Structure and diversity of a natural temperate sessile oak (Quercus petraea L.) – European Beech (Fagus sylvatica L.) forest

Any Mary Petritan, Ioov Adrian Biris, Oliver Merce, Daniel Ond Turcu, Ion Catalin Petritan

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A B S T R A C T

The paper details an investigation of the stand structure and patterns of diversity observed in the Runcu-Grosi Natural Reserve (western Romania), one of the best preserved natural mixed sessile oak forests in Europe. The effect of the proportion of sessile oak in the stand composition on specific patterns was also studied.

Comparable with other natural forests, the stands of Runcu-Grosi are characterised by a high volume (mean living tree volume of 577 m³ ha⁻¹ in the sessile oak dominated plots and 675 in the pure beech plots), a highly differentiated diameter distribution and a large quantity of dead wood, especially in the mixed plots (approx. 135 m³ ha⁻¹, compared to 75 in the pure beech plots). The higher volume of coarse woody debris in the mixed plots is due to the higher proportion of dead sessile oak in the reserve, which accounted for about 70% of the total dead wood in both the sessile oak and the beech dominated plots. The over-proportional representation of dead sessile oak, and a very low number of oak saplings taller than 1.3 m, indicated a declining tendency of sessile oak in the stand in future. The sessile oak dominated stands exhibited a higher level of tree species diversity than those dominated by beech. Where beech was the dominant species, a high percentage of the sessile oak was present in pure groups (36%), whereas in the oak dominated stands, most of the sessile oaks were surrounded either by shade tolerant beech or by other species (ca. 75%), and were classed as either dominant or codominant trees. These species-specific patterns correspond with the silviculture of mixed oak-beech forests: without interventions to favour oak, the dominance of beech will increase.

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1. Introduction

The conceptual model for forestry that targets greater naturalness in stand management (i.e., ‘close-to-nature silviculture’) is an important objective throughout much of the European forestry sector at present. Since, in order to manage forests in a natural way, it is necessary to know more about the patterns and processes that occur naturally in forests (Butler-Manning, 2007), the number of studies conducted in natural forests sharply increased in the last decades. They highlighted the great importance of these forests in harbouring high biological diversity (Lindenmayer and Franklin, 2002; Burascano et al., 2009) and in terrestrial carbon storage (Luyssaert et al., 2008; Keith et al., 2009). Furthermore, they provide useful information for silviculturists to maintain or restore a degree of old-growth character in managed forests (Bauhus et al., 2009; Wirth et al., 2009; Keeton et al., 2010).

As temperate broadleaved forests are one of the most severely exploited ecosystem types, particularly in Europe (Röhrig, 1991; Parviainen et al., 1999), the few examples of this forest type exhibiting a higher degree of naturalness have come into focus as references for forest management (Meyer et al., 2003). The most ecosystem types that may be characterised as virgin or old-growth forests in Europe are remnants of pure coniferous forests, coniferous forests mixed with beech (e.g., Nagel et al., 2007, 2010; Nagel and Svoboda, 2008; Kuchel et al., 2010) and pure beech forests (Tarko, 2000; Dörländer and Lüpfke, 2007; Veen et al., 2010), whereas pure and mixed sessile oak forests showing no signs of human impact are very rare and furthermore have been poorly investigated (Korpe, 1995; Smjeikal et al., 1995). Since almost all of the oak forests in Europe have been very intensively managed, even the best examples of semi-natural forests that have been exempted from silvicultural management and been left to develop naturally, are “often the result of centuries-old management regimes” (Vandekerhove et al., 2009). Therefore, the investigation of mixed oak forests with high naturalness degree would be welcome.

In the face of expected climate change and higher probability of extreme events such as storms or droughts, the establishment of
mixed stands is increasingly being recommended (Lüpke, 2009). The reason for this is that species of contrasting ecological characteristics combined in one stand can increase overall stand stability by increasing the resistance of the stand to stress and by distributing the risks of climate change (Lüpke, 2004). European beech (Fagus sylvatica) is the most important of the European deciduous broadleaf species (Bohn et al., 2004). It is, therefore, and will remain, one of the main species found in mixed stands in combination with other productive broadleaved tree species. In addition to beech, oak species (Quercus sp., in particular sessile oak (Q. petraea) and pedunculate oak (Q. robur)) are important broadleaf species of Europe – both economically and ecologically – with a good natural occurrence in Central Europe and particularly in Eastern Europe. Despite of oak decline in Europe in the past decades, caused by a complex interaction of abiotic and biotic factors (Thomas et al., 2002), the oak species might have an important role in European forests in the future, particularly in their natural range. Recent ecological studies that investigated the reaction of these species to warming and modification of precipitation regime (Friedrichs et al., 2009; Mérian et al., 2011), attributed a lower climate sensitivity and a higher drought tolerance to sessile oak (Brëda et al., 2006; Friedrichs et al., 2009). Thus this species which is adapted to a large range of ecological conditions (Berger et al., 2005) seems to be better to cope with the expected climate change in pure and mixed stands. However, more ecological studies as well as new insights concerning the patterns and processes that occur naturally in such stands are needed. The recent inventory of the virgin and natural forests of Romania conducted by the Forest Research and Management Institute (Giurgiu et al., 2001; Veen et al., 2010) led to the designation of the Runcu-Grosi Natural Reserve, dominated by stands of pure beech and mixed beech and oak (especially sessile oak). Due to the inaccessibility of the area in the past, this forest was never commercially exploited. Only a few management interventions (between 0 and 4, with a median of 1) of a low intensity (generally < 30 m³ ha⁻¹ wood volume removed) took place in the period 1977–1987. The wood removed during these interventions was predominantly dead wood and sick and windthrown trees. Minimal human influence in the forests of the Runcu-Grosi Natural Reserve provides a rare opportunity to investigate and understand the processes occurring in natural mixed sessile oak forests. Due to the scarcity of mixed oak and beech forests without or with only minimal human influence, this study will provide valuable insights into the structure, diversity and amount of dead wood of such mixed forests. Furthermore, the effects of the participation of different species in the stand composition on forest structure and diversity will be investigated. The following two hypotheses will be tested:

1. The structure and diversity of the investigated natural mixed sessile oak-beech forest are similar to those of other virgin or near-natural forests;
2. The predominance of different species in the stand composition (i.e., beech as the dominant species or sessile oak as the dominant species) implies specific patterns of stand structure and diversity.

2. Materials and methods

2.1. Study site

The study area Runcu-Grosi Natural Reserve is situated in the western part of Romania (46°11′N and 22°07′E), in the Zarand Mountains at an altitude of 350–620 m a.s.l. The climate is temperate continental with a slight Mediterranean influence. The mean annual temperature varies between 7.6 °C and 9.4 °C, and the mean annual precipitation between 750 and 925 mm, 420–580 mm of which falls during the growing season. The natural reserve covers an area of 261.8 ha and is dominated by sessile oak and European beech. The soils are cambisols and luvisols, predominantly with a good water and nutrient supply. The potential natural vegetation is Neutrophile mixed beech-sessile oak-hornbeam forests (Donita et al., 2008).

2.2. Field measurements

A total of 134 circular plots of 1000 m² covering the entire reserve were traced out systematically in a rectangular grid of 150 × 200 m. Among them, 34 plots were randomly scattered throughout the sampling network, where the data were recorded in 2009. Within each plot, all trees with a diameter at breast height (dbh) > 5 cm were mapped using the Field Map Data Collector. For each living tree, the height was measured to within 0.5 m and the dbh, taken in two perpendicular directions, was measured to the nearest centimetre. The trees were classed according to three canopy layers: overstorey > 2/3 top height, midstorey 1/3–2/3 top height and understory < 1/3 top height (Leibundgut, 1993). The top height is the average height of the 20% largest trees in the stand (Kramer and Akça, 1995). The coarse woody debris (CWD) consisted of standing dead wood or snags (dbh ≥ 5 cm, height ≥ 1.3 m) and lying dead wood or logs (small-end diameter ≥ 5 cm). In the case of snags, the tree species, dbh and height were measured. For the logs, the species, the diameter at both ends and the total length were recorded.

Trees belonging to the natural regeneration (all individuals < 6 m in height) were identified by species and counted in four circular subplots. These subplots had a radius of 1 m and were situated 9 m from the plot centre in the four cardinal directions (N, S, W, E). The seedlings and saplings were attributed to four height classes: <1.3 m, 1.3–2 m, 2–4 m and 4–6 m.

The volume of living and standing dead wood was determined using the double-logarithmic regression equation:

\[ \log V = a_0 + a_1 \log d + a_2 \log h + a_3 \log^2 d + a_4 \log^2 h, \]

where \( V \) is tree volume, \( d \) is dbh, \( h \) is height and \( a_0, a_1, a_2, a_3, a_4 \) are regression coefficients for different species established by Giurgiu and Drăghiciu (2004).

The volume of lying dead wood was calculated using the formula to calculate the volume of a truncated cone.

Of the 34 circular plots sampled, 7 consisted only of beech, 14 were dominated by beech (>50% of total volume), 11 by sessile oak (>50% of total volume) and 2 by other species. In order to investigate the specific structural pattern induced by different species compositions, the sampled plots were classified according to three stand types: pure beech, beech dominated and sessile oak dominated. The two plots dominated by other species were excluded from subsequent analyses.

2.3. Data analysis

The forest stand diversity within each type was characterised by tree layer species richness and the Shannon index:

\[ H' = \sum_{i=1}^{N} p_i \ln p_i \text{ where } p_i = \frac{n_i}{N}, \]

\( n_i \) is the number of trees of the \( i \)th species and \( N \) is total tree number.

The spatial structure of the three stand types was characterised by the spatial distribution of the tree positions using the contagion
index ($W_i$), the spatial mingling of different tree species using the mingling index ($M_i$) and the spatial arrangement of tree dimensions using the size differentiation index ($U_i$) (refer to Aguirre et al., 2003). For more detail regarding these indices refer to Hui and Gadow (2002). A short description is provided below:

The contagion index ($W_i$) describes the regularity of the spatial distribution of the four trees nearest to a reference tree $i$, and is based on the comparison of the angles $\alpha_j$ between these four neighbours with a reference standard angle $\alpha_0$, which is expected in a regular point distribution.

$$W_i = \frac{1}{4} \sum_{j=1}^{4} v_j$$

with $v_j = \begin{cases} 1, & \alpha_j < \alpha_0 \\ 0, & \text{otherwise} \end{cases}$ and $0 \ll W_i \ll 1$

The species diversity in the vicinity of a reference tree is described by the mingling index ($M_i$), defined as the proportion of the four nearest neighbours that do not belong to the same species as the reference tree:

$$M_i = \frac{1}{4} \sum_{j=1}^{4} v_j$$

with $v_j = \begin{cases} 0, & \text{neighbour } j \text{ belongs to the same species as reference tree } i \\ 1, & \text{otherwise} \end{cases}$

The size differentiation index ($U_i$) is defined as the proportion of the four nearest neighbours of a given reference tree that are bigger than the reference tree:

$$U_i = \frac{1}{4} \sum_{j=1}^{4} v_j$$

with $v_j = \begin{cases} 0, & \text{neighbour } j \text{ is smaller than reference tree } i \\ 1, & \text{otherwise} \end{cases}$ and $0 \ll U_i \ll 1$

All three indices were computed using Winkelmass 1.0 (Hui and Gadow, 2002).

The above indices measure horizontal structure. To assess the vertical structure the index $A$ proposed by Pretzsch (1996) was adopted. This is a measure of vertical species diversity combining Shannon indices after stratification into three height layers.

$$A = -\sum_{i=1}^{S} \sum_{j=1}^{Z} p_{ij} \ln p_{ij}$$

with $S = \text{number of species}$, $Z = \text{number of height layers}$, $p_{ij} = \text{proportion of species } i \text{ in layer } j = \frac{n_{ij}}{N}$, $n_{ij} = \text{number of individuals of species } i \text{ belonging to height layer } j$, $N = \text{total number of trees}$.

The differences between the three stand types were tested by means of an analysis of variance (Anova) using the HSD test unequal $N$. Where the data did not comply with the requirements...
of parametric test methods (normality of residuals and homogeneity of variance), non-parametric tests (Kruskal–Wallis test or Mann–Whitney U test) were used. All data analyses were performed using Statistica 9.1 (StatSoft, Inc., USA).

Following the approach of Westphal et al. (2006), for each of the three stand types we fitted two parametric distributions to the empirical diameter distributions: negative exponential function and a mixture of two Weibull functions (seven-parameter form). More information about the functions and the start values used in the iterative process can be found in Zhang et al. (2001) and Westphal et al. (2006). The parameters were estimated using the maximum likelihood method. All the computations were done with R software (R Development Core Team, 2010), using the “mixdist” package (Macdonald with contributions from Du, 2010). The goodness of fit was examined by the likelihood-ratio $\chi^2$ test.

3. Results

3.1. Living trees

The mean stocking density of living trees $\geqslant 5$ cm dbh was similar in the pure beech and beech dominated plots (499 ha$^{-1}$ and 487 ha$^{-1}$, respectively). In the sessile oak dominated plots the value was roughly 200 trees ha$^{-1}$ greater (713 ha$^{-1}$). Of these, ca. 15–21% had a dbh of 5–7 cm (Fig. 1A). In spite of their relatively high number, the living trees with 5–7 cm dbh amounted to a mean volume $< 1$ m$^3$ ha$^{-1}$. The mean volume of living trees $\geqslant 7$ cm dbh was lowest in the sessile oak dominated plots at 577 m$^3$ ha$^{-1}$, and highest in the pure beech plots (675 m$^3$ ha$^{-1}$) (Fig. 1B). The comparatively low volume of the sessile oak dominated plots in spite of the high stocking density arises from the lower tree height and mean dbh values (Fig. 1C and D).

In the mixed stands about 75% of the total volume was accounted for by the main species (beech or sessile oak), followed by principal mixing species (sessile oak or beech) with 20% (Table 1). Other species as Carpinus betulus, Quercus frainetto, Quercus cerris, Acer pseudoplatanus, Prunus avium, Ulmus glabra, Tilia cordata and Sorbus torminalis comprised not more than 1–2% of volume, each of them.

In each of the three stand types, about 30% of the trees were situated in the overstorey. Trees attributed to this layer accounted for 95% of the total living tree volume. The mean stocking density of this layer was significantly higher (HSD test unequal N, Fig. 1A) in the sessile oak dominated plots than in either the pure beech or the beech dominated plots. No significant difference was observed in terms of volume, however. The lower tree volume asso- ciated with the overstorey of the sessile oak dominated plots was due to a significantly lower mean dbh (44.4 cm) and mean height (11.9 m) and a comparatively low volume of the sessile oak dominated plots in spite of the high stocking density arising from the lower tree height and mean dbh values (Fig. 1C and D).

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In each stand type, the main species accounted for 77% of the volume in the overstorey. Whereas in the beech dominated plots beech was also the dominant species in the mid- and understory, in terms of both stocking density and volume, in the sessile oak dominated plots, oak was only dominant in the overstorey. The predominance of beech increased in the mid- and understory, in terms of the tree number per hectare (ca. 70% in both layers) and in volume (53% in the mid- and 70% in the understory). The sessile oak dominated plots were characterised by a standing density in the midstorey nearly double that of the other stand types (Table 1).

For comparison with other studies, the analysis of the diameter distribution included only the living trees with dbh $\geqslant 7$ cm. The fi-
nite mixture of the two Weibull functions gave the best fit for pure beech and sessile oak dominated stand types \( (p < 0.05, \chi^2\text{ test}) \) (Fig. 2), whereas the negative exponential function was not able to describe any stand type. Although, the bimodal Weibull function did not fit significantly the empirical diameter distribution of beech dominated stand type, the absolute discrepancy value \( (\text{Gregorius, 1974}) \) was lower compared to that of negative exponential function. The significant differences observed between the three distributions \( (p < 0.05, \text{Kolmogorov-Smirnov test}) \) were caused by the differing numbers of trees in the smallest diameter class and the presence of a second maximum in the 59 cm diameter class in the pure beech and in the 51 cm diameter class in the sessile oak dominated plots (Fig. 2).

The negative exponential tendency in the mixed stand types was a consequence of the high beech participation in small diameter classes (Fig. 3A and B). In the beech dominated stand type, the few sessile oaks (mean of 56 trees ha\(^{-1}\), Table 1) were characterised by a bimodal diameter distribution (first maximum in the 11 cm diameter class and the second at 51 cm) (Fig. 3C). In the sessile oak dominated plots, the diameter distribution followed a normal pattern, with most individuals (ca. 108 trees ha\(^{-1}\)) concentrated in the middle diameter classes (43–67 cm) (Fig. 3D). In the beech dominated stand type, the individuals of other species were approximately uniformly distributed throughout the diameter classes (11–51 cm) with a lower density in the higher diameter classes (Fig. 3E). In the sessile oak dominated stand type the other species were found amongst the smallest diameter classes (Fig. 3F).

3.2. Dead wood

The average volume of CWD reached 75 m\(^3\) ha\(^{-1}\) (13–161 m\(^3\) ha\(^{-1}\)) in the pure beech plots, 135 m\(^3\) ha\(^{-1}\) (29–325 m\(^3\) ha\(^{-1}\)) in the beech dominated plots and 134 m\(^3\) ha\(^{-1}\) (32–296 m\(^3\) ha\(^{-1}\)) in the sessile oak dominated plots (Table 2). The volume of CWD corresponded to only 11% of the total volume of living trees in the pure beech plots, 21% in the beech dominated and 23% in the sessile oak dominated plots. The CWD volume was made up predominantly of logs, with 93% in the pure beech plots and 72% in both mixed tree stand types. In both the beech and the sessile oak dominated plots, the CWD consisted mostly of sessile oak trees. Separated on the basis of the various forms of dead wood, the proportion of dead oak present as snags was 92% in the beech dominated plots and 87% in the sessile oak dominated plots, compared to a lying dead oak wood fraction of 64% and 95%, respectively. Generally, the beech snags were trees of small dimensions (23 beech snags per hectare corresponded to a volume of 4 m\(^3\) ha\(^{-1}\)) (Table 2). By contrast, the sessile oak snags were mostly larger dimension trees (14 sessile oak snags had a volume of 35 m\(^3\) ha\(^{-1}\)).

3.3. Natural regeneration

The mean density of the natural regeneration was about 25,000 individuals ha\(^{-1}\) in the pure beech plots, 20,000 in the beech dominated and 10,000 in the oak dominated plots (Fig. 4). The between-plot variation was very high (coefficient of variation: 95–133%). Whereas in the pure beech plots only 4% of the regeneration was higher than 1.3 m, in the sessile oak dominated plots the corresponding value was higher (14%). In the pure beech and beech dominated plots, the main species in the natural regeneration was beech, at 98% and 89%, respectively. In the oak dominated plots, the regeneration consisted mostly of sessile oak (55%), followed by beech (38%) and other species (7%). Most of the juvenile sessile oaks (97%) were shorter than 1.3 m; the remaining 3% belonged to the height class 2–4 m. Greater proportions of juvenile beech (13% in height class 1.3–2 m, 6% in 2–4 m and 8% in 4–6 m) and other species (18% in 1.3–2 m and 18% in 2–4 m) were observed in the greater height classes in the oak dominated plots than in either the pure beech or beech dominated plots. The other species mainly comprised hornbeam.

3.4. Diversity

The three stand types differed significantly in their diversity. The mean tree species richness increased from 1 in the case of the pure beech plots to 3.1 in the beech dominated plots (with a maximum of 5 species) and to 4.7 in the oak dominated plots (with a maximum of 9). The Shannon index was significantly higher in the oak (1.0) than in the beech dominated plots (0.5) (Table 3).

The mean contagion index \( (W_i) \) of all three stand types was similar (0.49–0.52), and indicated a random tree distribution \( (\text{Hui and Gadow, 2002}) \). Within each stand type the mean diameter differentiation index \( (U_i) \) had values of about 0.5 (Table 3), indicating that two of the four neighbours were smaller than the reference tree, or that 50% of all trees were codominant \( (\text{Hui and Gadow, 2002}) \). The mingling index \( (M_i) \) was significantly lower in the beech dominated plots than in the sessile oak (Table 3). The pure beech forest was characterised by a lower degree of vertical structure \( (A = 0.96) \).
Fig. 3. Mean diameter distributions of beech trees (A and B), sessile oak trees (C and D) and trees of other species (E, F) in the beech dominated (A, C, E) and sessile oak dominated plots (B, D, F). Bars indicate the standard error.

Table 2
Coarse woody debris (total, lying and standing dead wood) and number of snags per three stand types (pure beech, beech dominated and sessile oak dominated plots).

<table>
<thead>
<tr>
<th>Species</th>
<th>Pure beech</th>
<th>Dom beech</th>
<th>Dom S. oak</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean (min.–max.) volume of CWD (m$^3$ ha$^{-1}$)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Beech</td>
<td>65 (8–148)</td>
<td>38 (1–144)</td>
<td>6 (0–47)</td>
</tr>
<tr>
<td>S. oak</td>
<td>8 (0–51)</td>
<td>97 (0–253)</td>
<td>123 (32–296)</td>
</tr>
<tr>
<td>Total</td>
<td>75 (13–161)</td>
<td>135 (29–325)</td>
<td>134 (32–296)</td>
</tr>
<tr>
<td>Mean (min.–max.) volume of lying dead wood (m$^3$ ha$^{-1}$)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Beech</td>
<td>62 (8–127)</td>
<td>35 (1–124)</td>
<td>2 (0–11)</td>
</tr>
<tr>
<td>S. oak</td>
<td>8 (0–51)</td>
<td>62 (0–183)</td>
<td>92 (13–189)</td>
</tr>
<tr>
<td>Total</td>
<td>70 (13–161)</td>
<td>97 (27–184)</td>
<td>97 (13–189)</td>
</tr>
<tr>
<td>Mean (min.–max.) volume of standing dead wood (m$^3$ ha$^{-1}$)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Beech</td>
<td>4 (0–21)</td>
<td>3 (0–20)</td>
<td>3 (0–35)</td>
</tr>
<tr>
<td>S. oak</td>
<td>0</td>
<td>35 (42–152)</td>
<td>33 (0–106)</td>
</tr>
<tr>
<td>Total</td>
<td>4 (0–21)</td>
<td>38 (0–152)</td>
<td>38 (0–120)</td>
</tr>
<tr>
<td>No. of snags per hectare, mean (min.–max.)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Beech</td>
<td>23 (0–80)</td>
<td>21 (0–80)</td>
<td>5 (0–30)</td>
</tr>
<tr>
<td>S. oak</td>
<td>1 (0–10)</td>
<td>14 (0–50)</td>
<td>20 (0–60)</td>
</tr>
<tr>
<td>Total</td>
<td>24 (0–80)</td>
<td>37 (0–100)</td>
<td>28 (0–80)</td>
</tr>
</tbody>
</table>
of the sessile oak trees in sessile oak dominated plots were surrounded by beech and other species (ca. 40% with $M_i = 0.75$ and 35% with $M_i = 1$, Fig. 5D). By contrast, in the beech dominated plots, most of the sessile oaks present were found in pure groups (36% of trees with $M_i = 0$, Fig. 5D).

With regard to the diversity of tree dimensions per species in the vicinity of a reference tree, the distribution of the sessile oak trees present in the sessile oak dominated plots was found to be left-skewed. This indicates that the majority of the reference trees represented the dominant trees in their immediate vicinity, and that these were surrounded by at least three smaller neighbours (Fig. 5F). By contrast, almost all of the sessile oak trees in the beech dominated plots were surrounded by at least two larger neighbours. Beech trees occurred in all classification categories in a similar manner in both the pure beech and the beech dominated plots. Only in the sessile oak dominated plots were there a higher percentage (33%) of individual beech trees dominant in the immediate vicinity (the distribution was slightly left-skewed).

### 4. Discussion

#### 4.1. The old-growth characteristics of Runcu Grosi Reserve

The Runcu Grosi Natural Reserve is dominated by beech forest (20% of the sampled plots consisted only of beech and 40% were dominated by this species, which accounted for >50% of the living tree volume). The mean volume of the three stand types investigated varied between 577 m$^3$ ha$^{-1}$ (in the sessile oak dominated plots) and 675 m$^3$ ha$^{-1}$ (in the pure beech). These volumes are similar to those found in beech and beech-oak virgin forests. The mean living tree volumes measured in the south-eastern European beech virgin forests lie between 705 m$^3$ ha$^{-1}$ (Havesova forest, Korpel', 1995) and 807 m$^3$ ha$^{-1}$ (Albanian virgin beech forests, Tabaku, 2000) (see also Commarmort et al., 2005; Drößler and Lüpke, 2007). However, lower values have also been reported, such as 451 m$^3$ ha$^{-1}$ in Kyjov forest (Drößler and Lüpke, 2007) and 559 m$^3$ ha$^{-1}$ in Mirdita (Tabaku, 2000). In Serbia (Leibundgut, 1993) and in four virgin beech forests of south-western Romania (Smejkal et al., 1995) mean volumes of between 527 m$^3$ ha$^{-1}$ and 682 m$^3$ ha$^{-1}$ were recorded. The few virgin sessile oak forests investigated exhibited living standing timber volumes comparable to those reported in this study, namely 594 m$^3$ ha$^{-1}$ in Sitno (Korpel', 1995) and 590 m$^3$ ha$^{-1}$ in Drinova (Smejkal et al., 1995).

The three dimensional stand structure represents one of the most important traits by which to characterise highly structured natural and mixed stands (Pretzsch, 1993). Although our knowledge of the relationships between stand structure, biodiversity and ecological functions is still limited (Pretzsch, 1997; Möldner et al., 2008), it is generally assumed that a rich forest structure is linked to greater plant and animal species diversity (Haber, 1982).

The stands in the Runcu Grosi Nature Reserve are characterised by a highly differentiated diameter distribution (Fig. 2, and $U_2 = 0.50$). The reverse J-shaped (negative exponential) curve is often used to describe the structure of virgin or near-natural forests in Europe (Leibundgut, 1993; Korpel', 1995; Tabaku, 2000). Westphal et al. (2006), however, showed for nine beech virgin forests that these forests are characterised by a great variety of structures, and that the negative exponential model was the best fit in only four of the nine forests studied. In some of the nine stands studied the descending curve of the diameter distribution exhibited a peak in the middle diameter classes. Similarly, Kucbel et al. (2012) and Roibu (2010) found that the most suitable function used for fitting the empirical diameter distributions of old-growth beech forests with a second peak in the mid-sized diameter classes was proved to be the bimodal Weibull function. The diameter distribution of

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**Table 3**

<table>
<thead>
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<th>Diversity indices (species richness, Shannon index, contagion index ($W_i$), diameter differentiation index ($U_i$), mingling index ($M_i$), and A index proposed by Pretzsch (1996)) per three stand types (pure beech, beech dominated and sessile oak dominated plots).</th>
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Significant differences between stand types are indicated by different letters.

than the two mixed stand types ($A = 1.47$ in beech and 1.64 in sessile oak dominated plots).

#### 3.5. Structural pattern of the two main species

Beech revealed a predominantly random distribution in all three stand types (more than 50% of all trees had a $W_i = 0.50$), with ca. 20% of trees regularly positioned ($W_i = 0.25$) and ca. 20% irregularly positioned ($W_i = 0.75$) (Fig. 5A). Similarly, most of the sessile oak trees were randomly positioned in both the beech ($p = 0.44$) and in the sessile oak dominated plots ($p = 0.56$), with ca. 20% irregularly distributed (Fig. 5B). Almost twice the number of sessile oaks were irregularly distributed ($W_i = 1.0$) relative to beech.

In the beech dominated plots, 66% of the beech trees formed pure groups of the same species ($M_i = 0$, Fig. 5C), whereas most

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**Fig. 4.** Regeneration density per species and in the three stand types (pure beech, beech dominated and sessile oak dominated plots). Values are mean values. Bars indicate the standard error of the mean.
the three stand types investigated as part of this study also showed a peak in the middle diameter classes (Fig. 2), and the finite mixture of two Weibull functions produced the best fit. This peak was more pronounced in the oak dominated plots as most of the sessile oak trees had diameters of 43–67 cm.

The pure beech plots showed a significant lower diversity in vertical structure compared to mixed stands with sessile oak (Table 3). Similarly, Korpel', 1995 showed that sessile oak virgin forests have a more differentiated structure “in space and height in the entire development cycle” compared to beech and beech-silver fir virgin forests.

Another very important descriptor of virgin or old-growth forests is the amount of dead wood present (Leibundgut, 1993). Generally, the volume of coarse woody debris varies with the stage of stand development. The values reported for virgin beech forests range between 30 and 200 m^3 ha^-1 (Leibundgut, 1993; Korpel', 1995; Tabaku, 2000; Saniga and Schütz, 2001; Commarmot et al., 2005; Dröißler and Lüpke, 2007). Dead wood volumes of between 70 and 160 m^3 ha^-1 have been reported for virgin oak forests (Korpel', 1995; Bobiec, 2002). The values found in Runcu-Grosi Natural Reserve lie within these ranges, with about 135 m^3 ha^-1 coarse woody debris in both mixed stand types, and 75 m^3 ha^-1 in the pure beech plots. In a meta-analysis of 109 unmanaged forest reserves dominated by beech and oak species, Vandekerkhove et al. (2009) found a dead wood volume of 10-75 m^3 ha^-1 in forests left unmanaged for <50 years. The higher values found in this study, especially in the mixed tree plots, indicated that the low levels of intervention in the past did not have a notable effect on the structure and dynamics of this forest. The average percentage of dead wood relative to the standing volume is 12% in the case of the pure beech plots and about 22% for the mixed plots. This ratio of living to dead wood corresponds to that found in other virgin forests (Tabaku, 2000; Commarmot et al., 2005; Dröißler and Lüpke, 2007). The higher volume of coarse woody debris in the mixed plots and the higher percentage relative to the living volume is due to a higher proportion of dead sessile oak trees, which accounted for about 70% of the total CWD in both mixed stand types. An explanation for this may be the slower decay process that oak trees undergo.

Fig. 5. Distribution of the contagion index (W), mingling index (M) and diameter differentiation index (U) per species (beech – A, C, E and sessile oak – B, D, E) within each three stand types (pure beech, beech dominated and sessile oak dominated plots).
compared to beech (Vandekerckhove et al., 2009) and the fact that most oak trees die standing (Peterken, 1996). In Runcu-Grosi Reserve the standing dead wood accounted about 28% of the CWD and consisted predominantly of sessile oak trees (91% in the beech dominated and 86% in oak dominated stands).

The results indicated a tendency towards a decline in the proportion of sessile oak. Compared with the species composition of living trees in terms of volume, an over proportional representation of dead sessile oak was obvious (71% vs. 20% in beech dominated plots and 92% vs. 73% in sessile oak dominated plots). This tendency is also apparent in the lower proportions of sessile oak present in the smaller diameter classes (Fig. 3) and in the regeneration (Fig. 5). Although the number of sessile oak seedlings in the oak dominated plots was a little greater that of beech, the analysis of the vertical structure of the regeneration showed that most of the oak seedlings were less than 1.3 m in height.

All of these results lead to the conclusion that beech will increasingly become the dominant species within the reserve. Similar conclusions were drawn in other studies conducted in natural reserves in central Europe (Emborg et al., 1996; Jedike and Hackes, 2005; Sielhorst et al., 2009), where, particularly on sites with a good water supply, it has been shown that without human intervention the participation of oak in central Europe’s forests will decrease considerably.

4.2. Differences induced by the dominance of one or other species

The comparative analysis of the stand structure and diversity of the plots dominated by sessile oak on the one hand and beech on the other showed that different structure and diversity patterns arise as a result of the species identity of dominant species.

The sessile oak dominated stands generally exhibited a higher level of tree diversity than those dominated by beech (Table 2). Although the mean tree species richness did not differ significantly between the two stand types, more tree species grow in the sessile oak dominated plots (maximum: 9) than in the beech (maximum: 5). Furthermore, the Shannon index value and the mingling index were significantly higher in the stands dominated by sessile oak. This may be explained by a lighter crown of sessile oak trees that allows for brighter conditions beneath the canopy, which is favourable for many species. On the contrary, the beech casts a heavy shade (Leuschner et al., 2001a) which limits the number of other species that can grow under their canopy. Our findings are in accordance with those of other studies that showed a marked decrease in both understory and overstorey diversity levels, which was associated with a higher beech participation in tree layer (Mölder et al., 2008; Burrascano et al., 2011).

A significant higher number of trees per hectare was found in the overstorey of oak dominated stands (Fig. 1) than in stands dominated by beech. The trees in the overstorey of the oak stands use better the space, with beech of smaller dimensions (mean dbh = 30 cm, height = 25 m) situated under the crowns of the larger oaks and in the immediate vicinity of large sessile oaks (dbh = 52 cm, height = 31 m, Table 1, Fig. 5). This is made possible by the relatively high shade tolerance of beech and by the higher crown transmittance of oak. By contrast, in the beech dominated stands, the oak trees belonging to the overstorey have diameters similar to those of the dominant beech (59 vs. 50 cm) and are virtually as tall (35 vs. 33 m).

The two stand types also differ in relation to the vertical distribution of trees. Whereas in the beech dominated stands most trees are found in the understorey (36%), in the sessile oak dominated stands the stocking density is highest in the midstorey (46%). At the same time, in the sessile oak dominated plots, the dominance of sessile oak disappears in the two lower canopy layers, whereas beech assumes dominance. By contrast, in the beech dominated stands beech remains the main species in all three canopy layers (Table 1).

A similar pattern was found in the small beech-sessile oak mixed nature reserve at Ludwigshain, where although the sessile oaks dominated the overstorey and accounted for the greater part of the volume, beech was the dominant species in the lower canopy layers (Detsch, 1999). Where beech was the dominant species, a high percentage of sessile oak (36%) arising in pure groups was observed (Fig. 5C). This observation supports Goreaud, 2000 finding that in oak dominated forests has a greater chance of survival when clumped in groups.

The contrasting patterns observed in the two stand types are due to the different shade tolerances and the contrasting competitiveness of the two dominant species. Whereas beech is a very shade tolerant species (Petritan et al., 2007, 2010), sessile oak is light demanding (Krahl-Urban, 1959). In the juvenile stage sessile oak can tolerate higher shade, but its light demand increases strongly with age (Lüpke and Hauskeller-Bullerjahn, 2004). Beech is also generally deemed to be a better competitor than oak, both above- and belowground (Leuschner et al., 2001b).

These findings are in agreement with the ecophysiological characteristics of the two species and also with experiences gleaned in the silviculture of mixed oak-beech forests. Without silvicultural interventions to favour oak, it is likely that in the absence of any major disturbance to the canopy, the dominance of beech will increase and significantly fewer oaks will be found in the next stand generation. For a deeper understanding of the natural tree species dynamics in this reserve, however, a study of the gap regime and dendochronological investigations are essential.

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References


