be modified by thinning. We therefore reject our starting hypothesis, assuming a similar effect of tree removal during natural mortality or/and thinning.

Mortality and thinning significantly modified the tree-size distribution. Through natural mortality only a few large beech trees, small beech trees and many small oak trees dropped out (Fig. 1b), showing that the regeneration of oak was difficult in unmanaged stands. With increasing thinning intensity, a higher number of large beech trees were cut (Fig. 1b). The mean quadratic diameter of beech therefore decreased with thinning, and that of oak increased. The change in tree-size distribu-

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**Fig. 3** - The height development of sessile oak and European beech trees in managed and unmanaged plots.
tion in the analysed beech and oak stands of this study explains the concerns of pro-
ducers of high-quality oak wood in regions of mixed beech-oak forests. In the case of
set-aside plans or restricted silvicultural management, their concern is a high mor-
tality of sessile oak (Hein & Dhôte 2006), or at least a lower production of high-quality
oak wood due to the lacking option of sup-
porting oak growth (Von Lupke 1998). Still,
sessile oak occurs naturally in pristine
forests as long as gaps open up during the
decay stage and provide the regeneration
with enough light. Natural disturbances
could provide those gaps needed for the
regeneration of oak (Larsen & Johnson 1998).
In most managed continuous-cover beech
stands, the phase of late senescence with
natural decomposition and the opening
of gaps, when old trees naturally die, is
shortened through harvesting at earlier
points in time, and a fostering of the regen-
eration of oak would therefore still be nec-
essary e.g., by artificially providing gaps.
The discussion of abandoning managed
forest areas for conservation must address
how to keep oak viable, which is consid-
ered a challenge (Varga et al. 2015). The
structural heterogeneity of forests in once
managed and abandoned forest stands was
found to be lower than in both managed
stands and pristine forests (Stiers et al.
2018). Since oak trees in mixtures with
shade-tolerant species are more likely to
die, the share of oak is expected to de-
crease after sudden abandonment.
The effects of mortality and thinning be-
came visible also in the spatial distribution
of the two species. Both mortality and thin-
ning decreased the tree density and led to
a higher regularity in the horizontal distri-
bution patterns of trees within the stand.
Natural mortality slightly reduced the
clumping pattern in beech and made the
spatial distribution of beech more homoge-
 nous. This is a logical consequence due to
the density-dependent mortality, or self-
thinning, when the regeneration of light-
demanding species is impeded by the shad-
ing of larger trees in their proximities.
Trees growing close to strong neighbours
are therefore more susceptible to stress
and more likely to die (Vacek & Leptš 1996).
The remaining trees will have a more ran-
dom or even a regular horizontal distribu-
tion (Pommerening 2002). Comparable to
the effect of natural mortality, thinning re-
 leased oak trees by removing the closest
neighbouring beech trees. This led to a
larger growing space and a higher survival
rate for oak. The horizontal distribution of
oak trees thus became more regular, which
is the usual effect of thinning with the aim
of reducing competition (Longuetaud et al.
2008).
Over the stand development, the inter-
mingling of oak and beech trees increased
during the mortality phase. As a shade tol-
ernant t-strategist species (Hamilton 1968),
beech usually occupies the gaps made
available through the drop-out of large and
old trees or any other disturbances. That
increased the probability for already-exist-
ing oaks to obtain more beech trees as
their nearest neighbours. This natural proc-
ess of beech replacing and suppressing oak
by occupying each possible location be-
came visible in our study and from other
previous studies (Ligot et al. 2013). With
progressing stand development, it is main-
lly the suppressed oak trees which drop out
(Vacek & Leptš 1996). Strong surviving oak
trees therefore remain at an appropriate
distance from neighbouring beech trees
and can enlarge their growing space. This
decreases the possibility of beech having
oak in close proximity. After thinning, the
intermingling of oak declined because of
the removed neighbouring beech trees,
which resulted in an increased intermin-
gling of beech. To regulate the interspecific
competition, thinning practices often aim
at maintaining a high number of oaks in the
overstorey while restraining beech (Von
Lupke 1998). This might explain our find-
ing of decreased and increased intermingling
in oak and beech surroundings, respec-
tively. Interspecific competition can thus
be managed by controlling the level of in-
termingling in mixed stands.
Natural competition is an important fac-
tor in mixed-species stands, particularly
when species depend on the same re-
ources (Sawicki & Szweczuk 2001). As
the analysed long-term experimental plots
used in this study have a favourable water
and nutrient supply, most of the intra- and
inter-specific competition is for light (Pret-
zesch & Biber 2010). The competition for
light is especially influenced by the vertical
and horizontal structural characteristics
of a stand. Note that the sensitivity to compe-
tition, crowding and overtopping changes
during the ontological development of
trees, and that the changes are different
for each species (Seifert et al. 2014), which
could not be well reflected in this study by
using only one competition index. In any
case, an analysis of the competition in
mixed beech-oak stands shows the high
competitiveness of European beech, as evi-
denced by the higher number of trees and
its relatively wide crown compared to ses-
sile oak (see Tab. 1). The strong competi-
tiveness of beech and the outcompeting
of oak (Hein & Dhôte 2006) also became visi-
able in our study, with a higher mortality
rate for oak than for beech and lower final
tree heights of oak in unmanaged stands
compared to managed stands (Fig. 3). We
found that oak experienced less competi-
tion from beech upon increasing natural
mortality. The competition load on trees of
both species, especially of oak, was re-
duced both by the drop-out of suppressed
small trees, and by thinning. Thinning
therefore intensified the natural process of
self-thinning, through the cutting of sup-
pressed, competing neighbour trees to
promote the growth of target trees (Bon-
cina et al. 2007). Consequently, our analysis
showed that in the case of a high natural
mortality of beech, a lower intensity of
thinning was necessary and vice versa. On
the experimental plots, thinning opera-
tions in favour of oak were required in or-
der to maintain the mixture of beech and
oak over all phases of stand development
(Ligot et al. 2013). Even though the experi-
mental plots used in this study were imple-
mented for testing different intensities of
thinning, their management might differ from
that in private-owned forests. None-
theless, the experimental plots may be use-
ful for providing an idea of the manage-
ment effect in mixed beech and oak stands
in the long term (Pretzsch et al. 2019).

Conclusions
Sessile oak in mixed beech-oak stands is
usually overshadowed and suppressed,
and both its basal area proportion and the
number of stems in the stands decrease
more strongly than those of beech do.
The strong competitiveness of beech over
oak is reflected by several stand-structural
traits. For maintaining a certain share of
oak in mixed beech-oak forests, either reg-
ular thinning interventions (Boncina et al.
2007) or an initial spatial or temporal sepa-
ratin of the two species (Pretzsch & Zen-
ner 2017) is necessary. Our results – which
are representative of a large area of the
common distribution range of European
beech and sessile oak in Germany – show the
need for thinning interventions when aim-
ing at a sustainable mixture of the two
species. In terms of climate change, the
competitiveness of European beech might
be decreasing and sessile oak is expected
to adapt better to climatic changes (such
drought) than beech (Rubio-Cuadrado
et al. 2018). This might make mixed oak
and beech stands even more attractive
when it comes to facing challenges around
future forest ecosystems. Understanding
and managing the structural processes be-
hind competition and facilitation between
beech and oak can therefore lead to a
more stabilised performance of mixed
stands providing multiple ecosystem func-
tions.

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Competition and silvicultural management in mixed beech-oak stands
Maleki K et al. - iForest 13: 80-88

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Competition and silvicultural management in mixed beech-oak stands


Supplementary Material
Tab. S1 - Overview of the structural indices used in this study.
Link: Maleki_3172@suppl001.pdf