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Relation between forest stand diversity and anticipated log quality in managed Central European forests

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ABSTRACT
This study examined the influence of tree species and structural diversity on the production of high-quality logs. The data were from the regional forest inventory of the University Forest Enterprise, Czech Republic, performed from 2009 to 2011 on 1188 sample plots. For every sample plot, we quantified 38 diversity indicators. The plots were divided into four age groups (young, middle-aged, old and uneven-aged stands). The anticipated proportion of high-quality logs was determined using local assortment tables. For each age group, the impact of species and structural diversity indicators on the volumetric proportion of high-quality logs was assessed using backwards multiple regression. The relationship between diversity measures and log quality changed with stand age. In old stands, horizontal structure had a more profound effect on the proportion of high-quality logs. In young stands, species diversity and vertical structure were more influential. In middle-aged stands, the impact of stand diversity on log quality was most complex. In uneven-aged stands, vertical structure was the diversity component most affecting the proportion of high-quality logs. Overall, the proportion of best quality logs increased with the increasing stand diversity in all age classes, suggesting that timber production and stand diversity are not contradictory management goals.

1. Introduction
Timber production and economic yield have always been primary forestry objectives. However, demands for timber and timber products are often considered to be in conflict with demands to maintain biodiversity (Fox et al. 2006). Forest production research has mostly dealt with the relationship between timber yields and species diversity (e.g. Belote et al. 2011; Pretzsch 2005; Liang et al. 2007; Wang et al. 2011). Recently, the impact of stand structural diversity (i.e. spatial and size differentiation of forest stands, Gadow & Hui 1999) on timber production has also received attention (e.g. Liang et al. 2007; Lei et al. 2009; Long & Shaw 2010; Wang et al. 2011).

Although stand productivity and assortment structure (i.e. quantity of logs of differing quality that can be produced from a stand and used for different products; Forest Research Agency 2015) are closely related, higher productivity does not necessarily generate better quality wood. Stands with similar timber stocks may significantly differ in the quality of the timber produced (i.e. in the assortment structure), which affects the income from forests, because the prices of fuel timber are several times lower than the prices of veneer or sawlogs (Suchomel et al. 2012). Therefore, one of the main goals of forest management is to produce high-quality timber assortments (assortments being pieces of timber of different quality into which a tree may be converted; Oxford English Dictionary 2015).

Stand assortment structure is influenced by a number of factors (Danilović 2008; Prka & Krpan 2010; Prka 2012). One of the main factors affecting the distribution of timber assortments in individual trees is the diversity of tree habitus (stem and crown shape; Prka 2012), which is largely influenced by forest structure. This was demonstrated by Liang et al. (2007), who showed that trees of the same size may be of a very different quality due to stand characteristics, such as density, spatial distribution of trees and species composition. However, information about the relationship between stand species and structural diversity, and timber quality is limited. Liang et al. (2007) reported that stands with greater species and structural diversity contained a higher percentage of high-quality timber. Similarly, Guldin and Fitzpatrick (1991) found better log quality in uneven-aged stands than in even-aged stands, while Macdonald et al. (2010) indicated insignificant differences between timber quality of even-aged homogeneous stands and structurally more diverse forests.

Since studies dealing with this issue are scarce, our goal was to fill this gap by analysing relationships between indicators of tree species and structural...
diversity and timber quality in Central European forest stands. We searched for the answers to the following questions: (1) How is the timber quality of a stand influenced by tree species and structural diversity? (2) What diversity elements (Table 1) have the most impact on timber quality? (3) Is the effect of diversity on log quality independent of stand age? We focused upon high-quality, economically most profitable timber (Suchomel et al. 2012) which is most valuable for the wood-processing industry. We hypothesised that the relationship between stand diversity and timber quality is positive, that management goals to achieve high stand diversity and high-quality timber are not contradictory, but complementary to each other. We also expected that their relationship is age-related, that is, the elements of diversity that affect timber quality are not constant over time, but change with age.

2. Materials and methods

Data was collected during the regional forest inventory of University Forest Enterprise ‘Kostelec nad Černými lesy’ of the Czech University of Life Sciences (Figure 1) performed from 2009 to 2011 (Merganič, Marušák et al. 2012). The total area of the enterprise is 6581 ha, 95.4% of which is covered with forests. The majority of the forests in the enterprise are managed, so their development is influenced to a large extent by human activities. Generally, small-scale clear-cutting is used in areas not exceeding 1 ha. Elevations range from 220 to 560 m a.s.l. The average length of the growing season is 153 days. Mean annual temperature varies from 7.0°C to 7.5°C, and mean temperature during the growing season ranges between 13.0°C and 13.8°C. Mean annual precipitation fluctuates from 600 to 650 mm. According to Czech typology (Pliva 1987), six forest types occur in the area of the enterprise. The most common types are Querceto-Fagetum acidophilum and Querceto-Fagetum mesotrophicum that cover almost 40% of the total area of the enterprise. Since these forest types are the most common in the Czech Republic (ÚHÚL 2007), and the tree species composition of the enterprise is similar to the species composition of Czech forests (Krejzar et al. 2015), the enterprise represents well the country’s forests.

In total, 1188 inventory sample plots were established over the whole forested area of the forest enterprise using a stratified sampling design (Merganič, Marušák et al. 2012). The sample plots were of a circular shape with an area of 500 m². On each plot, approximately 100 variables describing site conditions (e.g. slope, aspect, soil moisture), stand development (e.g. stand age, canopy cover, number of layers, level of tree aggregation and mixture) and tree status (e.g. tree species, tree diameter at breast height (DBH), tree height, stem quality, health condition) were assessed. Canopy cover was defined as a ratio of the sum of tree crown projections (i.e. the area of the vertical projections of the outermost perimeter of the crowns on the horizontal plane, Gschwantner et al. 2009) with canopy overlaps removed, to the total area of the sample plot. Hence, the maximum value of canopy cover is 100%. Canopy cover was visually estimated in the field as per cent cover at 5% intervals, separately for trees with DBH less than and greater than 7 cm (hereafter referred to as young and old trees, respectively). Tree canopy layers (NLay, Table 1) were identified after Zlatník (1976) as (1) dominant (significantly above the trees that form the main canopy), (2) co-dominant (trees that form the main canopy), (3) subdominant (trees that are higher than a half of the mean height of dominant trees, but do not reach the main canopy), (4) intermediate (trees and shrubs with a height greater than 1.30 m and smaller than a half of the mean height of dominant trees) and (5) undergrowth (trees smaller than 1.3 m). Undergrowth was further divided into three layers: (5a) trees between 20 cm and 1.30 m in height, (5b) seedlings smaller than 20 cm but older than 1 year and (5c) seedlings up to a year old.

Overall, 29 tree species were identified within the inventory, all occurring in the class of old trees and 22 occurring in the class of young trees. Norway spruce (Picea abies L. Karst.) was the most common tree species in both young and old trees (26% and 53% calculated from the number of young trees and stand volume of old trees, respectively). Other common tree species were silver fir (Abies alba), Scots pine (Pinus sylvestris), European larch (Larix decidua), common beech (Fagus sylvatica), oak (Quercus spp.), hornbeam (Carpinus betulus) and birch (Betula pendula syn. Betula verrucosa). The proportion of some light-demanding species (e.g. Scots pine or larch) was lower in young trees than in old trees, while the proportion of silver fir, which is a shade-tolerant species, was greater in young than in old trees.

In the study, we included stands of all ages because they all represent potential sources of timber, and because their current state affects their future quality, and hence future income from the forests. Since all growth parameters of trees are age-dependent and they do not develop linearly over time, for the analysis, sample plots were divided into four age groups (young, middle-aged, old and uneven-aged stands). Young stands had a mean tree age less than 40 years, middle-aged stands had trees with a mean age between 40 and 100 years and old stands had trees with a mean age greater than 100 years. Stands were classified as uneven-aged if the crown cover of young
Table 1. Species and structural diversity indicators used in this study.

| Type of stand diversity | Category of diversity indicators | Acronym | Explanation | Equation | Reference |
|-------------------------|----------------------------------|---------|-------------|----------|-----------|
| Species diversity       | Species richness                 | R1      | $(S_{tree} - 1)/\ln(N_{tree})$ | Hill (1973) |
|                         |                                  | R2      | $S_{tree}/\sqrt{N_{tree}}$ | Margalef (1958) |
|                         |                                  | N0Shrub | $S_{shrub}$ | Menhinick (1964) |
|                         |                                  | N0Moss  | $S_{moss}$ | Bengtsson (1972) |
| Species evenness        |                                  | D       | $\left(\frac{N_{tree} - \sqrt{\sum_{i=1}^{n} n_i^2}}{N_{tree} - \sqrt{\sum_{i=1}^{n} n_i^2}}\right)$ | McIntosh (1967) |
|                         |                                  | E1      | $H / \ln(S_{tree})$ | Pielou (1957, 1977) |
|                         |                                  | E3      | $(e^{H}) - 1)/(S_{tree} - 1)$ | Heip (1970) |
|                         |                                  | E5      | $((1 - S) - 1)/(e^{H} - 1)$ | Hill (1973) |
|                         |                                  | BP      | $N_{tree}/n_{max}$ | Berger and Parker (1970) |
| Species heterogeneity   |                                  | HB      | $\left(\ln(N_{tree}) - \sqrt{\sum_{i=1}^{n} \ln(n_i)}\right)/N_{tree}$ | Brillouin (1956) |
|                         |                                  | H       | $-\sum_{i=1}^{n} p_i \cdot \ln(p_i)$ | Shannon and Weaver (1949) |
|                         |                                  | Si      | $1 - \frac{\sum_{i=1}^{n} p_i^2}{\ln(n_{max})}$ | Simpson (1949) |
| Species similarity      |                                  | ED2     | $\frac{\sum_{i=1}^{n} (p_i \cdot \ln(p_i))}{\sum_{i=1}^{n} \ln(n_i)}$ | Lance and Williams (1966) |
|                         | between young and old trees      | DF2     | $\frac{\sum_{i=1}^{n} (p_i \cdot \ln(p_i))}{\sum_{i=1}^{n} \ln(n_i)}$ | Lance and Williams (1966) |
|                         |                                  | BC1     | $\frac{\sum_{i=1}^{n} \max(p_{iA}, p_{iB}) - \sum_{i=1}^{n} \min(p_{iA}, p_{iB})}{\sum_{i=1}^{n} \max(p_{iA}, p_{iB})}$ | Lance and Williams (1966) |
|                         |                                  | BUB     | $\frac{\sum_{i=1}^{n} \min(p_{iA}, p_{iB}) + \sum_{i=1}^{n} \max(p_{iA}, p_{iB}) - \sum_{i=1}^{n} \max(p_{iA}, p_{iB}) - \sum_{i=1}^{n} \min(p_{iA}, p_{iB})}{\sum_{i=1}^{n} \max(p_{iA}, p_{iB}) - \sum_{i=1}^{n} \min(p_{iA}, p_{iB})}$ | Lance and Williams (1966) |
|                         |                                  | Y       | $\frac{\sum_{i=1}^{n} \min(p_{iA}, p_{iB}) + \sum_{i=1}^{n} \max(p_{iA}, p_{iB}) - \sum_{i=1}^{n} \max(p_{iA}, p_{iB}) - \sum_{i=1}^{n} \min(p_{iA}, p_{iB})}{\sum_{i=1}^{n} \max(p_{iA}, p_{iB}) - \sum_{i=1}^{n} \min(p_{iA}, p_{iB})}$ | Lance and Williams (1966) |
|                         |                                  | QS1     | $\frac{2\sum_{i=1}^{n} \min(p_{iA}, p_{iB})}{\sum_{i=1}^{n} \max(p_{iA}, p_{iB})}$ | Lance and Williams (1966) |
|                         |                                  | QS2     | $1 - QS1$ | Lance and Williams (1966) |
|                         | Proportional similarity          | PS      | $\sum_{i=1}^{n} \min(p_{iA}, p_{iB})$ | Lance and Williams (1966) |

(Continued)
| Type of stand diversity | Category of diversity indicators | Acronym | Explanation | Equation | Reference |
|------------------------|----------------------------------|---------|-------------|----------|-----------|
| Structural diversity   | Horizontal structure             | AG      | Species aggregation | 1 – Clustered |          |
|                        |                                  |         | 2 – Random   |          |          |
|                        |                                  | SM      | Species mixture | 3 – Single tree-wise |          |
|                        | Vertical structure               | N0Lay   | Number       | = number of tree canopy layers | Zlatník (1976) |
|                        |                                  | LayRel  | Ratio        | = N0Lay/7 |          |
|                        |                                  | Var1    | Range        | = Xmax – Xmin (absolute range of tree heights) |          |
|                        |                                  | Var2    | Range        | = Var1/Xmin (relative range of tree heights) |          |
|                        |                                  | PmS     | Ratio        | = number of trees with diameter above 7 cm/number of trees with diameter below 7 cm |          |
|                        |                                  | PmM     | Ratio        | = number of trees with diameter below 7 cm/number of trees with diameter above 7 cm |          |
|                        | Structural similarity between young and old trees | ED1     | Euclidian distance | = \sqrt{\sum_{i=1}^{n} (n_A - n_B)^2} | Lance and Williams (1966) |
|                        |                                  | DF1     | Canberra distance | = \sqrt{\sum_{i=1}^{n} n_A - n_B} \sum_{i=1}^{n} Ntree |          |
|                        |                                  | BC2     |                | = 2 \sum_{i=1}^{n} n_A n_B \sum_{i=1}^{n} Ntree | Bray and Curtis (1957) |
|                        | Woody debris                     | VolCWD  | Volume       | = \sum_{i=1}^{a} \frac{d_i}{1} (volume of coarse woody debris) – Smalian formula | Šmelko (2007) |
|                        |                                  | VolFWD  | Volume       | = 0.0033 \cdot \frac{d_{av}}{1}^{0.5} \cdot \frac{A_i}{V_i} (volume of fine woody debris) | Šmelko (2010) |
|                        |                                  | PmH     | Ratio        | = volume of coarse woody debris/volume of fine woody debris |          |
|                        |                                  | PmT     | Ratio        | = volume of fine woody debris/volume of coarse woody debris |          |
|                        |                                  | PHZ     | Ratio        | = volume of coarse woody debris/volume of living trees |          |
|                        |                                  | PTZ     | Ratio        | = volume of fine woody debris/volume of living trees |          |
|                        |                                  | POZ     | Ratio        | = volume of woody debris/volume of living trees |          |

Young and old trees are with diameter at breast height less than and greater than 7 cm, respectively.
d: Diameter of coarse woody debris piece; l: length of coarse woody debris piece; d_{av}: average diameter of fine woody debris; A_i: area of i-th sample plot; N_{tot}: total number of trees per sample plots; n_i: number of i-th tree species per sample plots; p_i: proportion of tree species per sample plots; A, B, C: class of trees: young, old, all; X: tree heights.
trees with diameters less than 7 cm exceeded 30%. From all inventory plots, 265, 530, 275 and 118 plots represented young, middle-aged, old and uneven-aged stands, respectively. These age groups enabled the analysis of the relationship between diversity and quality while excluding the non-linear impact of stand age. At the same time, it allowed us to examine if and how the relationship changes with stand age.

2.1. Quantification of plant diversity
Stand diversity was quantified using different indicators representing plant species and structural diversity. Species diversity is based on species composition that refers to the identity and variety of elements in a group (Noss 1990). Depending on how the species composition is evaluated, species diversity indicators can be placed in three groups (Ludwig & Reynolds 1988; Krebs 1989): (1) species richness expressed as a number of species in a stand (Krebs 1989), (2) species evenness referring to the equality in species composition in a stand (Bruciamacchie 1996) and (3) species heterogeneity encompassing both species richness and evenness (Bruciamacchie 1996). In addition to these three categories, we identified the fourth group of species diversity indicators representing species similarity between young and old trees in a stand (Magurran 2004) (Table 1). Structural diversity of a stand is defined as the specific arrangement of stand components (Gadow 1999). In our analysis, we identified four groups of structural indicators: (1) horizontal structure (i.e. spatial distribution of the elements in the stand; Neumann & Starlinger 2001), (2) vertical structure (i.e. vertical differentiation of the stand; Kint et al. 2000), (3) structural similarity between young and old trees in a stand (Ludwig & Reynolds 1988; Krebs 1989) and (4) woody debris (Humphrey & Watts 2004; Woodall & Williams 2005) (Table 1).

The selection of the individual indicators in each group was based on review of the literature (Ludwig & Reynolds 1988; Humphrey & Watts 2004; Woodall & Williams 2005; Merganič, Merganičová et al. 2012). The selected indicators are presented in Table 1.

2.2. Calculation of tree volume
Tree volume was calculated using two-parameter regressions derived for volumetric tables of Czechoslovakia by Petráš and Pajtík (1991) for the most common 11 tree species: 7 broadleaved (beech, oak, hornbeam, birch, ash, poplar, poplar clone, alder) and 4 coniferous tree species (spruce, fir, pine, larch). The equations were derived from felled sample trees measured in 2 m sections, including stem and crown woody parts. The mathematical form and the regression coefficients differed for individual tree species because each tree species is
characterised by a different tree habitus. The specific formulations for individual species can be found in Petráš and Pajtík (1991).

The general form of the relationship was
\[ v = f(dbh, h) \]
where \( v \) is total volume in cubic metres, \( dbh \) is the tree DBH in centimetres and \( h \) is the tree height in metres.

2.3. Log grading

Log grading was performed using assortment tables of Petráš and Nociar (1990, 1991) that quantify the proportion of six different product classes ranging from logs of the highest quality that can be used for veneer production to low-quality fuel wood. Log grading of each tree is dependent on the region, tree species, age, tree DBH, stem quality and stem damage assessed in the field. For the purposes of this study, for each stand, we used the proportion of the two top assortment classes containing the highest quality logs, which can be used for veneer, musical instruments, sport equipment and barrels. For each plot, an indicator of anticipated production of high-quality logs, or quality log proportion (QLP), was quantified as the volumetric proportion of the two best assortment classes from the total timber volume of the plot. The proportion of the logs was chosen instead of the absolute volume to ensure the comparability of the individual plots, because the coefficient of variation of volume was high (61%). We focused upon this high-quality timber because it is economically the most profitable and most valuable for the wood-processing industry. Our preliminary analysis showed that the mean proportion of this high-quality timber in our region was 26%, indicating that the two top assortment classes represented one-fourth of the whole timber stock of the enterprise.

2.4. Multiple regression between diversity indicators and indicators of anticipated log quality

The analysis was carried out in several steps. First, plots were segregated into the four age groups previously discussed to exclude the impact through time of non-linear development of the proportion of high-quality timber. Then, diversity indicators were divided into eight groups characterising species richness, species evenness, species heterogeneity, species similarity, horizontal structure, vertical structure, structural similarity and woody debris (Table 1). This was done because the high number of indicators and their multi-collinearity would cause difficulty in estimating variable coefficients.

For each stand age group, multiple linear regression was then performed separately for each group of diversity indicators, using all the indicators in that category, to determine which indicators had the greatest effect on the volumetric proportion of high-quality logs (QLP):

\[
QLP = a + b_1 \times DI_1 + b_2 \times DI_1 + \ldots + b_n \times DI_n
\]
where \( a \) and \( b \) are regression coefficients of the linear regression and \( i \) is the index for \( n \) diversity indicators (ranging from 1 to \( n \)) for a given category of diversity indicators. In addition to diversity indicators, these regressions included five covariates as independent variables: total volume of living trees (VolTotal), mean age of young and old trees per stand (AgeYoung, AgeOld) and canopy cover of young and old trees per stand (CanopyYoung, CanopyOld). The selection of these covariates was based on factors known to affect forest growth and yield processes (Pretzsch 2009) and previous analyses of our data which showed that stand age, stocking and forest type had a significant impact on both species richness and the economic value of timber in the stands of the forest enterprise (Merganič, Marušák et al. 2012). Stand volume and canopy cover can be considered as indirect measures of site conditions (i.e. of forest types).

In the next step, independent variables included in the preliminary analyses (both diversity indicators and covariates) were excluded from the regression using backwards selection based on their tolerance, variance inflation factor (VIF) and \( t \) value. The tolerance of each indicator should be above 0.1 and the higher the value of tolerance the better (Quinn & Keough 2002). VIF should be below 10, preferably as low as possible, to avoid strong multi-collinearity between the independent variables (Marquardt 1970). Diversity indicators should also have \( t \) values greater than or equal to 1.96 (for \( df > 100 \) and \( \nu = 0.05 \)) to significantly contribute to explaining the variance of QLP, the dependent variable.

In the final step, for each stand age group, all significant diversity indicators from each diversity group and all covariates were included in one multiple regression and those that were insignificant and/or showed strong collinearity to other independent variables were excluded using backwards selection. The final multiple regressions for each stand age group comprised only significant independent variables that were not collinear.

3. Results

For the evaluated stands, plant species and structural diversity had a significant impact on the anticipated...
production of high-quality logs (QLP). However, the adjusted $R$-squared of the derived multiple regressions did not exceed 0.5, indicating that the combination of significant diversity indicators and covariates explained less than 50% of the total variance in QLP for a given stand age group. The highest correlation coefficient was obtained for the age group of uneven-aged stands ($R = 0.68$), and the lowest for old stands ($R = 0.38$).

The number of indicators included in the regressions and their combination differed between the age groups. The highest number of independent variables was in the regression of middle-aged stands (8), for which we found the second highest correlation ($R = 0.62$). The minimum number of independent variables (3) was in the regression derived for uneven-aged stands (Table 2).

Every regression contained at least one covariate variable (Table 2). In old and young stands, the age of young trees (AgeYoung) had a negative significant impact on the proportion of best quality logs, while in middle-aged and uneven-aged stands it was the age of old trees (AgeOld) which had a positive significant relation to QLP (Table 2). Stand volume (VolTotal) as another covariate was included in two regression models for middle-aged and young stands, in which it had the greatest positive impact on the proportion of best quality logs (Table 2, Figure 2). Another covariate, canopy cover of old trees (CanopyOld), remained only in the regression for old stands (Table 2), where it was the second most influential indicator and had a positive relation with QLP. All significant species diversity indices except for BC1 had a positive relation to the proportion of best quality logs in all regressions (Table 2). Species diversity indicators were included in all regressions except in the equation for uneven-aged stands. Three species diversity indicators were included in the regressions for middle-aged stands, one representing species richness (R2), one species heterogeneity (Si) and one species similarity between young and old trees (Y) (Table 2). In young stands, the proportion of high-quality timber was significantly correlated with two species diversity indicators representing species richness and species similarity between young and old trees (R2 and BC1, respectively). In the regression derived for old stands, the number of shrub species representing species richness (N0Shrub) was the only species diversity indicator with significant impact on QLP (Table 2).

All regressions contained structural diversity indicators (Table 2), but their character differed among stand age groups. Indicators of vertical structure occurred in the regressions for the uneven-aged, young, and middle-aged stands. Indicators of horizontal structure had significant impacts on QLP in middle-aged and old stands, and woody debris had a significant impact on QLP in old stands (Table 2). All indicators of structural diversity were positively correlated with QLP except for the ratio of volume of fine to coarse woody debris (PmT) (Table 2).

For old forest stands, six independent variables entered the final multiple regression model (Table 2),

Table 2. Statistics of multiple linear regressions calculated for age groups.

| Stand age group | Multiple $R$ | Adjusted $R$-squared | $F$ | Variable | Beta | Standard error of beta |
|-----------------|--------------|-----------------------|-----|----------|------|------------------------|
| Old stands >100 years | 0.38 | 0.15 | 43.95 | CanopyOld | 0.212 | 0.058 |
| | | | | AgeYoung | −0.118 | 0.057 |
| | | | | PmT | −0.145 | 0.057 |
| | | | | SM | 0.176 | 0.062 |
| | | | | AG | 0.231 | 0.063 |
| | | | | N0Shrub | 0.116 | 0.057 |
| | | | | R2 | 0.219 | 0.048 |
| | | | | AgeOld | 0.102 | 0.048 |
| Middle-aged 40–100 years | 0.62 | 0.38 | 33.12 | Si | 0.123 | 0.054 |
| | | | | SM | 0.102 | 0.042 |
| | | | | DF1 | 0.187 | 0.045 |
| | | | | Y | 0.151 | 0.054 |
| | | | | LayRel | 0.156 | 0.042 |
| | | | | VolTotal | 0.407 | 0.047 |
| | | | | N0Shrub | 0.116 | 0.057 |
| | | | | R2 | 0.219 | 0.048 |
| | | | | AgeYoung | −0.137 | 0.063 |
| Young <40 years | 0.54 | 0.27 | 18.25 | BC1 | 0.359 | 0.076 |
| | | | | DF1 | −0.214 | 0.083 |
| | | | | PmS | 0.293 | 0.060 |
| | | | | N0Shrub | 0.136 | 0.057 |
| | | | | R2 | 0.219 | 0.048 |
| | | | | AgeOld | 0.229 | 0.102 |
| Uneven-aged | 0.68 | 0.44 | 32.16 | LayRel | 0.245 | 0.071 |
| | | | | N0Shrub | 0.485 | 0.101 |

Multiple $R$ is the coefficient of multiple correlation for all independent variables included in the equation. The adjusted $R$-squared indicates the coefficient of determination adjusted for the number of independent variables included in the multiple regression. Beta is the standardised regression coefficient of the independent variable.

AG: species aggregation; AgeOld: mean age of trees with diameter above 7 cm; AgeYoung: mean age of trees with diameter below 7 cm; BC1: index of similarity (Bray & Curtis 1957) between trees with diameter below and above 7 cm; CanopyOld: canopy cover of trees with diameter above 7 cm; DF1: index of similarity (Canberra distance, Lance & Williams 1966) between the trees with diameter below and above 7 cm; LayRel: ratio of number of tree layers to maximum number of tree layers; N0Shrub: number of shrub species; PmS: ratio between the number of trees with diameter above 7 cm and the number of trees below 7 cm; PmT: ratio of volume of fine woody debris to volume of coarse woody debris; R2: index of species richness (Menhinick 1964); Si: index of species heterogeneity (Simpson 1949); SM: species mixture; Var1: absolute range of tree heights; VolTotal: total volume of living trees in m$^3$; Y: similarity index by Boyce (2003).
of which two were covariates (canopy cover of old trees [CanopyOld] and stand age of young trees [AgeYoung]), one represented species richness (number of shrub species [N0Shrub]) and two represented horizontal structural diversity (species aggregation [AG], species mixture [SM]) and one represented dead wood (ratio of volume of fine woody debris to coarse woody debris [PmT]). SM had the highest impact on QLP followed by canopy cover of old trees and AG (see Pareto graph, Figure 2).

In the multiple regression derived for middle-aged forest stands, stand volume (VolTotal) was the variable with the greatest effect on QLP (Figure 2), followed by age of old trees (AgeOld), and an index of structural similarity between young and old trees (DFI). This regression contained indicators that represented six out of the eight groups of diversity indicators (only species evenness and woody debris were not included).

The multiple regression for young forest stands contained five significant variables, of which two were covariates (stand volume [VolTotal], age of young trees [AgeYoung]), one represented species richness (R2), one species similarity between young and old trees (BC1) and one vertical structure (PmS). Stand volume had the greatest effect on QLP, as was also the case for middle-aged stands (Figure 2). In the uneven-aged stands, the range of tree heights (Var1) had the greatest impact on QLP (Figure 2). This regression contained only diversity indicators representing vertical structure (Table 2).

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The multiple regression for young forest stands contained five significant variables, of which two were covariates (stand volume [VolTotal], age of young trees [AgeYoung]), one represented species richness (R2), one species similarity between young and old trees (BC1) and one vertical structure (PmS). Stand volume had the greatest effect on QLP, as was also the case for middle-aged stands (Figure 2). In the uneven-aged stands, the range of tree heights (Var1) had the greatest impact on QLP (Figure 2). This regression contained only diversity indicators representing vertical structure (Table 2).

4. Discussion

Our results indicate that structural diversity had a greater effect on the proportion of best quality timber than species diversity, since the regressions comprised more structural indicators than species indicators (Table 2, Figure 2). In addition, species diversity indices had usually a lower impact on the proportion of best quality logs than structural diversity indicators, since their beta coefficients were smaller compared to those for structural diversity indicators (Table 2). The results also confirmed our hypothesis that the impact of species and structural diversity changed with stand age. In young stands, species diversity seemed to be more important for generating timber of high quality, while in old stands horizontal structure of the stands was more influential. In middle-aged stands, the impact of species and structural diversity on the proportion of high-quality logs was the most complex, because the derived regression contained indicators representing all groups of diversity except for species evenness and woody debris (Table 2). In uneven-aged stands, vertical structure seemed to be the diversity feature controlling log quality, since the regression comprised only indicators of vertical diversity (number of tree layers and range of tree heights) and a covariate (Table 2).

Most diversity indicators had a positive impact on the proportion of high-quality logs (Table 2), which indicated that promoting greater stand species and structural diversity can, at the same time, result in better...
timber quality. All significant vertical diversity indicators included in the regressions were positively correlated with the proportion of best quality logs (Table 2). This is in accordance with silvicultural experiments that have shown the positive impact of multi-layer vertical structure on overall stand productivity (Coomes et al. 2014; Pretzsch 2014; Jucker et al. 2015).

Horizontal structure had the most significant impact on QLP in old stands, where it was represented by two indicators (Table 2, Figure 2): SM and AG. Both positively affected the proportion of best quality logs. The values of these two diversity indicators increase with increasing mixture and intermingling of tree species in the stand (Table 2). This result suggested that better log quality can be expected in the old stands characterised by greater intermingling of species in the stand. This positive effect can be explained by so-called complementary demands for resources of different tree species, which has been demonstrated in different studies (e.g. Morin et al. 2011; Jucker et al. 2015) and has been shown to increase with age (Cardinale et al. 2007). Similarly, Liang et al. (2007) found that timber quality depends on the spatial distribution of trees.

The last structural diversity indicator in the regression for old stands was the ratio of volume of fine woody debris to coarse woody debris (PmT) (Figure 2, Table 2), which had a negative impact on QLP. The group of old stands in our study included stands in the regeneration period. More fine woody debris in a stand suggested that when coarse timber was extracted, fine material was left on the site. The previous felling may have removed higher quality trees, leaving those of lower quality for the next felling. In addition, overstory trees remaining in a stand develop, creating larger crowns in reaction to changes in the local competitive environment induced by canopy openings (Jucker et al. 2015), with proportionately higher investment in crowns or fine material than in high-quality boles. Hence, the next felling may generate more fine woody debris that usually remains in the stand. Thus, the combination of extraction of higher quality trees during first rotation fellings and the subsequent increase in crown biomass on remaining trees may result in a negative relationship between PmT and QLP.

The positive relations of all significant diversity indicators to the proportion of high-quality logs in middle-aged stands (Table 2) indicated that the timber quality was higher in the stands that were more differentiated in their species composition and stand structure. Our results suggest that promoting species and structural diversity by thinning may increase the quality of the remaining stand and generate more future income from the mature forest. In middle-aged stands, future timber production is improved by thinning treatments that influence the growth of individual trees (Pretzsch 2009). Several authors (Danilović 2008; Prka & Krpan 2010) have shown thinning may greatly improve final timber quality, as this changes the final habitus of individual trees, which improves log quality for a given tree (Prka 2012). In addition, species diversity may help increase forest productivity by promoting denser and more structurally complex canopies (Jucker et al. 2015). Hence, thinning treatments that increase species and structural diversity of stands may generate both higher timber production and quality.

Four out of five significant species diversity indices for the even-aged stands were positively correlated with the proportion of best quality logs (Table 2). This suggested that when species diversity was higher, the proportion of best quality logs was greater for such stands. This is in accordance with Liang et al. (2007), who found that the proportion of peeler logs was positively correlated with species diversity. This finding may help to promote mixed forest stands for forestry, although the timber yields of mixtures may not always reach the timber yields of pure stands (Knoke et al. 2008).

The only exception was the BC1 species similarity index between young and old trees in the regression for young stands, which had a negative relationship with the proportion of best quality logs (Table 2). The value of this indicator is 0 if the species composition of the two classes of trees is the same, and increases as the differences in the species composition of the tree classes increase, to a maximum value of 1. Hence, its negative impact suggested that the proportion of high-quality logs was greater in stands with fewer species. A slight tendency towards lower stem quality with increasing tree species diversity on the stand level was also reported by Benneter and Bauhus (2014). Nevertheless, the negative effect of BC1 was smaller than the positive influence of the ratio between the numbers of old trees and young trees representing vertical structure and the R2 index of species diversity, since the absolute value of the beta coefficient of BC1 was smaller than the beta coefficients of the other two diversity indicators (Table 2). Hence, overall we can state that in young stands the proportion of high-quality logs increased with increasing stand species and structural diversity.

The present study indicated that under the conditions encountered in Central Europe, species and structural diversity and quality of timber production are not in conflict to each other. Hence, promoting both biologically and structurally diverse stands may enhance the economic value of the final timber production from temperate forests of Central Europe. Similarly, Benneter and Bauhus (2014) showed that diverse stands are capable of providing highly valuable timber while at the same time providing other ecosystem services.
The fact that species and structural diversity indicators explained less than 50% of the total variance in QLP points to the influence of other factors on log quality. In addition to already mentioned management treatments, site conditions also play an important role (Danilović 2006). For example, Jucker et al. (2014) presented that the productivity of mixed stands may be significantly hampered by drought. More research is needed on the relationship between log quality, diversity and other factors. Such studies provide us with information needed to modify modern forest management to support sustainability.

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