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First signs of old-growth structure and composition of an oak forest after four decades of abandonment

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First Signs of Old-growth Structure and Composition in an Oak Forest

Abstract

The lack of natural references of dry-mesic oak forests creates conceptual obstacles for their conservation and close-to-nature management in Central Europe. Single-tree inventory was used to investigate stand characteristics and old-growth attributes of a *Quercus petraea* (Matt.) Liebl. and *Q. cerris* L. dominated, 120-year-old stand in a Hungarian forest reserve, abandoned approximately 40 years ago. All individuals were recorded with diameter ≥ 5 cm on the 3 ha study site. Logs, stumps, saplings and seedlings were also surveyed. 582 woody stem/ha belonging to 14 species were measured with single-tree inventory. Basal area values showed the total dominance of oaks in the canopy layer (99%) as a legacy of the long-term human exploitation. In contrast, young individuals of oak species were almost missing, and *Acer campestre* L. dominated the lower layers, indicating the transitional nature of the stand. Diameter classes showed a marked bimodal distribution. Both the abandonment of the reserve and the precedent severe oak decline contributed to the relatively high amount of dead wood (46 m^3/ha). Four decades of abandonment is rather short time interval to generate a diverse forest composition and structure in a mature dry-mesic oak forest. The dense regeneration and shrub layer and the upsurgence of admixing species indicate the shift towards the uneven-aged and compositionally more diverse old-growth oak forest state. Among the structural forest features the dead wood had similar values as old-growth forests. If the recent trend continues, the studied oak forest develops towards a mixed forest with significantly lower ratio of oak species.

keywords: dry-mesic oak forest, *Quercus petraea*, forest structure, single-tree inventory, dead wood, forest reserve

Introduction

Old-growth forest stands can be described with mature structural and functional characteristics (Peterken 1996, p.17), which gradually appear if different silvicultural actions are stopped in a forest stand. There are no standard general criteria for this state, they were separately defined for North America (Old-Growth Definition Task Force 1986, Hale et al., 1999) and for European forests (Gilg 2005, Chiavetta et al. 2012). Many authors argue that no standard definition can be given, as different forest types have markedly different compositional, structural, functional and disturbance characteristic (Hilber & Wiensczyk 2007). However, certain structural and compositional features are individually proposed as main indicators of the old-growth status, such as presence of large trees; high tree species diversity; greatly varying tree height, diameter and age; reverse J-shape frequency distribution in diameter classes; multi-layered canopies; gaps in the canopy layer; well-developed shrub- and regeneration layers; large amount of dead wood with various size categories and decay stages (Hardt 1993, Oliver & Larson 1996; Goodburn & Lorimer 1999, Franklin et al. 2002, Gilg 2005, Piovesan et al. 2005, Chiavetta et al. 2012).

The knowledge of the natural species composition, structure and dynamics of temporal deciduous forests of Central Europe is unbalanced. Beech (*Fagus sylvatica* L.) dominated and other mesic deciduous forests, often occurring on higher altitudes of mountainous regions, have several virgin sites or patches with long time-span of non-intervention (Veen et al. 2010). Numerous papers discuss their composition (Chiavetta et al. 2012), amount of large trees (Nilsson et al. 2002), dead wood characteristics (Bobiec 2002; Nilsson et al. 2002, Christensen et al. 2005, Piovesan et al. 2005, Vandekerkhove et al. 2009), stand structure (Piovesan et al. 2005, Westphal et al. 2006, Horváth et al. 2012), biodiversity (Ódor et al. 2006, Heilmann-Clausen et al. 2014), dynamics and history (Koop & Hilgen 1987, Korpeľ 1995, Standovár & Kenderes 2003). On the contrary, virgin or old-growth oak stands are extremely rare in Europe, especially on dry and dry-mesic sites (Parviainen 2005, Rahman et al. 2008, Veen et al. 2010, Petritan et al. 2013, Saniga et al. 2014).

The scarcity of old-growth or virgin oak stands on dry and dry-mesic forest sites as natural references, and missing published information on them creates conceptual obstacles for nature conservation and close-to-nature forest management (Rahman et al. 2008), especially where natural regeneration of the dominant oak species is missing. This scientific obstacle presumably could be overcome by the comprehensive and detailed investigation of abandoned dry-mesic oak forests (Horváth et al. 2012). Several stands in Europe are ceased to be managed from different reasons, like designation as conservation area, or economic considerations. Long-term research of the abandoned oak stands is crucial to provide useful information for the sustainable and close-to-nature forest management of oak dominated forests of Europe (Rahman et al. 2008), active conservation supporting their structural and functional complexity and maintaining biodiversity (Carvalho 2011, Petritan et al. 2013), and understanding of natural disturbance regimes and natural shifts in their tree composition.

Central Europe maintains a considerable diversity of dry-mesic oak forests, situated between mesic mixed forests and dry open oak forests (Borhidi 2003, Roleček 2005). The Pannonian-Balkanic Turkey oak-sessile oak forest (dominated by *Quercus petraea* (Matt.) Liebl. and *Q. cerris* L.) is the main representative of these vegetation types in Hungary, covering the major part of foothills. It is the second most frequent forest type composed of native species of Hungary, one of the most important forest types concerning economic, conservation and cultural aspects (Bölöni et al. 2008).

This study focuses on the composition and structure of a 120-year old *Q. petraea* stand on dry-mesic site, set aside for nature protection 40 years ago. The objectives of the study were: (1) to quantify species composition and stand structural attributes of the main layers of the stand after 40 years of spontaneous development and (2) to compare how these attributes relates to the ones originated from oak-dominated stands with old-growth character. In case of (1) we focused on the assessment of:

- density, basal area and volume values of the tree layer species,
- status of tree regeneration in the sampling and seedling layers,
- qualitative and quantitative characteristics of dead wood,
- diameter class distributions of the tree layer,
- spatial patterns performed by snags and by thin and thick diameter classes of the tree layer.

To evaluate the old-growth characteristics of the studied stand, we selected some well-studied virgin or old-growth oak forests as references for the comparison. The majority of the European examples are mesic *Quercus robur* L. dominated forests, like Białowieża in Poland (Faliński 1986), and mesic *Q. petraea* forests, as Kasivárová and Bujanov in Slovakia (Saniga et al. 2014), mixed *Q. petraea* forest of Runcu-Grosi Natural Reserve, Romania (Petritan et al. 2012), and most of the stands of Lange-Leitn Natural Forest Reserve in Austria (Rahman et al. 2008). Well-documented old-growth forests on dry-mesic sites are the most relevant references, as the virgin *Q. petraea* dominated Boky National Nature Reserve in Slovakia (Saniga & Shütz 2002, Halamová & Saniga 2006, Saniga et al. 2014), the mature *Q. robur*-*Q. suber* L. and *Q. pyrenaica* Willd.-*Arbutus unedo* L. mixed-oak forests in thermo-temperate, dry and sub-humid climate in Portugal (Carvalho 2011), and some of the drier *Q. petraea*-*Q. cerris* forest types (*Luzulo-Quercetum typicum*) in the old-growth Lange-Leitn Natural Forest Reserve, Austria (Rahman et al. 2008). Results on oak forests of the extensive North American literature were also included. Some of the oak dominated forests in Missouri, Illinois, Pennsylvania, Virginia, Kentucky, North Carolina, Ohio, Tennessee states have similar site conditions as dry-mesic oak forests in Europe (Goebel & Hix 1996, Pallardy et al.

1988, Fralish et al. 1991, Mikan et al. 1994, Shifley et al. 2000, Hart et al. 2012). Although due to biogeographical reasons tree species diversity is higher in general in North America than in Europe (Latham & Ricklefs 1993), structural attributes and some compositional features are important references for understanding dry-mesic oak forests in Central Europe.

Materials and methods

1. Site description

The study site is located in the Vár-hegy Forest Reserve (VFR) in the Bükk Mountains, designated in 1993. This middle-range mountain that belongs to the Inner Western Carpathians is consisted mainly of mesozoic limestones, its scenic undulating karst plateau is surrounded by deep valleys and several peaks around 900 m a.s.l. The 669 m high, Triassic limestone hill called Vár-hegy is located a bit isolated from the inner massive of the Bükk Mountains to the direction of southwest. The annual average temperature is 8 ^{o}C, the annual precipitation is 650 mm, of which 400 mm falls in the growing period. The average duration of snow cover is 45 days, the average maximum snow depth is 18 cm. The 341 ha area of the reserve is covered mainly by close-to-nature oak dominated forests typical for the oak woodland zone of the Bükk Mts. (Natura 2000 habitat types; 91G0: Pannonic woods with *Quercus petraea* and *Carpinus betulus* L., 91H0: Pannonian woods with *Quercus pubescens* Willd., 91M0: Pannonian-Balkanic Turkey oak-sessile oak forests, Council of EU 1992). Its 94 ha core area has been set aside for preservation in 1991, though several previous conservation acts had already secured almost spontaneous natural development of the VFR stands.

A 3 ha sized site was selected for this study in the VFR in 2003. The primary criteria for study site selection were that it should be located in the core area of the reserve, and it should represent Pannonian-Balkanic Turkey oak-sessile oak forest. The selected site is located in the southern part of the VFR, approximately at 600 m a.s.l., on a 20° steep, south-facing slope. The soil is shallow silty rendzina (Bidló et al. 2004). Based on the forest management plan and land use data, the stand is approximately 120 years old. The sessile oak (*Quercus petraea*) dominated stand has developed from coppice wood. Beside sessile oak, the second most dominant species is Turkey oak (*Quercus cerris*). *Acer campestre* L. and *Cornus mas* L. form a dense shrub- and sub-canopy layer. *Melica uniflora* Retz. is the dominant species in the herb layer, other frequent species are *Scutellaria altissima* L., *Dactylis polygama* Horv., *Vincetoxicum hirundinaria* Medik., *Poa nemoralis* L., *Clinopodium vulgare* L., *Buglossoides purpurocoerulea* (L.) I.M.Johnst., *Stellaria holostea* L.

The history of the study site can be traced by archive data (Gesztes 1887) and by the detailed data of forest management plans of the second part of the last century (Anonymus 1953-2005). According to a title deed dating from 1261, a forest area approx. 6000 ha around the VFR had been an estate of the Episcopate in Eger since then until World War II. The first management plan of the forest dates from 1887. Before that time, irregular cuttings were made to fulfil the needs of the manorial estate in terms of charcoal burning, lime burning, fire wood, and timber for the extensive agricultural estates. Most of the present VFR area was cut around 1880 (Gesztes 1887), however, several over-mature trees were retained (Mázsa et al. 2013). The intensive use in the previous centuries and during the world wars left a sessile oak dominated, 120-year-old, mostly coppice forest with a rather homogeneous structure. The last management action with commercial goal took place in 1968/69, when partial preparation-cutting of shelterwood forestry system was performed on the half of the study site. Few years later the shrub-layer was supposedly eradicated in the whole area. Since mid-1970s the stand has remained almost untouched, however in 1988 – after a severe oak decline – a moderate sanitary cutting (20-25 m3/ha, Kovács 2005) of desiccated oaks took place (Szepesi 1997) and had substantially opened the canopy layer.

2. Field measurements

We established twelve 50 m × 50 m collateral quadrats, covering 3 ha altogether (150 m × 200 m) on the southern slope of the VFR in 2003. The designation of the quadrats was made by SOKKISHA SET-2 Electronic Total Station with geodesical accuracy. All standing woody stems, alive or dead, with diameter at breast height (DBH) greater than or equal to 5 cm got a unique identification number and were marked with dye. The dyed individuals were positioned and measured in 2003 and 2004 (Table 1, single-tree inventory). The following data were collected:

1) species of the woody individual; 2) location: X and Y geographical coordinates using the EOV Hungarian projection; 3) diameter at breast height (DBH), 4) height of the tree measured with VERTEX III.

Coarse woody debris of the stand was assigned to three categories (Table 1): standing dead trees and broken snags (snags) were sampled along with the single-tree inventory described previously. In case of stumps (upper diameter > 20 cm, height < 50 cm) the following data were recorded: position (X, Y coordinates), species (if recognizable), diameter measured at the base, height, decay phase. In case of lying dead wood (logs) items thicker than 20 cm in diameter at the thicker end were surveyed. In addition to the considered stump characteristics (except for height), length of the section from the root collar to the point where diameter reached 20 cm, and the distance from that point to the top were also measured. The decay stages of DW were evaluated on an ordinal scale (I-V, Spetich et al., 1999), where class I is the least decomposed and class V is the most decomposed.

In order to characterize the sapling and seedling layer, another method was applied (Table 1). The 15 sampling points of the 3 ha study site were placed systematically in a 50 m × 50 m grid. Individuals of all woody species were numbered in two size categories: saplings (height ≥ 130 cm, DBH < 5 cm) were counted within circular plots having 5.64 m radius (100 m^2)

around the sampling points; seedlings (50 cm < height < 130 cm, stem diameter < 5 cm) were subsampled within four smaller circular plots (radius = 1.49 m, 7 m^2) placed in each greater circle in the direction of the four points of the compass. Data of the four smaller circular plots were handled together and were assigned to each sampling point.

3. Data analysis

Tree species composition and structure of the stand were characterized by descriptive statistics, as total density (stems/ha), total basal area (=dominance, m^2/ha), total volume (m^3/ha). The volume of tree individuals was calculated by species specific equations based on DBH and height (Sopp & Kolozs 2000). Density, relative density (%), basal area, relative basal area (%) and volume values were calculated for all living woody species measured by the single-tree inventory. Standard deviation values were determined on the basis of the data of the twelve 50 m × 50 m collateral quadrats. Living trees were then divided into two classes; thin class: 5 cm ≤ DBH < 20 cm and thick class: DBH ≥ 20 cm (Table 1), and these values were given separately for the two classes.

Descriptive statistics (means and standard deviation values) were also calculated for the regeneration data from circular plots: density and relative density values of sapling and seedling populations.

Density, basal area and volume of snags, logs and stumps were calculated separately and in total. Volume of the whole snags was calculated with the same function as that of the living trees (Sopp & Kolozs 2000). Stumps and broken snags were considered as geometric cylinder, volume of logs was assessed with the formula for truncated cone and cone. Standard deviations were determined by the data of the twelve 50 m × 50 m collateral quadrats.

Distributions of tree frequencies in DBH classes of dead and alive individuals of the tree layer were calculated. Ripley's K statistic with isotropic edge correction (Ripley 1976) was used as a measure of spatial pattern of the thick and the thin classes of the tree layer and the snags, and the variance-stabilized version of the K function called Ripley's L was graphed. Observed L functions were compared to confidence intervals obtained from L functions calculated for 200 random point patterns. Statistical analyses were performed in the R software environment (R Core Team 2014), using the spatstat (Baddeley & Turner 2005) package.

Results

1. Living trees of the tree layer

Altogether 1,745 living stems belonging to 14 species were measured with single-tree inventory (DBH ≥ 5 cm) of the tree layer on the 3 ha study site (Fig 1). Density of stems was 582 living stems/ha, and basal area was 30.74 m^2/ha (Table 2). Total volume of living trees was 354.8 m^3/ha.

The most abundant species in the tree layer (individuals ≥ 5 cm DBH) were *Acer campestre* and *Quercus petraea* with 219 and 197 stems/ha, respectively (Table 2). Less numerous were *Q. cerris* (77 stems/ha), *Cornus mas* (25 stems/ha), *Q. pubescens* (24 stems/ha), and *Fraxinus excelsior* L. (22 stems/ha). Together these six species represented more than 96% of all stems in the tree layer.

With regard of basal area, the most dominant species in the tree layer was *Quercus petraea* (19.78 m^2/ha, 64.4%), followed by *Q. cerris*, *Q. pubescens* and *Acer campestre* with 7.6 m^2/ha (24.7%), 1.65 m^2/ha (5.4%) and 1.17 m^2/ha (3.8%), respectively (Table 2). The mean DBH of *Q. petraea*, *Q. cerris*, *Q. pubescens*, and *A. campestre* was 35, 35, 29 and 8 cm, respectively (Table 3). The total basal area of the other 10 species was only 0.54 m^2/ha. Volume values showed the same trends; over 98% of tree volume was represented in the four most dominant species alone (Table 2).

The density and basal area of the oak thick tree class showed the total dominance of oaks in the canopy layer (99% of density and basal area, Table 4). Opposite trend could be traced in the thin class: oak species were almost missing, and the other woody species, especially *Acer campestre* and *Cornus mas* dominated (Table 4).

2. Saplings and seedlings

Ten species, with 1,750 stems/ha were documented in the sapling layer (Table 5). The most abundant species was *C. mas* with 750 stems/ha, representing 42.9% of all stems. *A. campestre*, *Crataegus monogyna* Jacq. and *C. laevigata* (Poir.) DC were the next most abundant species, with 23.8%, 15.5%, and 7.1% respectively. No other species had more than 100 individuals/ha or represented over 4% of total stem density. The seedling layer contained 5313 stems/ha and species number was 16 (Table 5). The most abundant species were *Fraxinus excelsior*, *Prunus spinosa* L., *Acer campestre,* and *Cornus mas*, with relative densities ranging 22.4% for *F. excelsior* to 12.2% for *C. mas*. No oak individuals were found among the saplings and very few among the seedlings.

3. Dead wood; snags, logs and stumps

In average 33 snags, 70 logs, 171 stumps were found in one hectare of the study site (Table 6). Concerning only the naturally generated dead wood, the ratio of snags and logs was 32% and 68% respectively. Volume of snags, logs, and stumps were 14.1, 27.9, and 3.8 m^3/ha, respectively; the total amount of dead wood were 45.8 m^3/ha (Table 6).

All snags were in early decay stages (I and II). Percentage proportions of the decay stages of log volumes (m^3) were the following: I: 30%, II: 41%, III: 22%, IV: 3%, V: 4. Stumps were usually more decomposed: I: 7.5%, II: 6.5%, III: 47%, IV: 15%, V: 24. Most of the DW species were identifiable. Altogether 7 species were detected; the vast majority was given by oak species (45 m^3, 98%), with *Quercus petraea* in the first place (38.3 m^3, 84%). Average DBH of snags (DBH ≥ 5 cm) was 21 cm; the thickest was a sessile oak with 63 cm. Several snags – mainly *Acer campestre* – had smaller DBH than 10 cm (11 stems/ha), the proportion of snags between 20 and 35 cm was also high (18 stems/ha), but individuals with DBH larger than 40 cm was almost missing.

4. Diameter distribution

Diameter classes of woody stems of the tree layer (DBH ≥ 5 cm) showed a marked bimodal distribution (Fig 2). When species were grouped into three categories (*Quercus* species, *Acer campestre*, other woody species) size-class patterns were apparent. The first category (5-10 cm) had very high share; this size class was given mainly by the sub-canopy layer dominated by *A. campestre* (Fig 2). Trees with DBH between 10 and 20 cm were almost missing, but size classes with larger DBH than 25 cm were well represented due to the matrix of old *Quercus* species in the canopy layer. The average DBH of the thick class trees was 34.8 cm. Size-class distribution of the oaks exhibited a normal distribution with no recent regeneration, while *A. campestre* showed a steady decline in stem density with increased size (Fig 2) resulting in a reverse J-shaped distribution.

5. Spatial patterns

According to the results of the Ripley's L-statistics, the thin class (5 cm ≤ DBH < 20 cm) of trees were highly aggregated at all examined scales (Fig 3A). The thick class (DBH ≥ 20 cm) of the tree layer showed a segregated pattern between 20 and 70 meters (Fig 3B). Snags were slightly aggregated (near the confidence intervals; Fig 3C).

Discussion

1. Dominance of oak species in the canopy layer

Concerning the species composition of the stand, the strong dominance of the three oak species was determinant in the tree layer (DBH ≥ 5 cm, 51% of stems, 94% of basal area, Table 1) in particular of in the thick class of the tree layer, where almost all admixing species were absent (relative density: 1% of stems, 1% of basal area, Table 4). These homogeneous oak forests are typical in Hungary; on the basis of 207 phytosociological relevés of dry-mesic *Q. petraea* dominated forests, the average relative dominance of oaks in the canopy layer is higher than 95% (Horánszky 1964, Szujkó-Lacza 1964, Isépy 1970, Papp & Jakucs 1976, Szollát 1989, Kun 2000, Király 2001, Csiky 2002). In the virgin Boky forest (Slovakia), which has the most similar site conditions among the primeval forests as VFR, the basal area and cubic meter data of oaks of the canopy layer (thick class, DBH ≥ 20 cm) are almost the same as those sampled in VFR (VFR: 29.03 m^2/ha, 344.3 m^3/ha; Boky Nature Reserve 29.44 m^2/ha, 313.8 m^3/ha), but the relative density and basal area is lower (VFR: 99%, Boky Natural Reserve: 93%, Halamová & Saniga 2006) due to the admixing species with larger diameters in the canopy layer. Similarly, in the natural, late-stage mixed-oak forests of Portugal the admixing species are represented also in the larger DBH categories and basal area of oaks are between 58% and 83% (Carvalho, 2011). In North American dry-mesic oak stands the dominance of oak species is markedly lower in almost all cases compared to the Central European dry-mesic stands. In old-growth stands oak species give the 59-84% of the basal area (Fralish et al. 1991, Mikan et al. 1994, Dodds & Smalidge 1999, Feist et al. 2004), exceptionally reaching 90% (Abrams et al. 1997). In some cases the relative basal area of oak species remains even under 50% (Elliott et al. 1999, Hart et al. 2012). We presume that this measure of oak-dominance and especially the almost total absence of admixing species with larger diameters are not natural in VFR, but is the effect of the direct human preference for oak species (primarily *Quercus petraea*) in the last centuries (Gesztes 1887). Evidently, the actions of the shelterwood system of the systematic forest management of the last 150-200 years – planting, spacing, thinning – played leading role in the overwhelming oak dominance in Central European commercial forests, which are aimed at maximizing the proportion of the principal tree species in the canopy layer (Danszky 1972).

2. Shade-tolerant species gain ground in the sub-canopy layer

The cessation of forest management and openings of the tree layer due to the oak decline in the 1980s resulted in a massive development of the sub-canopy layer dominated by *Acer campestre*. Declining oak dominance and increasing ratio of other woody species is a Europe-wide process in oak forests without silvicultural management. The spatially closest example is Síkfőkút site, established in 1972 for the long-term monitoring of forest ecosystems. It shows similarly dense sub-canopy layer dominated by *A. campestre* under the *Quercus petraea* and *Q. cerris* canopy (Kotroczó et al. 2012). Several examples of forest reserves and protected oak forests of Europe show that protection and cessation of management result in significant change of mixture ratios at the expense of oak species, like in Forêt de Fontainebleau in France, Białowieża in Poland, Neuenburger Urwald in Germany (Koop & Hilgen 1987, Bernadzki et al. 1998, Vera 2000, pp. 189-276). Saniga et al. (2014) found the displacement of oak species by shade-tolerant species in three Slovakian oak forest reserves (Boky, Kasivarova and Bujanov) on the basis of a study of four-decade succession. Petritan et al. (2013, 2014) found similar processes in the mesic virgin *Q. petraea* stands of Runcu-Grosi Natural Reserve in Romania. In several North American oak forests different maple (*Acer saccharum* Marshall, *A. rubrum* L.) and other shade-tolerant species gain ground in the sub-canopy layer (Lorimer 1984, Pallardy et al. 1988, Shotola et al. 1992, Goebel & Hix 1996, McCarthy & Bailey 1996, Abrams et al. 1997, Lin & Augspurger 2008). The transitional nature of oak forests are often explained by the exclusion of fire in North America in the last century (Abrams 1992, McCarthy et al. 2001, Shumway et al. 2001, Signell et al. 2005), except oak forests on xeric sites, which experiences less successional pressure (Abrams et al. 1997). In Europe, one of the leading theories is the wood-pasture concept (Vera 2000), which states that large herbivores maintained an open landscape in the primeval landscape of Europe, and the recent extent of oak-dominated forests is a consequence of that (Vera 2000). The concept was developed for the lowlands of Europe; its applicability was investigated and challenged for the Central European oak forests (Bobiec et al. 2011, Saniga et al. 2014).

3. Low ratio and absence of oaks in the seeding and sapling layers

In accordance with the trends described above, among tree seedlings and saplings the shade-tolerant and/or r-strategist species dominated, like *Carpinus betulus*, *Acer platanoides* L., *A. campestre* and *Fraxinus excelsior*. Besides the tree species, also shrub species typical for dry-mesic oak forests were present in the undergrowth (*Cornus mas, Crataegus laevigata, C. monogyna*, *Rosa canina* L., *Prunus spinosa*). The total absence of oaks in the sapling layer can probably be explained by the enhanced acorn eating and browsing of the increased wild game population of the Central European region (Côté et al. 2004, Götmark et al. 2005, Ammer et al. 2010). Most saplings of the study site have been grazed several times and often have no, or very damaged buds showing the high impact of game, such as mouflons (*Ovis orientalis* Gmelin), red deer (*Cervus elaphus* L.), and roe deer (*Capreolus capreolus* L.). However, in case of this measure of the absence of oaks in the lower layers, it should be considered that light-demanding oaks of Europe (like *Q. petraea* and *Q. robur)* need open space for recruitment (Reif & Gärtner 2007). If this is provided, they can eventually successfully develop even in the presence of high amount of browsing animal (Bobiec et al. 2011).

The results of our study support that, if open space is not created by humans or other disturbance factors, like fire or wind, there is little chance for the oak forest to regenerate. This conclusion is in accordance with the several other authors' findings from North American (Pallardy et al. 1988, Shotola et al. 1992, Mikan et al. 1994, Abrams et al. 1997, McCarthy et al. 2001, Hart et al. 2012) and from European oak forests (Bobiec et al. 2011, Petritan et al. 2014). In a relatively dry North American *Quercus alba* L. dominated site, a detailed dendroecological study proved that the majority of oak individuals reached the canopy by subsequent releases of stand-wide disturbances, like wind and ice storms (Hart et al. 2012). In our understanding the absence of oak regeneration in our study area is a combined effect of increased browsing and acorn consumption of wild games, and the light deficit.

4. High amount of dead wood

Forty-six cubic meters per hectare of deadwood of the VFR can be considered as a relatively high amount in a dry oak forest. This is much more than in typical managed oak forests with coarse woody debris volume ranging between 1 and 12.5 m^3/ha (Bretz Guby & Dobbertin 1996, Lombardi et al. 2008). The number of snags and logs (43/ha altogether) was also relatively high, most of these individuals were killed during the oak decline in the 1980s. The other oak-dominated stands in dry-mesic site conditions, like Boky Nature Reserve have similar values; dead wood ranges between 10 and 90 m^3/ha within the developmental cycle (Saniga & Schütz 2002). The volume of snags and logs was 6.9 m^3/ha in early stand stage and 65.4 m^3/ha in late stages of natural mixed-oak stands of Portugal (Carvalho 2011). In the drier vegetation types of Lange-Leitn Natural Forest Reserve (*Luzulo-Quercetum-typicum* and *Luzulo-Quercetum* with *Calluna*) the mean volumes of dead wood were 83 m^3/ha and 57.2 m^3/ha (Rahman et al. 2008). Examples of dry-mesic oak forests of North America show similar values; the total amount of dead wood ranges between 30 and 60 m^3/ha (Goebel & Hix 1996, Shifley et al. 1997). The ratios of snags and logs in VFR (32%, 68%) meet the old-growth criteria of Nilsson et al. (2002), which defines that about 30% of the volume of dead trees is standing in old-growth forests. Nilsson's other criterion states that 10% of standing trees are dead in old-growth forest – in VFR it is only 6%. Regarding the high quantity of dying oak individuals, this proportion will rapidly grow in the near future.

5. Diameter classes

Diameter classes of trees maintained bimodal shape, indicating the absence of the medium sized-trees. The recovery of the shrub- and sub-canopy layer (left peak in the diameter distribution) was the result of the last four decades, as the last eradication of shrub-layer took place in the 1960s. The distribution of oak size classes showed normal distribution, which is typical for stands managed in clearcutting silvicultural system (Goodburn & Lorimer 1999, Rouvinen & Kuuluvainen 2005). The average DBH of the thick class of the tree layer was 34.8 cm. We think that the absence of large trees, in spite of the relatively old age of canopy trees, can be attributed to the lower site quality and the coppice origin of the stand. Old stands on dry sites often have fewer large trees compared to old-growth stands on mesic sites (Hart et al. 2012).

6. Spatial patterns

Thick class off the tree layer, basically the oak individuals of the canopy performed segregated pattern, similarly to several investigated old-growth forest, like Moravian alluvial floodplain forests and fir-beech forests of the Western Carpathians (Janik et al. 2013), *Quercus petraea-Fagus sylvativa* forest of Romania (Petritan et al. 2014), *Q. macrocarpa*

Endl. forest of Indiana (Ward et al. 1996), and cove forest of the Great Smoky Mountains (Busing, 1998). Competitive exclusion and self-thinning are the general arguments for the segregated (or random) pattern of the canopy layer trees (Ward et al. 1996, Collins & Klahr 1998); we argue that former forest management, like regular thinning could also contribute to the segregated pattern in our case. After the abandonment of VFR the new dynamic processes of regeneration and appearance of dead wood material created more aggregated patterns. This result coincides with that of European and North American oak and mixed-oak forest examples, like the old-growth forest with patchy *Acer saccharum* invasion in Illinois (Lin & Augspurger 2008), the aggregated sub-canopy trees of Indiana (Ward et al. 1996) and Oklahoma stands (Collins & Klahr 1998), as well as the clumped suppressed trees of Rancu Grosi Natural Reserve in Romania (Petritan et al. 2014).

Conclusions

Four decades of abandonment of a mature dry-mesic oak forest is rather short time to generate a more diverse forest composition and structure in these site conditions. It created a stand with two main, compositionally relatively poor layers instead, a canopy layer dominated by *Quercus petraea*, and a sub-canopy layer dominated by *Acer campestre*. However, certain features of old-growth structure and composition could be detected. Among the structural forest features the dead wood had similar values as old-growth forests, one of the most important indicators of old-growth state (Hale et al. 1999). A dense regeneration layer with *A. campestre* and shrub-species *Cornus mas* has developed. Segregated pattern of the mature oak trees and the aggregated patterns of the regeneration layer and the snags show old-growth character. Headway of admixing species was traced in all lower forest layers, leading to compositional diversification in the sub-canopy-, the seeding- and the sapling layers.

If the recent trend continues, the studied non-intervention oak forest develops towards a mixed forest with significantly lower ratio of oak species. However, the future development of the stand seems to be very uncertain and open for multiple pathways. The slow changes towards the old-growth state, the marked decline of oaks and the implied uncertain future trends pose several conceptual and practical conservation management questions that can be answered just with intensive and comprehensive investigation of the old-growth and abandoned oak stands on dry-mesic sites.

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Table 1. Definition and sampling methods of the different forest layers

name	definition	sampling method
tree layer, thick class (canopy layer)	DBH ≥ 20 cm	single-tree inventory on 3 ha study site
tree layer, thin class (sub-canopy layer)	5 cm ≤ DBH <20 cm	single-tree inventory on 3 ha study site
sapling layer	DBH < 5 cm, height ≥ 130 cm	15 × 100m^2 circular plot
seedling layer	stem diameter < 5 cm, 50 cm < height < 130 cm	60 × 7m^2 circular plot
snag	entire standing dead trees and broken snags, DBH ≥ 5 cm, height ≥ 50 cm	single-tree inventory on 3 ha study site
log	lying dead trees, thicker end diameter > 20 cm	dead wood inventory
stump	upper diameter > 20 cm, height < 50 cm	dead wood inventory

Table 2. Composition, density, basal area and volume of living tree stems of the tree layer with DBH ≥ 5 cm, arranged by relative basal area. Values are means and standard deviations (±)

Species	Density (stems/ha)	Relative density (%)	Basal area (m^2/ha)	Relative basal area (%)	Volume (m^3/ha)
Quercus petraea (Matt.) Liebl.	197 ± 48	33.9	19.78 ± 5.31	64.4	247.6 ± 80.3
Quercus cerris L.	77 ± 73	13.2	7.60 ± 7.13	24.7	81.3 ± 74.9
Quercus pubescens Willd.	24 ± 34	4.1	1.65 ± 2.25	5.4	15.4 ± 19.4
Acer campestre L.	219 ± 125	37.7	1.17 ± 0.74	3.8	6.1 ± 4.1
Fraxinus excelsior L.	22 ± 21	3.8	0.22 ± 0.33	0.7	2.2 ± 4.9
Cornus mas L.	25 ± 7	4.2	0.09 ± 0.1	0.3	0.4 ± 0.4
Acer platanoides L.	6 ± 7	1.0	0.11 ± 0.20	0.3	1.0 ± 2.1
Carpinus betulus L.	5 ± 7	0.9	0.08 ± 0.17	0.2	0.5 ± 1.3
Others	7 ± 6	1.3	0.05 ± 0.10	0.2	0.3 ± 0.9
Total	582 ± 172	100	30.74 ± 4.28	100	354.8 ± 46.3

Table 3. Minimum, maximum and mean values of DBH of living tree stems of the tree layer with DBH ≥ 5 cm, arranged by the number of stems found on the 3 ha study site

Species	Nr. of stems	DBH

	(3 ha)	Mean	Min.	Max.	SD
Acer campestre L.	657	8	5	20	2.2
Quercus petraea (Matt.) Liebl.	591	35	6	70	7.4
Quercus cerris L.	230	35	17	60	6.9
Cornus mas L.	74	7	5	10	1.2
Quercus pubescens Willd.	71	29	14	46	7.1
Fraxinus excelsior L.	66	9	5	59	6.7
Acer platanoides L.	18	11	5	42	10.6
Carpinus betulus L.	16	11	5	25	7.6
Crataegus monogyna Jacq.	12	6	5	9	1.1
Cerasus avium (L.) Moench	4	9	5	21	7.7
Sorbus torminalis (L.) Crantz	3	12	5	26	11.8
Pyrus pyraster (L.) Burgsd.	1	8			
Sorbus domestica L.	1	5			
Ulmus glabra Huds.	1	12			
Total	1745	22	5	70	14.4

Table 4. Density and basal area of oak species (*Q. petraea, Q. cerris, Q. pubescens*) and all other woody species separately in the thin (5 cm ≤ DBH < 20 cm) and the thick (DBH ≥ 20 cm) class of the tree layer

Species	Density (stem/ha)	Relative density (%)	Basal area (m^2/ha)	Relative basal area (%)
		thin class		
oak species	6	2	0.13	8
all other woody species	281	98	1.45	92
		thick class		
oak species	292	99	28.90	99
all other woody species	3	1	0.26	1

Table 5. Composition and density of saplings (DBH < 5 cm and height ≥ 130 cm) and seedlings (50 cm < height < 130 cm), arranged by sapling density. Values are means and standard deviations (±)

Species	Density; saplings/ha	Relative density of the saplings (%)	Density; seedlings/ha	Relative density of the seedlings (%)
Cornus mas L.	750 ± 1062	42.9	646 ± 948	12.2
Acer campestre L.	417 ± 807	23.8	729 ± 897	13.7

Crataegus monogyna Jacq.	271 ± 513	15.5	167 ± 232	3.1
Crataegus laevigata (Poir.) DC.	125 ± 350	7.1	125 ± 230	2.4
Rosa canina L.	63 ± 129	3.6	333 ± 652	6.3
Prunus spinosa L.	42 ± 110	2.4	1021 ± 1496	19.2
Carpinus betulus L.	21 ± 81	1.2	167 ± 286	3.1
Fraxinus excelsior L.	21 ± 81	1.2	1188 ± 1808	22.4
Ligustrum vulgare L.	21 ± 81	1.2	354 ± 612	6.7
Pyrus pyraster (L.) Burgsd.	21 ± 81	1.2		
Acer platanoides L.			250 ± 670	4.7
Cerasus avium (L.) Moench			83 ± 143	1.6
Malus sylvestris (L.) Mill.			63 ± 175	1.2
Sorbus torminalis (L.) Crantz			63 ± 175	1.2
Quercus petraea (Matt.) Liebl.			63 ± 175	1.2
Quercus cerris L.			42 ± 110	0.8
Tilia cordata Mill.			21 ± 85	0.4
Total	1750 ± 1356	100	5313 ± 4449	100

Table 6. Composition and amount of dead wood of 1 ha of the study site. Values are means and standard deviations (±). Totals may not add up exactly due to rounding error

dead wood	snag		log		stump		total	
species	stem/ha	m^2/ha	m^3/ha	items/ha	m^3/ha	stem/ha	m^3/ha	m^3/ha
Quercus petraea (Matt.) Liebl.	17.3	1.18	11.9 ± 10.8	53.3	23.4 ± 11.9	156.3	3.1 ± 1.6	38.3 ± 20.1
Quercus cerris L.	2.0	0.15	0.8 ± 1.2	7.7	2.2 ± 3.7	13.0	0.6 ± 0.8	3.7 ± 5.0
Quercus pubescens Willd.	2.7	0.15	1.2 ± 2.7	7.0	1.8 ± 4.4	1.0		3.0 ± 7.2
Acer campestre L.	11.0	0.05	0.2 ± 0.2	0.3				0.2 ± 0.2
Cerasus avium (L.) Moench	0.3			0.7				0.1 ± 0.1
Carpinus betulus L.				0.3	0.3 ± 0.1			0.3 ± 0.1
unidentifiable				0.3	0.1 ± 0.5	1.0		0.2 ± 0.7
total	33.3	1.52	14.1 ± 11.1	70.0	27.9	171.0	3.8 ± 1.3	45.8 ± 20.9

Fig 1. Map of the living trees on the 3 ha study site

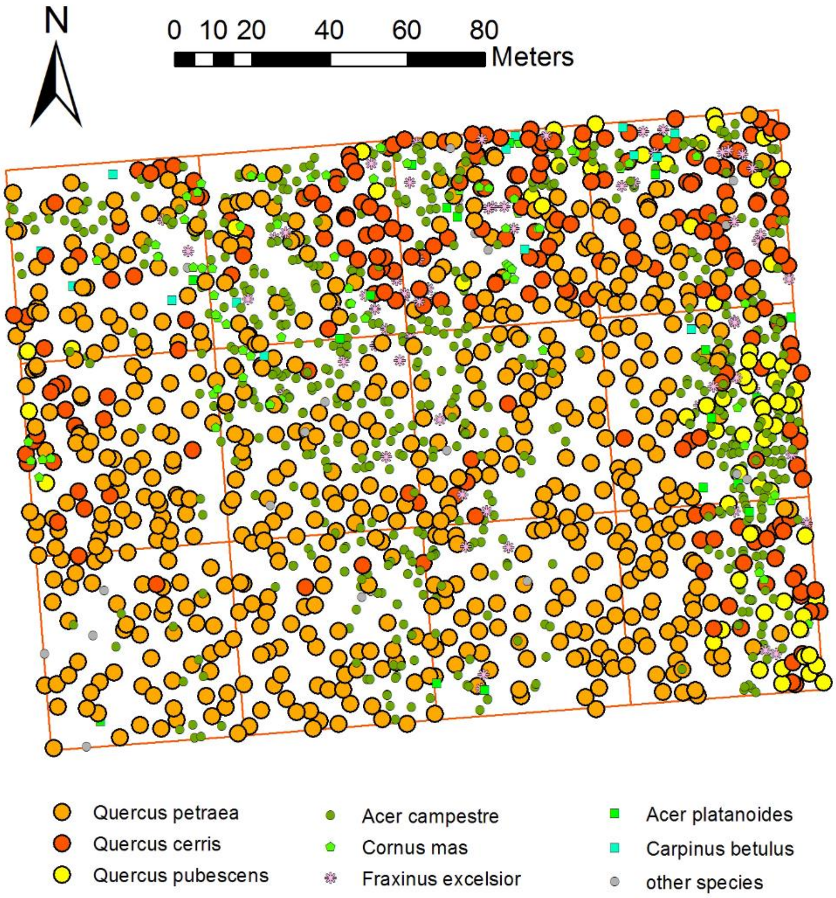


Fig 2. DBH distributions of *Quercus* species, *A. campestre* and other woody species

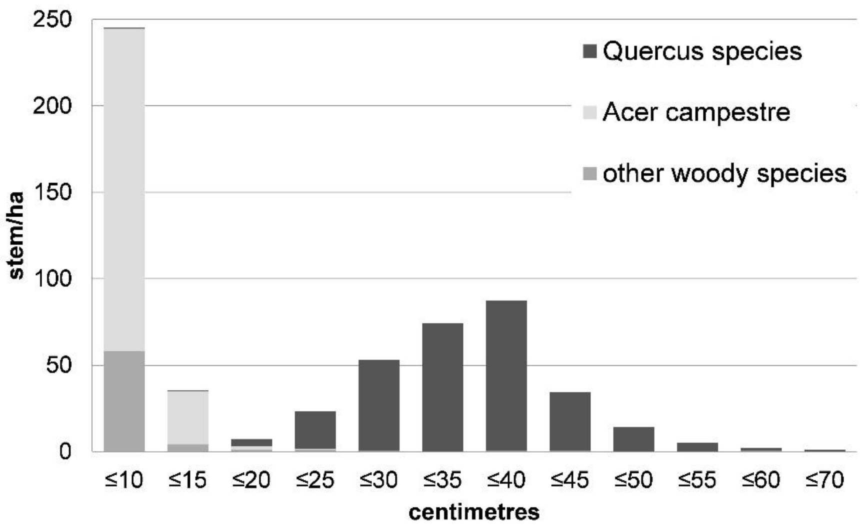


Fig 3. Ripley's L functions of the A) thin class of the tree layer (5 cm ≤ DBH < 20 cm), B) thick class of the tree layer (DBH ≥ 20 cm), and C) snags. Black line (Observed) above the grey lines of confidence interval (CI) indicates aggregated pattern, black line under the CI indicates segregated pattern.

Fig 3A

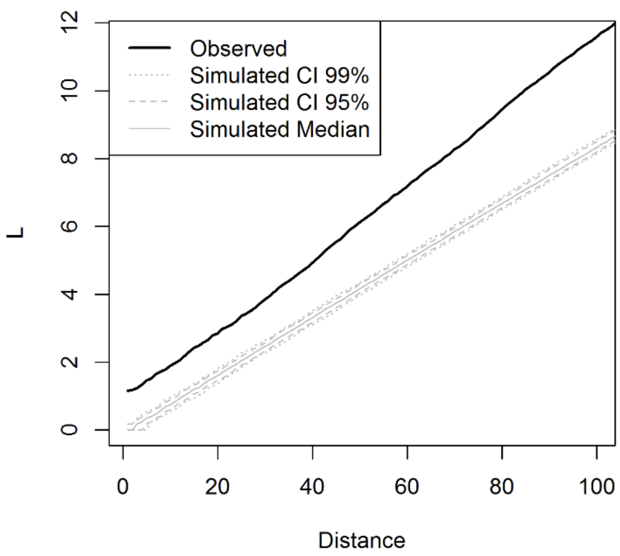


Fig 3B

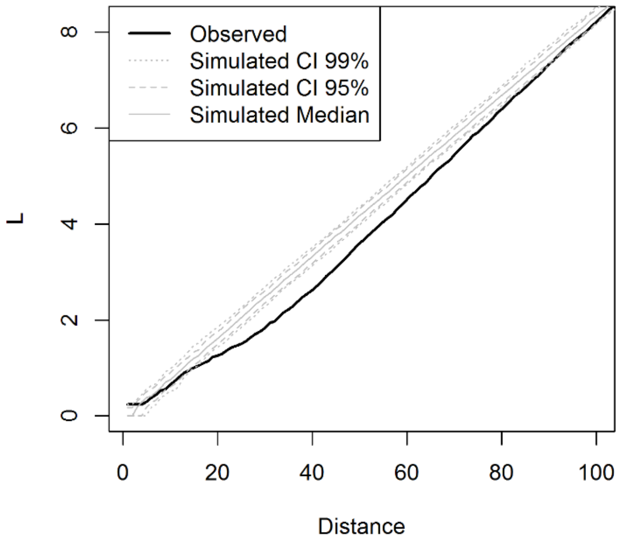
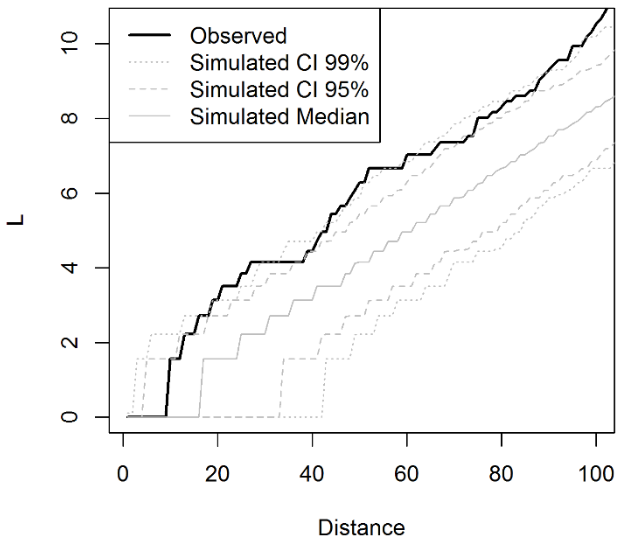

Observed
Simulated CI 99%
Simulated CI 95%
Simulated Median
L
Distance
0
2
4
6
8
0
20
40
60
80
100

Fig 3C


Observed
Simulated CI 99%
Simulated CI 95%
Simulated Median
L
Distance
0
2
4
6
8
10
0
20
40
60
80
100