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# Time needed to achieve sufficient richness of structural elements and bryophytes in deciduous forest stands

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**Abstract**

In Northern Europe, one of the tools that has been used in nature conservation is set-aside of the so-called woodland key habitats (WKHs). We determined the period of time after start of passive restoration to attain the threshold quality needed to be recognized as a WKH. Richness of bryophyte species and structural elements in stands with different past history was determined. We found that most of the studied forest stands designated, as WKHs had regenerated after clearcut or selective spruce removal during the last century. Stands (n = 12) were grouped as managed and less-managed WKHs, based on evidence of human disturbance. The term less-managed WKHs was used to describe stands that probably had been regenerated on previous clearcuts or past agricultural land before year 1900. Managed and less-managed stands slightly differed in amounts of coarse woody debris and richness of bryophyte species. The results show that passive restoration of a managed deciduous tree stand, by setting it aside from management in a period of 45 to 90 years, can allow to reach the sufficient biological value, as defined by WKH inventory criteria. However, this amount of time is not sufficient to reconstruct quality of dead wood that is typical of old-growth forests.

**Key words:** Logging, passive restoration, species richness, structural elements.
**Abbreviations:** CWD, coarse woody debris; DBH, diameter at breast height; GLM, generalized linear model;WKH, woodland key habitat.

## Introduction

Forest fragmentation and degradation of habitat quality have caused decline of biological diversity (Kuuluvainen 2002; Hanski 2005), and despite efforts the decline has not been halted (Angelstam et al. 2011). Parties to the Convention on Biological Diversity have set new targets for the year 2020, which call for the Aichi target of 17% of the terrestrial area conserved in protected areas or by other means (Secretariat of the Convention on Biological Diversity 2011). In Northern Europe, one of the tools that has been used in nature conservation is set-aside of woodland key habitats (WKHs), which are small forest stands with high biological diversity (Timonen et al. 2010). WKHs are identified by old-growth characteristics, including structural elements and specialist species (Ek et al. 2002; Timonen et al. 2010). Within particular regions, the WKHs are considered to be among the least human-disturbed forests, as they by definition have large amounts and diversity of dead wood, and threatened species in different organism groups (Jönsson, Jonsson 2007; Pykälä 2007; Timonen et al. 2011). On the other hand, some studies have shown (Gustafsson et al. 2004a; Junninen, Kouki 2006) that WKHs are not really hotspots of diversity for some organism groups, which is likely due to the long period of time required for old-growth characteristics to develop (Jönsson, Jonsson 2007). Thus, WKHs might be better considered as stands that have been less human-disturbed than typical industrial forests, and that contain varying amounts of structural features of natural forest (Ericsson et al. 2005; Hottola, Siitonen 2008; Ikauniece et al. 2012). Also, in some cases, amounts and diversity of structural elements of old-growth forests can be just as high in commercial forests as in protected areas (Lõhmus et al. 2005). In view of the above, rather than being old-growth forest, WKHs might represent conservation networks that simply have more characteristics of a natural forest than other stands. Thus, these set-aside areas can be regarded as stands in which non-intentional passive restoration (Suding 2011) is taking place.

In Latvia, where there has been a long legacy of commercial forestry and shifting agriculture, the area of forests older than 150 years is extremely small for all tree species (Tērauds et al. 2011). However, due to non-intensive methods of forest management used prior to 1940 (Tērauds et al. 2011), many forest stands have developed structures that can support diversity of species characteristic of natural forests (Madžule et al. 2012).

The aim of our study was to determine the period of time that had been required after start of passive restoration (no or minimal wood removal) to attain the threshold of quality needed to be recognized as a WKH. We determined richness of bryophyte species and structural elements in the stands with different past history. As a case study, we focused on deciduous tree WKHs, as they have high importance in conservation of many species groups, such as bryophytes (Snäll et al. 2004) and birds (Roberge et al. 2008).

## Materials and methods

### *Study area*

The study was conducted in the Ziemelvidzeme Biosphere Reserve of Latvia (Fig. 1). The region (terrestrial area 457 600 ha) is located in the northern part of Latvia in the boreo-nemoral vegetation zone (Sjörs 1963) of Europe. The mean annual temperature is 5.6 °C and the mean precipitation is 630 mm yearly. The forests form a mosaic of site types on dry and wet soils, and most of the wet forest area has been drained (Tērauds 2011). Forests occupy an area of 221 383 ha in the Ziemelvidzeme Biosphere Reserve. The greater part of the forest area of the landscape is dominated by coniferous trees *Pinus sylvestris* and *Picea abies* (Tērauds 2011). The main deciduous tree species are *Betula pendula, Betula pubescens, Populus tremula, Alnus glutinosa*, and *Fraxinus excelsior* (Tērauds 2011).

The region contains more than 3 400 WKHs, which have been voluntary protected from logging by agreement within the Forest Stewardship Council forest certification scheme. Stand age of the deciduous WKHs ranges from 61-220 years, estimated by forest inventory records (Tērauds 2011). The oldest WKHs are *Quercus robur* forests, but these are rare in the region.

### *Field sampling*

In total, 12 WKHs dominated by deciduous tree species (*A. glutinosa, Betula* spp. and *P. tremula*) were chosen subjectively from the WKH database (obtained from the State Forest Service) to represent a wide range in stand age, but blindly without prior visitation to the stands. The WKH database, which is linked to the State forest Register, contains stand-level information on tree composition, approximate age and site type. Size of the stands varied from 0.8 to 4.6 ha. Eight of the stands were on wet mineral soils, two on drained peat soils, one on drained mineral soil and one on peat soil. According to site type, the stands represented *Myrtillosoi-polytrichosa* (five stands), *Drypteriosa* (three stands), *Oxalidosa turf. mel.* (two), *Mercurialosa mel.* (one) and *Dryopterioso-caricosa* (one). The fieldwork was conducted from June to October in 2010. Plots (20 × 50 m) were established at randomly chosen coordinates in each of the selected stands.

In each sampling plot, diameter at breast height (DBH) and tree height were determined for all living trees over 10 cm DBH and cores were removed from these for age estimation. The two birch species (*B. pendula* and *B. pubescens*) were considered together due to similarity in epiphytic communities (Barkman 1958). All coarse woody debris (CWD) originating inside plots and with diameter > 10 cm (breast height from base) was measured by tree species. DBH and tree height of standing dead trees were measured. For downed trees diameter in the middle of logs

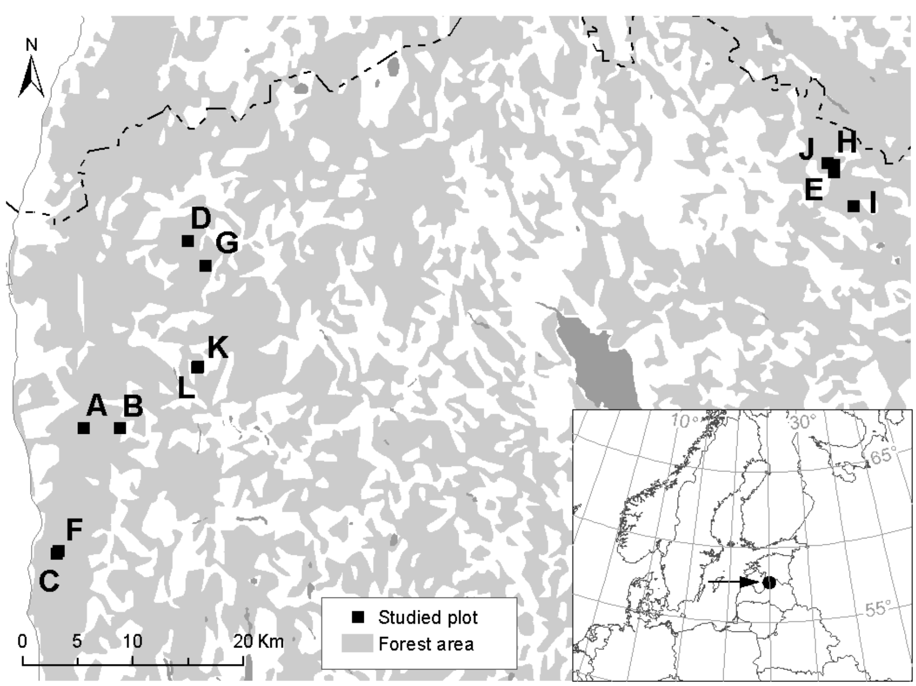


**Fig. 1.** Map of study area with location of 12 studied woodland key habitats (WKHs) in the Ziemelvidzeme Biosphere Reserve, modified from Tērauds et al. (2011).

and length were recorded. Dead branches were not recorded. Diameter of all stumps was measured. A count was made of the number of cut stumps (those with a plane surface and/or lacking a log that might have originated from the stump). We calculated total volume of downed trees as sum of volume of log pieces estimated as cylinders and volume of dead standing trees using equations for living trees. The total volume of CWD was the sum of volume of downed and dead standing trees.

We recorded all bryophyte species found from tree base up to 2 m height on all living and standing dead trees (DBH > 10cm) and all species on fallen CWD (DBH >10 cm) and stumps. Unknown species were collected and later examined in laboratory. Nomenclature followed by Hill et al. (2006) for mosses and Grolle and Long (2000) for liverworts. Decay stage of CWD was estimated using a five-point scale (Pyle, Brown 1998).

Archive inventory data in the form of maps and journals stored at the Latvian State Forest Research Institute "Silava" were used to reconstruct the forest history of the 12 WKHs since 1928. The inventory years and level of detail of descriptions differed between the stands that had been designated as WKHs. In five of the studied plots, the present area of the WKH had earlier been divided into two stands differing in tree composition and age. Data on stand composition and stand age from archived journals and notes on planned forest activity were used to infer type and time of logging events. In cases when between subsequent inventories the tree age had switched from cutting age to a young stand, it was assumed that the stand had been logged, or at least that wood had been removed after a major natural disturbance. Based on past logging events in the WKH territories, they were divided into two groups: managed (clearcut and selective wood removal in the past 90 years) and less-managed stands. The area of the stands designated as WKHs (ha) was obtained from the State Forest Service. Stand age was calculated as the mean value of all cored trees within studied plots.

*Data analysis*

For stand structural characteristics that did not deviate from normality (P > 0.05, Shapiro-Wilk normality test), a two-sample t-test was used to test for significant differences between managed and less-managed WKHs. The Mann-Whitney U test was used to test significance of differences of variables that differed from normality.

## Results

*Management history*

Forest inventory data indicated that tree species composition in stands A, B and C changed from spruce with age 70 to 95 years in 1928 – 1941 to deciduous trees with age 44 to 88 in 2011 (Table 1, Fig. 2A–C). Considering the major change in species composition, the stand age in inventory records and the present-day tree age distribution in 2011, it was assumed that spruce had been cut. Stand A was recorded as a clearcut in 1950. The presence of many deciduous trees with age over 100 years in stand B suggests that saplings of perhaps subcanopy trees were retained in the clearcut (Fig. 2B). Stand C was in part (earlier spruce stand) likely cut soon after 1929. This stand was harvested by clearcut again in 1972 – 1982, indicated by a change from mature black alder to young ash, which in 2011 had age 31 to 40 years (Fig. 2C). Abundant stumps were also present in this stand. In 1941, spruce with age 100 dominated in stand D (Table 1). The inventory records of that year noted a planned clearcut in the next 10 years. Presently the stand is dominated by birch and spruce with age 80 to 130 (Fig. 2D). The above suggests that selective removal of spruce did occur in the stand, and stumps were also present, but the present age of trees in the stand indicates that it was not clearcut. Stand E, which was recorded as a clearcut in 1932, presently is dominated by birch and black alder, with age of most trees approximately matching the time since logging (Fig. 2E).

In stands F to L, the inventory records showed a progressive increase in age of the stands, indicating lack of harvest of at least a major part of the oldest trees (Table 1). In the 1920s – 1930s, these had been stands with age 15 to 65 years, and had probably regenerated on previous clearcuts or on past agricultural land. In stand K, cut spruce stumps were observed, but considering the progressive increase in stand ages given in inventory, from 65 years in 1935 to 90 in 1960 and 128 in 2011 (Table 1), major wood removal seems unlikely. Nevertheless, the stumps indicate that probably some of the older spruces were removed, perhaps after suffering mortality.

Further, the stands were grouped by past intensity of logging. Stands A-E are referred to as managed, and stands F–L as less-managed.

*Structural elements*

The managed stands (clearcut or selective spruce removal) had more living deciduous trees in the DBH class 0.20 – 0.29 m (Table 2). Age of the oldest trees did not much differ between the two groups of stands (managed and less-managed) and all stands except stand G had some trees with age > 100 years (Fig. 2). Two stands (one managed and one less-managed) lacked deciduous trees with age > 100 years, and three stands (two managed) lacked coniferous tree with age > 100 years (Fig. 2).

The total volume of coarse woody debris (CWD) did not differ significantly between the two groups of stands (Table 2) and ranged from 62.35 to 139.30 m$^3$ in less-managed stands and from 19.30 to 138.62 m3 in managed stands. Downed tree volume per hectare ranged from 44.19 to 101.9 m$^3$ in less-managed stands and from 8.63 to 113.85 m$^3$ in managed stands. The volume of downed trees < 0.30 m was significantly greater in less-managed stands (Table 2). There were no significant differences between managed and less-managed forests in numbers of downed trees in

**Table 1.** Logging history of the studied stands. Mean and maximum tree age in stands is given for deciduous and coniferous trees

| Stand | Mean tree age in 2011 (max tree age) | Stand description in records | Time of clearcut/ wood removal | Number of cut stumps (species) |
|---|---|---|---|---|
| A | 60 (black alder –148, spruce – 62) | 1928 – mixed spruce, birch stand (70 years); 1950 – clearcut; 1960 – young spruce stand; 1973 – young birch stand | Clearcut 1928-1950 | – |
| B | 88 (black alder – 131, spruce – 91) | 1928 – mixed spruce, birch stand (70 years); 1950 – young black alder stand; 1960 – young black alder stand | Selective cut 1928-1950 | – |
| C | 44 (ash – 165, spruce – 57) | 1929 – spruce stand (95 years), mixed black alder, birch stand (80 years); 1941 –mixed black alder, birch stand (85 years); 1960 – mature black alder stand; 1972 – mature black alder stand; 1982 – young ash stand | Clearcut 1929-1941, clearcut 1972-1982 | 3 (spruce); 3 (black alder), 1 (ash) |
| D | 105 (aspen – 130, spruce – 232) | 1941 – spruce stand (100 years); 1960 – birch stand | Selective cut 1941-1960 | 1( aspen), 4 (unknown) |
| E | 76 (black alder – 99, spruce – 150) | 1932 – clearcut; 1982 – young birch stand | Clearcut 1932 | – |
| F | 77 (black alder – 136, spruce – 110) | 1929 – mixed black alder, young birch stand; 1941 – mixed black alder, birch stand (55 years); 1960 – black alder stand; 1972 – black alder stand (80 years); 2011 –mixed black alder, birch stand | | – |
| G | 65 (lime – 84, aspen – 83, spruce – 100) | 1928 – mixed aspen, birch, spruce stand (55 years); 1941–1945 – mixed aspen, birch, spruce stand (70 years); 1960 – aspen stand (80 years); 1973 – mature aspen stand; 2011 – mixed aspen, birch, spruce stand | | – |
| H | 84 (ash – 131, spruce – 102) | 1936 – mixed spruce, birch stand (25 years), mixed birch, grey alder stand (25 years); 1960 – birch stand (50 years); 1972 – birch stand; 1982 – birch stand (60 years); 2011 –mixed birch, aspen stand | | – |
| I | 82 (black alder – 110, spruce – 173) | 1936 – mixed spruce, birch stand (15 years), mixed spruce, black alder stand (110 years); 1960 – mature spruce stand; 1972 – mature spruce stand; 1982 – mature spruce stand; 2011 – mixed spruce, black alder stand | | – |
| J | 82 (black alder – 111, spruce – 115) | 1936 – mixed spruce, birch stand (25 years), mixed grey alder, birch stand (20 years); 1960 – young spruce stand; 1972 – spruce stand; 1982 – spruce stand; 2011 – mixed birch, spruce, black alder stand | | – |
| K | 80 (birch – 125, aspen – 118, spruce – 130) | 1935 –mixed spruce, aspen stand (65 years); 1960 – aspen stand (90 years); 2011 – mixed aspen, black alder stand | | 3 (spruce) |
| L | 120 (aspen – 194, spruce – 178) | 1934 – mixed birch, aspen stand (55 years), mixed aspen, spruce stand (70 years); 1960 – aspen stand (90 years); 2011 – mixed aspen and black alder stand | | – |

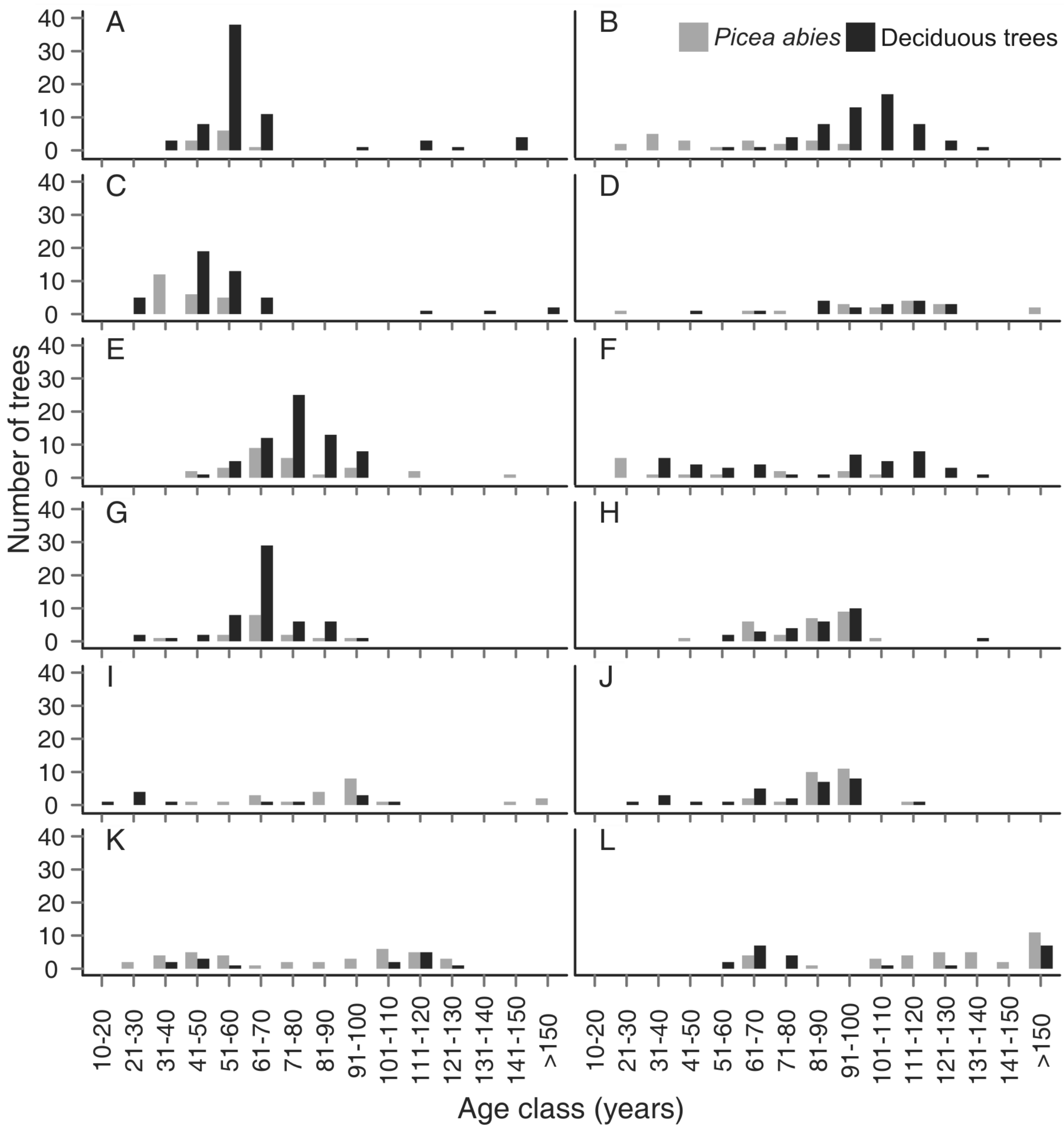


**Fig. 2.** Age distribution of cored trees in the studied stands.

various decay stages (Table 2). The proportion of downed wood in decay stage V was very low for all stands (Table 2).

*Bryophyte species richness*

In total, 73 bryophyte species including 12 indicator species were recorded in the studied plots, of which most occurred on living trees (Table 3). The lowest number of bryophyte indicator species was found on stumps. The number of indicator species in plots on CWD (stumps plus downed trees and plus snags) was significantly higher in less-managed stands, compared to managed stands. Indicator species richness in plots on downed trees was also higher in less-managed stands, but the difference only approached significance in the Whitney-U test (Table 2).

## Discussion

The historical records and mean stand ages of less-managed and managed WKHs clearly showed that the most of the studied forest stands designated as WKHs

**Table 2.** Comparison of mean values between managed (n = 5) and less-managed (n = 7) stands. U test, Whitney-U test

| Variables | Range | Less-managed stands | Managed stands | p value | Used test |
|---|---|---|---|---|---|
| **Number of structures** | | | | | |
| Age of deciduous trees | 0 – 49 | 4.14 | 20.4 | 0.87 | U test |
| | 50 – 99 | 16.71 | 33.2 | 0.2 | t-test |
| | 100 – 149 | 4.86 | 9.8 | 0.463 | U test |
| | > 150 | 1 | 0.2 | 1 | U test |
| Age of coniferous trees | 0 – 49 | 3 | 4.6 | 0.453 | U test |
| | 50 – 99 | 14.43 | 9.6 | 0.274 | t-test |
| | 100 – 149 | 5.71 | 5.4 | 0.741 | U test |
| | > 150 | 1.86 | 0.6 | 1 | U test |
| DBH of deciduous trees | 0.10 – 0.19 | 8.14 | 27.2 | 0.623 | U test |
| | 0.20 – 0.29 | 5.86 | 19.2 | 0.028 | U test |
| | > 0.30 | 12.71 | 17.2 | 0.551 | t-test |
| DBH of coniferous trees | 0.10 – 0.19 | 13.14 | 16.2 | 0.414 | t-test |
| | 0.20 – 0.29 | 8.71 | 3.4 | 0.084 | t-test |
| | > 0.30 | 3.14 | 0.6 | 0.108 | U test |
| Stumps | | 1.86 | 3.8 | 0.218 | U test |
| Decay class of downed trees | I | 4.28 | 2.2 | 0.505 | U test |
| | II | 0.42 | 2.4 | 0.287 | U test |
| | III | 2 | 3.8 | 0.371 | t-test |
| | IV | 2 | 1 | 0.615 | U test |
| | V | 0.71 | 0.4 | 0.41 | U test |
| **Volume ($m^3$ $ha^{-1}$)** | | | | | |
| Coarse woody debris | Total | 100.22 | 63.72 | 0.164 | t-test |
| | Downed trees | 65.19 | 46.47 | 0.389 | t-test |
| | Dead standing trees | 35.03 | 17.26 | 0.085 | U test |
| Diameter of downed trees | 0.10 – 0.19 | 22.78 | 14 | 0.236 | t-test |
| | 0.20 – 0.29 | 20.53 | 27.32 | 0.646 | t-test |
| | > 0.30 | 20.77 | 5.14 | 0.047 | t-test |
| **Number of species** | | | | | |
| Species in plot | All species | 33.43 | 33.8 | 0.943 | t-test |
| | Indicator species | 5.42 | 5.2 | 0.851 | t-test |
| Species on coarse wood debris | All species | 24.71 | 20.8 | 0.218 | t-test |
| | Indicator species | 3.86 | 1.8 | 0.041 | t-test |
| Species on downed trees | All species | 20.57 | 16 | 0.144 | t-test |
| | Indicator species | 2.57 | 1.4 | 0.085 | U test |
| Species on snags | All species | 9.85 | 7.8 | 0.588 | t-test |
| | Indicator species | 1.57 | 1 | 0.494 | U test |
| Species on stumps | All species | 3.57 | 5 | 0.548 | t-test |
| | Indicator species | 1.29 | 0 | 0.261 | U test |
| Species on living trees | All species | 26 | 28.8 | 0.398 | t-test |
| | Indicator species | 3.71 | 4.4 | 0.605 | t-test |

were affected by forestry during the last century. Of the 12 stands, three had been clearcuts, and in two spruce had been selectively removed. However, the presence of trees older than the estimated time of clearcut indicates that the harvest methods were less destructive to non-timber trees than the typical practice of intensive methods used in Nordic countries. Also, some of less-managed stands were very young forests in the year 1930, and considering the past intensive use of forests in Latvia (Tērauds et al. 2011), it is likely that they developed after cutting or on agricultural land. Rouvinen and Kouki (2008) stressed the need for historical data in the assessment of naturalness of forests. In this respect, according to the age of stands and signs of previous cutting, the studied deciduous tree WKHs

**Table 3.** Number of plots (n = 12) in which bryophyte species were recorded, by different substrates and management type: managed (n = 5) and less-managed (n = 7) woodland key habitats (WKHs). Woodland key habitat (WKH) indicator species are indicated in bold

| **Bryophyte species** | **Substrate** | | | | **Management** | |
|---|---|---|---|---|---|---|
| | **Living trees** | **Downed trees** | **Dead standing trees** | **Stumps** | **Managed** | **Less-managed** |
| Liverworts | | | | | | |
| *Blepharostoma trichophyllum* | 2 | 5 | 0 | 0 | 3 | 3 |
| *Calypogeia azurea* | 0 | 1 | 0 | 0 | 0 | 1 |
| *Calypogeia neesiana* | 0 | 1 | 0 | 0 | 0 | 1 |
| ***Calypogeia suecica*** | 0 | 4 | 0 | 1 | 1 | 3 |
| *Cephalozia bicuspidata* | 1 | 2 | 0 | 1 | 2 | 2 |
| *Chephalozia connivens* | 0 | 1 | 0 | 1 | 0 | 2 |
| *Chephalozia lunulifolia* | 0 | 2 | 0 | 0 | 1 | 1 |
| *Chephaloziella elachista* | 0 | 1 | 0 | 0 | 1 | 0 |
| *Chephaloziella spinigera* | 0 | 1 | 0 | 0 | 0 | 1 |
| *Chiloscyphus pallescens* | 0 | 2 | 0 | 0 | 0 | 2 |
| *Frullania dilatata* | 7 | 1 | 2 | 0 | 3 | 4 |
| ***Frullania tamarisci*** | 1 | 0 | 0 | 0 | 1 | 0 |
| ***Jamesoniella autumnalis*** | 10 | 6 | 0 | 1 | 5 | 5 |
| ***Lejeunea cavifolia*** | 5 | 0 | 1 | 0 | 3 | 3 |
| *Lepidozia reptans* | 11 | 7 | 4 | 2 | 5 | 6 |
| *Lophocolea heterophylla* | 12 | 12 | 4 | 1 | 5 | 7 |
| ***Metzgeria furcata*** | 2 | 0 | 1 | 0 | 1 | 2 |
| ***Nowellia curvifolia*** | 0 | 8 | 1 | 0 | 3 | 5 |
| *Plagiochila asplenoides* | 10 | 4 | 2 | 2 | 4 | 6 |
| *Ptilidium pulcherrimum* | 12 | 8 | 4 | 0 | 5 | 7 |
| *Radula complanata* | 12 | 6 | 9 | 0 | 5 | 7 |
| ***Riccardia palmata*** | 0 | 2 | 0 | 0 | 0 | 2 |
| Mosses | 0 | 0 | 0 | 0 | 0 | 0 |
| *Amblystegium serpens* | 5 | 1 | 1 | 0 | 0 | 5 |
| *Atrichum undulaturm* | 1 | 0 | 0 | 0 | 1 | 0 |
| *Aulacomnium androgynum* | 1 | 0 | 0 | 0 | 1 | 0 |
| *Brachythecium campestre* | 0 | 0 | 0 | 1 | 0 | 1 |
| *Brachythecium rutabulum* | 10 | 10 | 5 | 0 | 5 | 7 |
| *Brachythecium salebrosum* | 3 | 7 | 1 | 0 | 3 | 5 |
| *Bryum subapiculatum* | 1 | 0 | 0 | 0 | 1 | 0 |
| *Calliergon cordifolium* | 0 | 3 | 0 | 0 | 2 | 1 |
| *Calliergonella cuspidata* | 1 | 1 | 0 | 0 | 1 | 1 |
| *Cirriphyllum piliferum* | 1 | 0 | 0 | 0 | 1 | 0 |
| *Climacium dendroides* | 1 | 2 | 0 | 0 | 1 | 1 |
| *Dicranum montanum* | 12 | 9 | 8 | 5 | 5 | 7 |
| *Dicranum polysetum* | 6 | 4 | 1 | 2 | 3 | 4 |
| *Dicranum scoparium* | 12 | 10 | 5 | 6 | 5 | 7 |
| *Eurhynchium angustirete* | 12 | 11 | 7 | 6 | 5 | 7 |
| *Eurhynchium striatum* | 1 | 0 | 0 | 0 | 1 | 0 |
| *Fissidens adianthoides* | 1 | 0 | 0 | 0 | 1 | 0 |
| *Fissidens taxifolius* | 0 | 1 | 0 | 0 | 0 | 1 |
| *Herzogiella seligeri* | 4 | 7 | 1 | 0 | 3 | 5 |
| ***Homalia trichomanoides*** | 9 | 3 | 5 | 0 | 4 | 6 |
| *Homalothecium sericeum* | 2 | 0 | 2 | 0 | 2 | 2 |

*(continued)*

**Table 3.** *continued*

| Bryophyte species | Substrate | | | | Management | |
|---|---|---|---|---|---|---|
| | Living trees | Downed trees | Dead standing trees | Stumps | Managed | Less-managed |
| *Hylocomnium splendens* | 8 | 8 | 4 | 3 | 4 | 6 |
| *Hypnum cupressiforme* | 12 | 11 | 9 | 3 | 5 | 7 |
| ***Isothecium alopecuroides*** | 2 | 0 | 0 | 0 | 1 | 1 |
| *Leucodon sciuroides* | 1 | 0 | 1 | 0 | 1 | 1 |
| *Mnium hornum* | 3 | 2 | 0 | 1 | 3 | 2 |
| ***Neckera complanata*** | 3 | 0 | 1 | 0 | 1 | 2 |
| ***Neckera pennata*** | 7 | 1 | 4 | 0 | 2 | 5 |
| *Orthotrichum affine* | 4 | 0 | 0 | 0 | 2 | 2 |
| *Orthotrichum speciosum* | 4 | 0 | 0 | 0 | 2 | 2 |
| *Oxyrrhynchium hians* | 4 | 1 | 0 | 0 | 1 | 3 |
| *Plagiomnium affine* | 6 | 1 | 0 | 1 | 2 | 4 |
| *Plagiomnium cuspidatum* | 11 | 9 | 9 | 3 | 5 | 7 |
| *Plagiomnium undulatum* | 6 | 4 | 2 | 1 | 3 | 3 |
| *Plagiothecium curvifolium* | 2 | 0 | 0 | 0 | 1 | 1 |
| *Plagiothecium denticulatum* | 1 | 0 | 0 | 0 | 0 | 1 |
| *Plagiothecium laetum* | 12 | 2 | 4 | 1 | 5 | 7 |
| *Platygyrium repens* | 4 | 2 | 0 | 1 | 2 | 3 |
| *Pleurozium schreberi* | 8 | 9 | 1 | 3 | 4 | 7 |
| *Pohlia cruda* | 1 | 0 | 0 | 0 | 0 | 1 |
| *Polytrichum juniperinum* | 1 | 1 | 0 | 1 | 2 | 0 |
| *Ptilium crista-castrensis* | 0 | 4 | 0 | 0 | 0 | 4 |
| *Pylaisia polyantha* | 5 | 0 | 0 | 0 | 3 | 2 |
| *Rhizomnium punctatum* | 4 | 4 | 0 | 0 | 3 | 3 |
| *Rhodobryum roseum* | 4 | 2 | 0 | 0 | 2 | 3 |
| *Rhytidiadelphus triquetrus* | 10 | 10 | 4 | 5 | 5 | 7 |
| *Sanionia uncinata* | 5 | 2 | 1 | 0 | 3 | 3 |
| *Tetraphis pellucida* | 9 | 3 | 1 | 5 | 5 | 4 |
| *Thuidium delicatulum* | 6 | 2 | 0 | 0 | 2 | 4 |
| *Thuidium tamariscinum* | 6 | 2 | 0 | 0 | 3 | 4 |
| ***Ulota crispa*** | 8 | 1 | 3 | 0 | 4 | 4 |

could be mainly classified as mature managed forests. Considering that in Latvia most of the logged forest area prior to 1930 was regenerated naturally and that planting when conducted had an extreme focus on coniferous species, the studied deciduous stands probably regenerated naturally (Tērauds et al. 2011).

Assuming the validity of the method used for identification of WKHs (Ek et al. 2002), our results show that non-intensive management during a period no longer than 90 years can result in deciduous forest with high biological value, as suggested in other studies (Ericsson et al. 2005; Pykälä 2007; Tērauds et al. 2011). One of the studied stands had even been logged twice during the last 90 years (Table 1), but contained some trees older than 130 years, suggesting that the previous method of clearcut harvest left retention trees and patches of advance growth undisturbed. After logging, which was probably much less intensive than that commonly practised today, the stands were unintentionally set-aside, which in essence could be termed passive restoration (Suding 2011). The past selective cutting of spruce in stand D, which was suggested by change in age structure, today might be called, for example, active restoration of deciduous woods as white-backed woodpecker habitat, as is being conducted in Sweden and Finland (Roberge et al. 2008).

There were only minor differences between managed and less-managed stands in structural variables. Total CWD volume and volume of downed trees showed high variation between stands and did not differ between managed and less-managed stands, as observed previously in a similar study in the UK (Kirby et al. 1998). However, one of the less-managed stands (stand L) had a large number of trees over 150 year of age, and may represent a stand that has been very minimally disturbed for a long period of time. In comparison to other regions (Ericsson et al. 2005; Lõhmus et al. 2005; Jönsson, Jonsson 2007; Pykälä 2007), the amounts of dead wood in the WKHs in Latvia were rather high, and two of the stands (one managed and one less-managed) contained CWD volume over 129 $m^3 ha^{-1}$, which is in the range of that typical of old-growth forest (Lõhmus, Kraut 2010). However, the two groups of stands differed in amounts of different size classes of living trees and CWD. The managed stands contained more living trees in the mid-size class (DBH 0.20 – 0.29 m) and less coarse woody debris with DBH > 0.30 m. This indicates less input of large diameter CWD in the managed stands, which can be explained by younger age (smaller size) of the trees. Only one of the managed stands had downed trees with DBH > 0.30 m, clearly indicating the relationship between past management and occurrence of large diameter CWD (Jönsson, Jonsson 2007). Also, downed trees in late stages of decomposition were relatively rare in both groups of stands, as is typical of WKHs in boreal Europe (Jönsson, Jonsson 2007), but very different from the distribution of large logs according to decay class in old-growth forest (Siitonen et al. 2000). Thus, a period longer than 90 years is needed to attain a more or less continuous recruitment of downed trees of all sizes.

Total bryophyte species richness did not differ significantly between managed and less-managed stands, as observed previously in other studies (Vellak, Paal 1999; Lõhmus et al. 2007; Lõhmus, Lõhmus 2008). WKHs do not necessarily have higher density of rare bryophyte species than productive forests (Gustafsson et al. 2004a) and high occurrence of rare bryophyte species can be found also in mature managed forests (Gustafsson et al. 2004b). Also, bryophyte species richness in old managed forests can be similar to that in WKHs (Perhans et al. 2007). Only the richness of indicator bryophyte species on CWD was significantly higher in less-managed stands, which can be explained by greater temporal continuity of dead wood supply. Many species with epiphytic habitat also were found on logs, suggesting that this tree-species effect might be explained at least partly by continued survival of epiphytes after tree fall. The highest bryophyte richness on CWD was observed on logs in the middle decay stages, as previously found (Söderström 1988; Andersson, Hytteborn 1991; Crites, Dale 1998; Ódor, van Hees 2004), but this might simply be due to the low amounts of CWD in late decay stages resulting from disturbed forest continuity (Crites, Dale 1998; Rambo, Muir 1998).

In conclusion, active restoration to provide greater and continuous input of CWD, as is being conducted in other countries in the boreal zone (Lilja-Rothsten et al. 2008; Berglund et al. 2011) would likely reduce the time needed to achieve a near old-growth condition.

Forest management has strongly reduced the diversity and volume of CWD within WKHs, which has affected wood inhabiting bryophyte species richness. Thus, while the WKHs are among the most natural forests in Latvia, many have been harvested in the last century. Missing elements of structural quality indicate that more than 90 years without human disturbance is needed to reconstruct the quality of CWD that is typical of old-growth forests. While the amounts of CWD in some of the studied stands were high, there were very few logs in late decay stages. This suggests that passive restoration efforts by setting aside of deciduous woods for development by natural succession, coupled with active restoration by creation of dead wood, can lead to high biological value of the stands in subsequent decades.

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