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Naturalness of *Quercus robur* stands in Latvia, estimated by structure, species, and processes

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Abstract. In seven *Quercus robur* stands in Latvia, the past history of stand development was determined by size and age structure of trees, dead wood amounts, cut stumps, and by forest inventory records and maps. All the stands met the criteria of Woodland Key Habitats. *Quercus robur* was the main canopy species in all stands. Since the time of the recruitment of canopy trees, there has been minimal release of the *Q. robur* in the >1-m height class, at least among those that have survived until today. One stand lacked evidence of natural successional processes, while the others were naturally regenerating with *Picea abies* or deciduous tree species, such as *Fraxinus excelsior*, *Ulmus glabra*, *Alnus glutinosa*, and *Tilia cordata*. The dead wood amounts in plots suggest a high level of naturalness. However, the ages of the canopy oaks (up to 226 years) indicate lack of long-term natural development. Also, the presence of cut stumps in three plots and lack of standing dead wood in four plots are signs of the impact of human disturbance on natural processes. Since the 1920s, one of the stands had converted from a *Populus tremula* and *Betula pendula* to a *Q. robur* canopy. Even though the studied stands can be considered as having low naturalness based on age structure and past management history, they each supported two to eight Woodland Key Habitat indicator species, including one to six protected species.

Key words: *Quercus*, Woodland Key Habitat, broad-leaved forest dynamics, epiphytes.

INTRODUCTION

Due to intensive forest harvest and exploitation for agriculture, all Western European forests of the temperate zone are to a great extent disturbed by man (Peterken, 1996). Very few fragments of the past virgin forest remain (Jones, 1945), causing a deficiency of reference areas to study structure and disturbance dynamics. In northern European forests in the temperate–boreal transition zone, human activities were responsible for a decline of broad-leaved forests and expansion of spruce (Bradshaw & Hannon, 1992; Lindbladh et al., 2000; Niklasson et al., 2002), particularly in the past 300 years (Lindbladh & Foster, 2010). The largest old-growth broad-leaved (*Quercus robur*, *Fraxinus excelsior*, *Ulmus* spp., *Tilia cordata*, *Acer* spp.) woodland in lowland Europe is the Bialowieza Primeval Forest on the Polish and Belarusian border (Falinski, 1986). However, even there the territory suffered from felling and overgrazing due to use as a hunting reserve in the late 1800s–1900s (Falinski, 1988), which caused an expansion of *Picea abies* (Mitchell & Cole, 1998).

The coverage of broad-leaved species in Latvia reached a maximum in the Atlantic period about 6000 years ago (Zunde, 1999). Since that time, climate cooling and human impact caused a decline of broad-leaved forest in Latvia, particularly in the 17th and 18th centuries to supply growing export of *Q. robur* for ship-building and slash and burn clearage of forest by peasants (Dumpe, 1999; Liepina, 1999). In northern Latvia, the total forest area dropped from 59.2% in 1710 to 19.4% in 1914 (Vasiļevskis, 2007). In 1924, broad-leaved forest occupied only 2.3 thousand ha (0.2% of forests) in Latvia (Matīss, 1987). However, by 2008, the forest area had increased to 53%, of which broad-leaved forests contributed 1.1% (data from the Latvian State Forest Register 2009). The *Q. robur* stands in Latvia are presently mostly small (<2 ha) and highly fragmented (Zunde, 1999).

It has been argued that the *Q. robur* primeval forest in lowland Europe formed an open landscape, due to grazing by large herbivores (Vera, 2000). According to this view, wooded meadows and pastures in the rural landscape today might resemble the forests of pre-industrial forestry. In contradiction to the grazing hypothesis, some palaeoecological evidence suggests that the natural *Q. robur* woodland that existed prior to human settlement formed a closed canopy, with or without grazers (Mitchell, 2005). Thus, knowing that regeneration of *Q. robur* is limited by light availability caused by competition with vegetation (Humphrey & Swaine, 1997; Küßner, 2003; Harmer & Morgan, 2007), natural disturbances such as fire, wind, and water-logging probably created gaps favouring regeneration (Bradshaw et al., 2003; Bradshaw & Hannon, 2004; Whitehouse & Smith, 2004). Regeneration of *Q. robur* and other broad-leaved species can be successful in floodplains (Küßner, 2003; Dobrowolska, 2008) and under conifer canopies, provided sufficiently lit conditions free from competitive vegetation (Götmark et al., 2005; Dobrowolska, 2006; Goris et al., 2007). In Poland (Falinski, 1986) and Russia (Ņesterovs, 1954), *Q. robur* mostly occurs in mixed woods with a closed canopy, and the tree species in mixed stands with *Q. robur* differ depending on the growth conditions. The controversy regarding whether *Q. robur* woods naturally occurred as open of closed woodland may never be fully resolved, but in Eastern Europe there is no evidence that an open landscape with oak existed before human settlement.

In Latvia, open parkland landscapes were created by slash and burn agriculture, whereby scattered *Q. robur* trees survived within tilled land, hayfields, and pastures (Dumpe, 1999). Regeneration of *Q. robur* on agricultural land can be successful in patches of unpalatable or spiny vegetation unfavoured by large herbivores, which can provide an explanation for long-term persistence of *Q. robur* in an open landscape (van Uytvanck et al., 2008). As pasture woodlands are of high conservation value in Europe, partial harvesting has been suggested to create more open stands (Götmark, 2007; Økland et al., 2008; Paltto et al., 2008). Also in Latvia, *Q. robur* trees in protected areas are often cleared from surrounding trees and shrubs to maintain their value for biological diversity (Anon., 2008), creating a setting that might have been typical under a traditional shifting agricultural regime.

Knowledge of the naturalness of *Q. robur* forests in Latvia could be used to guide conservation management, particularly regarding possible restoration measures. The naturalness of forests can be estimated using criteria within three dimensions: structures, species, and processes (Brūmelis et al., 2011b). The aim of the present study was to determine the level of naturalness of *Q. robur* stands in Latvia, based on the age and size structure, amounts of dead wood, cut stumps, archival inventory data and maps, as well as richness of Woodland Key Habitat (WKH) indicator species (Ek et al., 2002). Considering the history of logging and conversion of forests to farmland in Latvia, we might expect that the naturalness of *Q. robur* forests is low. Of the 6554 ha of forest area dominated (over 50% relative wood volume) by *Q. robur*, 14.5% (953 ha) has age over 150 years and only 2.3% (147 ha) is over 200 years old (State Forest Service, 2008). A large part (803 ha) of these forests are WKHs, which in Latvia are identified based on the presence of species that cannot persist under industrial forestry and on the amounts of structural elements, such as coarse wood debris. Considering the legacy of forest harvesting in Latvia, we hypothesize that the structural features of naturalness of *Q. robur* WKHs, which might be considered to be among the most natural *Q. robur* forests, have developed over a relatively short period of time. Further, part of the oak forests today are probably secondary forests on abandoned agricultural land.

MATERIAL AND METHODS

Study area

Latvia is located in the boreo-nemoral zone, where *Q. robur* can occur in mixed forest together with coniferous boreal species (Sjörs, 1963). The climate is moderate continental with a mean temperature of –5.3 °C in January and 14.8 °C in July, and precipitation of 700–800 mm, of which about 500 mm falls in the warm period (Central Statistical Bureau of Latvia). Moraine relief dominates with sandy clays and clay sands (Nikodemus et al., 2008). The climate is more continental towards the east.

Stands of *Q. robur* were chosen from the State Forest Register based on dominance of *Q. robur* (at least 50% of total wood volume), *Q. robur* age (>120 years), stand size (>2 ha), and WKH criteria (Ek et al., 2002). It was considered that the above criteria would select a subset of stands that might be expected to be among the most natural. From the register, seven stands were selected without prior visit to the site (Fig. 1). These forest stands were Audile (area 4.2 ha), Pededze (7.9 ha), Barkava (11.7 ha), Salenieki (5.2 ha), Kinguru (6.5 ha), Mezotne (18.1 ha), and Rauda (2.9 ha). Four *Q. robur* stands (Audile, Pededze, Barkava, and Salenieki) were chosen in the Lubana Lowland, central eastern Latvia, as it was generally considered that this area might support old relict stands. In the early 1700s, the largest part of the remaining uncut *Q. robur* stands were found in

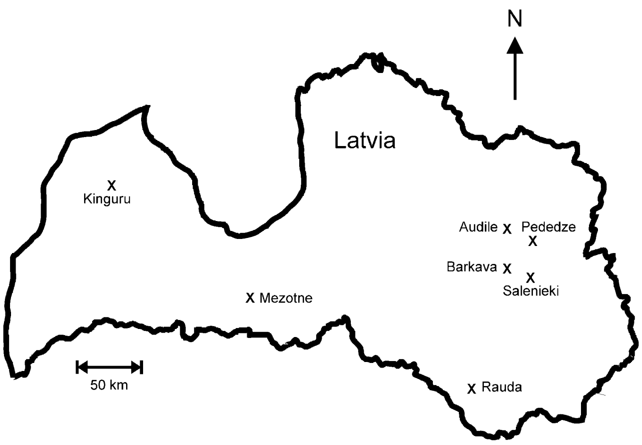

Fig. 1. Map of Latvia showing location of the studied stands.

the Lubana area, but even so, most of the stands along rivers had been harvested and wood floated by rafts to Riga (Zunde, 1999). The Lubana Lowland had been subject to major floods and the water levels in Lake Lubana (then about 90 km^2) could in spring rise by 2–4 m, flooding an area of over 600 km^2 (Šķiņķis, 1998). Drainage in the area began in the 1850s, and continued to the 1930s, but with little effect on flooding. All the stands in the Lubana area are located in the previous flood zone of the lake. After a major drainage project, begun in the 1950s, the lake covered about 80 km^2, and the surrounding forests were much less subject to floods.

The other three stands, Kinguru, Mezotne, and Rauda, were located in western, central, and south-eastern Latvia, respectively. Except one stand, Kinguru, the sampled forest stands were protected as nature reserves or microreserves. The protected areas were established for conservation of biologically valuable forest habitats. The conservation values of the Mezotne forest, protected as a micro-reserve, are a natural broad-leaved forest and populations of *Dendrocopos medius* and *Osmoderma eremita*.

In the studied forest stands in the Lubana area (Audile, Pededze, Barkava, and Salenieki), *Q. robur* and *F. excelsior* were dominant species in the tree layer mixed with *Alnus glutinosa*. *Tilia cordata* was abundant only in Salenieki. A different pattern of regeneration was observed in the other stands. *Picea abies* was abundant in the sapling layer at Kinguru and Rauda, and scattered spruce had also entered the upper canopy of the former stand. The Mezotne stand generally lacked a sapling layer. Vegetation in the stands was dominated, in variable composition and cover, by typical nemoral species, such as *Paris quadrifolia*, *Galeobdolon luteum*, *Pulmonaria officinalis*, *Anemone nemorosa*, and *Glechoma hederacea*. The Rauda and Kinguru stands supported also boreal herbs, such as *Oxalis acetosella*. A dense *Rhamnus cathartica* shrub layer occurred in the Salenieki plot.

Sampling methods and data analyses

One sample plot was established in each of the seven selected *Q. robur* stands in 2007–2008. The plots were located in the centre of the stands to avoid edge disturbance. Plot size was 20 m × 50 m (0.1 ha). This plot size was considered to be representative of the stand, as visual inspection of the stands suggested similar forest structure at this scale, except at edges.

Stem height was measured for all trees with height over 10 m. Smaller trees were counted in height classes (<1.0 m, 1.1–2.0 m, 2.1–5.0 m, and >5.0 m). For trees over 10 m in height, cores were removed 0.5 m above tree base with an increment borer (at 1-m height for oak due to the physical difficulty of coring this species). Trees were cored below breast height to obtain a better estimate of true tree age.

A total of 301 trees were measured and from these cores were obtained. The number of tree cores used in age structure analysis was 52 in Audīle, 54 in Barkava, 37 in Pededze, 37 in Salenieki, 60 in Kinguru, 48 in Rauda, and only 13 in Mezotne. In Mezotne, trees were sparse with wide canopies. *Betula pendula*, *Populus tremula*, and *Alnus incana* were excluded from the age structure analysis due to their very small number in plots (<2 in each plot except in Barkava).

A search was made for WKH indicator epiphyte species on cored trees in the plots. Because the epiphytic species composition varied considerably between trees in the selected stands, in addition a search for WKH indicator epiphyte species was made in the entire stands and recorded as present when found. The search was conducted in each stand for approximately 1 h.

Tree cores were glued in mounting boards and sanded to a fine polish. The cores were then scanned and tree rings were measured with Lignovision 1.37 (RINNTECH). If the pith was missed, the age was corrected by adding the number of missing years by estimation based on ring curvature and mean ring width of the innermost 10 increments. In some cases of extensive wood rot around the pith, the distance from the innermost ring to the geometric tree centre was estimated by subtraction of the core length from the tree radius. The number of missing rings was extrapolated based on the mean ring width of the oldest visible 10 increments. This estimation method assumes symmetry of tree rings, which will rarely occur, but this inaccurate method was considered more suitable than omitting the trees from analysis.

The volume of living trees was estimated using volume tables for the respective species (Sacenieks & Matuzāns, 1964). For fallen logs over 10 cm in diameter at mid length, the volume was calculated as cylinders using log length and diameter in the middle. Dead standing tree volume was estimated from volume tables for the respective species (Sacenieks & Matuzāns, 1964). Cut stumps were counted.

Archival forest inventory data for the stands was obtained from forest management plans stored at the Latvian State Forest Research Institute 'Silava'. For each tree species, the mean tree age in the canopy layer was given as well as the relative timber volume in 10% classes. If a tree species formed more than one canopy layer, the volume and age were given for each cohort.

RESULTS

Archival inventory records

The inventory maps and records for the stands had been produced in different years from 1924 to 1937 (Table 1). The maps indicated that the Kinguru and Rauda stands were open with scattered trees, while the others were shown as closed forest. Ages of *Q. robur* ranged from 70 to 150 years, with the oldest in Mezotne. *Quercus robur* dominated in all stands (90–100% of the relative timber volume), except in the Salenieki stand where in 1927 it was reported as absent; the dominant trees there were *Betula pendula* and *Populus tremula*. Along with the dominant *Q. robur*, in 1937 the Barkava stand also contained *B. pendula*, *P. tremula*, and *A. glutinosa*, which were recorded as contributing each less than 10% of the total volume. At Kinguru in 1927, an understorey of *B. pendula* and *P. tremula* mixed with *P. abies*, with age about 15 years, was recorded.

Size and age structure of living trees

The maximum tree height in the plots was 30–36 m. In all plots the upper canopy over 25 m in height (>20 m in the Barkava plot) was dominated by *Q. robur* (Fig. 2), mixed with *F. excelsior* and *Ulmus glabra* in the Audile site (Fig. 2). While *Q. robur* was abundant in all plots in the below 1 m height class and in the upper canopy, it was in low numbers or missing in other height classes (Table 2, Fig. 2). The understorey tree layer at 1–10 m height (Fig. 1) was dominated by *T. cordata* in the Salenieki plot, *F. excelsior* in the other sites, with also *U. glabra*

Table 1. Stand inventory data for the years 1924–1937. Age and wood volume of dominant tree species are given. * Relative volume was not estimated for tree species with volume <10, but their presence was recorded

Site	Map (description)	Species	Age	% volume
Audile	1924 (forest)	*Quercus robur*	130	100
Pededze	1934 (forest)	*Quercus robur*	90	90
		Fraxinus excelsior	90	10
Salenieki	1927 (forest)	*Populus tremula*	50	50
		Betula pendula	50	50
Barkava	1937 (forest)	*Quercus robur*	80	90
		Populus tremula	70–90	10
		Betula pendula	70–90	<10*
		Alnus glutinosa	70–90	<10*
Kinguru	1927 (scattered trees)	*Quercus robur*	80	100
		Populus tremula	15	<10*
		Betula pendula	15	<10*
		Picea abies	15	<10*
Mezotne	1926 (forest)	*Quercus robur*	150	100
Rauda	1929 (scattered trees)	*Quercus robur*	70–80	100

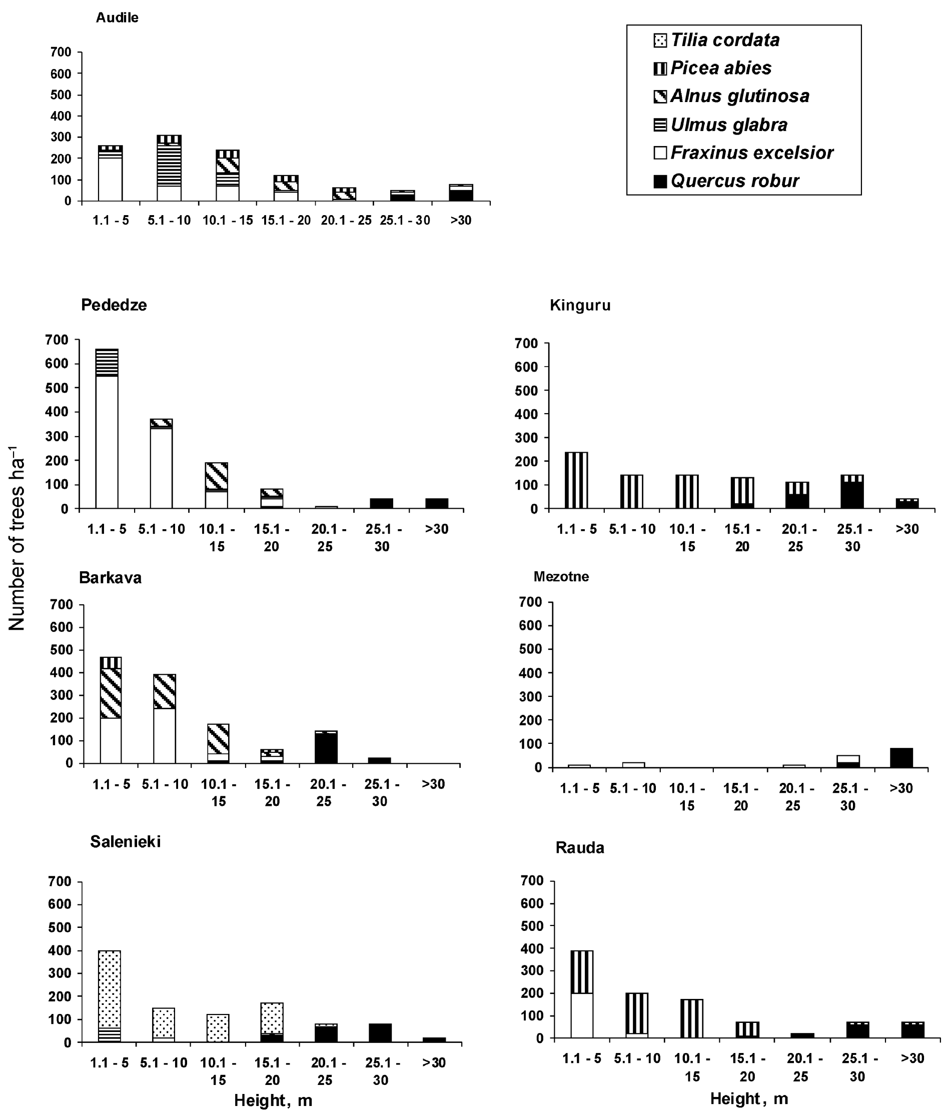

Fig. 2. Distribution of height of trees >1 m in plots.

at Audile and *B. pendula*, *P. tremula* (not shown), and *A. glutinosa* at Barkava. The successional understorey species was *P. abies* at Kinguru and Rauda. At Mezotne, *F. excelsior* formed a subcanopy layer and was abundant together with *Q. robur* in the below 1 m layer, but otherwise the stand lacked a tall sapling stage.

The maximum *Q. robur* ages observed in the Salenieki, Kinguru, and Rauda plots were low (140, 170, and 171 years, respectively) compared to those in the other plots. The maximum age of *Q. robur* was over 200 years in three plots (Fig. 3), with a maximum age of 242 years in Mezotne. Most (80%) of the tree

Table 2. Density of stems with height <1 m (number ha^{-1}). Qr – *Quercus robur*, Fe – *Fraxinus excelsior*, Ag – *Alnus glutinosa*, Tc – *Tilia cordata*, Pa – *Picea abies*, Ai – *Alnus incana*, Ug – *Ulmus glabra*, Bp – *Betula pendula*, and Pt – *Populus tremula*

Site	Qr	Fe	Ag	Tc	Pa	Ai	Ug	Bp	Pt	Total
Audile	430	24 500			60		80		20	25 090
Pededze	640	4 940	10	30		10	3 040			8 670
Barkava	370	660			110	50		20	1 710	2 920
Salenieki	390			180						570
Kinguru	210				20					230
Mezotne	22 250	16 500								38 750
Rauda	70	100			70				10	250

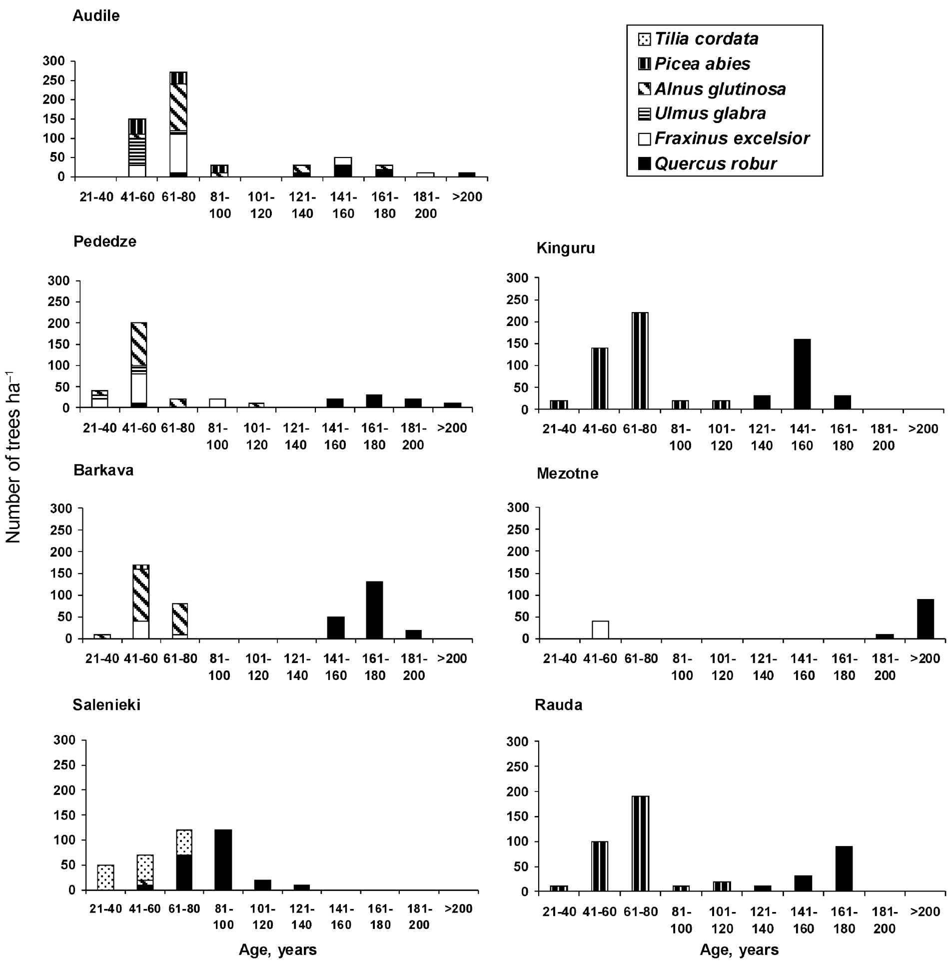

Fig. 3. Distribution of age of trees >10 m height in plots.

cores passed close to the pith and thus the age could be estimated fairly accurately. Only four cored trees had rot near the core, resulting in very approximate ages, but these were not the oldest trees, as suggested by size, and thus most likely did not affect the above-mentioned maximum ages.

In the Audile plot, some *F. excelsior* and *A. glutinosa* trees were over 100 years old. Most of the *A. glutinosa*, *U. glabra*, and *F. excelsior* in the plots had ages of 41 to 80 years; a small proportion of the trees were in the 21–40 year age class (Fig. 3). In the Salenieki plot, *T. cordata* was abundant in the 21–80 year age classes. A peak of *P. abies* regeneration occurred in about 1930–1950 in the Kinguru and Rauda sites, corresponding to the 61–80 year age class (Fig. 3). *Betula* was common in the 41–80 year classes at Barkava (not shown).

Dead wood

The highest total dead wood volume (Table 3) was at Audile (198 m^3) and the lowest at Barkava (109 m^3). In all plots the dead wood volume was comprised mostly of *Q. robur* (over 100 m^3 ha^{-1}). The dead *Q. robur* volume mostly consisted of large, over 30 cm diameter stems (not shown). Significant proportions of dead wood volume were also contributed by *A. glutinosa* (43 m^3 ha^{-1}) at Audile and *P. abies* (52 m^3 ha^{-1}) at Kinguru. The ratio of dead to living wood volume ranged

Table 3. Volume (m^3 ha^{-1}) of dead and living stems and number of cut stumps (number ha^{-1}). The proportion (%) of dead standing wood volume is also given. For abbreviations of tree species see Table 2

Site	Qr	Fe	Ag	Tc	Pa	Ai	Ug	Bp	Pt	Total	Proportion standing dead wood, %	Cut stumps
					Volume dead, ha^{-1}							
Audile	150	5	43		5	1				198	50	
Pededze	108	10	13							133	0	
Barkava	103	<1	2			4				109	0	10
Salenieki	129									129	69	
Kinguru	34				52					86	0	60
Mezotne	67	8								75	0	60
Rauda	132				4	5		2		143	80	
					Volume living, ha^{-1}							
Audile	286	122	49		42		12	1	1	513		
Pededze	742	16	36			7	19			820		
Barkava	406	6	21		4	1		10	12	460		
Salenieki	352		2	34				5		393		
Kinguru	505			5	280					790		
Mezotne	736	30								766		
Rauda	463				105					568		

from 0.10 at Mezotne to 0.38 at Audile. Cut stumps, all of which were *Q. robur*, were observed in Barkava, and in greater numbers at Kinguru and Mezotne. These three plots, and also Audile, lacked standing dead wood (Table 3).

Indicator species

All the recorded WKH indicator species were found on *Q. robur*, except for *Lecanactis abietina*, which was found on *P. abies*. The most frequent indicator species found in the plots were *Arthonia spadicea*, *A. byssacea*, and *Homalia trichomanoides* (Table 4). No indicator bryophyte spcecies were found at Salenieki. The highest numbers of species occurred in the Pededze stand, followed by Kinguru, Audile, and Rauda. Of the recorded indicator species, six are protected in Latvia: *Arthonia spadicea*, *A. byssacea*, *A. vinosa*, *A. leucopellea*, *Lobaria pulmonaria*, and *Dicranum viride*.

DISCUSSION

Quercus robur is a typical early successional species that can invade disturbed habitats such as gaps, forest edges, and grassland (Lawesson & Oksanen, 2002). Moreover, *Q. robur* can persist for multiple generations in a closed canopy at a

Table 4. Woodland key habitat indicator epiphytes recorded in the studied forest stands in Latvia

	Audile	Pededze	Barkava	Saleniece	Kinguru	Mezotne	Rauda
Lichens							
Acrocordia gemmata	+						
Arthonia byssacea	+	+	+	+			+
Arthonia leucopellea		+					
Arthonia spadicea	+	+	+	+	+	+	+
Arthonia vinosa		+			+		
Bacidia rubella		+					
Lecanactis abietina					+		
Lobaria pulmonaria		+					
Bryophytes							
Anomodon spp.	+	+					+
*Dicranum viride**							+
Homalia trichomanoides	+	+			+	+	+
Isothecium alopecuroides					+		
Neckera pennata					+		

* Recorded in the forest stand during WKH inventory but not found in the plots.

stand level (Mitchell, 2005), probably due to natural disturbances that create gaps (Bradshaw et al., 2003; Bradshaw & Hannon, 2004; Whitehouse & Smith, 2004). It might be expected that a natural *Q. robur* forest would contain structures such as old large trees close to their maximal age, abundant dead wood, and a sapling layer of shade tolerant species, but would lack cut stumps. In the relatively undisturbed mesic deciduous forest in the Bialowieza reserve in Poland, *Q. robur* reaches 400 years of age, occurs mostly in mixed woods with other broad-leaved tree species, and coarse dead wood amounts are mostly over 100 m^3 ha^{-1} (Falinski, 1988; Bobiec, 2002).

The presence of cut stumps in Barkava, Kinguru, and Mezotne indicates past removal of dead or damaged trees or selective cutting. However, the lack of standing dead wood in these plots suggests that the former was more likely. Despite the evidence of past wood removal, the densities of canopy trees are in the range of those reported for old-growth forests in the nemoral and borenemoral zones (Nilsson et al., 2003). Also, the volumes of dead wood at the sites (75–198 m^3 ha^{-1}) correspond to, or are close to, volumes (>100 m^3 ha^{-1}) in old-growth mesic deciduous and riparian forests in Poland (Bobiec, 2002). It has been estimated (Nilsson et al., 2003) that a volume of 130–150 m^3 ha^{-1} dead wood was common in productive European forest before human exploitation. The mean volume of dead wood in eutrophic bore-nemoral stands in Estonia was estimated to be 198 m^3 ha^{-1} (Lõhmus & Kraut, 2010). Thus, while the dead wood amounts accumulated in the studied *Q. robur* forests are approaching or have reached those in natural nemoral forest, the lack of standing dead wood in four plots indicates that the level of naturalness in terms of structures is far from that in old-growth forest.

Considering that *Q. robur* can attain an age of 400–500 years (Falinski, 1986) or even 800 years (Jones, 1959), the sampled stands in Latvia are certainly not old-growth forests. The oldest trees in the plots in the Lubana area (Audile, Pededze, and Barkava) had ages just over 200 years, with origin in about 1800 to 1810. Among the seven studied stands, in one the age of the oldest tree was less than 140 years, and in three stands less than 250 years. Considering the history of forest harvest and conversion to agricultural use in Latvia (Tērauds et al., 2011), these stands most likely regenerated naturally after logging or on agricultural land, although natural catastrophic disturbance such as fire cannot be ruled out. Water-logging, which was common in the Lubana area in spring at that time, might have facilitated recruitment of *Q. robur* (Bradshaw & Hannon, 2004). Forest inventory conducted in the early 1700s indicated that, while *Q. robur* woodland had already suffered major depletion over much of Latvia, it was abundant along the Pededze River, with stems reaching 1.4 m DBH (Zunde, 1999). However, these stands were close to rivers and thus were most likely prime harvest targets at a time when *Quercus* forests were already extremely depleted.

The inventory of the Barkava stand in 1937 reported a dominant *Q. robur* overstorey with a minor component of *P. tremula*, *B. pendula*, and *A. glutinosa* with ages of 70–90 years. The same species are seen in the stand today, but there are no *P. tremula*, *B. pendula*, and *A. glutinosa* over 80 years of age. Considering the cut stumps at Barkava, the continued presence of early successional *P. tremula* and *B. pendula* might be due to regeneration in gaps created by natural mortality or perhaps selective cutting. In contrast to the other six stands, stand inventory data from 1927 for the youngest (Salenieki) stand indicated a mixed *P. tremula* and *B. pendula* forest without *Q. robur*. In this stand, the age structure of *Q. robur* today (Fig. 3) suggests that most of the trees in 1927 were 1–20 years of age, and hence their wood volume would not have been recorded in the inventory. The *P. tremula* and *B. pendula* were most likely cut, releasing the *Q. robur* understorey. Planting or sowing of *Q. robur* was unlikely in the pre-1930 period, as natural regeneration of clearcuts was predominantly used, followed by sowing of pine (Tērauds et al., 2011). The Kinguru and Rauda stands were described in 1926/1929 as having scattered *Q. robur* about 70–80 years old, with an understorey of *P. tremula*, *B. pendula*, and *P. abies* in the former. In these sites, the open canopy might have been due to previous use as pasture, as was common in Latvia at that time (Dumpe, 1999).

Despite the large numbers of stems of less than 1 m height, recruitment of *Q. robur* to taller height classes after the post-initiation stage of the canopy has been lacking. In addition, the age structure of plots (Fig. 3) shows that in the Barkava plot, and partly also at Pededze, Kinguru, and Rauda, there was a gap in, or minimal, regeneration of all tree species between about 1870 and 1930, corresponding to the 81–140 year age classes (Fig. 3). A shorter 20-year period of no regeneration occurred at Audile in 1890–1910, and a longer period in Mezotne from 1830 to 1950. These periods might be related to human disturbance to the understorey, for example, by livestock grazing. The method used for identifying overgrowing meadow and pasture woodland of European importance in Latvia is partly based on an observation of a gap in the regeneration of tree species (Lārmanis, 2010). It is argued that if a period of no regeneration is observed, then the canopy was more open, i.e., grazed. On the other hand, time gaps in cohort structure can result from poor light availability caused by competition (Harmer et al., 2001; Küßner, 2003). Shading might also explain the succession to relatively more shade tolerant species, such as *P. abies* (Kinguru and Rauda), *F. excelsior* (Audile, Pededze, and Barkava), and *T. cordata* (Salenieki), as reported previously for the Moricsala Reserve in Latvia (Brūmelis et al., 2011a). Succession of mixed *Q. robur* stands to species-rich spruce–deciduous forest has occurred also on Abruka Island in West Estonia (Meikar et al., 2004). Thus, the age structure in the plots, except for Mezotne, probably shows a pattern of natural succession since stand intitiation, with shade tolerant species being more successful than *Q. robur*. In the stands in the Lubana area, the *Q. robur* dominated canopy might be expected to change to a mixed broad-leaved forest in the future, as is common in alluvial flood plains, or perhaps to a *P. abies* successional stage (Falinski, 1986). In the Republic of Bashkortorstan and South-Western Russia, natural succession of *Q. robur* forests to a mixed canopy is common, but in the long-term a return of *Q. robur* can occur in large canopy gaps (Ņesterovs, 1954).

The Mezotne stand lacked evidence of past regeneration of trees in the understorey over a 120-year period, it contained the least amounts of dead wood

($75\ m^3\ ha^{-1}$) and there were numerous stumps ($60\ ha^{-1}$). This long period of no regeneration cannot be explained solely by a period of canopy closure, and suggests long-term management as an open park forest with or without pasture use. The stand is located in an old rural area and is surrounded by agricultural land, which is consistent with this idea. The present lack of a sapling/shrub layer might explain the copious numbers of *Q. robur* (22 250 ind. ha^{-1}) and *F. excelsior* (16 500 ind. ha^{-1}) in the lower than 1 m layer.

Of the recorded eight lichen species, six (except *Bacidia rubella* and *Lecanactis abietina*) are protected. However, only one (*Dicranum viride*) of the five WKH indicator bryophyte species is protected. In a study of epiphytes in nemoral forests of Latvia, in which more stringent criteria of naturalness and a larger number of stands were used (Mežaka et al., 2008), of the species listed as WKH indicator species (Ek et al., 2002), 12 lichens and 7 bryophytes were recorded, of which respectively 8 and 5 were found on *Q. robur*. Thus, in terms of indicator species numbers, the stands sampled in our study are likely representative of the set of most natural oak forest in Latvia, and we are confident that the search for species in the plots and stands was sufficient. However, we recorded WKH indicator species only, and full species lists would provide additional information on epiphyte diversity in the stands. Even though all the studied stands were relatively young, each contained at least one protected species. The largest number (5) of protected species occurred in Pededze. The species richness of these epiphytes did not appear to be related to stand age, as even the youngest stands (Kinguru and Rauda) supported six and five WKH indicator species, respectively, while the highest richness, observed at Pededze, was eight species. Of the lichen species found in the studied stands, *Arthonia leucopellea*, *A. spadicea*, *A. vinosa*, and *Bacidia rubella* have been reported as frequent on *Q. robur* in wooded meadows in Estonia (Leppik & Jüriado, 2008) and may be limited by availability of large diameter substrate rather than human disturbance. *Arthonia byssacea* is rare in Estonia (Thor et al., 2010) and has been found to be associated with old large diameter *Q. robur* (Jüriado et al., 2009). However, we found *A. byssacea* in five stands, including in the youngest (Salenieki). Perhaps this species requires more shaded conditions in closed forests, as found in the Latvian *Q. robur* stands compared to the Estonian wooded meadows.

Lobaria pulmonaria and *Neckera pennata*, recorded each in one stand in the present study, are dependent on habitat connectivity (Snäll et al., 2004, 2005; Paltto et al., 2006). Both of these species readily utilize other deciduous species, particularly *P. tremula*, as a substrate and are probably not limited by presence of *Q. robur* in the landscape. *Homalia trichomanoides*, *Isothecium alopecuroides*, and also *Anomodon longifolius* (we did not identify *Anomodon* to species) have been observed to be limited by habitat quality features, such as moisture, substrate pH, tree size, and forest age, and also by present and/or past habitat connectivity (Löbel et al, 2006; Löbel & Rydin, 2009).

Some of the stands may have had past agricultural use (grazing, meadows). Traditionally managed wooded meadows and pasture usually contain old legacy trees. The age of the oldest *Q. robur* tree in a traditionally managed woodland on

Saaremaa Island, Estonia, was estimated to be about 500 years (Läänelaid et al., 2008). This raises the question to what extent the present occurrence of species on oak is due to past non-forest land-use. As pasture woodlands have high conservation value in Europe, partial harvesting has been recommended for generating more open stands (Götmark, 2007; Økland et al., 2008; Paltto et al., 2008). Also in Latvia, *Q. robur* trees in protected areas are often cleared from surrounding trees and shrubs to maintain their value for biological diversity (Anon., 2008), creating a setting that might have been typical of that under a traditional shifting agricultural regime. However, none of the studied sites contained legacy trees of a meadow setting, i.e., they might be secondary forests on past agricultural land but they do not represent traditional long-term wooded meadow/pasture management. An exception might be the Mezotne stand. This stand also supports an *Osmoderma eremita* population. This rare beetle species has a small dispersal distance and requires large diameter and hollow *Q. robur* that are well lit (Ranius & Hedin, 2001). Therefore, management by shrub cutting might be warranted when required.

The studied *Q. robur* WKH stands, which can be considered to be among the most natural stands of this forest type in Latvia, were found to be mature (in terms of cutting age, which is 100–120 years for oak in Latvia) to overmature *Q. robur* woodland developed under minimal to moderate human disturbance. Similarly, in southern Sweden, WKHs have not escaped human disturbance, but nevertheless are among the most natural stands in the region (Ericsson et al., 2005; Jönsson et al., 2009). While the amounts of dead wood were in the range of those reported for old-growth forest, or approaching these, there were no very old *Q. robur* close to its maximal age, and standing dead wood was lacking in four stands. Nevertheless, protected species were found in the stands. The small size of the stands (2.9–18.1 ha) suggests that the full range of variability of pre-industrial broad-leaved forest cannot be expected, either now or in the future. In the studied stands, considering the long age span of *Q. robur*, we predict that the *Q. robur* canopy will persist for at least another 200 years, and certainly the conservation value of the stands will increase with time. The studied *Q. robur* stands are among the most natural in Latvia, but assessment based on the age and size structure, amounts of dead wood, and past evidence of cutting and possibly agricultural use suggests a rather low level of naturalness. Nevertheless, the richness of WKH indicator species was in some cases high.

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Hariliku tamme *Quercus robur* puistute looduslikkus Lätis, hinnatuna struktuuri, liikide ja arengu järgi

Sandra Ikauniece, Guntis Brūmelis ja Toms Kondratovičs

Seitsmes hariliku tamme *Quercus robur* puistus Lätis tehti puude suuruse ja vanuselise struktuuri, surnud puidu hulga, kändude ning metsainventuuri tulemuste ja kaartide järgi kindlaks puistu arengu ajalugu. Kõik uuritud puistud vastasid

metsa vääriselupaikade kriteeriumidele. Tamm oli kõigis puistutes peapuuliigiks. Puurinde kujunemisest peale on üle 1 m kõrguste tammede lisandumine olnud minimaalne, vähemalt tänapäevani elanud tammede osas. Ühes puistus ei olnud loodusliku suktsessiooni märke, kuid teistes toimus looduslik uuendus hariliku kuuse, hariliku saare, hariliku jalaka, sanglepa ja hariliku pärnaga. Surnud puidu suur hulk proovialadel näitab kõrget looduslikkuse taset. Ent esimese rinde tammede vanus (kuni 226 aastat) viitab pikaajalise loodusliku arengu puudumisele. Inimmõjule osutavad ka kännud kolmel proovialal ja seisvate surnud puude puudumine neljal proovialal. Ühel proovialadest on alates 1920. aastatest toimunud puuliikide vaheldumine: harilik haab ja arukask on esimeses rindes asendunud hariliku tammega. Kuigi uuritud puistud võib vanuselise struktuuri ja majandamise ajaloo järgi pidada madala looduslikkusega puistuteks, esineb neist igaühes 2–8 metsa vääriselupaikade indikaatorliiki, nende seas 1–6 kaitstavat liiki.