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FOREST STRUCTURAL ELEMENTS AND BRYOPHYTE SPECIES RICHNESS IN MANAGED FOREST LANDSCAPE

Doctoral Thesis

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Summary

Linda Gerra Inohosa, 2013. Forest structural elements and bryophyte species richness in managed forest landscape

Today, high biodiversity in Latvia is associated with deciduous forests, of which a part has been recognized as woodland key habitats (WKHs), but which may have been previously managed. The aim of the present study was to characterize richness of bryophyte species in relation with structural elements such as living trees and coarse woody debris (CWD) in forests with different history of management. The following objectives were established to reach the aim of the study:

1. To characterize structural elements and bryophyte species richness in managed forest landscape.
2. To determine the history of deciduous WKHs with different stand ages.
3. To characterize relationships between structural elements and bryophyte species richness in deciduous WKHs.
4. To compare bryophyte species richness and structural elements in managed and less-managed WKHs.
5. To evaluate relationships between structural elements and bryophyte species richness in *Quercus robur* forests.

Generalized linear model (GLM) and generalized linear mixed model (GLMM) analyses were used to obtain the best models to explain the total and indicator species richness in the studied managed forest landscape and WKHs. Archive inventory data in the form of maps and journals were used to reconstruct the forest history of 12 WKHs since 1928. Based on past logging in the studied territories, the WKHs were divided into two groups: managed and less-managed. Significant differences were found between managed and less-managed WKHs in stand structural characteristics and bryophyte species richness variables. In additional, five *Quercus robur* stands were described, of which one, in Moricsala Nature Reserve, was considered as a more natural forest stand.

The results showed that high bryophyte species richness was related with the occurrence of large diameter broad-leaved trees and aspens in managed landscape. However, the studied managed forest landscape did not support high bryophyte species richness on CWD, due to lack of large dead wood and low forest continuity.

The historical study on deciduous WKHs confirmed that some of the high-value stands of today had been harvested in the last 90 years. The deciduous WKHs had sufficient bryophyte species richness on living trees as long as there was high diversity of deciduous tree species, in particular large old deciduous trees. However, the past management had a negative effect on the quality of dead wood and the richness of species found on CWD.

In summary the results showed that a 90-year period without human disturbance is not a sufficient time to obtain structures such as large CWD and continuity of decay classes of downed trees. Also, more time is needed to reach high richness of bryophytes on dead wood.

The present research was carried out at the Department of Botany and Ecology, Faculty of Biology, University of Latvia from 2007 to 2012. The supervisor of the study was *Dr.biol.*, prof. Guntis Brūmelis.

Key words: deciduous forests, woodland key habitats, coarse woody debris, indicator species.

Abbreviations: AIC (Akaike information criterion), CWD (coarse woody debris), DBH (diameter at breast height), GLM (generalized linear model), GLMM (generalized linear mixed model), WKH (woodland key habitat).

Kopsavilkums

Linda Gerra Inohosa, 2013. Mežaudžu strūktūrelementu un sūnu sugu bagātība apsaimniekotā meža ainavā.

Mūsdienās Latvijā liela bioloģiskā daudzveidība ir saistīta ar lapu koku mežiem. Neskatoties uz to, ka daļa no lapu koku audzēm ir uzskatāmas par dabiskajiem meža biotopiem, šie meži var būt bijuši iepriekš apsaimniekoti. Veiktā darba mērķis bija raksturot sūnu sugu bagātību saistībā ar strūktelementiem kā dzīvi koki un mirusī koksne mežos ar atšķirīgu apsaimniekošanas vēsturi. Lai sasniegtu darba mērķi izvirzīti sekojoši uzdevumi:

1. raksturot strūktūrelementus un sūnu sugu bagātību apsaimniekotā meža ainavā;
2. apskatīt vēsturi dažāda vecuma lapu koku dabiskajiem meža biotopiem;
3. raksturot savstarpējo saistību starp struktūrlementiem un sūnu sugu bagātību lapu koku dabiskajos meža biotopos;
4. salīdzināt sūnu sugu bagātību un struktūrelementus apsaimniekotos un mazāk apsaimniekotos lapu koku dabiskajos meža biotopos;
5. novērtēt savstarpējos saistību starp struktūrelementiem un sūnu sugu bagātību *Quercus robur* mežos.

Lai atrastu labākos modeļus, kas izskaidro kopējo un indikatorsugu bagātību apsaimniekotā mežaudzē un dabiskajos meža biotopos, izmantota ģeneralizētā lineārā modeļu (GLM) analīze un ģeneralizētā lineārā miksēto modeļu (GLMM) analīze. Savukārt 12 dabiskajiem meža biotopiem rekonstruēta vēsture, izmantojot arhīva materiālus kopš 1928. gada karšu un žurnālu viedā. Izvērtējot saimniecisko darbību apskatītajā laika periodā, dabiskie meža biotopi iedalīti divās grupās: apsaimniekotās un mazāk apsaimniekotās mežaudzēs. Būtiskākās atšķirības noteiktas starp struktūrelementu un sūnu sugu bagātību apsaimniekotajos un mazāk apsaimniekotajos dabiskajos meža biotopos. Papildus aprakstītas piecas *Quercus robur* mežaudzes, no kurām viena, kas atradās Moricsalas dabas rezervātā, uzskatāma par mežaudzi ar lielāku dabiskumu.

Rezultāti rādīja, ka liela sūnu sugu bagātība apsaimniekotā meža ainavā saistīta ar liela diametra platlapju koku un apšu klātbūtni. Tomēr pētītā apsaimniekotā meža ainava nenodrošina lielu sūnu sugu skaitu uz mirušās koksnes, pateicoties liela diametra mirušās koksnes iztrūkumam un zemai meža kontinuitātei.

Vēsturiskie dati par lapu koku dabiskajiem meža biotopiem apstiprināja faktu, ka dažas augstas vērtības mežaudzes ir bijušas pakļautas koksnes izvākšanai pēdējo 90 gadu laikā. Dabiskajos meža biotopos bija pietiekama sūnu sugu bagātība uz dzīvajiem kokiem, kamēr šajos mežos bija sastopama augsta lapu koku dažādība, it īpaši lieli veci lapu koki. Savukārt apsaimniekošana ir negatīvi ietekmējusi mirušās koksnes kvalitāti un sūnu sugu bagātību uz mirušās koksnes.

Galvenie darba rezultāti parādīja, ka 90 gadu ilgs laika periods bez cilvēka darbības nav pietiekams, lai pastāvētu tādas struktūras kā liela mirusī koksne un kontinuitāte starp kritalu sadalīšanās pakāpēm. Tai pat laikā, lielāks laika posms ir nepieciešams, lai sasniegtu augstu sūnu sugu bagātību uz mirušās koksnes.

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Atslēgas vārdi: lapu koku meži, dabiskie meža biotopi, mirusī koksne, indikatorsugas.

Introduction

The fragmentation and loss of quality of old natural forests are among the largest threats to biological diversity (Kuuluvainen 2002, Hanski 2005). Today, conservation of nature is especially focused on old-growth forests, mainly because many features of habitats need a long time to develop. The remaining unprotected patches of old forests need to be considered important for biodiversity. Presently, there is still a need to evaluate the amounts of structural elements to maintain sensitive species in managed forests (Mönkkönen et al. 2009).

Human activities have resulted in habitat loss of many species. Decline has been observed also for rare and threatened bryophytes (Berg et al. 1995). For many bryophyte species the small fractions of old-growth forests or even individual elements of old-growth forests (that remain in the fragmented landscape areas) are very important for nature conservation (Söderström 1988a, Jonsson et al. 2005, Löbel et al. 2006a, Brūmelis et al. 2011).

In the last decades, one of the ways of supporting the biological diversity of managed forestland is the conservation of woodland key habitats (WKHs). WKHs are mostly small patches hosting red-listed species (Timonen et al. 2010). However, WKHs can also be considered as having formed after management and thus cannot be represented as remnants of old-growth forests (Ericsson et al. 2005, Jönsson and Jonsson 2007).

In Latvia, during the last 70 years, the area of deciduous tree forests has increased. This has happened due to non-intensive methods of forest management used prior to 1940 and the overgrowing of agricultural land. On the other hand, the area of old stands have decreased and the area of forests older than 150 years has become extremely small for all tree species. In addition, a large proportion of deciduous forest stands have been recognized as WKHs and are considered to have high quality, large quantities of coarse woody debris (CWD), and high occurrence of rare species. Historical studies have shown that part of today's defined WKHs have been logged in the beginning of the last century (Tērauds 2011, Tērauds et al. 2011), meaning that at least for deciduous forests the non-intensive forestry methods of the past are compatible with attaining the biodiversity levels of today.

The present study is focused on two main questions. Firstly, what are the structural elements that support high bryophyte species richness in managed landscape? Secondly, how long does it take a managed stand to attain the necessary conditions to be considered as WKH.

The aim of the study

To characterize richness of bryophyte species on living trees and CWD in relation with structural elements in forests with different history of management impact.

The objectives of the study

1. To characterize structural elements and bryophyte species richness in managed forest landscape.
2. To determine the history of deciduous WKHs with different stand ages.
3. To characterize relationships between structural elements and bryophyte species richness in deciduous WKHs.
4. To compare bryophyte species richness and structural elements in managed and less-managed WKHs.
5. To evaluate relationships between structural elements and bryophyte species richness in *Quercus robur* forests.

The hypothesis of the study

1. The occurrence of epiphytic indicators of WKHs is related with the presence of large diameter aspens and broad-leaved trees in a stand.
2. The richness of epixylic species of WKHs is low in both managed forests and WKHs. This is due to the low quality of downed trees, despite the high volume of CWD.
3. Most WKHs have been under forest management impact during the last century, and therefore do not provide all characteristics of old-growth forests.

The theses of the study

1. High bryophyte species richness can develop in managed forests, including species that are sensitive to various human activities, provided that there are structural elements that support species growth.
2. High bryophyte species richness is related with deciduous forest stands. Deciduous forests can develop in a short time period structural elements that ensure suitable growth conditions for WKH indicator species.

1. Literature

1.1. Managed landscape and richness of bryophyte species

Managed landscape can be considered as a matrix of different types of habitats in which human activities interact with species. If human impact is considered in a small scale like a forest stand then the changes could be small, but if the management is evaluated in a larger scale then it can be more severe, which indicates the importance of landscape scale approaches (Villard and Jonsson 2009).

J.F. Franklin (1993) considered that large scale studies are the only way to conserve the vast majority of biological diversity, and that landscape has three important roles in conservation of biological diversity: 1) it includes smaller habitats, 2) landscape increases the importance of reserve areas and 3) in the landscape it is possible to control connectivity between reserves. However, the word “reserves” might also refer to individual structures such as dead trees, which are important for many species and for which maintenance is dependent on management.

One of the most common ways of how to evaluate biodiversity in landscape is to use useful biodiversity indicators like single species or a limited set of species (Villard and Jonsson 2009). The number of indicator species in combination with the number of old-growth forest structure elements may show the value of a forest area (Nilsson 2009), or on the opposite they may indicate the most important structures needed in the particular forest area (Nilsson 2009). Therefore, to achieve conservation targets, it is important to choose good indicators.

One of the options is to use bryophytes as a species group to evaluate the value of naturalness in a forest (Suško 1998), since they can: be good indicators of one seral stage or a rare substrate, they are relatively easily detected, and are present during most of the year (Nilsson 2009). U. Suško (1998) in his work about structures of biological diversity and threatened species in Latvia mentioned that bryophytes with high biological value are mostly connected with living trees (epiphytic species) and dead wood (epixylic species).

Ecological investigations of bryophytes have shown that specific bryophyte species are associated with stand structures such as large living trees (Snäll et al. 2003, Kouki et al. 2004) and dead wood in particular decay stages (Söderström 1988a, 1988b). U. Suško (1998) affirmed that some of the substrates for indicators need more than 100 years to develop, for example very old deciduous trees or downed trees of large diameter. Thus, many bryophyte species are associated with substrates that indicate long-term absence of human disturbance (Peterken 1996, Kuuluvainen 2002).

Studies at the landscape scale have shown that substratum diversity (Lõhmus et al. 2007, Pharo et al. 2004) is the main factors for bryophyte species richness. Substrate quality and quantity are particularly important for red-listed and indicator species (Fritz et al. 2008). Significant structures are large broad-leaved trees, large aspens, decorticate snags, downed trees and wind throws (Lõhmus et al. 2007). These old-growth forests remnants in a landscape can even provide suitable habitats that support high richness of bryophyte species when located in young forests (Lõhmus and Lõhmus 2008). In this way, species that are sensitive to various human activities can exist in new naturally afforested lands (Lõhmus and Lõhmus 2008).

As changes in species distribution patterns in a changing landscape require dispersal to new patches and extinction from old patches (Paltto et al. 2006), an important factor for bryophyte species at the landscape scale is the connectivity between available substrates (Snäll et al. 2003, Snäll et al. 2004, Snäll et al. 2005, Löbel et al. 2006a). S. Löbel et al. (2006a) showed that stand quality and connectivity are important for both asexually and sexually dispersal species. Therefore, the reduction of deciduous trees in the landscape and cutting of old-growth forests of old age and quality negatively affect populations of epiphytic bryophyte species (Löbel and Rydin 2009).

The abundance of rare species can also be explained by historical landscape structure (Löbel et al. 2006a), i.e. the present distribution was formed when connectivity was higher than that found today (Snäll et al. 2004). In contrast, H. Paltto et al. (2006) showed in a study on red-listed and indicator species in old temperate broad-leaved forests that species density in the landscape is more associated with the existing area of broad-leaved forests.

Ö. Fritz et al. (2008) found that forest continuity was associated with richness of red-listed bryophytes, which can be explained by the increase in colonization probability of species with time of continuous forest cover. Also, more structures are abundant and substrate quality is higher in stands having continuity (Fritz et al. 2008). P.A. Essen et al. (1997) mentioned two explained mechanisms why bryophyte species depend on canopy continuity of forests. One is associated with species that require habitats with specific structural elements present only in old-growth stands, for example very large trees and CWD. Second, it could be that species are depending on specific microclimate conditions in old-growth forests. At the same time N.J. Fenton and Y. Bergeron (2008) found that bryophyte species richness at the landscape could also be primary influenced by habitat availability rather than forest continuity. Thus, the age of a forest is not the most important factor for high moss and forest liverwort richness (Fenton and Bergeron 2008).

Additionally, it is important to have a stable microclimate and adequate shading (Suško 1998) because bryophyte species are very sensitive to changes in the environment (Hallingbäck and Hodgetts 2000). They are especially considered to be sensitive to forestry operations (Snäll et al. 2003, 2004). Thus, the fragmentation of forests is most detrimental to bryophytes living on dead wood because many of these species are depend on moist and shaded forest climate and suffer from an edge effect (Ódor et al. 2006).

1.2. The effects of management on bryophyte species richness

The effect of management on the bryophyte species richness and composition has been studied in forests of different types. Several authors have described that higher bryophyte species richness occurs in old natural forests in comparison with younger and/or managed ones (Andersson and Hytteborn 1991, Vellak and Paal 1999, Meier et al. 2005, Vellak and Ingerpuu 2005). The higher species richness in forests less disturbed by humans is related with a larger heterogeneity of microsites, which provide additional habitats for species with different ecological requirements. The presence of big trees and abundance of CWD creates more diverse substrates in old growth stands (Andersson and Hytteborn 1991, Gustafsson and Hallingbäck 1988). In contrast to natural forests, the lower species richness in managed forests is attributed to complete lack of suitable substrates, lower average amount or quality of substrates and gaps in the continuity of substrates (Siitonen 2001).

Managed forests are usually different from more natural ones since large dead trees are virtually missing (Ódor and Standovár 2001) and the input of CWD is reduced (Essen et al. 1997, Ekbom et al. 2006). Management has changed the character of forests by removal of dead wood (Kirby et al. 1998, Krankina et al. 2002, Rajandu et al. 2009) and logging of old living trees (Bobiec 2002, Nilsson 2009). J. Sittonen et al. (2000) showed that logging in northern Sweden strongly reduced CWD amounts, especially the number and volume of large downed trees, as well as the quality of dead wood, and the abundance of logs in advanced stages of decay. The volume of CWD in managed landscape in Sweden is low and the distributions of diameter and decay classes are uneven with low amounts of large dead trees and late decay stages (Kruys et al. 1999).

Especially large diameter dead wood provides more valuable substrate for bryophytes than small diameter dead wood (Humphrey et al. 2002). Thus, dead wood has high importance in maintaining high bryophyte richness and plus an extremely key role in the conservation of epixylic bryophyte populations (Ódor and Standovár 2001). It has been shown that rare species richness increases with larger proportions of CWD (Kruys and Jonsson 1999). On the other hand, forest management has not reduced all CWD. The volume of small diameter dead wood has not declined in managed forest landscape and may even increase because of harvesting operations (Siitonen 2001). It has been found that the small diameter CWD could support part of species richness of wood inhabiting cryptogams, including also bryophytes (Kruys and Jonssons 1999).

L. Söderström (1988a) found that drought sensitive epixylic liverworts confined to intermediates stages of log decay are most threatened by modern forest management. Their occurrence is restricted by large decaying downed trees in managed stands (Söderström 1988a). In addition, the liverworts confined to large, fallen downed trees demand a high and unchanged humidity which is not found in the managed stands (Gusstafsson and Hallingbäck 1988). Other studies have also found that dead wood is especially rich in liverworts (Crites and Dale 1998, Pharo et al. 2004, Meier and Paal 2009). Not only rare species but also total bryophyte species richness is positively related to diameter of downed trees and to decay class (Humphrey et al. 2002). While CWD is one of the most lacking substrates in managed stands and thus many rare species existence is threatened, it is important to note that forestry also eliminates substrate for epiphytic organisms (Essen et al. 1997).

Despite the differences described above, other studies have shown contrasting results. While modern forest management has led to loss of key features of old-growth forests in the landscape, in Estonia a managed landscape did not differ between reserves in total volume of CWD (Löhmus et al. 2005). A. Friedel et al. (2006) did not find a significant difference in richness of bryophytes between unmanaged and managed stands in beech forests in Germany. E. Rajandu et al. (2009) in a study of coniferous forests in southern Estonia did not observe a noticeable difference in bryophyte species richness between unmanaged and managed forests. Different management impact did not create differences in epiphytic bryophyte species richness in mixed deciduous-coniferous forest in Western Hungary (Király and Ódor 2010). It is also known that managed forests can support high occurrence of red-listed bryophyte species (Gustafsson et al. 2004a).

1.3. Woodland key habitats and richness of bryophyte species

One of the tools used to sustain biodiversity in managed forest landscape is the conservation of small habitat patches – the so called WKHs. The concept of WKH exists in the forests of Scandinavian and Baltic countries (Timonen 2010, Timonen et al. 2010). In

Latvia, the WKHs represent a system that is not based on the conservation concept of protection of individual territories for particular species of ecosystems (Priedītis 2002), but instead to protect small parcels of forest with large ecological value (Timonen et al. 2011). Thereby, they are supposed to be valuable for biodiversity of production forests (Timonen et al. 2011).

By definition, a WKH is an area that contains habitat specialists that cannot sustainably survive in a stand managed for timber (Ek et al. 2002). WKH can also be recognized based on sufficient amounts of structural elements and/or indicator species, which in theory can provide evidence of high probability of finding habitat specialists (Ek et al. 2002). Thus, WKHs are supposed to be sites where red-listed, rare or specialist species occur or are likely to occur (Timonen et al. 2011).

As mentioned above the methodology of WKHs separates two divisions of species: habitat specialists and indicators. A habitat specialist is a species that depends on specific habitat and that is threatened. An indicator species is not so specialized for a certain habitat but also has high demands on its living conditions. This means that indicator species are more common in WKHs but do not have as high value as habitat specialists (Ek et al. 2002). It needs to be noted that these definitions only applies to the WKH methodology, and that elsewhere these terms are used differently.

Table 1. The list of woodland key habitat (WKH) specialists and indicator species (Ek et al. 2002, Auniņš 2010).

Species	
Habitat specialists	**Indicator species**
Anastrophyllum hellerianum	*Anomodon* spp.
Antitrichia curtipendula	*Homalia trichomanoides*
Barbilophozia attenuata	*Isothecium alopecuroides*
Bazzania trilobata	*Jamesoniella autumnalis*
Buxbaumia viridis	*Jungermannia leiantha*
Calypogeia suecica	*Lejeunea cavifolia*
Frullania tamarisci	*Leucobryum glaucum*
Geocalyx graveolens	*Metzgeria furcata*
Hylocomnium umbratum	*Neckera complanata*
Lophozia spp.	*Neckera pennata*
Neckera crispa	*Nowellia curvifolia*
Plagiothecium latebricola	*Odontoschisma denudatum*
Scapania spp.	*Rhytidiadelphus subpinnatus*
Trichocolea tomentella	*Ulota crispa*
	Sphagnum wulfianum

The WKH specialist and indicator species represent the following organism groups: polypores, lichens, vascular plants, insects, mollusks and also bryophytes. A total of 28 bryophyte species are mentioned in the method used for inventory of WKH in Latvia, from which 14 bryophyte species are habitat specialists and 14 species are indicators (Ek et al. 2002). Over time some changes have been made in the list of habitat specialist and indicator species. In the work published by A. Auniņš (2010) 29 species are described as WKH indicators and specialists. The latest list combined species *Lophozia ascendens, Lophozia incisa, Scapania apiculata* and *Scapania nemorea* into the two genus *Lophozia* spp. and *Scapania* spp. (Auniņš 2010). All species from these two genera have the status of WKH specialists. In addition, bryophyte species *Barbilophozia attenuata* as habitat specialist and species *Nowellia curvifolia* and *Sphagnum wulfianum* as indicator species have been added (Table 1) (Auniņš 2010).

A number of studies have considered if WKHs are hotspot areas for bryophyte species richness. The WKHs are generally more important for threatened bryophytes than for vascular plants (Pykälä 2007). K. Perhans et al. (2007) showed that WKHs contain high bryophyte species richness and an even higher number of red-listed and indicator species than old managed forests, as previously observed (Gustafsson et al. 1999).

However, in a study about red-listed bryophyte species in two regions in south east Sweden, it was observed that WKHs were not always rich in red-listed bryophyte species (Gustafsson 2004b). This is likely because WKH networks support species with good dispersal abilities, but for poor dispersers the WKH system consists mainly of isolated patches (Aune et al. 2005).

In Latvia, there has been very little published information on epiphytic bryophyte richness in WKHs. A. Mežaka et al. (2012) described that high epiphytic species richness in deciduous WKHs of Latvia is mostly related with habitat quality. S. Ikauniece et al. (2012a) showed that directly WKHs of nemoral forests together with old aspen forests have high importance for conservation of rare epiphytic species.

The higher species diversity in WKHs (Timonen et al. 2011) can be explained by higher volumes and greater diversity of CWD than mature managed (stand age 81 – 120 years) and over mature managed (stand age 121 – 140 years) stands (Jönsson and Jonsson 2007). Past forest management has strongly reduced the volume and diversity of CWD within WKHs in comparison with the situation in old-growth forests (Jönsson and Jonsson 2007). Because of that most of WKHs cannot be defined as remnants of undisturbed forests (Ericsson et al.

2005). Nevertheless the mean age and timber volume have increased compared with that in the surrounding forest during the last 50 years (Ericsson et al. 2005).

Å. Berg et al. (2002) found that red-listed bryophyte species occurrence in WKHs is not only restricted by suitable substrate (high quality substrates), but also by historical land-use, as most rare bryophytes were restricted to WKHs with no management history.

1.4. The history of woodland key habitats

L. Hansson (2001) in the study on Swedish WKHs accented that many of these forest stands occur in areas where a long history of management has been observed, including timber harvesting. This has been confirmed in other studies. E. Hellberg et al. (2003) studied the history of three deciduous WKHs in boreal Sweden. All of them represented the products of previous land use patterns and logging. Thus, deciduous WKHs can not be defined as old growth forests. However, earlier management has not reduced the value of the sites for conservation of rare species and their substrates.

T.S. Ericsson et al. (2005) examined the past history of WKHs in Sweden, where the forests were classified as being untouched, or exposed to different types of forestry. They found that mostly WKHs had been managed in the past and approximately from around 1930 and afterwards most of them were left fairly unaffected by forestry activities.

A study by M.T. Jönsson et al. (2009) found similar results, as selected WKHs had been harvested in the second half on the 19th century and first half of the 20th century. After that, the territories that are now considered as WKHs were left to regenerate naturally. This suggests that even 100 years after management in forests can be enough to develop structures including dead wood and a range of tree ages and sizes. However, some of the old-growth structures could not be reached in less than 150 years.

The studies above confirm the observations of A. Tērauds (2011) about the history of deciduous WKHs in northern Latvia. In that study, the structural changes in forest landscape during the last 70 years were described (Tērauds 2011). Despite the fact that the work was based only on database material, he made some assertions about the present biodiversity in managed landscape. The historical archive material showed that forest stands which are designated as WKHs had been managed during the last century. Especially the area that is nowadays dominated by black alder had a large number of logged stands around the year 1930. He also noted that WKH can occur on previous agriculture land when these territories had been naturally afforested. He concluded that 70 years period with low intensity management could allow to achieve high biological diversity and to maintain structures at the level of those in WKH. Since deciduous species such as silver birch *Betula pendula*, downy birch *Betula pubescens*, grey alder *Alnus incana* and European aspen *Populus tremula* are capable of rapid colonization (Priedītis 2002), logging of spruce forests 90 years ago was followed by development of deciduous stands, many of which are now considered as WKHs (Tērauds 2011).

In a study of oak WKHs in Latvia it was shown that the stands considered to be among the natural stands of *Quercus robur,* had been affected by minimal or moderate human disturbances, and that some had a low level of naturalness. These forests were missing dead standing trees and the ages of living trees did not reach the maximum ages of the species. However, most did have high amounts of dead wood that were characteristic of old-growth forests and the richness of WKH indicator species was high (Ikauniece et al. 2012b).

2. Materials and methods

The study was divided in two parts. In the first part woodland in a managed forest setting was described by transect method. In the second part, plots were used to describe forest stands. In this dissertation, the data analysis and interpretation of the studies were made separately.

The studied territories were mostly located in the Ziemelvidzeme Biosphere Reserve. In addition, three forest stands were chosen outside of the Ziemelvidzeme Biosphere Reserve, one in the district of Aluksne, one in the district of Gulbene and one in the district of Ventspils (Figure 1).

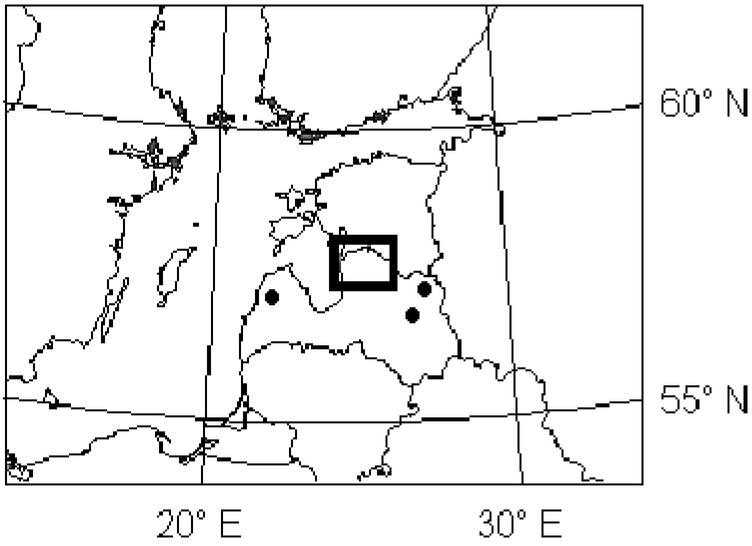


Figure 1. Location of Ziemelvidzeme Biosphere Reserve and studied plots in districts of Aluksne, Gulbene and Ventspils.

2.1. Study areas

The studied sites were located in the boreo-nemoral vegetation zone, where boreal coniferous forests are mixed with nemoral forests (Sjörs 1963). In the studied territories, the Ziemelvidzeme Biosphere Reserve and districts of Aluksne and of Gulbene are located in a region where the mean annual temperature is 5.0 – 5.2°C (Lizuma et al. 2007) and the annual average precipitation is about 703 mm (Briede and Lizuma 2007).

The Ziemelvidzeme Biosphere Reserve was founded in the year 1997 with the main aim to protect cultural landscape and recreation resources, and to decrease the anthropogenic load to protected areas. The Reserve is located within the administrative borders of the Salacgriva, Rujiena, Aloja, Mazsalaca, and Naukseni districts and part of the Reserve crosses the borders of the Limbazi, Strenci and Valka districts. The Reserve has a total area of 475514 ha (including territory of sea), of which about 221383 ha are covered by forest. Together, the Reserve has 25 Nature Reserves and one Nature Park (Ziemeļvidzemes biosfēras rezervāts 2010). In addition, the region includes more than 3400 WKHs, which have been voluntary protected within the Forest Stewardship Council (FSC) forests certification scheme.

Outside of the Ziemelvidzeme Biosphere Reserve, a plot was established in Gulbene district in the Nature Reserve Pededze Lower Reaches. The Nature Reserve was established in 1999 to protect the unique, biologically diverse forest complex and habitats of rare species. Since 2009 it has been included in Nature Reserve “Lubānas mitrājs”. The Pededze Lower Reaches is located in Dauksti and Stradi parishes of the Gulbene district, Rugaju parish of the Balvi district, and Indrani parish of the Madona district. The total area of the Reserve is 4663 ha in which the Pededze River with oxbows and floodplain meadows found on its banks are the most important nature values of the Reserve. The Reserve also includes forests that are dominated by broadleaf tree species (mostly oaks). These forests are protected habitats in Latvia and Europe. The age of oak stands reaches 150 – 200 years (Pededzes lejtece 2007).

Another plot was established in the district of Aluksne. The stand was located in the parish of Markalne near to Lake Aluksne. It is situated in the highland of Aluksne and hillock of Maliena about 100 m above the sea level (Balode 2012).

In addition, one plot, that represented a more natural oak stand, was chosen in district Ventspils on Moricsala Island. Moricsala Island is located in the Nature Reserve Moricsala which was established in the year 1912. The Reserve of Moricsala is located in the parish of Usma. The total area of Reserve is 818 ha, of which 83 ha are occupied by Moricsala Island. The aim of the Reserve is to conserve broad-leaved forests that have been minimally disturbed by humans and biodiversity in these forests. Especially important are stands dominating by oaks and small-leaved lime *Tilia cordata*. The oak stands in Moricsala Island are important for conservation in the Europe Union. In this region the mean annual temperature is 5.5 – 5.8°C and the annual average precipitation is 750 mm (Reihmanis 2009).

2.2. Studied transects

Four landscapes composed mainly of state-owned forests were chosen within the Ziemelvidzeme Biosphere Reserve (Figure 2). The total area was about 30000 ha. State forests were chosen for study as digital inventory data was available. Approximately 10.4 % of the chosen region had forest management restrictions (such as only selective cutting allowed or complete restriction of wood removal). Despite the fact that there are some patches of protected areas, the region can generally be defined as managed landscape.

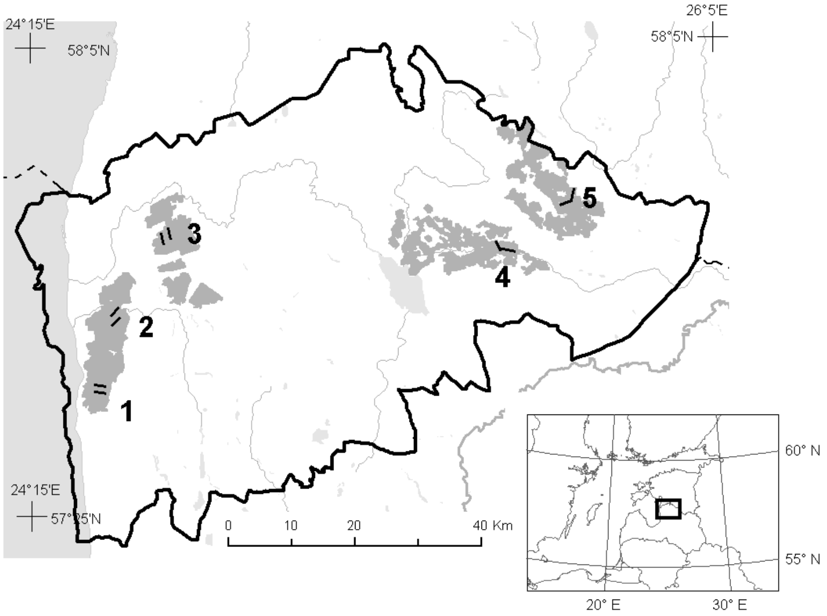


Figure 2. Studied transects in Ziemelvidzeme Biosphere Reserve modified after A. Tērauds et al. (2011).

In the chosen forest landscapes, about 37 % of the area was on dry soils, 27 % percent was on wet mineral soil, 14 % on peat, and the remaining 22 % was drained. The forest stands were dominated by coniferous tree species (Norway spruce *Picea abies* and Scots pine *Pinus sylvestris*). The most common deciduous tree species were *Betula pendula*, *Betula pubescens*, black alder *Alnus glutinosa*, *Alnus incana*, and *Populus tremula*. *Tilia cordata* and ash *Fraxinus excelsior* were less common, and *Quercus robur* was rare in the area (Tērauds et al. 2011).

In the four study areas, five transects with a total length of 20 km were drawn without prior site visitation on digital orthophoto maps (Figure 2). However, private and agricultural land was avoided. The first three transects were divided in two similar parts (Figure 2). Each transect was 4 km long and divided in eight sections (500 m long) and each section was divided in five subsections. Plots with size 50 x 2 m (100 m^2) were placed every 100 m along transects, giving a total of 200 plots. Coordinates of global positioning system (GPS) were used to locate the studied plots (Appendix 1).

2.3. Studied forest stands

In total, 17 forest stands were chosen to represent a wide range in stand age, but blindly without prior visitation to the stands. Within the Ziemelvidzeme Biosphere Reserve, 14 forest stands dominated by deciduous tree species were chosen from the WKH database (obtained from the State Forest service) (Figure 3) (Appendix 2). In the study, two oak stands (stand N in Pededze Lower Reaches and stand P in region of Aluksne) (Figure 3) (Appendix 2) were described to enlarge the examined data set, as oak was rare in the Ziemelvidzeme Biosphere Reserve.

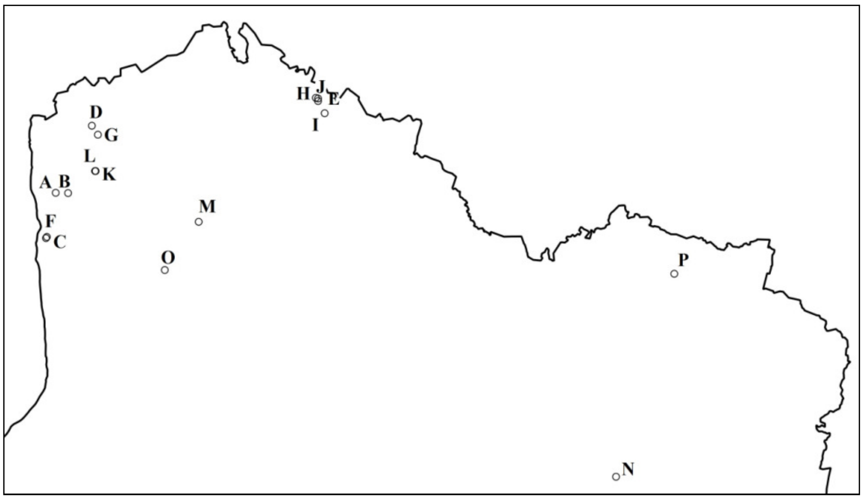


Figure 3. Location of studied stands in Latvia.

In additional, a control (most natural forest stand) plot in oak forest stand of Moricsala was used (Figure 4) to describe richness of structural elements. The main criteria in choosing the sampled stands was the deciduous tree species composition (Table 2), as they are important structures for bryophyte species (Snäll et al. 2003).

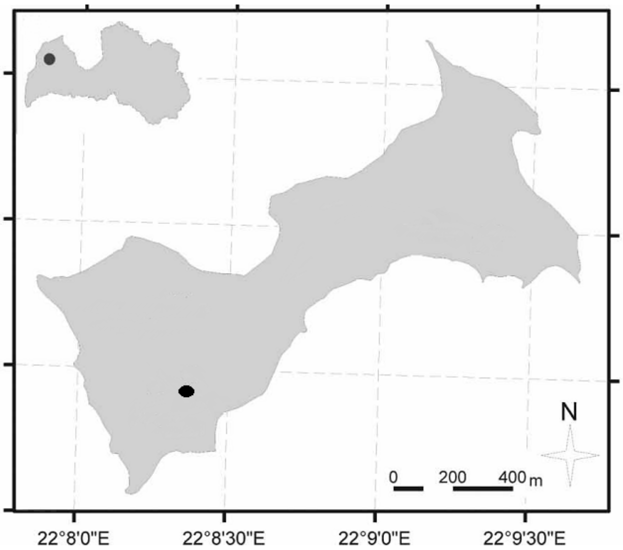


Figure 4. Location of studied stand in Moricsala.

Table 2. Information about the 17 studied plots. Bet – *Betula* spp., Alngl – *Alnus glutinosa*, Fraex – *Fraxinus excelsior*, Picab – *Picea abies*, Poptr – *Populus tremula*, Quero – *Quercus robur*, Tilco – *Tilia cordata.* The composition of the tree layer is given as proportion of wood volume (scale of 10). Information on age of tree layers is also given, obtained from State Forest service (2012).

Studied plot	**Coordinates**		**District**	**Area (ha)**	**Composition and age of tree layer**
Symbol	**X**	**Y**			
A	526960	6394947	Salacgrīva	4.6	7Bet 3Alngl 63
B	530225	6394872	Salacgrīva	1.7	9Alngl 1Bet 103
C	524467	6383290	Salacgrīva	0.8	6Alngl 3Bet 1Fraex 46
D	536419	6412180	Salacgrīva	2.3	4Fraex 3Alngl 1Picab 1Poptr 1Bet 118
E	595231	6418544	Rūjiena	1.7	5Alngl78 3Bet78 1Fraex98 1Picab 98
F	524690	6383613	Salacgrīva	2	7Alngl 118 1Bet 118 1Alngl 58 1Fraex 118
G	537988	6409892	Aloja	1.5	6Poptr 2Betpu 1Picab 1Alngl 115
H	595231	6419204	Rūjiena	6.2	6Bet 3Poptr 1Picab 88
I	596943	6415386	Rūjiena	1.7	5Picab118 2Alnglu 68 Fraex68 1Bet118 1Alngl118
J	594632	6419327	Rūjiena	4.2	4Bet 3EPicab3Alngl 88
K	537336	6400544	Limbaži	3.9	4Poptr 4Alngl 1Picab 1Bet 128
L	537210	6400520	Limbaži	2.4	5Poptr128 3Alnglu88 2Bet128
M	564186	6387428	Valmiera	8.9	8Quero180 2Picab130
N	672774	6321873	Gulbene	5	6Quero141 2Quero201 1Bet141 1Picab141
O	555349	6375075	Limbaži	5.6	7Quero180 2Picab120 1Picab180
P	687933	6374087	Alūksne	3.3	5Quero101 3Picab101 1Bet86 1Poptr86
Moricsala	387445	6340197	Ventspils	1.6	8Tilco 2Quero158

Size of the stands varied from 0.8 to 8.9 ha. Eight of the stands were on wet mineral soils (stands A, C, F, G, H, I, K, L), two on drained peat soils (stands E, I), one on drained mineral soil (stand D) and one on peat soil (stand B). The stands represented *Myrtillosoi-polytrichosa* (stands A, C, F, G, L), *Drypteriosa* (stands H, J, K), *Oxalidosa turf. mel.* (stands E, I), *Mercurialosa mel.* (stand D) and *Dryopterioso-caricosa* (stand B) site types. The studied oak forests represented *Oxalidosa* (stand M, O and Moricsala stand), *Aegipodiosa* (stand N) and *Hylocomiosa* (stand P) forest site types on mineral soils. The dominsant tree species were *Alnus glutinosa*, *Betula* spp., *Populus tremula* and *Quercus robur* (Table 2). In each forest stand one plot (20 x 50 m) was established at randomly chosen coordinates (Table 2) (Appendix 2).

The stand in Moricsala was dominated by tree species *Tilia cordata* and *Quercus robur* (oak canopy with lime subcanopy) (Appendix 2) (Table 2) with mean stand age 158 years (State Forest service 2012). The plot size was 180 x 20 m in this mixed oak-lime forest.

2.4. Collected data

The collection of data along the five transects was carried out from August to October 2009. In each sampling plot, diameter at breast height (DBH) was recorded for each living tree species by height classes: canopy, subcanopy and sapling layer. Diameter for all dead wood originating in plots (also when broken into logs) was measured at breast-height length from tree base. Dead branches from trees were not recorded. Each dead tree was measured only once and stumps were counted by tree species. The stand age was considered to be the age of the oldest tree layer for the stand in which the plot occurred. This, along with the designation of the protection status, was taken from inventory data from the Latvian State Forest Register. In each plot along the five studied transects all bryophyte species found on three randomly chosen living trees in the canopy, three stumps and three downed trees (if present) were recorded.

The data for the 16 stands (second part of the study) was collected in June, September and October 2010, and August 2011. In each sampling plot, DBH was determined for all living trees ≥ 10 cm DBH. All CWD originating inside the plots and with diameter ≥ 10 cm (breast height from the base) was measured and tree species was recorded. The CWD was divided into dead standing trees and downed trees. DBH and tree height of standing dead trees were measured. For downed trees diameter in the middle of logs and length was recorded. Dead branches were not recorded. Diameter of all stumps was measured. A count made of number of sawed stumps (those with a flat surface and/or older stumps lacking a log that might have originated from stump). Decay stage was estimated on a five-point scale (Pyle and Brown 1998) for each downed tree and stump.

The determined decay stages were: (1) wood cannot be penetrated with thumbnail, wood is sound, bark is intact, smaller to medium branches are present; (2) thumbnail penetrates in the bark till three centimeters, bark may or may not be attached, wood is sound, bark is decay; (3) thumbnail penetrates till seven centimeters, bark may or may not be attached, wood is somewhat rotten, the biggest trunks and only larger stubs are present; (4) thumbnail penetrates readily, bark is lightly attached, sloughing off or detached, wood texture is soft, decayed log may assume oval shape; (5) all wood texture is squashy and powdered, bark is detached or absent, can be decayed in pieces, wood is indistinguishable from ground. If different parts of log were in several decay stages, the predominant stage was chosen. Thus, each downed tree was assigned one decay stage.

Bryophyte species on all living and standing dead trees (DBH ≥ 10 cm) and on all fallen CWD (DBH ≥ 10 cm) and all stumps were recorded in the studied 16 stands. On tree stems, bryophytes were recorded from tree base up to a height of 2 m.

In addition, in the studied 16 stands, cores were removed from all living trees with DBH ≥ 10 cm to estimate the tree ages. Core samples were glued in boards with grooves. The cores were sanded and later growth rings were counted under a microscope. In cases when some of the rings were missing, estimation of the number of missed ages was made. Mean tree age was calculated as the mean value of all cored trees within the studied plots.

In the studied plot of Moricsala only structural elements were described without determination of bryophyte species. The aim was to compare data with other studied *Quercus robur* forests. The fieldwork was conducted in summer of 2007. Description of living and dead trees was conducted as for other plots.

In the study, the two birch species *Betula pendula* and *Betula pubescens* were considered together since their epiphytic communities are similar (Barkman 1958) and because they are considered together in the forest inventory. Unknown species were collected and later examined in the laboratory. The species were determined using Smith (1990, 2004), Jukoniene (2003), Игнатов & Игнатова (2003, 2004). Nomenclature followed by Hill et al. (2006) for mosses and Grolle and Long (2000) for liverworts.

2.5. Historical information

Archive inventory data as maps and journals stored at the Latvian State Forest Research Institute "Silava" were used to reconstruct the forest history of the 12 WKHs for the period after 1928 (stands A – L). The inventory years and recorded information differed between the stands. The studied plots could easily be designated to a stand in the records (Tērauds 2011). Depending on the dominant tree species and mean stand age in different years, sometimes present stands had been spatially delineated differently during the last century. In five of the studied plots (stands C, H, I, J and L), the present area of the WKH was earlier split into two stands differing in tree composition and stand age. Records on stand composition and stand age from archived journals and notes on planned forest activity were used to reconstruct type and time of logging events. In cases when (between subsequent inventories) the recorded tree age had changed from approximately cutting age to a young stand, it was assumed that the stand had been logged. In some cases this might have been removal of wood after a major natural disturbance. Based on past logging events in the studied territories, the WKHs were divided into two groups: managed (clear-cut and selective wood removal in the past 90 years) and less-managed stands. The inventory data for four oak stands (stands M – P) was obtained from the year 1952. The stand in Moricsala represented one of the most natural broad-leaved forests in Latvia and has been protected since 1912.

2.6. Data analysis

In the studied stands total volume of downed trees was estimated as volume of log pieces calculated as cylinders and volume of dead standing trees using equations for living trees (State Forest service 2000). The total volume of CWD was the sum of volume of downed and dead standing trees.

To determine significant differences between managed and less-managed WKHs (stands A – L) in stand structural characteristics and bryophyte richness variables that did not deviate from normality ($P>0.05$, Shapiro-Wilk normality test), a two-sample t-test was used. The Mann-Whitney U test was used to test the significance of differences of variables that differed from normality.

For the studied transects the effects of substrate variables on bryophyte richness in each plot were determined using a generalized linear model (GLM) with a Poison error distribution and log link function. For living trees the quantitative substrate variables were the total number of stems, number of stems in diameter classes (≤10.0 cm, 10.1–20.0 cm, 20.1-30.0 cm, 30.1–40.0 cm, >40.0 cm), mean DBH, maximum DBH and basal area (m^2) for each tree species in plots, and grouped by coniferous species (*Pinus sylvestris*, *Picea abies*), broad-leaved tree species (*Fraxinus excelsior*, *Quercus robur, Tilia coradata,* Wych elm *Ulmus glabra,* Norway maple *Acer platanoides)* and other deciduous tree species (*Alnus glutinosa, Betula* spp*., Populus tremula*). These variables were also calculated for downed trees, dead standing trees and total dead wood (downed trees plus dead standing trees). Additional variables for living trees were basal area (m^2) of each tree species in the canopy and subcanopy. The total number, total basal area (m^2) as well as basal area for each tree species in the sapling layer were also used as variables. In addition the number of stumps, stand age (quantitative variables) and designation as a WKH (binomial variable) were included as environmental variables. Together, 317 variables were used to find the best GLM models.

Models that predict bryophyte and indicator species richness were built using an iterative process. At first, GLM models were tested for each variable. Then, the statistically significant ($P<0.05$) model with the lowest Akaike's information criterion (AIC) was chosen from all possible models with two independent variables (using only variables with P-values <0.1). This best model was further used to build a multi-factor model, with increasing number of independent variables, but only when the new model was significant and a decrease of AIC was found. The proportion of variance explained by the variables in the GLM models was calculated by Anova. Models were derived separately for total bryophyte species richness and WKH indicator species (Auniņš 2010) on living trees and on CWD (downed trees plus stumps). The sets of substrate explanatory variables for living trees and dead wood were examined separately, as their species pools differ, especially for non-generalist species (Ek et al. 2002).

A Generalized linear mixed model (GLMM) (with a Poison error distribution and log link function) was used to examine the effects of substrate variables on bryophyte richness on living trees and on dead wood (downed trees plus stumps) in the studied 12 deciduous forest WKHs (stands A – L). The study plot was used as random effect in all models. Models were derived for total bryophyte species richness and WKH indicator species (Auniņš 2010). Here specialist species under the term indicator species were included. In addition, the bryophyte species *Riccardia palmata* was considered as indicator species, as it is a species included in the list of specially protected species (Regulations of Minister Cabinet Nr. 396). For living trees the substrate variables used were tree species, tree diameter, tree height and tree age. Tested tree-level variables in GLM models of derived bryophyte richness on downed trees plus stumps were diameter, CWD type (downed tree or stump), CWD tree species, and decay stage. Stand variables was also included in the GLM analysis for species richness in deciduous WKHs. The examined variables for living trees were: WKH area (ha), mean tree age and past history of management (WKH managed or less-managed). Stand-level variables for bryophyte richness on downed trees plus stumps were mean tree age, volume of downed trees (m^3/ha), total volume of CWD (m^3/ha), density of downed trees divided in three diameter classes (10-19, 20-29, >30 cm), past history of management (managed or less-managed) and WKH area (ha). All stand variables were treated as repeated observations for living trees, downed wood and stumps within plots.

First, the effect of each variable was tested one by one and those with p-values less than 0.1 were selected for further modelling. Initial multi-factor models were built using these variables. The models were simplified using stepwise variable selection by optimizing AIC. Models were derived for total bryophyte species richness and WKH indicator species (Auniņš 2010) richness on living trees and on downed trees plus stumps. The R programme 2.15.2 version "stats" package was used in the statistical tests (Zuur et al. 2007).

The structure and bryophyte richness in the oak forests were analyzed separately from other WKHs due to different amounts of dead wood and composition of bryophytes

(Ikauniece et al. 2012b). The GLMM models were not applied to explain the main factors for bryophyte species richness in oak forests due to the low number of studied plots (existing data).

3. Results

3.1. Structural elements in managed forest landscape

Of the studied 200 plots along the transects, 38 were in WKHs in which the dominant tree species were *Pinus sylvestris* (in coniferous WKHs) and *Alnus glutinosa* (in deciduous WKHs). Five of the studied plots had developed on clearcuts. The plots greatly varied in tree species composition and age. All plots were divided in three age groups: 65 plots were in stands with maximum tree-layer age less than 50 years and 79 studied plots had age between 51 – 100 years. The remaining plots (56 plots) were located in stands older than 100 years. The oldest deciduous WKHs had age 139 years and the dominant tree species were *Fraxinus excelsior*, *Populus tremula*. The coniferous WKHs reached age of 159 years with dominant tree species *Pinus sylvestris*.

Table 3. Summary statistics of living trees and coarse woody debris (CWD) (downed trees plus dead standing trees) recorded in the 200 plots.

	Living trees			**CWD**		
Tree composition	**Number of plots**	**Mean diameter (cm)**	**Maximum diameter (cm)**	**Number of plots**	**Mean diameter (cm)**	**Maximum diameter (cm)**
Pinus sylvestris	52	30	53	26	13	30
Picea abies	139	17	53	120	10	44
Betula spp.	114	18	53	77	11	46
Alnus incana	15	11	23	13	8	18
Populus tremula	18	32	78	11	20	33
Alnus glutinosa	59	20	46	24	13	30
Salix caprea	7	9	17	5	7	13
Fraxinus excelsior	23	16	39	26	9	26
Tilia cordata	22	14	40	9	12	36
Ulmus glabra	7	18	31	2	7	9
Acer platanoides	4	12	22	-	-	-
Sorbus aucuparia	1	11	11	-	-	-
Quercus robur	-	-	-	1	26	26
Broad-leaved trees	45	15	40	36	10	36
Coniferous trees	153	20	53	128	10	44
Other deciduous species	137	19	78	97	11	46

The most common tree species in the plots were *Picea abies*, *Betula* spp., and *Alnus glutinosa* (Table 3). More than 1/5 of the studied plots contained broad-leaved (nemoral) trees. The most common tree DBH for living trees was 10.0 – 20.0 cm (Figure 5). None of the plots contained broad-leaved trees with DBH > 40.0 cm (Figure 5). *Populus tremula* had the largest mean (32 cm) and maximum (78 cm) DBH (Table 3), but this species was found only in 18 plots.

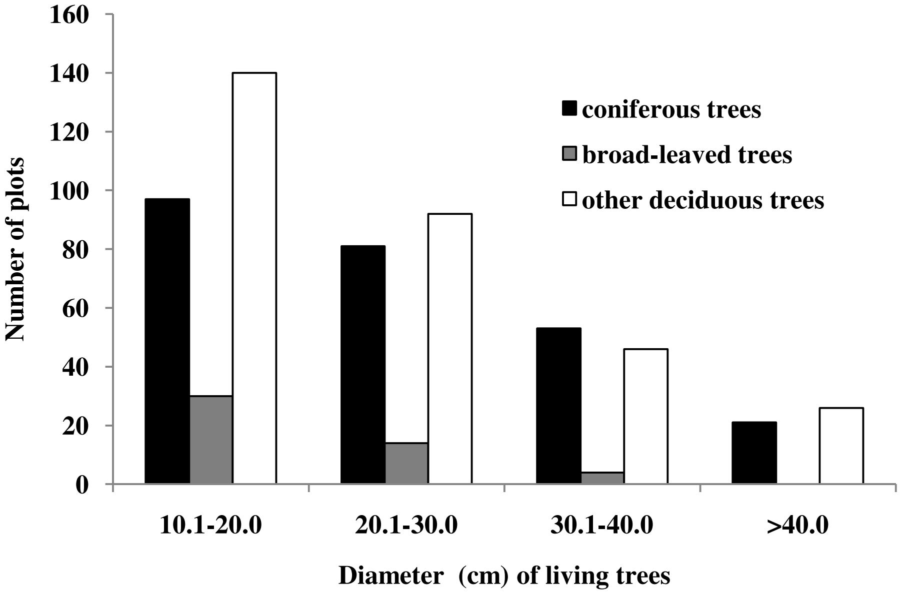


Figure 5. Number of plots containing living trees in different diameter classes. Diameter was measured at breast-height.

The majority of plots (162 of 200) also contained CWD. Downed trees were recorded in 124 plots and dead standing trees in 132 plots. More than half of the studied plots (122 of 200) contained stumps, which were mostly *Picea abies*. Most of the CWD was also *Picea abies* (Table 3).

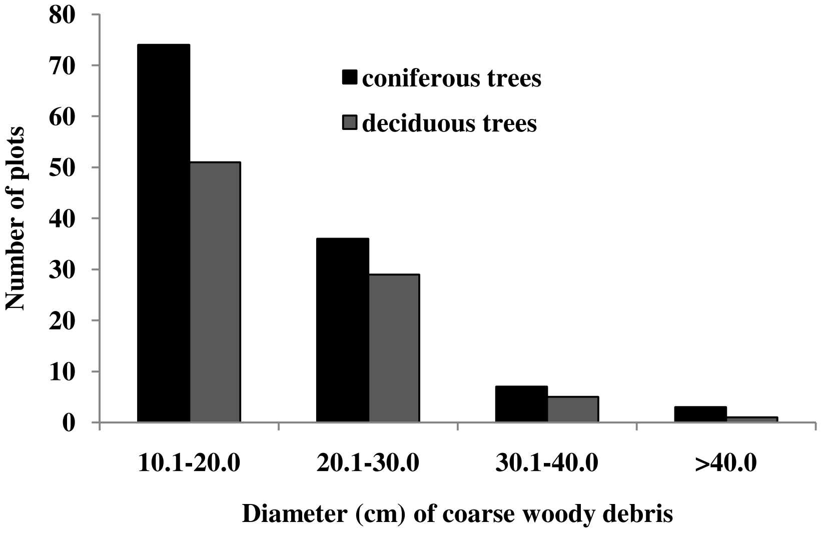


Figure 6. Number of plots containing coarse woody debris (downed trees plus dead standing trees) in different diameter classes.

The maximum diameter for CWD was 46 cm for deciduous trees (downed tree of *Betula* spp.), and 44 cm for coniferous trees (downed tree of *Picea abies*) (Table 3). Dead standing trees had maximum diameters of 39 cm for coniferous trees (*Picea abies*) and 33 cm for deciduous trees (*Populus tremula*) (Table 3). Only 16 plots contained CWD that had DBH > 30 cm (seven plots had coniferous trees with DBH 30.1-40.0 cm, five had deciduous trees with DBH 30.1-40.0 cm; three plots had coniferous trees and one plot had deciduous trees with DBH > 40.0 cm) (Figure 6). The tree species *Quercus robur* was recorded only once and it was a downed tree with DBH 26 cm (Table 3).

3.2. Richness of bryophyte species in managed forest landscape

In total, 56 bryophyte species (45 mosses and 11 liverworts) were recorded in the studied sites (Table 4). Of the total number, 46 species (37 mosses and 9 liverworts) were found on living trees and 41 species (33 mosses and 8 liverworts) on downed trees and stumps. Of the bryophyte species, 18 were found only on living trees and 10 species only on decayed wood. Eight bryophyte species were found once in the 200 plots. The maximum total number of species found in the studied plots was 16 species. On each substrate separately the maximum numbers of bryophytes in plots were: 14 species on living trees, 13 species on downed trees and nine on stumps. The most common species on living trees were *Dicranum montanum* and *Plagiothecium laetum* (Table 4). The moss *Pleurozium schreberi* was the most common species on downed trees and stumps. Downed trees were important substrates for the liverwort *Lepidozia reptans* (Table 4).

Table 4. Number of plots (n=200) in which moss and liverwort species were recorded on different substrates. Woodland key habitat (WKH) indicator species are indicated in bold.

Species	**Number of plots**			
	Substrate			**Total number of plots**
	Living trees	**Downed trees**	**Stumps**	
Liverworts				
Anastrophyllum hellerianum		**1**		**1**
Blepharostoma trichophyllum	5	2		7
Frullania dilatata	10			10
Lejeunea cavifolia	**1**			**1**
Lepidozia reptans	36	27	10	44
Lophocolea heterophylla	50		6	72
Metzgeria furcata	**1**			**1**
Nowellia curvifolia		**12**	**1**	**13**

Table 4 (Continued). Number of plots (n=200) in which moss and liverwort species were recorded on different substrates. Woodland key habitat (WKH) indicator species are indicated in bold.

Species	**Number of plots**			
	Substrate			**Total number of plots**
	Living trees	**Downed trees**	**Stumps**	
Liverworts				
Plagiochila asplenioides	14	4	1	16
Ptilidium pulcherrimum	64		9	81
Radula complanata	35	4		36
Mosses				
Amblystegium serpens	4			4
Brachythecium campestre		1	1	2
Sciuro-hypnum oedipodium	1			1
Brachythecium rutabulum	40	17	7	57
Brachythecium salebrosum	13	2		15
Calliergon cordifolium		4		4
Calliergonella cuspidata	4			4
Chiloscyphus pallescens		3		3
Climacium dendroides	6	2	1	7
Dicranum montanum	118	15	23	136
Dicranum polysetum	29	11	12	43
Dicranum scoparium	71	23	25	96
Eurhynchium angustirete	51	13	10	60
Oxyrrhynchium hians	5		1	6
Herzogiella seligeri	4	10	3	16
Homalothecium sericeum	5			5
Hylocomium splendens	34	22	21	61
Hypnum cupressiforme	51	8	7	61
Fissidens taxifolius	3			3
Homalia trichomanoides	**17**	**4**		**19**
Mnium hornum	5			5
Neckera complanata	**1**			**1**
Neckera pennata	**19**	**1**		**20**
Orthotrichum affine	10			10
Orthotrichum rupestre		1		1
Plagiomnium affine	8	6	3	16
Plagiothecium curvifolium			1	1
Plagiomnium cuspidatum	26	14	4	39
Plagiothecium laetum	101	4	4	103
Plagiomnium medium	1			1
Plagiomnium undulatum	3	3		4
Platygyrium repens	3	2		5
Pleurozium schreberi	59	28	31	87

Table 4 (Continued). Number of plots (n=200) in which moss and liverwort species were recorded on different substrates. Woodland key habitat (WKH) indicator species are indicated in bold.

Species	**Number of species**			
	Substrate			**Total number of plots**
	Living trees	**Downed trees**	**Stumps**	
Mosses				
Polytrichum commune		2	5	7
Polytrichum juniperinum			2	2
Ptilium crista-castrensis	3	2	1	5
Pylaisia polyantha	6			6
Rhytidiadelphus triquetrus	14	14	8	31
Rhizomnium punctatum	6			7
Rhodobryum roseum	3	7	2	11
Sanionia uncinata	8	5	3	15
Tetraphis pellucida	23	5	20	45
Thuidium delicatulum		3		3
Thuidium tamariscinum	24		3	15
Ulota crispa	**9**			**9**

In total, eight WKH indicator species were found in the plots, of which four were mosses and four were liverworts (Table 4). The maximum number of indicator species found in a plot was four and in this case all were recorded on living trees. Most of the indicator species were found on living trees (four mosses and two liverworts), with the most common being *Neckera pennata* and *Homalia trichomanoides* (Table 4). Two bryophytes considered to be epixylic species by A. Āboliņa (2008), *Anastrophyllum hellerianum* and *Nowellia curvifolia*, were recorded on downed trees, of which the liverwort *Anastrophyllum hellerianum* was found only once. The second epixylic species *Nowellia curvifolia* was recorded once on a stump, but it was more abundant on downed trees. Only 30 of 200 plots contained at least one indicator species.

3.3. GLM models for bryophyte species richness in managed forest landscape

A total of 40.56 % of the variation in total bryophyte species richness on living trees was explained by explanatory variables in the best GLM model obtained (Table 5). The maximum DBH for deciduous species was the best explanatory variable, with maximum DBH of *Betula* spp., *Populus tremula* and *Alnus glutinosa* together explaining 35.25 % of the total variance. Maximum DBH of *Betula* spp. explained almost half of the variation in total bryophyte richness (Table 6). Stand age was also a significant variable, but explained a relatively small amount of variation.

Table 5. Summary statistics for building of Generalized Linear models (GLMs). Models were produced for total and indicator bryophyte richness on living trees and on coarse woody debris (CWD) (downed trees plus stumps). For each GLM model, the amount of variance explained, significance level and Akaike's information criterion (AIC) are shown. The best models are given in bold. Two models are shown for indicator species richness on living trees. MaxD – maximum diameter at breast height (DBH).

	Model	**Explained variance %**	**Pr(>|z|)**	**AIC**
	Living trees			
Total species richness	MaxD of *Betula* spp.	18.23	***	1030.2
	MaxD *Betula* spp.+MaxD *Populus tremula*	26.2	***	993.1
	MaxD *Betula* spp.+MaxD *Populus tremula*+MaxD *Alnus glutinosa*	35.25	***	950.67
	MaxD *Betula* spp.+MaxD *Populus tremula*+MaxD *Alnus glutinosa*+MaxD *Fraxinus excelsior*	38.57	***	936.33
	MaxD *Betula* spp.+MaxD *Populus tremula*+MaxD *Alnus glutinosa*+MaxD *Fraxinus excelsior*+Stand age	**40.56**	*******	**928.55**
Indicator species richness	**Model A**			
	MaxD of *Ulmus glabra*	21.75	***	231.61
	MaxD *Ulmus glabra*+MaxD *Populus tremula*	35.97	***	204.2
	MaxD *Ulmus glabra*+MaxD *Populus tremula*+MaxD *Fraxinus excelsior*	43.66	***	190.28
	MaxD *Ulmus glabra*+MaxD *Populus tremula*+MaxD *Fraxinus excelsior*+MaxD CWD	48.34	***	182.59
	MaxD *Ulmus glabra*+MaxD *Populus tremula*+MaxD *Fraxinus excelsior*+MaxD CWD+MaxD *Tilia cordata*	51.26	***	178.57
	MaxD *Ulmus glabra*+MaxD *Populus tremula*+MaxD *Fraxinus excelsior*+MaxD CWD+MaxD *Tilia cordata*+MaxD *Acer platanoides*	**53.95**	*******	**175**
	Model B			
	MaxD of broad-leaved trees	35.93	***	202.27
	MaxD of broad-leaved trees+MaxD *Populus tremula*	50.53	***	174.08
	MaxD of broad-leaved trees+MaxD *Populus tremula*+MaxD CWD	**52.72**	*******	**171.53**
	Dead wood (downed trees+stumps)			
Total bryophyte richness	Basal area of downed trees (m^2)	13.43	***	992.36
	Basal area of downed trees (m^2)+number of stumps	**16.1**	*******	**975.76**
Indicator species richness	**MaxD of CWD**	**11**	******	

‘***’ $p \leq 0.001$, ‘**’ $p \leq 0.01$, ‘*’ $p \leq 0.05$

Table 6. Summary statistics for explanatory variables in Generalized Linear models (GLMs) with lowest Akaike's information criterion (AIC). Standardized coefficients, variance explained and significance levels of explanatory variables are shown. Proportion of variance explained by variables in the GLM models was calculated in an Anova test. MaxD – maximum diameter at breast height (DBH).

	Variable	Coefficient	Variance %	Pr(>|z|)
	Living trees			
Total bryophyte richness	**MaxD *Betula* spp.+MaxD *Populus tremula*+MaxD *Alnus glutinosa*+MaxD *Fraxinus excelsior*+Stand age**			
	MaxD of *Betula* spp.	0.0171	18.2	***
	MaxD of *Populus tremula*	0.0147	9	***
	MaxD of *Alnus glutinosa*	0.0127	7.9	***
	MaxD of *Fraxinus excelsior*	0.0173	3.3	***
	Stand age	0.0025	1.9	**
Indicator species richness	**Model A**			
	MaxD *Ulmus glabra*+MaxD *Populus tremula*+MaxD *Fraxinus excelsior*+MaxD CWD+MaxD *Tilia cordata*+MaxD *Acer platanoides*			
	MaxD of *Ulmus glabra*	0.0937	21.7	***
	MaxD of *Populus tremula*	0.0300	14.2	***
	MaxD of *Fraxinus excelsior*	0.0481	7.2	***
	MaxD of CWD	0.0455	4.7	**
	MaxD of *Tilia cordata*	0.0299	3.9	*
	MaxD of *Acer platanoides*	0.0743	3.3	**
	Model B **MaxD of broad-leaved trees+MaxD *Populus tremula*+MaxD CWD**			
	MaxD of broad-leaved trees	0.1022	35.9	***
	MaxD of *Populus tremula*	0.0346	14.6	***
	MaxD of CWD	0.0321	2.1	*
	Dead wood (downed trees+stumps)			
Total bryophyte richness	**Basal area of downed trees (m^2)+number of stumps**			
	Basal area of downed trees (m^2)	8.1631	13.4	***
	Number of stumps	0.0392	2.6	***
Indicator species richness	**MaxD of CWD**			
	MaxD of CWD	0.0646	11	**

'***' $p \leq 0.001$, '**' $p \leq 0.01$, '*' $p \leq 0.05$

A greater amount of variation (almost 54%) was explained in the GLM model for indicator species richness on living trees (Model "A") (Table 5). The significant important variables were maximum DBH of nemoral tree species (*Ulmus glabra, Fraxinus excelsior, Tilia cordata* and *Acer platanoides*), as well as maximum DBH of *Populus tremula*, and maximum DBH of CWD (dead standing trees plus downed trees). The most important explanatory variables were maximum DBH of the tree species *Ulmus glabra* and *Populus tremula*, which together explained 35.9 % of the variation in the GLM model (Table 6). A similar amount of variation (53%) was explained in Model "B" (Table 5, 6). This model used the maximum DBH of all of the four broad-leaved tree species in Model "A" as one explanatory variable. All broad-leaved trees together explained 35.9 % of the total variance (Table 5). The explained variance of CWD decreased in Model "B" compared with Model "A" (Table 6).

Less variation of total species richness (16.1%) and indicator species richness (11%) on dead wood was explained by the variables used (Table 5). The only significant variables in explaining total bryophyte species richness were basal area of downed trees and number of stumps in plots. Basal area of downed trees explained the greatest part of total variance (13.4 %). Only the variable maximum DBH of CWD had significant effect on indicator species richness. Designation as WKH was not significantly related to species richness in any of the models

The maximum DBH of deciduous trees was the most important variable explaining richness of indicator species. The probability of recording one indicator species on living tree was higher if the studied plot contained at least one broad-leaved tree with DBH > 30 cm (Figure 7).

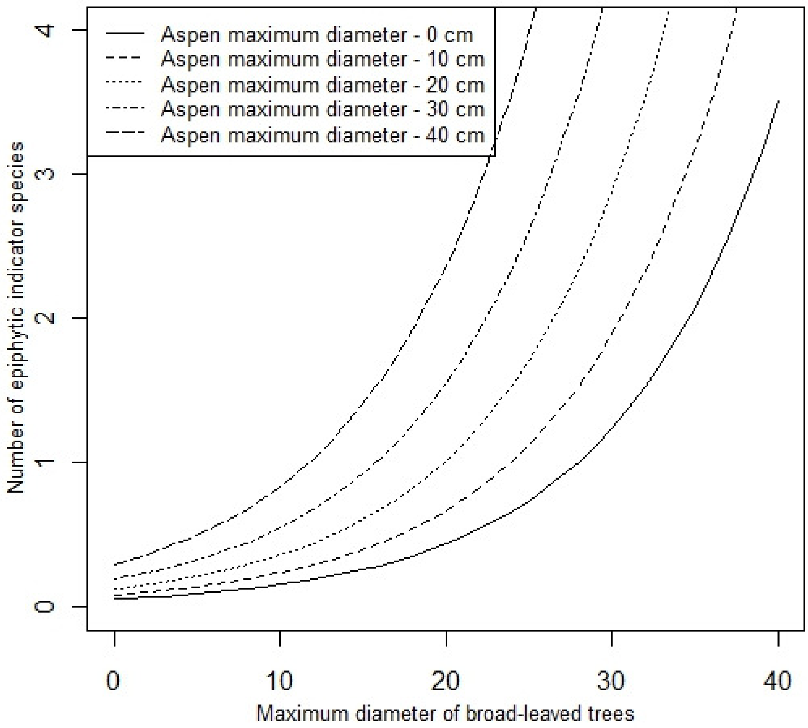


Figure 7. Predicted number of woodland key habitat (WKH) indicator species depending on the maximum diameter (cm) of broad-leaved trees and the maximum diameter (cm) of *Populus tremula*. These variables explained 50.3% of the total variance for indicator species richness on living trees.

3.4. History of woodland key habitats

Forest inventory data indicated that tree species composition in stands A, B, and C had switched from spruce with age 70 – 95 years to deciduous trees with age 44 – 88 in 2011 (Appendix 3). Considering the drastic 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 removed.

Stand A was a clearcut in 1950. This forest stand was dominated by tree species *Alnus glutinosa* and *Betula* spp. and the most common ages of trees were 51 – 60 years in 2011.

A selective cut was probably conducted in stand B, due to the absence of spruce and birch today that were older than 100 years (Figure 8). The presence of many deciduous trees (tree species *Alnus glutinosa*) with age over 100 years suggests that saplings of perhaps subcanopy trees were retained during logging in stand B.

Stand C (earlier spruce stand) was in part likely cut soon after 1929. This stand was cut by clearcut again during the time period from 1972 – 1982, as there was a change from mature black alder to young ash, which in 2011 had age 31 – 40 years (Appendix 3) (Figure

8). Abundant stumps were also present in this stand. The result of the logging was that today the plot had only four deciduous trees older than 70 years.

In 1941, spruce with age 100 dominated in stand D. The inventory data showed that in 1941 a clearcut was planned in the next 10 years. Today the stand is dominated by birch and spruce with age 80 – 130. This suggested that selective removal of spruce did occur in the stand D, but the present age of trees in the stand indicates that it was not clearcut. Also, stumps were recorded.

Stand E was a clearcut in 1932 (Appendix 3). Today, it is dominated by birch and black alder, with age of most trees approximately matching the time since logging. The plot had three spruce trees older than 100 years in 2011, but mostly they had age from 60 – 70 years (Figure 8).

In stands F to L, the inventory records showed a progressive increase in age of the stands, suggesting no harvest of at least a major part of the oldest trees (Appendix 3). In the 1920s to 1930s, these stands had age 15 – 65 years. Likely, they had regenerated on previous clearcuts or on past agricultural land.

Stand F was considered to have missed logging, as black alder was consistently noted in the records with old age more than 100 years.

Three stands (G, H, K and L) had the tree species *Populus tremula* in 1928, 1935 and 1934 and in 2011, indicating continuous development without logging of this species. In stand K, cut spruce stumps were observed (Appendix 3) but considering the progressive stand ages given in inventory, from 65 years in 1935 to 90 years in 1960 and 128 years in 2011, major wood removal seems unlikely. Nevertheless, the stumps indicate that probably some of the older spruces were removed, perhaps after suffering mortality. In addition stand L is the oldest studied forest with aspens older than 160 years.

Despite the fact that most trees in stand G had age 61 – 70 (Figure 8), it had probably not been logged, based on continuity of aspen in the inventory records.

Stands I and J were young forests in 1936. The dominant tree species changed from spruce to black alder (stand I) or birch (stand J) during the last 90 years, but the gradual increase in age indicates that likely they were not logged.

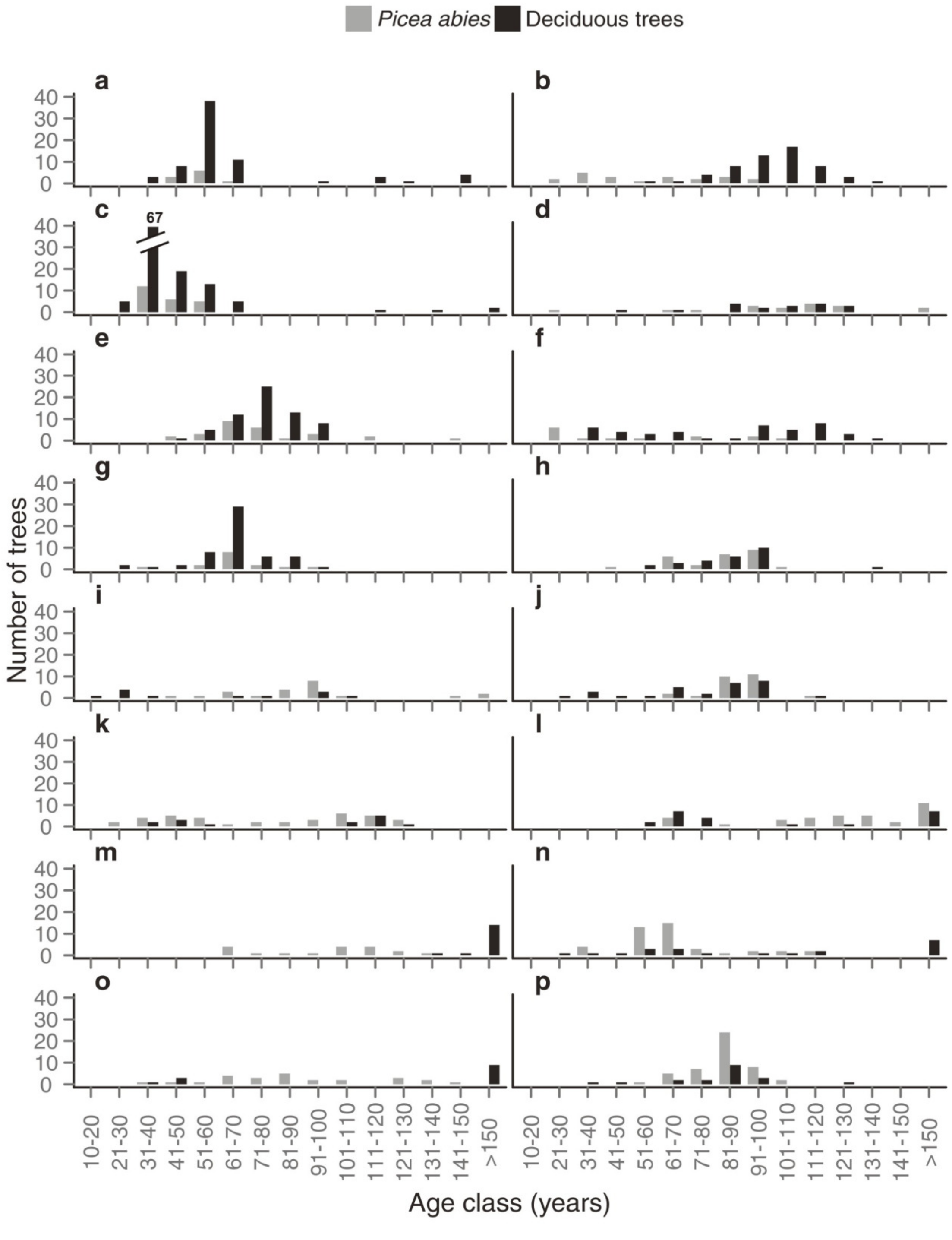


Figure 8. Age distribution of cored trees in the studied woodland key habitats (WKHs) (a – l) and *Quercus robur* stands (m – p).

Oak forests were represented by stands M – P (Appendix 3) (Figure 8). Stands M and N did not show any signs of logging. Stand M was the oldest studied oak stand, in which all oak trees were older than 130 years. Stand N contained oak trees older than 300 years. In two stands O and P, cut stumps indicated logging. But there was no evidence of wood removal in the inventory materials. The four cut stumps of the tree species *Quercus robur* in stand O might represent tree removal after natural disturbances in the forest.

Stand P was a young forest (60 years) in 1960. Today, cut stumps were evident and the oldest tree was only 92 years old. Thus, it could be that stand P was affected by harvesting before 1961.

Further, the stands were grouped by past intensity of logging. Stands A to E are referred to as managed and stands F to L as less-managed. The stands M to P were grouped and analyzed separately as *Quercus robur* forests.

3.5. Richness of structural elements in woodland key habitats

In total, 10 tree species were recorded in the studied deciduous tree plots. The most common coniferous tree was *Picea abies*, which occurred in all plots; common deciduous trees were *Alnus glutinosa, Betula* spp. and *Fraxinus excelsior.* The highest number of tree species occurred in one managed stand (stand C) and one less-managed stand (stand G) (Table 7). The plot in the managed stand C also had the highest tree density (136) and all of the coniferous trees in this plot had DBH < 20 cm (Figure 9).

Table 7. Number of living trees in the studied woodland key habitats (WKHs) by tree species. Symbol m – managed stand.

Tree species	**Plots**												**The total number of trees**
	(Am	**Bm**	**Cm**	**Dm**	**Em)**	**F**	**G**	**H**	**I**	**J**	**K**	**L**	
Acer platanoides	1	-	1	3	-	2	3	-	-	-	-	-	10
Alnus glutinosa	24	54	84	-	45	23	-	1	6	2	-	11	250
Alnus incana	-	-	3	-	1	-	14	-	-	-	2	-	20
Betula spp.	27	2	15	3	16	-	3	22	-	16	6	3	113
Fraxinus excelsior	6	-	7	1	2	4	2	3	-	6	-	-	31
Populus tremula	-	-	2	7	-	-	7	-	-	-	3	8	27
Tilia cordata	8	-	1	1	-	14	7	-	5	4	-	-	40
Ulmus glabra	1	-	-	3	-	-	3	-	2	1	-	-	10
Picea abies	10	22	23	19	27	14	11	26	22	25	37	35	271
Pinus sylvestris	-	-	-	-	-	-	-	1	-	-	-	-	1

All of the studied stands had deciduous trees with DBH > 30 cm (Figure 10). The plot in the managed stand B had 41 deciduous trees with DBH > 30 cm. The highest number of coniferous trees with DBH > 30 cm in one plot was seven (the plot in less-managed stand I). The maximum DHB for *Picea abies* was found in the plot of less-managed stand K (DBH =

47 cm) and the largest deciduous trees were recorded in plots of managed stands: DBH = 64 cm (*Populus tremula*, stand D) and DBH = 57 cm (*Fraxinus excelsior,* stand F).

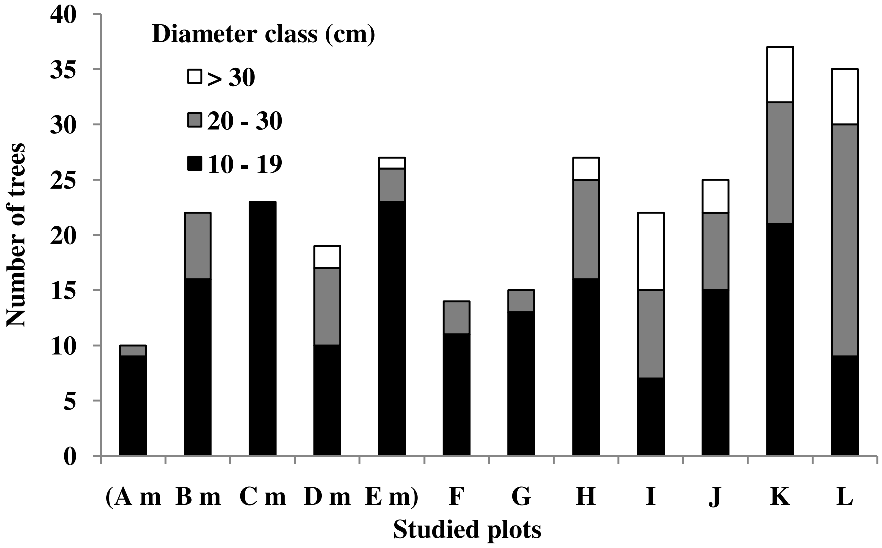


Figure 9. Diameter classes of living coniferous trees in the studied woodland key habitats (WKHs). Symbol m – managed stand. Diameter was measured at breast-height.

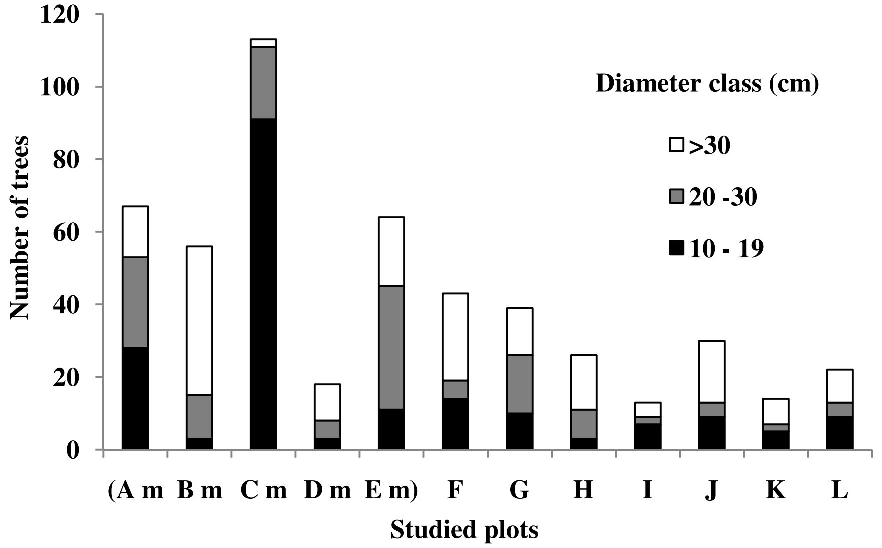


Figure 10. Diameter classes of living deciduous trees in the studied woodland key habitats (WKHs). Symbol m – managed stand. Diameter was measured at breast-height.

The total volume of CWD varied from 19.31 – 139.30 m^3/ha, of which the volume of downed trees varied from 8.63 – 113.85 m^3/ha and the volume of dead standing trees from 6.25 – 75.3 m^3/ha. The greatest part of all CWD was formed by downed trees (Figure 11), except in the plots of stands A, C, H. The lowest volume of CWD was in three plots of managed stands (stands A-C) (Figure 11).

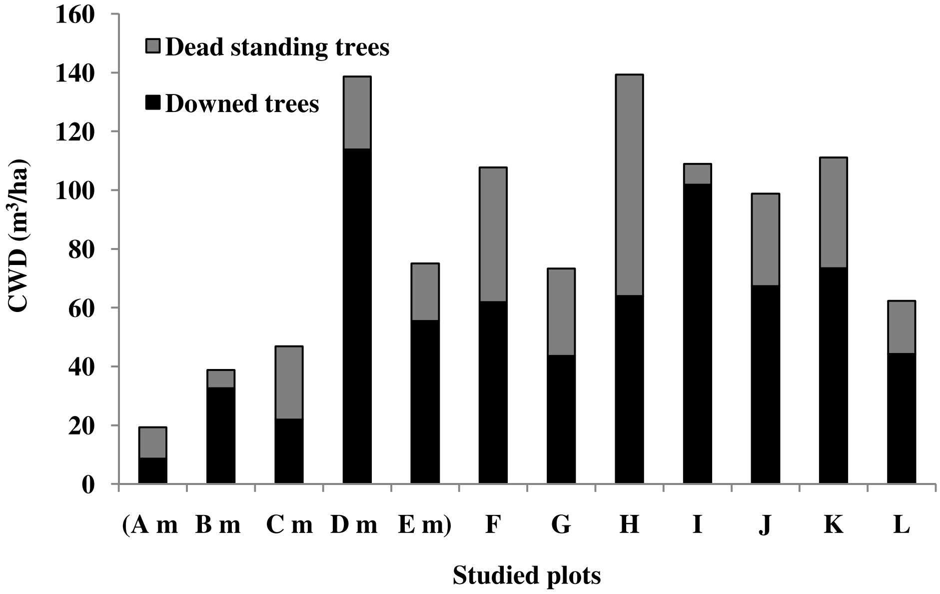


Figure 11. The volume of coarse woody debris (CWD) in the studied woodland key habitats (WKHs). Symbol m – managed stand.

The highest number of downed trees was in the smallest diameter class. Eight plots (in both managed and less-managed stands) contained downed trees > 30 cm in diameter (Figure 12). All downed trees in managed stand A were less than 20 cm in diameter.

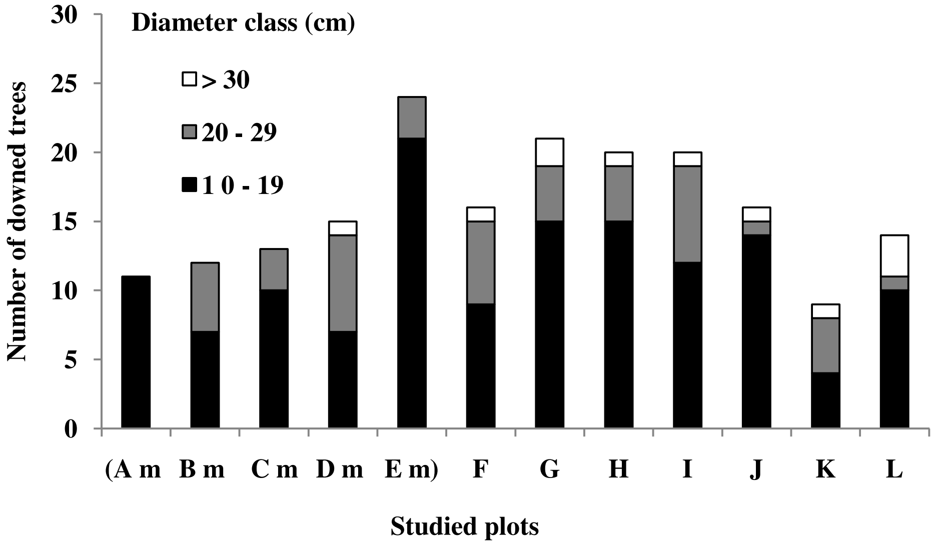


Figure 12. Number of downed trees in different diameter classes in the studied woodland key habitats (WKHs). Symbol m – managed stand.

The volume of downed trees in the smallest diameter class varied from 5.4 – 37.3 m^3/ha, diameter class 20 – 29 cm from 3.7 – 75.8 m^3/ha and in the largest diameter class from 7.8 –

43 m^3/ha (Figure 13). The plot in less-managed stand K had the highest volume of downed trees in the last diameter class (Figure 13).

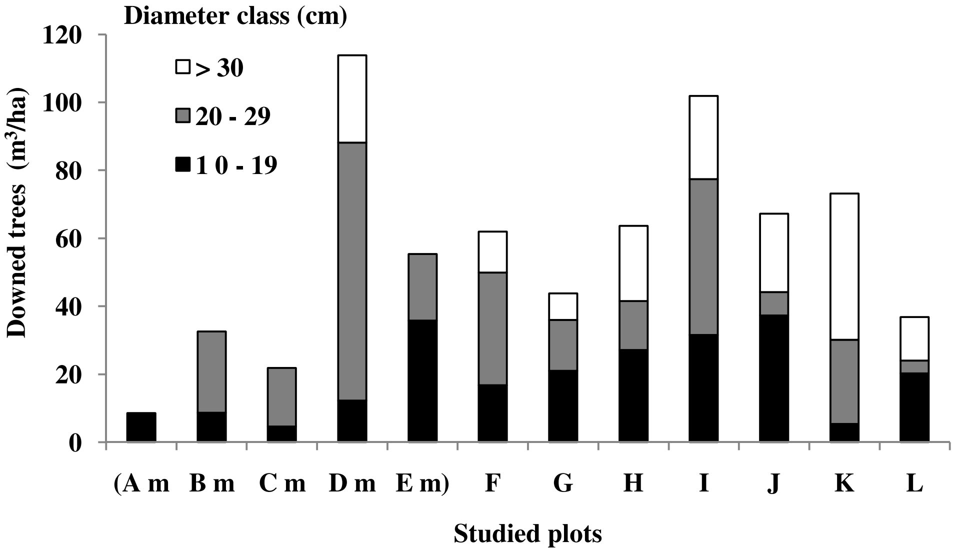


Figure 13. The volume of downed trees in different diameter classes in the studied woodland key habitats (WKHs). Symbol m – managed stand.

The comparison between managed and less-managed woodland key habitats showed that the age of the oldest trees did not much differ between the two groups of stands (Table 8) and all studied plots except one in less-managed stand had some trees with age > 100 years (Figure 7). Two plots (one in managed and one in less-managed) lacked deciduous trees with age > 100 years, and three plots (two in managed stands) lacked coniferous trees with age > 100 years. The managed stands (clearcut or selective spruce removal) had more living deciduous trees in the DBH class 20 - 29 cm (Table 8). Managed stands had more stumps, but the difference was not significant. The proportion of downed wood (the number of downed trees) in decay stage IV and V was very low for all stands. There were no significant differences between managed and less-managed forests in numbers of downed trees in various decay stages.

The total volume of CWD debris did not differ significantly between the two groups of stands (Table 8). The volume ranged from 62.35 to 139.30 m^3/ha in less-managed stands and from 19.30 to 138.62 m^3/ha in managed stands. Downed tree volume per hectare ranged from 44.19 to 101.9 m^3/ha in less-managed stands and from 8.63 to 113.85 m^3/ha in managed stands. The volume of downed trees > 30 cm DBH was significantly greater in less-managed stands (Table 8).

Table 8. Comparison of mean values between managed (n=5) and less-managed (n=7) stands. U test: Whitney-U test.

Variables		Less-managed stands	Managed stands	p value	Used test
Number of structures					
Age of deciduous trees	0-49	4.1	20.4	0.87	U test
	50-99	16.7	33.2	0.2	t-test
	100-149	4.9	9.8	0.463	U test
	>150	1.0	0.2	1	U test
Age of coniferous trees	0-49	3.0	4.6	0.453	U test
	50-99	14.4	9.6	0.274	t-test
	100-149	5.7	5.4	0.741	U test
	>150	1.9	0.6	1	U test
DBH of deciduous trees (cm)	10-19	8.1	27.2	0.623	U test
	20-29	**5.9**	**19.2**	**0.028**	**U test**
	>30	12.7	17.2	0.551	t-test
DBH of coniferous trees (cm)	10-19	13.1	16.2	0.414	t-test
	20-29	8.7	3.4	0.084	t-test
	>30	3.1	0.6	0.108	U test
Stumps		1.9	3.8	0.218	U test
Decay class of downed trees	I	4.3	2.2	0.505	U test
	II	0.4	2.4	0.287	U test
	III	2.0	3.8	0.371	t-test
	IV	2.0	1.0	0.615	U test
	V	0.7	0.4	0.41	U test
Volume (m^3/ha)					
Coarse woody debris	Total	100.2	63.7	0.164	t-test
	Downed trees	65.2	46.5	0.389	t-test
	Dead standing trees	35.0	17.3	0.085	U test
Diameter of downed trees (cm)	1 0-19	22.8	14.0	0.236	t-test
	20-29	20.5	27.3	0.646	t-test
	>30	**20.8**	**5.1**	**0.047**	**t-test**
Number of species					
Species in plot	All species	33.4	33.8	0.943	t-test
	Indicator species	5.4	5.3	0.851	t-test
Species on CWD	All species	24.6	20.8	0.221	t-test
	Indicator species	**3.7**	**1.8**	**0.036**	**t-test**
Species on downed trees	All species	20.6	16.0	0.144	t-test
	Indicator species	2.6	1.4	0.085	U test
Species on dead standing trees	All species	9.9	7.8	0.588	t-test
	Indicator species	1.6	1.0	0.494	U test
Species on stumps	All species	4.6	5.0	0.855	t-test
	Indicator species	0.3	0.0	0.259	U test
Species on living trees	All species	26.0	28.8	0.398	t-test
	Indicator species	3.6	4.4	0.523	t-test

3.6. Richness of bryophyte species in woodland key habitats

In total, 74 bryophyte species (51 mosses and 23 liverworts) were recorded in the studied plots (Appendix 4) of which most occurred on living trees. The most common species on living trees were *Ptilidium pulcherrimum*, *Radula complanata*, *Dicranum montanum, Dicranum scoparium*, *Eurhynchium angustirete, Hypnum cupressiforme* and *Plagiothecium laetum*. The liverwort *Lophocolea heterophylla* was found in all studied plots on both substrates – on living trees and downed trees. The liverwort *Radula complanata* and mosses *Hypnum cupressiforme* and *Plagiomnium cuspidatum* were found on dead standing trees in more than half of the studied plots (Appendix 4). Thirteen species were found only once.

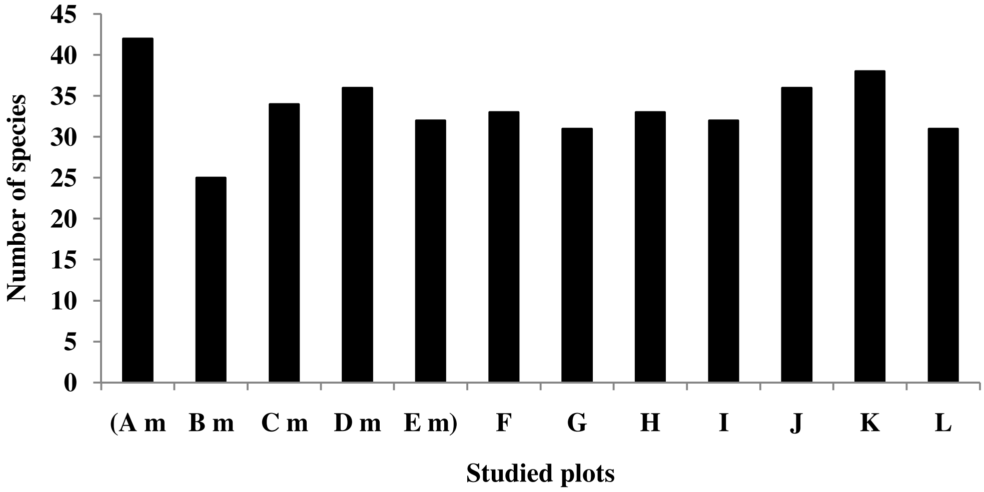


Figure 14. The total number of species in the studied woodland key habitats (WKHs). Symbol m – managed stands.

The highest number of species was found in the plot of managed stand A (42 species), and the plot in the managed stand (stand B) had the lowest number of bryophyte species (Figure 14). The highest number of species on living trees was found in the plot of managed stand A (34 species); on downed trees in the plot of less-managed stand K (30 species); on dead standing trees in the plot of less-managed stand H (17 species) and on stumps in the plot of less-managed stand J (13 species) (Figure 15). Almost in all studied plots most of the species were recorded on living trees (Figure 15). Only in two plots (in less-managed stands I and K) did the majority of species occur on downed trees (24 species and 30 species) (Figure 15). The poorest substrates in the richness of species were stumps (Figure 15). The maximum number of species on one living tree was nine, on one downed tree – 15 species, on one dead standing tree – nine species and on one stump – eight species.

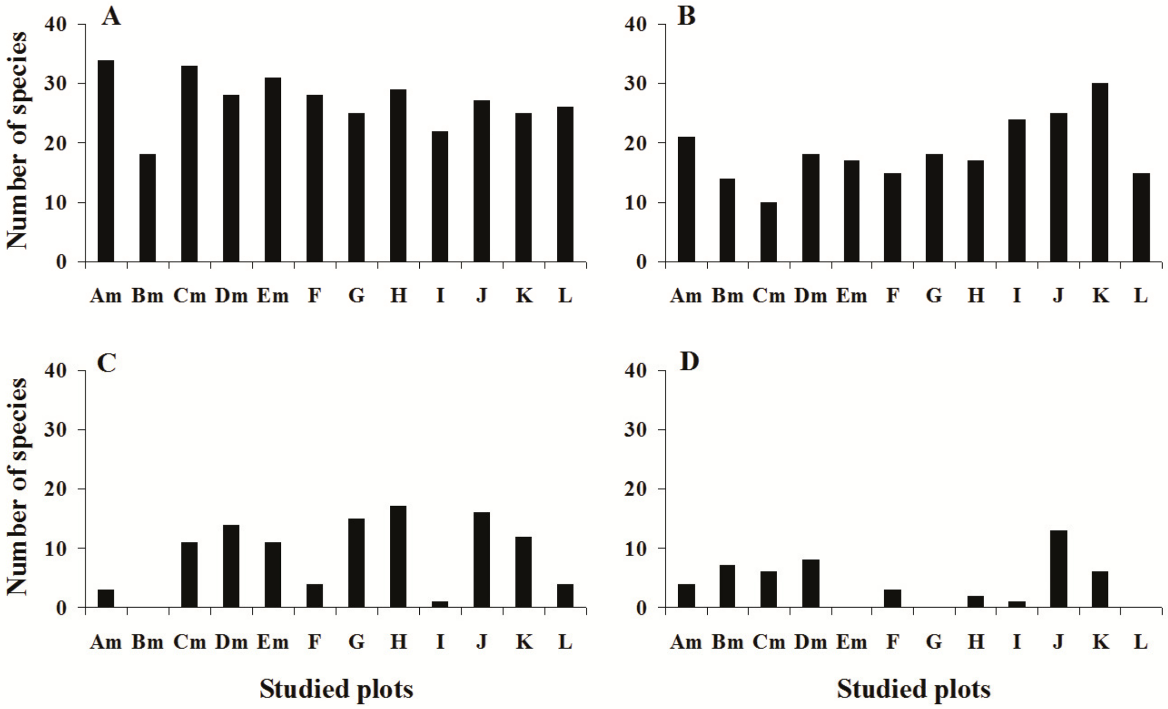


Figure 15. The total number of species in the studied woodland key habitats (WKHs) on different substrates. Symbol m – managed stands. A – on living trees, B – on downed trees, C – on dead standing trees, D – on stumps.

Together 12 WKH indicator species were found in all studied stands. The most common indicator species were *Jamesoniella autumnalis* and *Homalia trichomanoides* on living trees and *Nowellia curvifolia* on downed trees. The indicator mosses *Homalia trichomanoides*, *Neckera pennata* and *Ulota crispa* were common on dead standing trees (Appendix 4). *Frullania tamarisci* was found once and on a living tree. WKH indicator species were recorded on stumps in only two plots (*Calypogeia suecica* and *Jamesoniella autumnalis*) (Appendix 4).

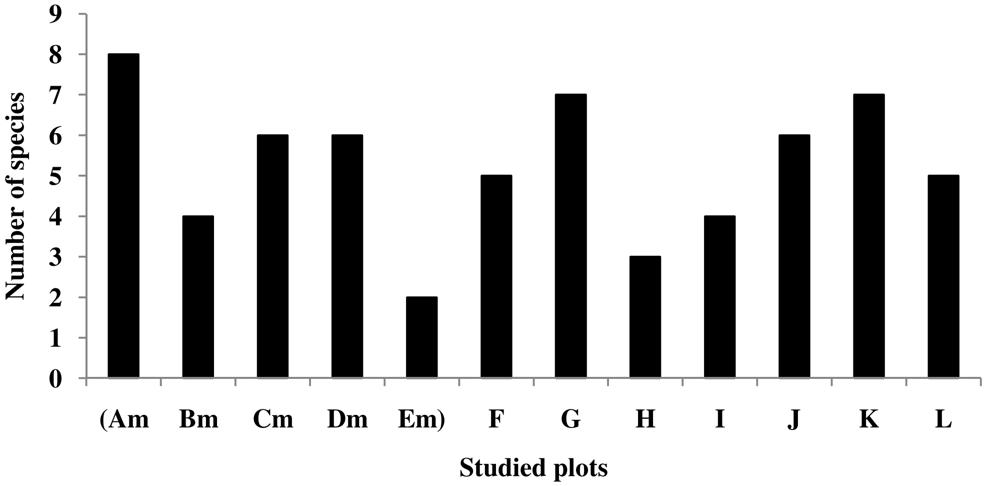


Figure 16. The total number of indicator species in the studied woodland key habitats (WKHs). Symbol m – managed stands.

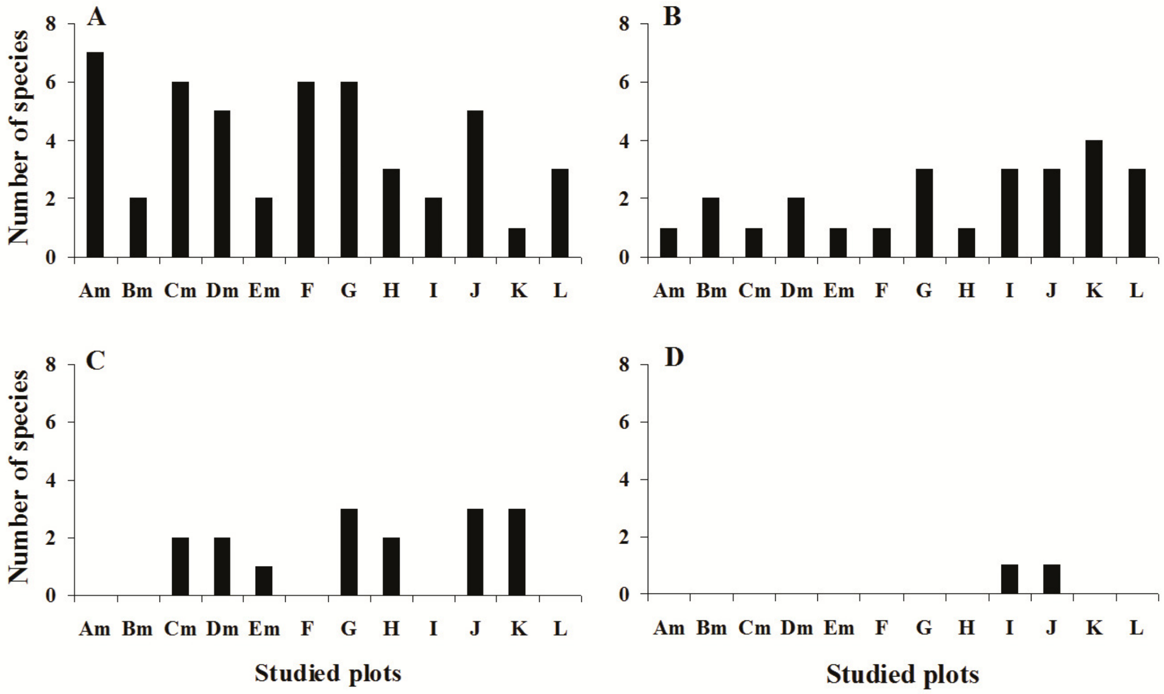


Figure 17. The total number of indicator species in the studied woodland key habitats (WKHs) on different substrates. Symbol m – managed stands. A – on living trees, B – on downed trees, C – on dead standing trees, D – on stumps.

The plot in managed stand A had the maximum number of indicator species (eight species) (Figure 16), the majority of which were found on living trees (Figure 17). The lowest number of WKH indicator species was two bryophytes in the plot of managed stand E (Figure 16). The plots in less-managed stands had the maximum number of indicators on downed trees (four species, stand K) and dead standing trees (three species, stand G, stand J and stand

K) (Figure 17). The lowest number of bryophyte indicator species was found on stumps (Figure 17). The maximum number of indicators on one living tree was four species, on one downed tree – three species, on one dead standing tree – three species and on one stump – one species.

The plots in managed stands had more species on living trees (also more WKH indicator species) and more species on stumps than plots in less-managed stands (Table 8). However, the number of indicator species in plots on CWD (stumps plus downed trees plus dead standing trees) was significantly higher in less-managed stands than in managed stands. Indicator species richness in plots on downed trees was also higher in less-managed stands, but the difference was only close to significance in the Whitney-U test (Table 8). Twelve species were found only in the plots of less–managed WKHs, of which only one was an indicator species (liverwort *Riccardia palmata*) (Appendix 4). The most common indicator species were *Homalia trichomanoides* in plots of less-managed stands and *Jamesoniella autumnalis* in plots of managed stands (Appendix 4).

The GLMM models showed the importance of factors for total bryophyte species and indicator species richness at a tree level in the plots. The selected significant variables were exactly the same both for total species richness and WKH indicator species richness on living trees (Table 9). The main factors explaining species richness were tree species, diameter and tree age. The created GLMM model for total species richness showed that species richness significantly differs between *Alnus glutinosa* (as reference in the model) and tree species *Acer platanoides, Alnus incana*, *Picea abies* and *Fraxinus excelsior*.

The indicator species richness on living trees significantly differed between chosen reference *Alnus glutinosa* and all other tree species (Table 9). The mean number of indicator species was higher on *Ulmus glabra* and *Acer platanoides* and the highest total number of species on *Populus tremula* and *Fraxinus excelsior* (Table 9). Almost all nemoral tree species (except *Tilia cordata*) had higher number of species compared with *Betula spp.*, *Alnus glutinosa* and *Picea abies*. The stand variables were not significant in the GLMM models for total and indicator bryophyte species richness on living trees (Table 9).

Table 9. Summary statistics for GLMM models explaining total and indicator bryophyte species richness on living trees. The significance level and Akaike's information criterion (AIC) are shown.

	Variable		**Coefficient/ mean value**	**Pr(>|z|)**	**AIC**
		Living trees			
Total species richness	**Tree species +Diameter +Tree age**		0.0663	***	854.8
	Tree species				
		Acer platanoides	4.6	*	
		Alnus glutinosa (as reference)	2.97		
		Alnus incana	4.67	**	
		Betula spp.	4.26		
		Fraxinus excelsior	5	***	
		Picea abies	2.68	***	
		Populus tremula	5.93		
		Tilia cordata	2.8		
		Ulmus glabra	4.6		
	Diameter			**	
	Tree age			***	
Indicator species richness	**Tree species +Diameter +Tree age**		-3.13	***	470.7
	Tree species				
		Acer platanoides	1.4	***	
		Alnus glutinosa (as reference)	0.19		
		Alnus incana	1.33	***	
		Betula spp.	0.34	*	
		Fraxinus excelsior	1.19	***	
		Picea abies	0.07	***	
		Populus tremula	1.14	***	
		Tilia cordata	0.37	**	
		Ulmus glabra	1.5	***	
	Diameter			*	
	Tree age			***	

'***' $p \leq 0.001$, '**' $p \leq 0.01$, '*' $p \leq 0.05$

Total bryophyte species richness on downed trees and stumps was best explained by decay stage and substrate type (downed tree or stump) (Table 10). In the obtained GLMM model the decay stages II, III, IV were significant for total species richness compared to decay stage I. The highest total species richness was found on downed trees in decay stages III and IV. More species were found on downed trees than on stumps (Table 10).

The best GLMM model for indicator species on dead wood (downed trees plus stumps) was found with two explained variables – tree species and decay stage (Table 10). The tree species *Alnus incana, Fraxinus excelsior* and *Populus tremula* were important for indicator species richness (as reference was chosen tree species *Alnus glutinosa*). The highest indicator species richness was on dead *Populus tremula* substrate (Table 10). The decay stages III and IV were significant in the GLMM model. There were no indicator species on dead wood in decay stage V. Similarly as in GLMM models for bryophytes on living trees also in models for species richness on dead wood stand variables were not important.

Table 10. Summary statistics for GLMM models explaining total and indicator bryophyte species richness on downed trees plus stumps. The significance level and Akaike's information criterion (AIC) are shown.

	Variable		**Coefficient/ mean value**	**Pr(>|z|)**	**AIC**
		Dead wood (downed trees+stumps)			
Total species richness	**Decay stage +Substrate**		0.9684	***	205.8
	Decay stage				
		I (as reference)	2.8		
		II	4.65	***	
		III	4.97	***	
		IV	6.31	***	
		V	2.86		
	Substrate				
		Downed tree (as reference)	4.43		
		Stump	3.04	***	
Indicator species richness	**Tree species +Decay stage**		-3.27	***	87.02
	Tree species				
		Alnus glutinosa (as reference)	0.14		
		Alnus incana	0.44	*	
		Betula spp.	0		
		Fraxinus excelsior	0.4	*	
		Picea abies	0.26		
		Populus tremula	1.2	*	
	Decay stage				
		I (as reference)	0.14		
		II	0.19		
		III	0.47	**	
		IV	0.47	**	

'***' $p \leq 0.001$, '**' $p \leq 0.01$, '*' $p \leq 0.05$

3.7. Richness of structural elements in *Quercus robur* forests

In total, seven tree species were recorded in the control plot in Moricsala. The most common species of living trees were *Tilia cordata* (48 trees), *Quercus robur* (26 trees), *Picea abies* (18 trees) and *Acer platanoides* (13 trees). The other deciduous tree species were seven *Alnus glutinosa*, two *Ulmus glabra* and one *Betula sp.*

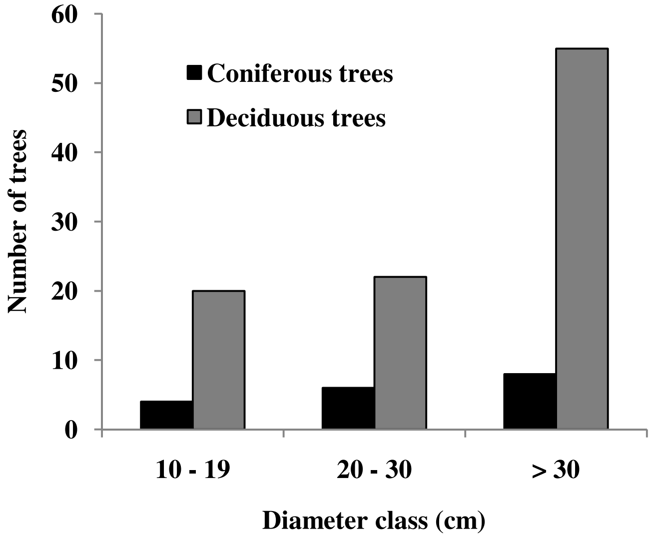


Figure 18. Number of living trees in different diameter classes in the studied plot in Moricsala. Diameter was measured at breast-height.

The highest number of deciduous trees with DBH > 30 cm was found in the plot in Moricsala (Figure 18). The most frequent species in the largest diameter class of living trees were *Quercus robur* and *Tilia cordata*. The maximum DBH for *Picea abies* was 54 cm and for *Quercus robur* was 88 cm.

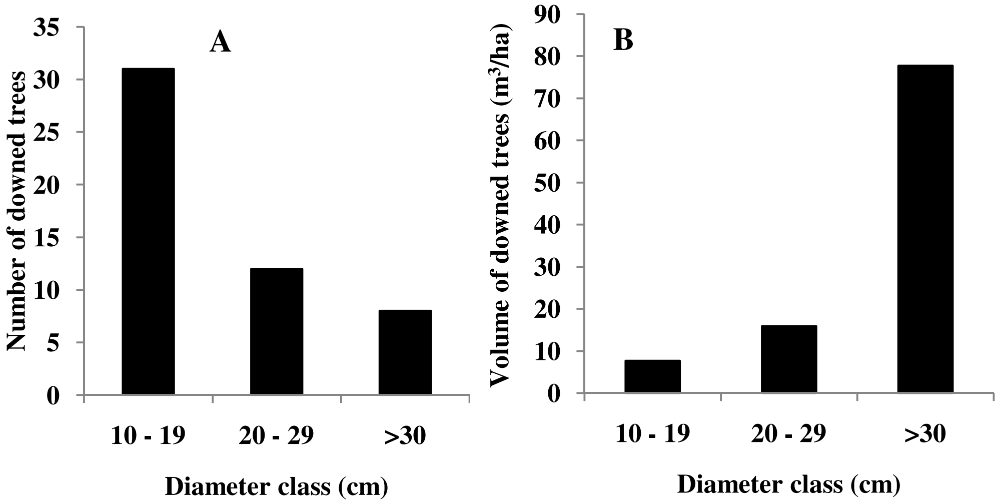


Figure 19. Amounts of downed trees in the studied plot in Moricsala. A - number of downed trees in different diameter classes. B - volume of downed trees in different diameter classes.

In the control plot of Moricsala the total volume of CWD was 219.43 m^3/ha, of which 101.40 m^3/ha was downed trees and the remaining volume (118.03 m^3/ha) was dead standing trees. The highest number of downed trees were in smallest diameter class (Figure 19), but the highest volume of downed trees was recorded in the > 30 cm diameter class (Figure 19). All five decay stages of downed trees were represented in the studied plot in Moricsala (Figure 20). The highest proportion of downed trees were in decay stage II (Figure 20).

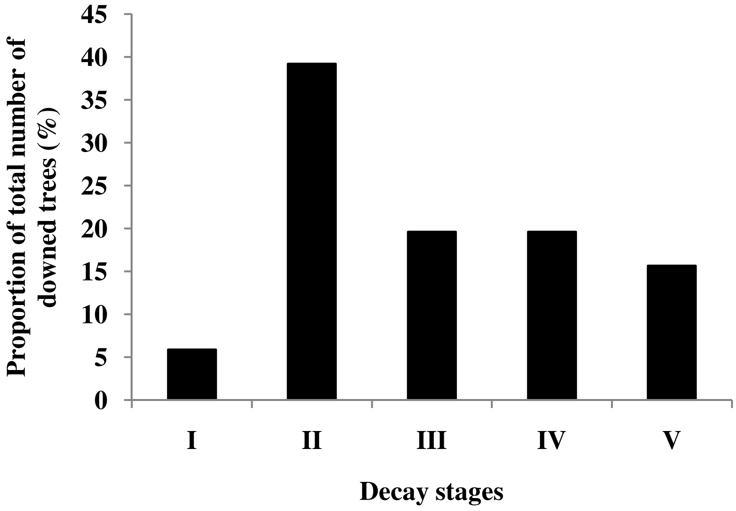


Figure 20. Proportion of total number of downed trees in different decay stages in the studied plot in Moricsala.

The other four studied oak plots (stands M – P) were mostly composed of the tree species *Quercus robur* and *Picea abies* (Table 11). *Pinus sylvestris* was recorded only once in the studied plots.

Table 11. Number of living trees in the studied *Quercus robur* forests according to the tree species.

Tree species	**Plots**			
	M	**N**	**O**	**P**
Acer platanoides	-	-	-	2
Alnus glutinosa	-	3	-	-
Betula spp.	-	2	-	1
Fraxinus excelsior	-	4	-	-
Populus tremula	-	1	-	4
Quercus robur	16	8	10	12
Ulmus glabra	-	3	4	-
Picea abies	29	42	25	48
Pinus sylvestris	-	-	-	1

The distribution of coniferous trees in diameter classes was similar in all the studied stands. All plots had spruce trees with DBH > 30 cm (Figure 21). Plot P had the highest number of coniferous trees in the highest diameter class. Plot M had no other deciduous trees besides oaks, and these had DBH > 30 cm. The maximum DBH for spruce was 55 cm (plot M) and for oak was 77 cm (plot O). The highest DBH (65 cm) of a deciduous tree (*Populus tremula*) was recorded in plot P.

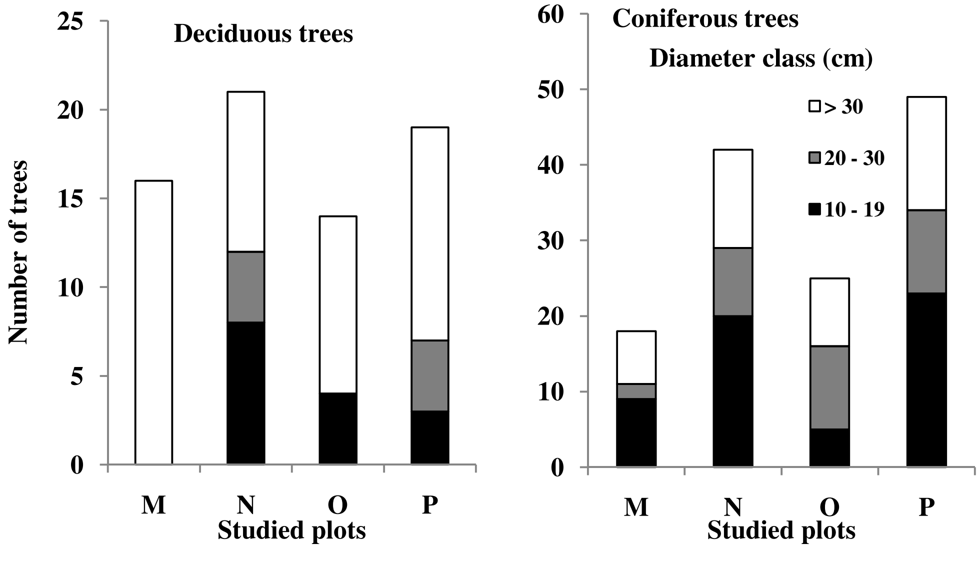


Figure 21. Diameter classes of living coniferous and deciduous trees in the studied four *Quercus robur* forests. Diameter was measured at breast-height.

In total, the volume of CWD varied from 16.10 - 239.56 m^3/ha. The lowest volume of CWD was recorded in plot O, which had no dead standing trees (Figure 22). The volume of downed trees varied from 8.23 –194.49 m^3/ha, and the volume of dead standing trees from

45.07 – 94.17 m^3/ha. Plots P and N had no downed trees with diameter > 30 cm (Figure 23). The maximum diameter for a downed tree was 83 cm for oak (stand M) and 28 cm for aspen (plot P).

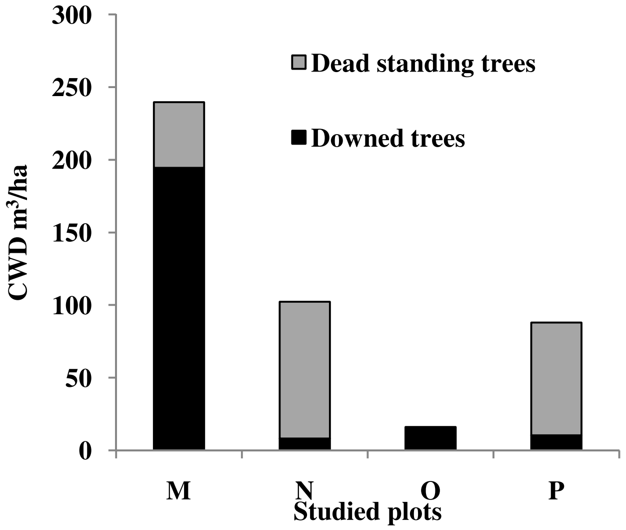


Figure 22. Volume of coarse woody debris (CWD) in the studied four *Quercus robur* forests.

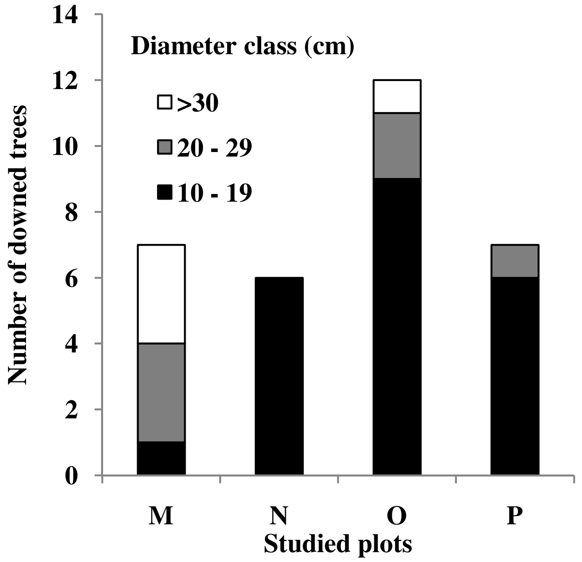


Figure 23. Number of downed trees in different diameter classes (CWD) in the studied four *Quercus robur* forests.

Plot M had the highest volume of downed trees in the largest diameter class (Figure 24). The total volume of downed trees in other studied plots was mostly composed of dead wood in the smallest diameter class.

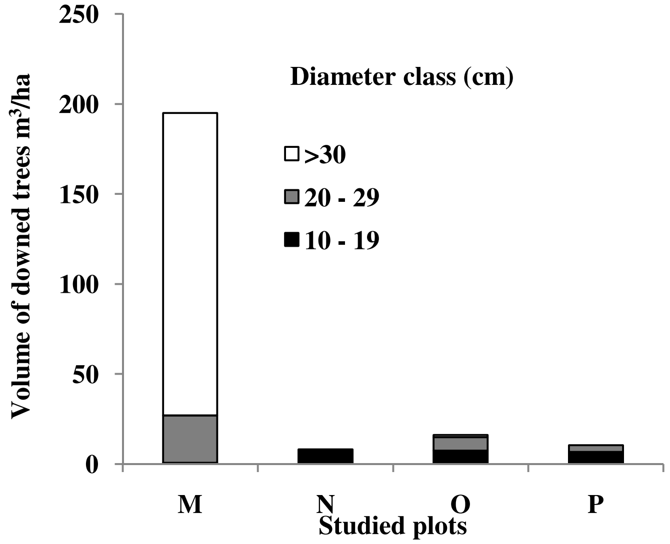


Figure 24. The volume of downed trees in different diameter classes in the studied *Quercus robur* forests.

The highest proportions of downed trees were in decay stages I and II. The last decay stage V was not recorded in any of the studied stands. Plot P was the only one of the studied stands that had downed trees in decay stages IV (Figure 25).

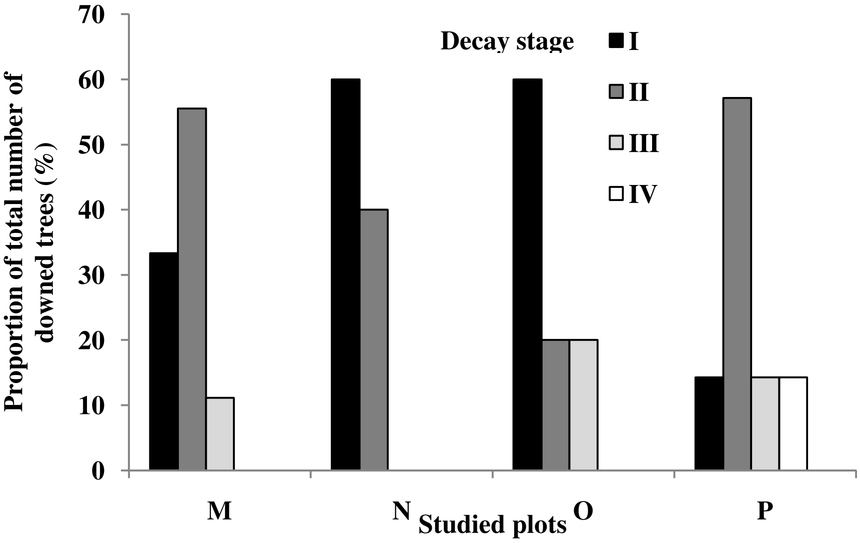
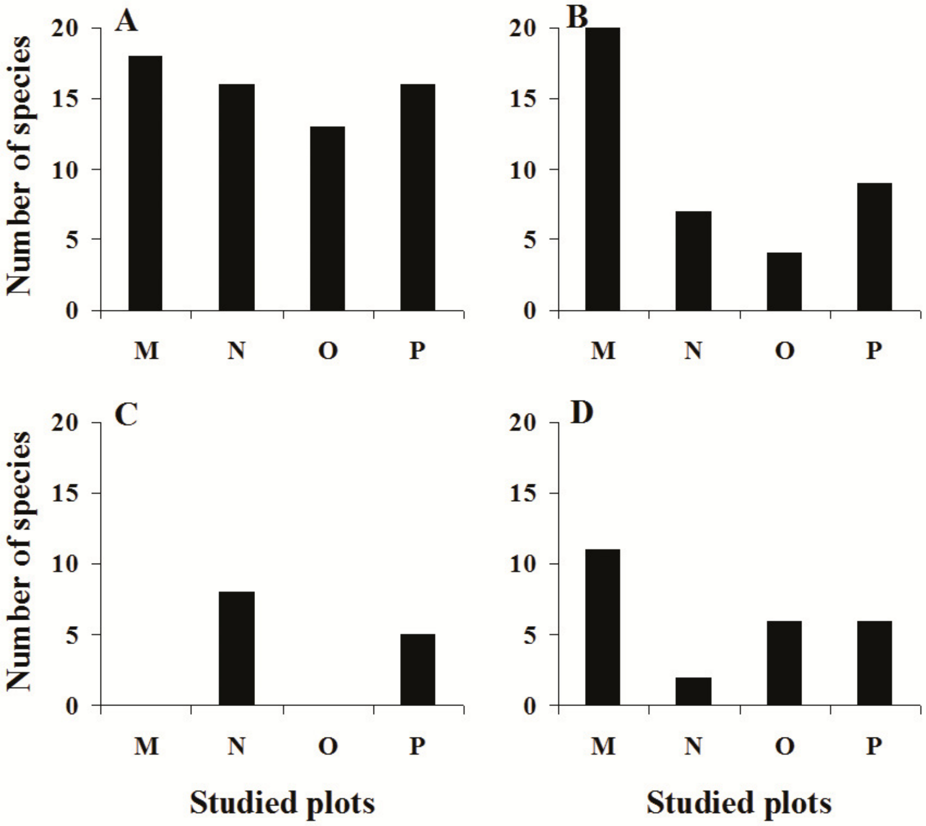


Figure 25. Proportion of total number of downed trees in different decay stages in the four studied *Quercus robur* forests.

3.8. Richness of bryophyte species in *Quercus robur* forests

In total, 42 bryophyte species were recorded in the studied oak forests (eight liverworts and 34 mosses) (Appendix 4). The richness of bryophytes was highest on living trees and downed trees, lower on dead standing trees. The most common species were mosses *Hypnum cupressiforme*, *Plagiomnium cuspidatum* and *Brachythecium rutabulum* and the liverwort *Radula complanata* (Appendix 4). Thirteen bryophyte species (three liverworts and 10 mosses) were found only in one studied plot and 12 of them only once.



Fiugure 26. The number of bryophyte species on different substrates in the studied *Quercus robur* forests. A – on living trees, B – on downed trees, C – on dead standing trees, D – on stumps.

The numbers of total species found in the plots were: 26 species (plot M), 19 species (plot N), 15 species (plot O) and 21 species (plot P). Mostly the highest number of species was found on living trees (plots N, O, P) (Figure 26). Except the plot of the stand M, where downed trees had more bryophyte species than living trees (Figure 26). The maximum number of species on a living tree was nine and on a downed tree was eight (plot M). The plot of stand N had the maximum number of species on a dead standing tree (five species). The highest species richness on stumps was in plot P (five species on one substrate).

The oak forest plots had six indicator species, of which two were recorded only once in the studied plots. Plots M and N had the highest number of indicators (three and four species). The lowest number of indicators were found in the plot O (one species) and plot P (two species). Four of the indicator species were found on living trees. The most common species was the moss *Homalia trichomanoides* (Appendix 4). The WKH indicator species were found on living trees in all studied plots (Figure 27). The maximum number of indicator species (three species) on one living tree and on one dead standing tree was in plot of stand N. The maximum number of indicators on a downed tree was two species (plot in stand M).

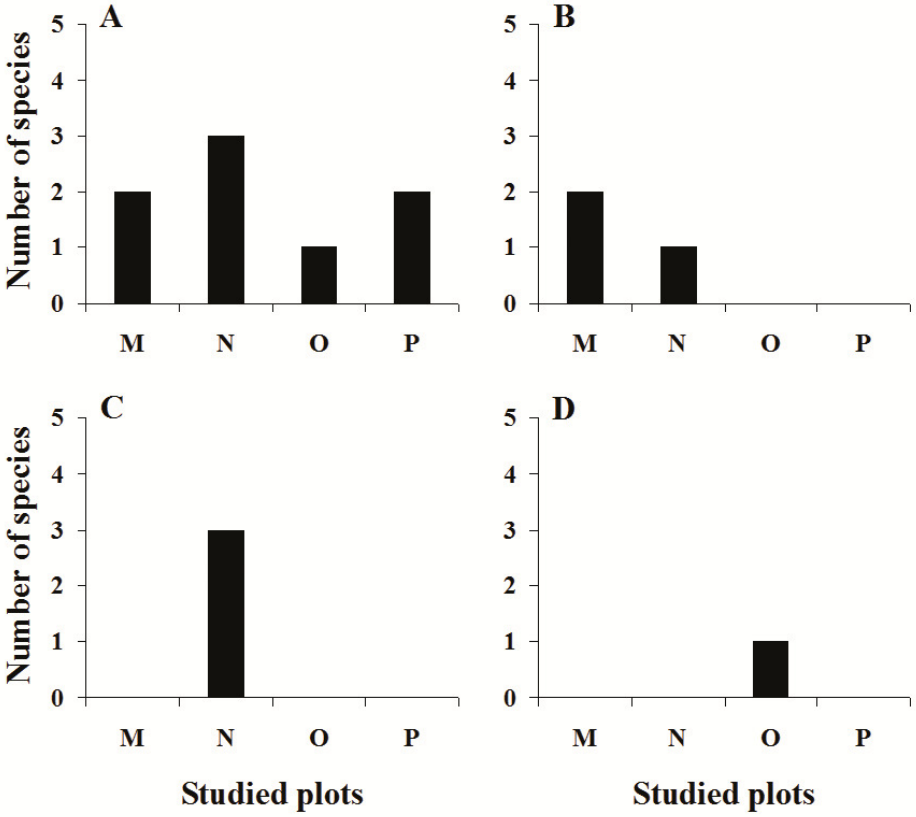


Figure 27. The number of indicator species on different substrates in the studied *Quercus robur* forests. A – on living trees, B – on downed trees, C – on dead standing trees, D – on stumps.

4. Discussion

4.1. Characteristics of managed forest landscape

The results showed that the studied forest landscapes mostly were dominated by spruce and deciduous tree species. Regarding structural elements that characterize old-growth forests, the forests were missing such old-growth structural elements as broad-leaved trees with DBH > 40 cm. Aspen was more abundant than broad-leaved trees, but nevertheless it was infrequent compared to most other tree species. Also, less than 1/10 plots had CWD > 30 cm in diameter.

The absence of the above structural elements indicate that the area had been mostly logged, as has been found in other studies (Ericsson et al. 2005, Lõhmus et al. 2005). This was confirmed also by the large number of plots (61%) with cut stumps. It has been shown that large dead wood is in low quantities in managed forest (Kruys et al. 1999, Fridman and Walheim 2000).

4.1.1. Bryophyte species richness on living trees

The results showed that in the studied forest area, total and indicator species richness on living trees was best explained by deciduous tree species availability and more by the combination of maximum diameter and tree species within the studied plots. This indicates the significance of tree DBH, as previously observed in other studies (Snäll et al. 2003, Snäll et al. 2004, Löbel et al. 2006a, Löbel et al. 2006b). This is also in accordance with the species-area relationship (MacArthur and Wilson 1967), where area reflects the tree DBH. It means that a number of species increases with tree size, because more microhabitats are provided. It has also been observed that deciduous trees at the landscape scale have greater importance than coniferous trees for epiphytic bryophyte richness (Löbel et al. 2006b, Mežaka and Znotiņa 2006, Vanderpoorten et al. 2004), which may be associated with differences in bark chemistry of the host tree (Barkman 1958).

The GLM analysis showed that the total bryophyte species richness was mostly explained by maximum DBH of *Betula* spp. as well the maximum DBH of *Alnus glutinosa*. In this case it could be that birch and black alder stands supported high richness of generalist species (Mežaka et al. 2008) which can live in a wide range of conditions, unlike to specialist species (Ek et al. 2002). The above is confirmed also by the fact that there were no indicator species found on *Betula* spp. or *Alnus glutinosa* in the present study. It is known that according to chemical and physical characteristics of bark (Barkman 1958), birch and black alder do not support high bryophyte diversity as a host tree. Thus, the epiphytic bryoflora of these species is usually low compared with nemoral tree species and *Populus tremula* (Mežaka et al. 2008, Darel and Cronberg 2011). Therefore, the relationship of total epiphyte richness with maximum diameter of *Betula* spp. and *Alnus glutinosa* is probably due to the presence of generalist bryophyte species richness on these substrates.

According to the results, presence of structural elements such as broad-leaved tree species as *Ulmus glabra*, *Fraxinus excelsior*, *Tilia cordata* together with tree species *Populus tremula* significantly increased the number of indicator bryophyte species. The results showed also that ash and aspen were significant variables for total bryophyte species richness. Nemoral tree species and *Populus tremula* with DBH > 30 cm can be considered as old-growth structures that support biological diversity in managed forests (Lõhmus et al. 2005, Lõhmus et al. 2007). Also, the importance of large aspen in a fragmented landscape (Ojala et al. 2000, Snäll et al. 2003) and managed forests (Vellak and Paal 1999) has been shown in studies of occurrence of some epiphytic bryophyte species.

The results showed that among the epiphytic WKH indicator species, the most common bryophytes were *Homalia trichomanoides* and *Neckera pennata.* Each of them was found in almost 2/3 of plots in which another WKH indicator was recorded. Previous studies on species occurrence in fragmented landscape showed that variables associated with habitat quality (habitat quality includes environmental variables like host tree species composition, total basal area of trees) and connectivity are important for both of these species (Löbel et al. 2006a, Löbel and Rydin 2009, Ikauniece et al. 2012a). This suggests that according to the high occurrence of both indicator species in the present study, possibly the connectivity of suitable substrates like large broad-leaved trees and aspen is not limiting the dispersal of these two species.

In addition, the observed relationship between maximum diameter of CWD (dead standing trees plus downed trees) and indicator species richness on living trees in GLM analyse might indicate that forest patches where the species were found had higher quality than stands where indicator species were not recorded. It has been shown in literature that higher quality forests can be distinguished from more managed by the presence of large deciduous trees, especially aspens (Siitonen et al. 2000) as well by large diameter dead wood (Ódor and Standovár 2001).

Interestingly, the GLM analysis did not show a relationship between designation as WKH and richness of indicator species. This might suggest that the past WKH inventory has been incomplete. However, it is possible that even a single deciduous tree in forest landscape of boreo-nemoral region creates a suitable patch for many bryophyte species to exist (Löbel et al. 2006a). Such broad-leaved trees could be more important for epiphytes than closed forest stands in mixed coniferous deciduous forest landscape (Snäll et al. 2005). In this case, a stand would probably not be designated as a WKH. Thereby, the present study certainly suggests that some of the WKH species can also be found in managed forests, as previously observed by studies in Estonia (Vellak and Paal 1999) and Sweden (Gustafsson et al. 2004a).

At the same time several epiphytic bryophyte species from the list of WKH indicators were absent in the present study. For example, *Anomodon* spp. and *Isothecium alopecuroides* were not found. Most likely they were not found because of the lack of sufficiently old deciduous trees in the studied area as these epiphytes are related with large diameter broad-leaved trees and aspens (Suško 1998, Löbel et al. 2006a, Löbel and Rydin 2009). Also, they need a stable microclimate (Suško 1998) that probably was missing in the studied forests. It is likely that these studied deciduous forests are also missing continuity as well, which is an important factor for rare species (Fritz et al. 2008). Another explanation could be related with biogeography differences in species distribution. For example, the WKH indicator bryophytes as *Antitrichia curtipendula*, *Frullania tamarisci* and *Neckera crispa* are more associated with old growth-forests in western of Latvia (Suško 1998), while the present studied area (Ziemelvidzeme Biosphere Reserve) was mostly located in the east of Latvia.

Stand age was significant only for total bryophyte richness and with low explained variance. The obtained result is in contrast to other studies in which older forest stands were observed to contain more bryophyte species, especially threatened and red-listed species (Löbel et al. 2006a, Fritz et al. 2008, Rajandu et al. 2009). Thereby, stand variables have only small effect on bryophyte richness and substrate diversity is the main factor affecting species richness.

In summary, the present study showed that species richness on living trees in coniferous deciduous forests is mostly related with the composition of deciduous trees. Especially high species richness of WKH indicator species is mainly associated with large living broad-leaved trees and aspens.

4.1.2. Bryophyte species richness on coarse woody debris

In the present study among the bryophyte species on dead wood, the number of WKH epixylic indicator species was low. One of the species *Anastrophyllum hellerianum,* which is the good indicator of boreo-nemoral forest communities (Meier et al. 2005) and old-growth forests (Andersson and Hytteborn 1991), was found only once. Another WKH species

Nowellia curvifolia was found in 6 % of plots on downed trees, and in one case on a stump. Together only six species of liverworts were recorded on CWD. In comparison to other studies (Lõhmus and Lõhmus 2008, Vellak and Paal 1999) in which dead wood was a rich substrate for liverworts, the number of bryophyte species observed in the present study, was also low. Although the results showed that dead wood was found in 81% of plots, the studied area was almost missing large diameter CWD, which can explain the low richness of bryophytes on CWD. It has been shown that bryophyte species *Anastrophyllum hellerianum* require large diameter downed trees (Āboliņa 2008). The other WKH indicator species *Nowellia curvifolia* is widely found in Latvia and its occurrence has increased in the last years (Āboliņa 2008). This could explain its more frequent recordings in the studied plots than other WKH indicator species. Despite the fact that the studied forest area has been mostly managed in the past (Tērauds 2011), many rare bryophyte species such as *Lophozia incisa, Jungermannia leiantha* and *Riccardia latifrons* can also be found in old managed forests (Perhans et al. 2007), but these species were not found in the present study.

The GLM analysis showed that the basal area of CWD and number of stumps were important for total bryophyte species richness. The maximum diameter was significant for indicator species richness. However, the examined factors explained a small part of both total and indicator species richness. It has been shown in literature that higher amounts of dead wood are associated with increase of the number of bryophyte species (Ohlson et al. 1997) and stumps can be important substrate to support bryophytes richness in the forest (Humphrey et al. 2002), especially in managed ones (Rajandu et al. 2009). Also, the positive relationship between downed tree diameter and frequency of epixylic bryophytes has been observed in previous studies (Söderström 1988b, Andersson and Hytteborn 1991, Ódor et al. 2006). Especially large downed trees are species rich with rare species (Ódor and van Hees 2004), including also WKH indicators. The importance of large downed trees for species richness reflects several different factors. Large decaying dead wood has grater surface area for colonisation and provides suitable substrate for a much longer time than small dead wood (Ódor and Standovár 2001, Ódor et al. 2006). Large pieces of dead wood decay slower and provide a greater range of microhabitats. Downed trees with large diameters can also hold more moisture than small branches, which is a key factor for many bryophyte species. In addition, larger downed trees are less likely to be overgrown by ground flora, thus providing freedom from competition of vascular plant species. In such a way downed trees could reach late decay stages without being hidden under vegetation cover and have richer bryophyte flora of late epixylic species (Söderström 1988b).

Generally, the present study showed that most likely the low number of species on downed trees is determined by the lack of presence of large diameter dead wood. The results showed that the management in the past has strongly reduced dead wood structures that could ensure high epixylic species richness.

4.2. Management history in woodland key habitats

The mean tree ages of stands of less-managed and managed WKHs, together with the historical records confirmed that most of the studied forest stands designated as WKHs were affected by forestry during the last century. According to the historical information, of the 12 stands, three had been clearcuts, and in two spruce had been selectively removed. Also, some of the less-managed stands were very young forests in the year 1930. Considering the past intensive use of forests in Latvia (Tērauds et al. 2011), these had probably been previously logged. For this reason the term less-managed was used to describe the unmanaged forests in the study. Recent studies demonstrate that many WKHs are forest fragments resulting from selective cutting and abandonment by modern forestry during the 20th century (Ericsson et al. 2005, Jönsson et al. 2009). The results of WKH history in the present study concurs with E. Hellberg (2003) results that a part of the present deciduous WKH forests has its origins in coniferous stands where timber harvesting have been conducted.

The results showed that non-intensive management during a period no longer than 90 years can result in forest stands that can be considered to have high biological value corresponding to WKH criteria. Similar findings have been 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 and now is a WKH with mean tree age of 44 years. However, the presence of deciduous trees with age more than 110 years could suggest that the previous method of cutting left some trees and patches of advanced growth undisturbed. Five of the studied WKHs (one managed and four less-managed) contained trees older than 150 years. The harvest methods in the studied forests allowed to maintain important structural features such as large living trees, which could not develop in less than 90 years (Jönsson and Jonsson 2009).

The historical information gives us the possibility to evaluate the time to attain conditions resembling old-growth forests after logging. According to the study of K.N. Suding (2011) such kinds of processes in the studied WKHs could be considered as passive restoration. Thus, the present structures in the stands can also be used to model the development of natural quality after passive restoration.

4.3. Richness of structural elements in woodland key habitats

In the present study the total CWD volume, volume of downed trees and volume of dead standing trees showed high variation between stands but did not differ significantly between managed and less-managed forests. There were minor differences in living and CWD variables between both forest groups.

The observed mean value of CWD in less-managed WKHs was 100.2 m^3/ha and 63.7 m^3/ha in managed stands, respectively. The volume of CWD in both studied forest groups was notably more than the average volume of CWD in Latvia (17.7 m^3/ha) reported by MCPFE (2011). In comparison with other studies the results showed that the mean volume even in managed WKH stands (63.7 m^3/ha) was twice higher than in the same type of WKH forests in Sweden (23.5 m^3/ha) (Jönsson and Jonsson 2007) and much higher than in south west Finland (6.6 m^3/ha) (Pykälä 2007). In addition, the values of CWD volumes in two of the stands - one managed (138.62 m^3/ha) and one less-managed (139.3 m^3/ha) - were in the range of the typical amounts of dead wood of old-growth forest in Estonia (129 m^3/ha) (Lõhmus and Kraut 2010). Thus, the WKHs might be considered as hotspot areas when the volume of dead wood is considered, as also decribed in Scandinavian countries (Timonen et al. 2011).

Comparing the results of the present study with characteristics of old-growth forests (Siitonen et al. 2000), the studied WKHs were similar in some aspects. Almost all of the studied plots had higher volumes of downed trees than dead standing trees, except in the less-managed stand H. The highest proportion of the number of downed trees was composed of substrates in small diameter classes (10-19 cm). However, the volume of large diameter downed trees (> 30 cm) represented only a minor proportion of the total volume, except in the less-managed stand K. This is in contrast with a study of WKHs in Sweden, in which large downed trees were found to account for 51 % of total downed tree volume (Jönsson et al. 2009).

Across the different decay stages, downed trees in late stages of decomposition were relatively rare in both groups of stands, as is typical of WKHs in boreal Europe (Jönsson and Jonsson 2007) Also, the distribution of decay classes in the studied forests largely differs from older forests (Siitonen et al. 2000), in such a way showing the past management impact in the studied WKHs (Gibb. et al. 2005, Green and Peterken 1997). The lower availability of downed trees in the later decay stages could be result from removal of large diameter trees, because the greater size of dead wood results in the greater number of downed trees in the later decay stages (Gibb et al. 2005). The past removal of CWD in different times can affect the present amounts of CWD in different decay classes present (Kruys et al. 1999). On the other hand, uneven distribution of decay stages could indicate that forest has not returned to a natural state after the activities of logging (Storaunet et al. 2005).

The managed stands contained more living trees in the mid-size class (DBH 20-29 cm) and significantly less volume of downed trees > 30 cm in diameter. This could indicate less input of large diameter dead wood in managed forest stands, which is explained with smaller size or younger age of the living trees. The results showed that only one of the managed stands had downed trees with DBH > 30 cm. In comparison with other studies (Jönsson and Jonsson 2007, Lõhmus and Kraut 2010), this clearly indicates the relationship between past management and occurrence of large diameter CWD.

In summary, the results showed that total amount of CWD was relatively high, in such a way demonstrating that less than 50 years (according to the history data about the youngest studied WKH) after clear cuts or spruce removal is enough to develop many important structural characteristics of WKHs forests like volume of dead wood, dead standing trees and downed trees. At the same time the quality of dead wood did not represent characteristics of old-growth forests in both studied forest groups: managed and less-managed WKHs. The management has strongly decreased the number of large well decayed downed trees. Thus, the effects of forestry on forest structures as CWD are visible for a long time. This indicates that a period longer than studied 90 years is needed to attain a more or less continuous recruitment of downed trees of all sizes and decay classes. At present, the studied WKHs indicated a lack of temporal continuity.

4.4. Richness of bryophyte species in woodland key habitats

The results showed that total bryophyte species richness on CWD and living trees, as well as indicator species richness on living trees did not differ significantly between managed and less-managed stands. The results concur with the findings of other studies where a management effect on species richness did not appear to be significant (Friedel et al. 2006, Lõhmus et al. 2007; Lõhmus and Lõhmus 2008, Rajandu et al. 2009). It has been shown before that WKHs do not necessarily have higher density of rare bryophyte species than productive forests (Gustafsson et al. 2004b). Also, bryophyte species richness in old managed forests can be similar to that in WKHs (Perhans et al. 2007).

According to the species number on different substrates, the results showed higher richness of epiphytes. In the present study the larger part of WKH indicator species were associated with living trees. The main factors explaining total and indicator species richness on living trees was heterogeneity in tree species, tree age and diameter. The results were in accordance with findings of previous studies that high epiphytic species richness in stands is associated with substrate diversity (Lõhmus et al. 2007, Fritz et al. 2008, Király and Ódor 2010), which in the present study were represented by diversity of tree species.

The results showed that the highest total species richness was found on *Populus tremula*, showing that aspens are high quality trees in epiphytic bryophyte species richness (Mežaka et al. 2012, Kuusinen 1996). The broad-leaved trees such as *Ulmus glabra, Fraxinus excelsior* and *Acer platanoides* also had high number of WKHs indicators, affirming that broad-leaved species are important for bryophyte species richness in managed forests (Lõhmus et al. 2007). These tree species are associated with high epiphyte richness because they have average high bark pH and moisture level comparing with spruce (Mills and Macdonald 2005).

The GLMM analysis showed that for epiphyte richness also tree age and tree diameter were significant factors. Tree age was clearly also an important factor, simply because old deciduous trees have larger stem diameter, which supports higher species richness, including also rare bryophyte species richness (Snäll et al. 2004, 2003, Berg et al. 2002, Lõhmus and Lõhmus 2008, Mežaka et al. 2008). Also, big trees have more species because they are characterized by larger heterogeneity of microsites and provide habitats for species with specific requirements (Friedel et al. 2006). However, it is known that also the diameter could reflect the time that tree has been available for colonization (Snäll et al. 2003). However, there were found no high correlation between tree age and diameter in the study, and therefore both variables were included in the GLMM analysis.

In conclusion our results suggest that sufficient bryophyte species richness on living trees typical of a WKH can be attained with time also in managed forests, given suitable diversity of deciduous tree substrate. In addition, the existence of large old trees that probably are left after clear-cutting is especially important to increase epiphytic species richness.

In comparison with the number of bryophytes found on living trees, the richness of bryophyte species on CWD was low. The results showed that only three epixylic indicator species were found. Less than 1/3 part from all WKH indicators was related with dead wood. It was found in the present study that indicator species difference on CWD was significantly higher in less-managed stands. Nevertheless, only one of the indicator species *Riccardia palmata* was found only in less-managed stands. Also, the observed difference between both forest groups could be related with epiphytic indicator species, which can still survive on dead standing trees and downed trees. In any case, the obtained results are in accordance with previous studies that showed negative impact of forest management on bryophyte species richness on CWD (Söderström 1988a, Andersson and Hytteborn 1991, Meier et al. 2005).

The significant relationship of total and indicator species richness with decay stage of downed trees in the GLMM analysis suggests that the higher richness was due to greater temporal continuity of dead wood supply. Also, the highest bryophyte richness on downed trees was in the middle decay stages, as previously found (Söderström 1988b, Andersson and Hytteborn 1991, Crites and Dale 1998, Ódor and van Hees 2004, Jansová and Soldán 2006). Other studies have shown higher bryophyte species richness on well decayed dead wood (Rambo and Muir 1998, Humphrey et al. 2002, Pharo et al. 2004). The higher bryophyte species richness in the middle decay stages can be explained by several factors. More decayed downed trees are closer to forest floor and less exposed to drying, and they hold more water and provide a moister substrate and humid microclimate favourable for many species, especially liverworts (Rambo and Muir 1998). Additionally, later decay stages provide more heterogeneous substrate and more niches are available (Kruys et al. 1999).

Overall, the observed low number of epixylic species might be due to different amounts of CWD in late decay stages and their past continuity of supply. Old-growth forests and even mature managed forests are dominated by middle and last decay stages (Lõhmus and Kraut 2010). Additionally, a low number of large diameter downed trees in the studied WKHs, especially in managed stands, probably reduced the possibility for many epixylic liverworts to exist, as suggested previously (Ódor and Van Hees 2004, Söderström 1988a). So far it has been proved that stands with longer continuity promote richness of bryophytes because they have more old-growth structures as CWD and they also provide necessary time for dispersal limited bryophytes like liverworts (Rambo and Muir 1998).

The GLMM results showed that substrate was an important factor for total bryophyte species richness. The highest number of species was found on downed trees. This might be explained by the different ecological conditions between stumps and downed trees. It is known that downed trees are more humid and thereby provide better habitat for dead wood depending bryophyte species (Rajandu et al. 2009). Also tree species was an important variable in GLMM model for indicator species richness. The richest substrate with indicator species was dead wood of *Populus tremula.* Thus, downed wood of deciduous trees could be important structures to sustain the richness of indicator bryophytes (Suško 1998). This is in accordance with the study of L.I. Andersson and H. Hytteborn (1991) where *Populus tremula* had the high number of epixylic species. None of the stand variables were significant in the created GLMM models showing that mostly species richness is explained by substrate (Mežaka et al. 2012).

As affirmed previously, bryophyte richness on CWD was best associated with substrate, tree species, decay stage of CWD and was negatively affected by management. This means that old-growth structural elements that were missing in the studied WKHs are related with low number of indicator species on downed trees. While in the present study it was not possible to found direct relationship between dead wood diameter and bryophyte species richness. The present results indicated that lack of large downed trees likely explains the low number of indicator species on downed trees in the studied WKHs.

Summarizing, the study showed that the bryophytes that indicated old-growth forests characteristics in the studied WKHs were mainly related with large old deciduous trees and large CWD in intermediate decay stages. The negative impact of clear-cutting and selective tree remove still remains in the managed forests even after 90 years. On another hand, the results indicates that by leaving WKHs unmanaged the amount of old trees and large diameter dead wood will increase, as well richness of bryophyte species.

4.5. Richness of structural elements and bryophyte species in studied *Quercus robur* forests

In the present study, the oak-lime stand in Moricsala was used as sample plot to illustrate structural elements of one of the most natural forest in Latvia. According to characteristics of living trees and amounts of CWD the studied stand represented an old growth forest.

The results showed high density of large diameter trees, from which the highest part of living trees with DBH > 30 cm were larger than 50 cm in diameter (not shown in results). This is consistent with characteristics of old growth forests in central Europe and southern Sweden (Nilsson et al. 2002), where large (> 40 cm in diameter) trees have dominance in these forests.

Secondly, the total volume of CWD in the present study was 219.43 m^3/ha, of which almost half was volume of downed trees. This is more than average amount of dead wood in old-growth forests in Europe (200 m^3/ha) (Nilsson et al. 2002). The dead wood amount was also higher than in old-growth forests in Estonia (Lõhmus and Kraut 2010). In addition, the present study showed that the volume of downed woody material (101.4 m^3/ha) reached the amounts that are typical of mesic deciduous forests in Białowieża National Park, Poland (84 – 157 m^3/ha) (Bobiec 2002).

The highest proportion of volume of downed trees was in the diameter class > 30 cm and reached volume that was more than > 70 m^3/ha. This is in accordance with typical amounts in in other studied old-growth forests (Siitonen et al. 2000, Lõhmus and Kraut 2010). All of the described features of the studied forest stand in Moricsala showed that this forest is structurally very rich.

The other four studied *Quercus robur* forests were structurally poor compared with the studied plot in Moricsala. According to the tree ages and volume of CWD only one (stand M) of the studied four oak plots had some characteristics of the Moricsala forest. The results showed that the plot of stand M had higher total volume of CWD (239.56 m3/ha) than Moricsala. Also plot M had a very large amount of downed trees, from which the largest part was formed by dead wood > 30 cm in diameter. Thus, this stand can be considered as a WKH that represents a hotspot area concerning CWD amounts.

In the other studied plots (stands N – P) the volumes of downed trees were very low. This is likely because the downed trees objects were dominated by small size classes. In the present study there was a deficit of large diameter downed trees in plot N. Also the decay stages of downed trees differed between Moricsala plot and other oak forests. The results showed that all decay stages were found in the Moriscala plot. The other studied plots (stands M – P) had uneven distribution of decay stages and most downed trees were in the first two decay stages.

The characteristics of dead wood in the three studied plots (stands N – O) clearly indicated the lack of temporal forest continuity. The historical material did not show any management during the last 50 years. However, evidence of logging activities was found in two of the studied stands (stands O and P). Perhaps, dead trees had been removed in the stand O. The cut stumps all had large diameter. The low mean tree age and presence of stumps in the plot P clearly indicated previous cutting. Also, plot P lacked living trees with DBH > 30 cm. This stand was not designated as a WKH or other protected area. Therefore, the stand represents a commercial forest. Although in the stand N, which was located in a Nature Reserve, representing one of the oldest oak forests in Latvia, the quality and quantity of CWD was lower than in plot P (commercial forest stand).

In the present study, bryophyte species richness was determined in four oak plots, but not in Moricsala. The results showed that the number of recorded bryophyte species was low in comparison with the richness of species in the studied deciduous WKHs. According to the low number of substrates, GLMM models were not made for bryophyte species richness in the oak forests. However, it could be expected that the same factors which were significant for species richness in the studied WKHs can explain low number of species in the oak forests. In addition, the species composition was similar in both studied forest type groups. Thus, the low number of bryophytes on downed trees in the studied oak forests was probably due to low occurrence of large dead wood and the absence of late decay stages. While the number of indicator species on living trees was also low, almost all of the studied oak plots contained large old deciduous living trees. The largest part of large deciduous trees (DBH > 30 cm) was recorded for oaks. Possibly, *Quercus robur* is not as important for rare bryophytes, when compared to other trees species, while the situation is reversed for lichen species (Berg et al. 2002).

The results showed that the plots in stand P and in stand O had low numbers of indicator bryophyte species of WKHs (two and one species, respectively). The other two stands (which were considered to be more natural than stands O and P), had a slightly higher number of indicators on CWD, most of which were epiphytes that still survived on the dead wood.

Summarizing, the studied four oak forests showed a low level of structural element richness and richness of indicator species that characterize old-growth forests, and also in comparison with the most natural oak forest in Latvia.

Conclusions

1. The obtained results showed that high bryophyte species richness based on occurrence of woodland key habitat species can exist in managed forests.
2. In the managed forest landscape the high bryophyte species richness on living trees is mostly determined by occurrence of large diameter broad-leaved trees and aspens.
3. The studied managed forest landscape does not support high bryophyte species richness on coarse woody debris, due to lack of large dead wood and low forest continuity.
4. The historical study on deciduous woodland key habitats confirmed that some of the high-value stands had been harvested in the last 90 years. The natural regeneration of forests resulted in stands that today are considered as deciduous woodland key habitats.
5. The studied woodland key habitats had high volume of coarse woody debris, which could be reached even in a 50-year period. However, even a 90-year period is not a sufficient time period to obtain high quality of coarse woody debris, like large diameter dead wood and continuity according to the decay stages of downed trees.
6. The deciduous woodland key habitats had sufficient bryophyte species richness on living trees in cases when there was high diversity of deciduous tree species.
7. Management has a negative effect on the quality of dead wood and the richness of species found on coarse woody debris.
8. The studied *Quercus robur* forests showed low relation to characteristics of natural forests according to structural elements and bryophyte species richness.

Theses

1. High bryophyte species richness can develop in managed forests, including species that are sensitive to various human activities, provided that there are structural elements that support species growth.
2. High bryophyte species richness is related with deciduous forest stands. Deciduous forests can develop in a short time period structural elements that ensure suitable growth conditions for woodland key habitat indicator species.

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Appendix

Appendix 1-1

Coordinates of plots in the five studied transects. Each transect was divided in eight sections and each section was divided in five subsections. The coordinates of established plots (50 m) are shown.

1 transect

Section	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**
1 subsection								
x	524825	525318	525811	526304	526806	526308	525809	525311
y	6383753	6383670	6383587	6383504	6384584	6384627	6384671	6384714
x	524874	525367	525860	526353	526756	526258	525759	525261
y	6383745	6383662	6383579	6383512	6384588	6384631	6384675	6384718
2 subsection								
x	524924	525417	525910	526403	526706	526208	525709	525211
y	6383736	6383653	6383570	6383521	6384593	6384636	6384680	6384723
x	524973	525466	525959	526452	526657	526159	525660	525162
y	6383728	6383645	6383562	6383529	6384597	6384640	6384684	6384727
3 subsection								
x	525022	525515	526008	526501	526607	526109	525610	525112
y	6383720	6383637	6383554	6383538	6384601	6384645	6384688	6384731
x	525072	525565	526058	526550	526557	526059	525560	525062
y	6383711	6383628	6383545	6383546	6384606	6384649	6384693	6384736
4 subsection								
x	525121	525614	526107	526600	526507	526009	525510	525012
y	6383703	6383620	6383537	6383554	6384610	6384653	6384697	6384740
x	525170	525663	526156	526649	526457	525959	525460	524962
y	6383695	6383612	6383529	6383563	6384614	6384658	6384701	6384744
5 subsection								
x	525219	525712	526205	526698	526407	525910	525410	524912
y	6383687	6383604	6383521	6383571	6384618	6384662	6384705	6384748
x	525269	525762	526255	526748	526358	525860	525361	524863
y	6383678	6383595	6383512	6383580	6384623	6384667	6384710	6384753

Appendix 1-2

Coordinates of plots in the five studied transects. Each transect was divided in eight sections and each section was divided in five subsections. The coordinates of established plots (50 m) are shown.

2 transect

Section	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**
1 subsection								
x	527639	527990	528342	528693	528786	528468	528149	527831
y	6394063	6394419	6394775	6395131	6397155	6396770	6396384	6395999
x	527674	528025	528377	528728	528754	528436	528117	527799
y	6394099	6394455	6394811	6395167	6397116	6396731	6396345	6395960
2 subsection								
x	527709	528060	528412	528763	528722	528404	528085	527767
y	6394134	6394490	6394846	6395202	6397078	6396693	6396307	6395922
x	527744	528095	528447	528798	528690	528372	528053	527735
y	6394170	6394526	6394882	6395238	6397039	6396654	6396268	6395883
3 subsection								
x	527779	528131	528482	528833	528659	528341	528022	527704
y	6394205	6394561	6394917	6395273	6397001	6396616	6396230	6395845
x	527815	528166	528518	528869	528627	528309	527990	527672
y	6394241	6394597	6394953	6395309	6396962	6396577	6396191	6395806
4subsection								
x	527850	528201	528553	528904	528595	528277	527958	527640
y	6394277	6394632	6394989	6395345	6396924	6396539	6396153	6395768
x	527885	528236	528588	528939	528563	528245	527926	527608
y	6394312	6394668	6395024	6395380	6396885	6396500	6396114	6395729
5 subsection								
x	527920	528271	528623	528974	528531	528213	527894	527576
y	6394348	6394703	6395060	6395416	6396847	6396462	6396076	6395691
x	527955	528306	528658	529009	528499	528181	527862	527544
y	6394383	6394739	6395095	6395451	6396808	6396423	6396037	6395652

Appendix 1-3

Coordinates of plots in the five studied transects. Each transect was divided in eight sections and each section was divided in five subsections. The coordinates of established plots (50 m) are shown.

3 transect

Section	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**
1 subsection								
x	535838	535725	535613	535500	536493	536607	536721	536834
y	6406971	6407458	6407945	6408433	6409770	6409283	6408796	6408309
x	535827	535714	535602	535489	536504	536618	536732	536845
y	6407020	6407507	6407994	6408482	6409721	6409234	6408747	6408260
2 subsection								
x	535815	535703	535590	535477	536516	536630	536744	536857
y	6407068	6407555	6408042	6408530	6409673	6409186	6408699	6408212
x	535804	535691	535579	535466	536527	536641	536755	536868
y	6407117	6407604	6408091	6408579	6409624	6409137	6408650	6408163
3 subsection								
x	535793	535680	535568	535455	536539	536653	536766	536880
y	6407166	6407653	6408140	6408628	6409575	6409088	6408601	6408114
x	535781	535669	535557	535443	536550	536664	536778	536891
y	6407215	6407702	6408189	6408677	6409527	6409040	6408552	6408066
4 subsection								
x	535770	535658	535545	535432	536561	536675	536789	536902
y	6407263	6407750	6408237	6408725	6409478	6408991	6408504	6408017
x	535759	535647	535534	535421	536573	536687	536800	536914
y	6407312	6407799	6408286	6408774	6409429	6408942	6408455	6407968
5 subsection								
x	535748	535635	535523	535410	536584	536698	536811	536925
y	6407361	6407848	6408335	6408823	6409381	6408894	6408406	6407920
x	535736	535624	535511	535398	536596	536710	536823	536937
y	6407409	6407897	6408383	6408871	6409332	6408845	6408358	6407871

Appendix 1-4

Coordinates of plots in the five studied transects. Each transect was divided in eight sections and each section was divided in five subsections. The coordinates of established plots (50 m) are shown.

4 transect

Section	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**
1 subsection								
x	588476	588689	588902	589116	589608	590102	590596	591090
y	6407575	6407123	6406671	6406218	6406307	6406232	6406156	6406080
x	588497	588710	588923	589165	589657	590151	590645	591139
y	6407530	6407078	6406626	6406227	6406299	6406224	6406148	6406072
2 subsection								
x	588519	588732	588945	589214	589707	590201	590695	591189
y	6407485	6407033	6406581	6406236	6406292	6406217	6406141	6406065
x	588540	588753	588966	589264	589756	590250	590744	591238
y	6407439	6406987	6406535	6406245	6406284	6406209	6406133	6406057
3 subsection								
x	588561	588774	588987	589313	589806	590300	590794	591288
y	6407394	6406942	6406490	6406254	6406277	6406202	6406126	6406050
x	588583	588796	589009	589362	589855	590349	590843	591337
y	6407349	6406897	6406445	6406263	6406269	6406194	6406118	6406042
4 subsection								
x	588604	588817	589030	589411	589905	590399	590893	591387
y	6407304	6406852	6406400	6406271	6406262	6406186	6406110	6406034
x	588625	588838	589051	589460	589954	590448	590942	591436
y	6407258	6406806	6406355	6406280	6406254	6406179	6406103	6406027
5 subsection								
x	588647	588860	589073	589510	590003	590497	590991	591485
y	6407213	6406761	6406309	6406289	6406247	6406171	6406095	6406019
x	588668	588881	589094	589559	590053	590547	591041	591535
y	6407168	6406716	6406264	6406298	6406239	6406164	6406088	6406012

Appendix 1-5

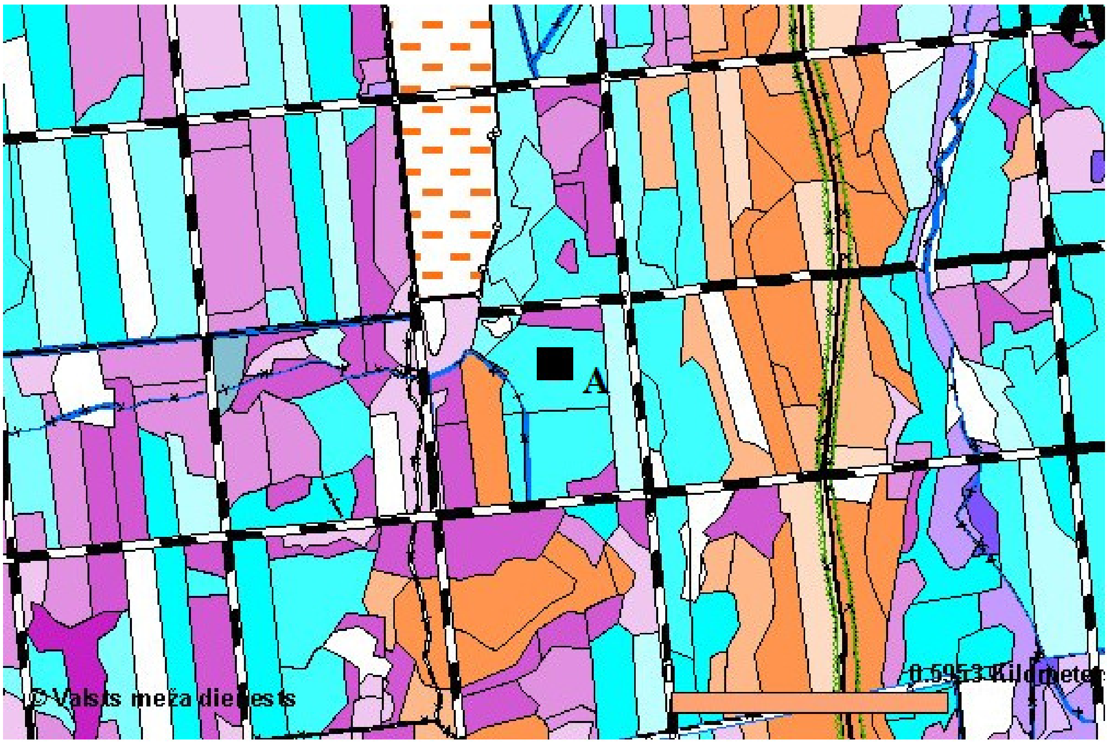
Coordinates of plots in the five studied transects. Each transect was divided in eight sections and each section was divided in five subsections. The coordinates of established plots (50 m) are shown.

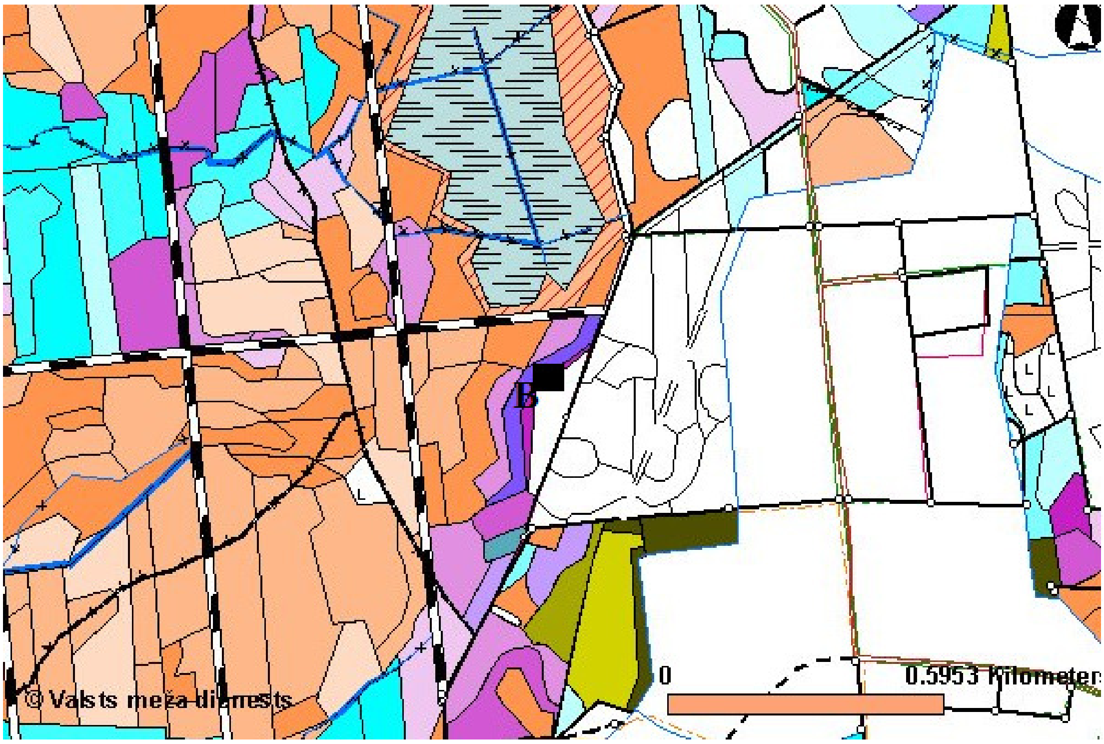
5 transect

Section	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**
1 subsection								
x	598573	599042	599511	599980	600449	600537	600625	600713
y	6413281	6413453	6413626	6413799	6413972	6414465	6414957	6415449
x	598620	599089	599558	600027	600458	600546	600634	600722
y	6413298	6413470	6413643	6413816	6414021	6414514	6415006	6415498
2 subsection								
x	598667	599136	599605	600074	600467	600555	600643	600731
y	6413315	6413488	6413661	6413834	6414070	6414563	6415055	6415547
x	598714	599183	599652	600121	600475	600563	600651	600739
y	6413333	6413505	6413678	6413851	6414120	6414613	6415105	6415597
3 subsection								
x	598761	599230	599699	600168	600484	600572	600660	600748
y	6413350	6413522	6413695	6413868	6414169	6414662	6415154	6415646
x	598808	599277	599746	600215	600493	600581	600669	600757
y	6413367	6413540	6413713	6413886	6414218	6414711	6415203	6415695
4 subsection								
x	598855	599323	599792	600261	600502	600590	600678	600766
y	6413384	6413557	6413730	6413903	6414267	6414760	6415252	6415744
x	598902	599370	599839	600308	600511	600599	600687	600775
y	6413402	6413574	6413747	6413920	6414317	6414810	6415302	6415794
5 subsection								
x	598949	599417	599886	600355	600519	600607	600695	600783
y	6413419	6413591	6413764	6413937	6414366	6414859	6415351	6415843
x	598995	599464	599933	600402	600528	600616	600704	600792
y	6413436	6413609	6413782	6413955	6414415	6414908	6415400	6415892

Appendix 2-1

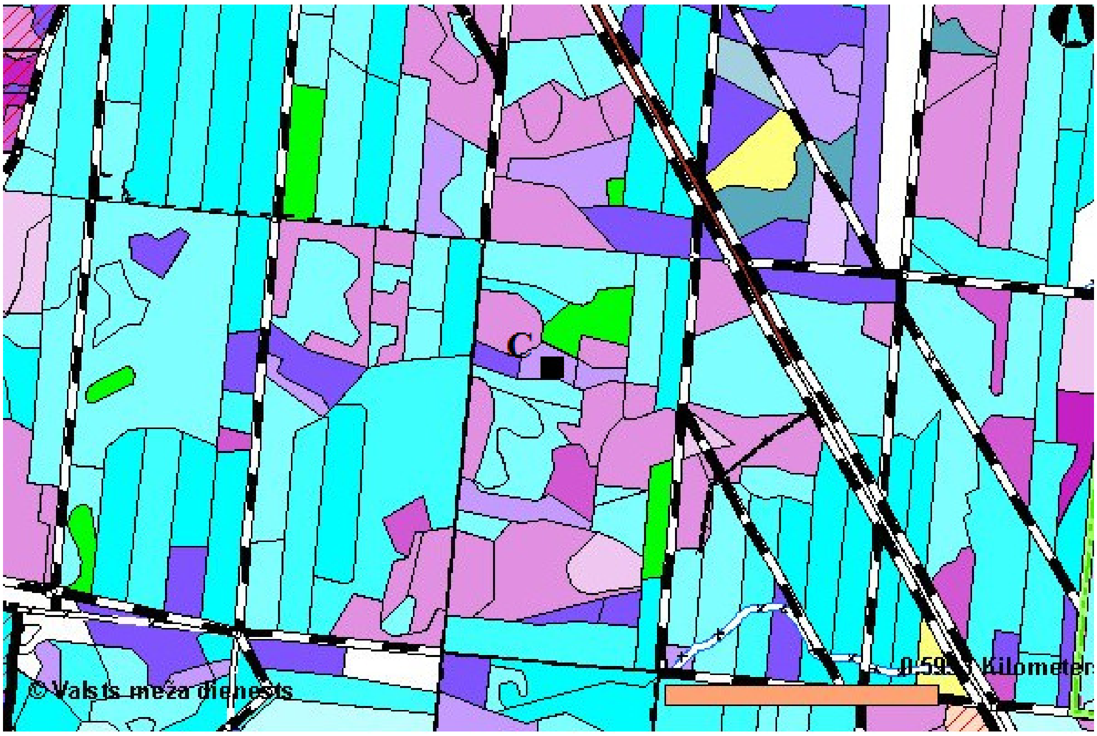
Location of studied stands (stands A – P, Moricsala) shown on forest inventory maps. Scale 1:15000.





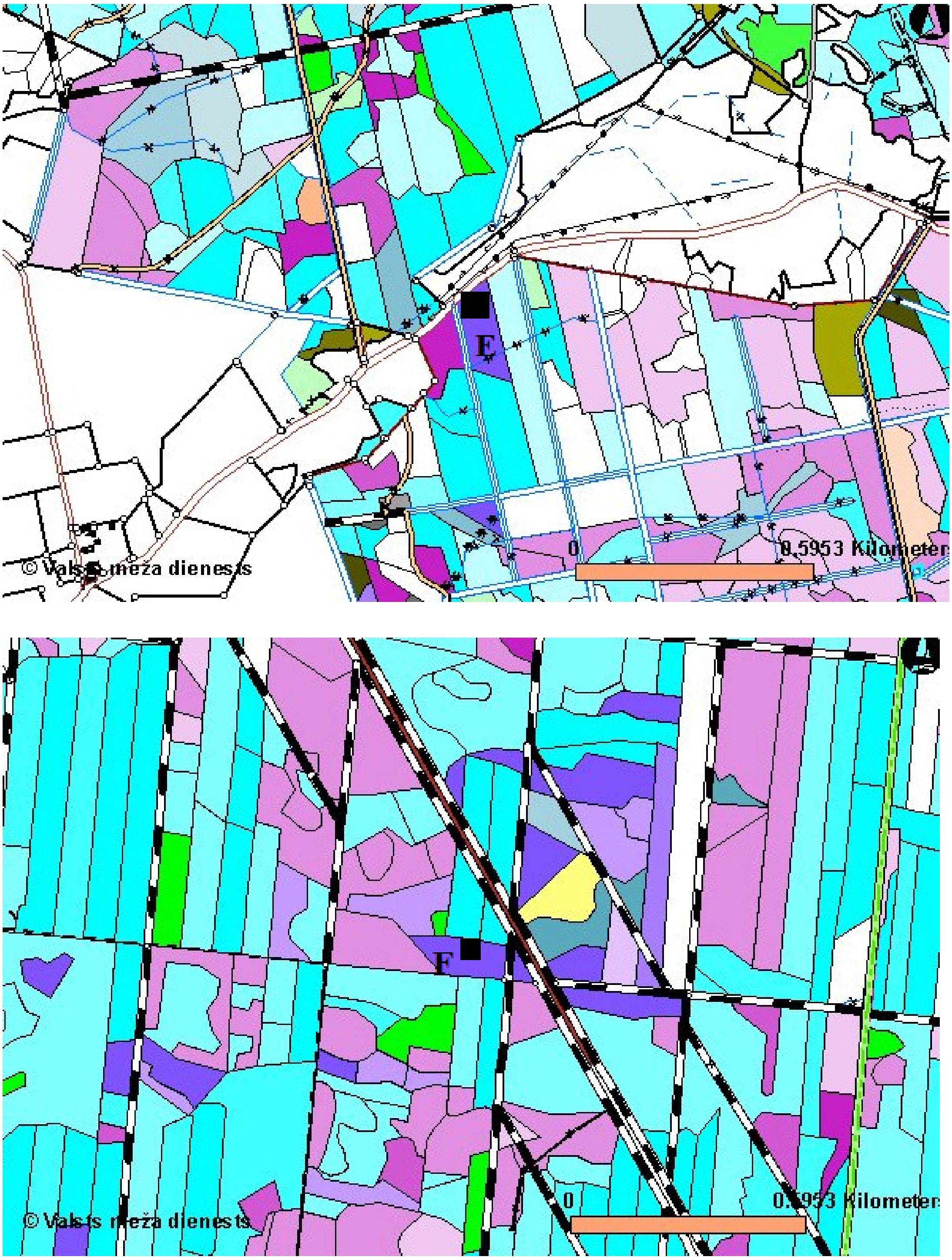
Appendix 2-2

Location of studied stands (stands A – P, Moricsala) shown on forest inventory maps. Scale 1:15000.



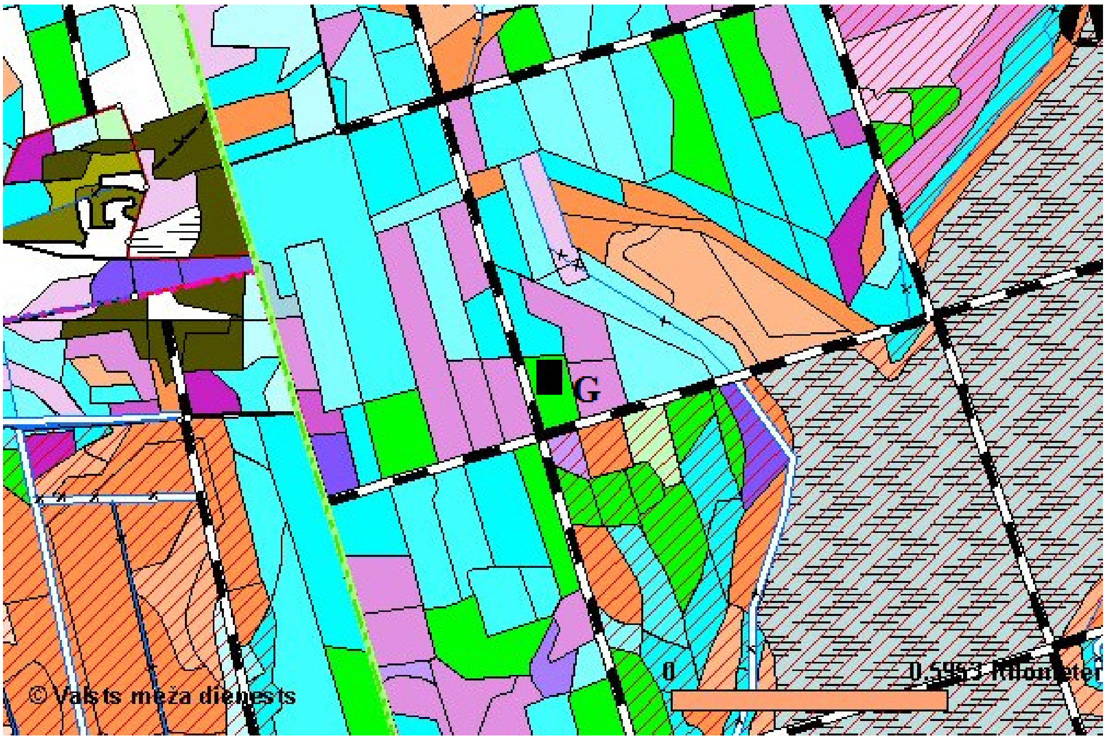
Appendix 2-3

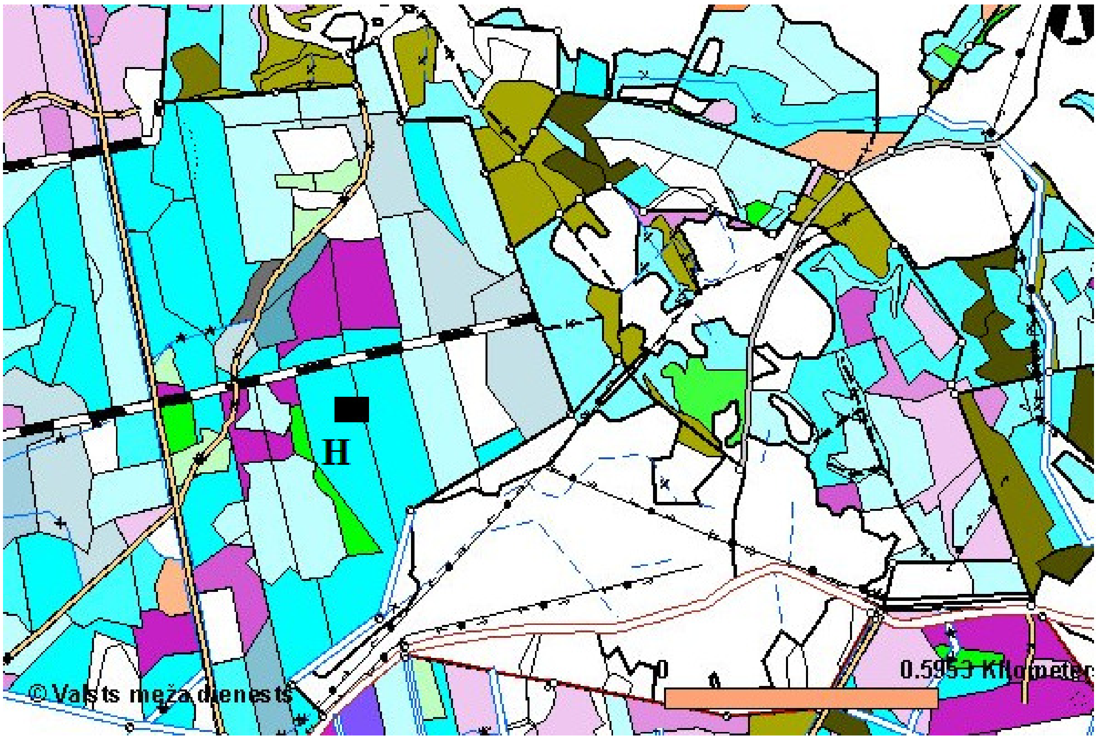
Location of studied stands (stands A – P, Moricsala) shown on forest inventory maps. Scale 1:15000.



Appendix 2-4

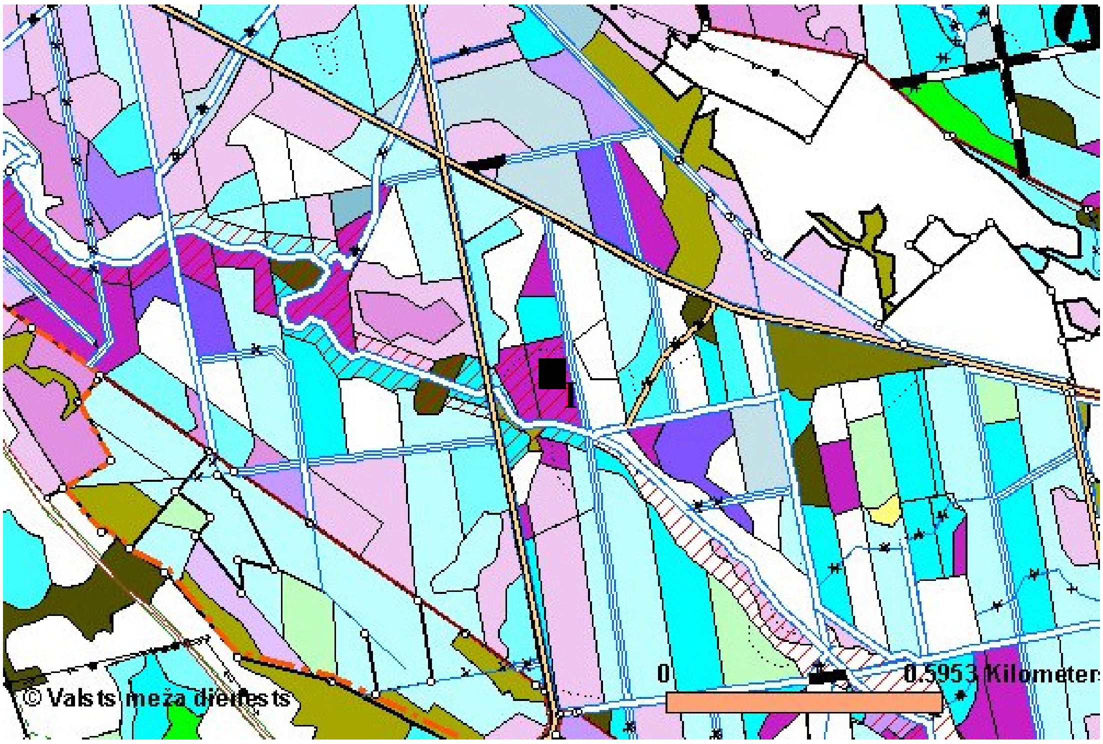
Location of studied stands (stands A – P, Moricsala) shown on forest inventory maps. Scale 1:15000.

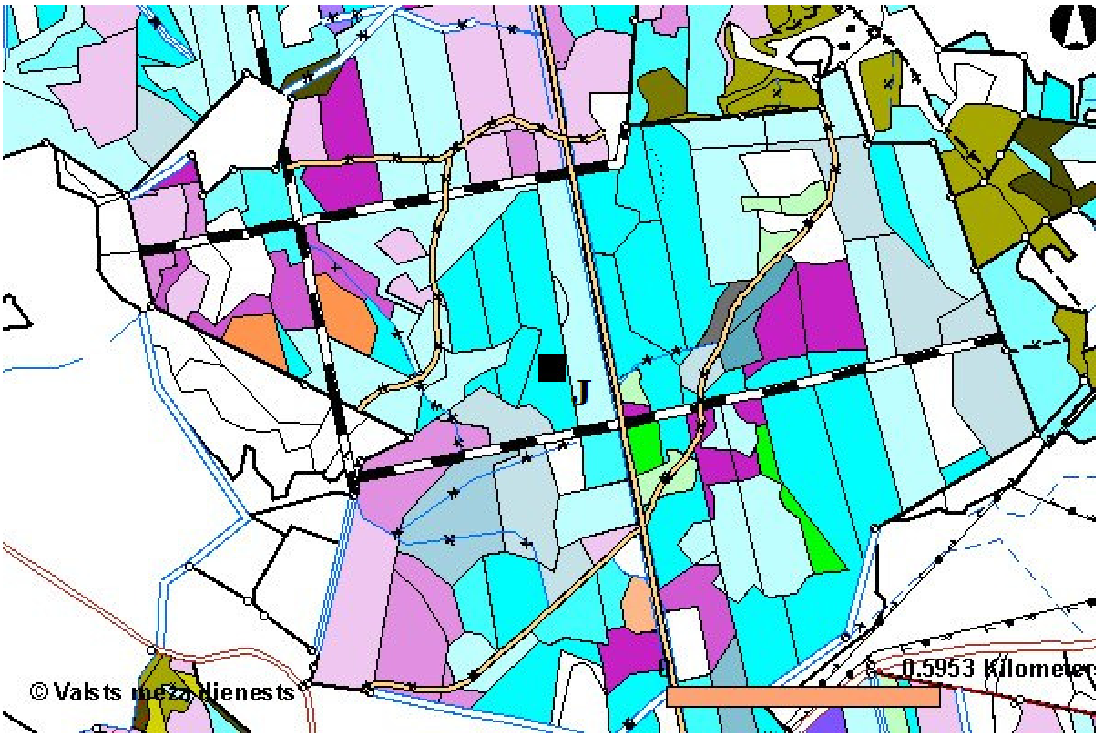




Appendix 2-5

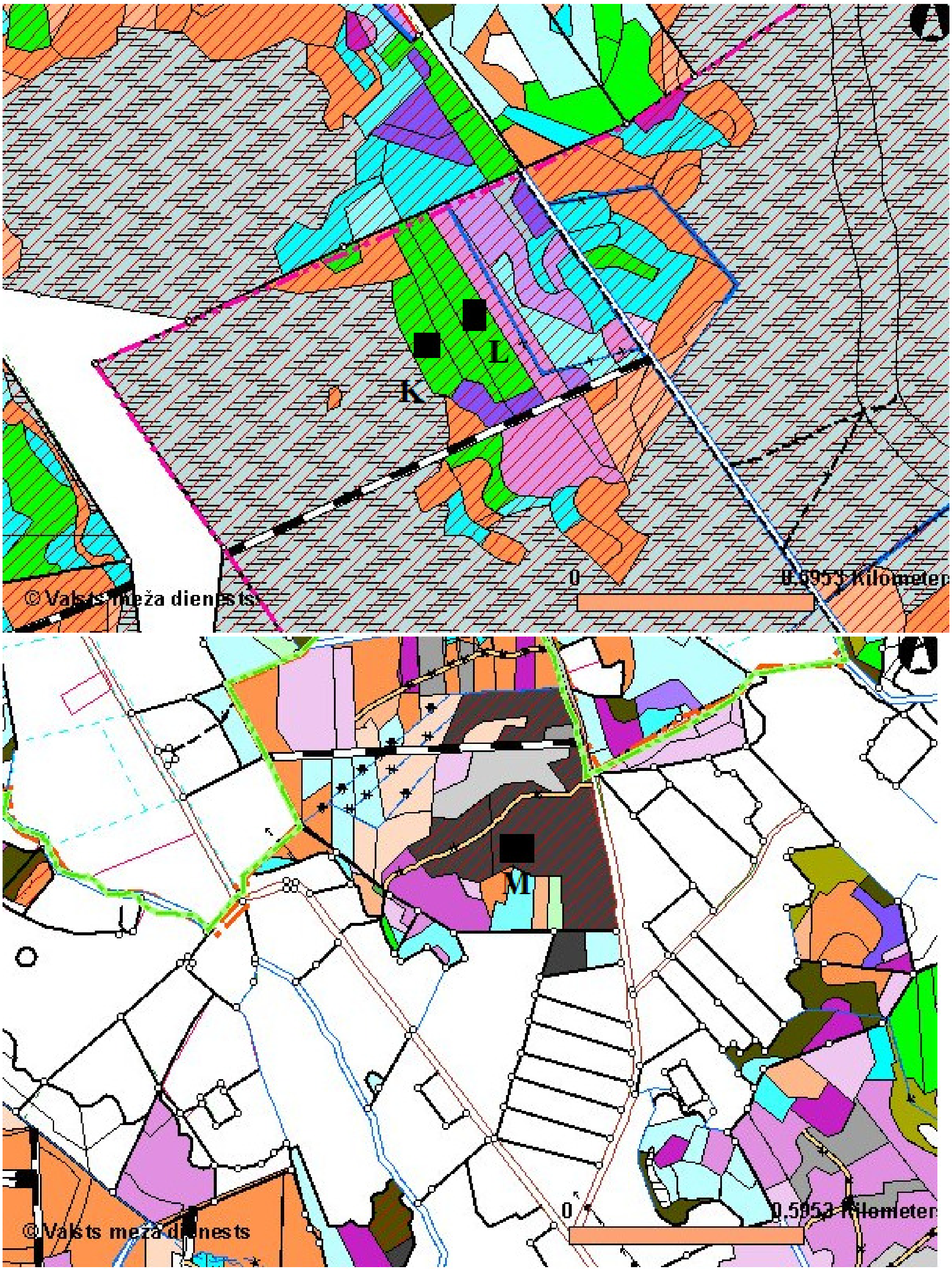
Location of studied stands (stands A – P, Moricsala) shown on forest inventory maps. Scale 1:15000.





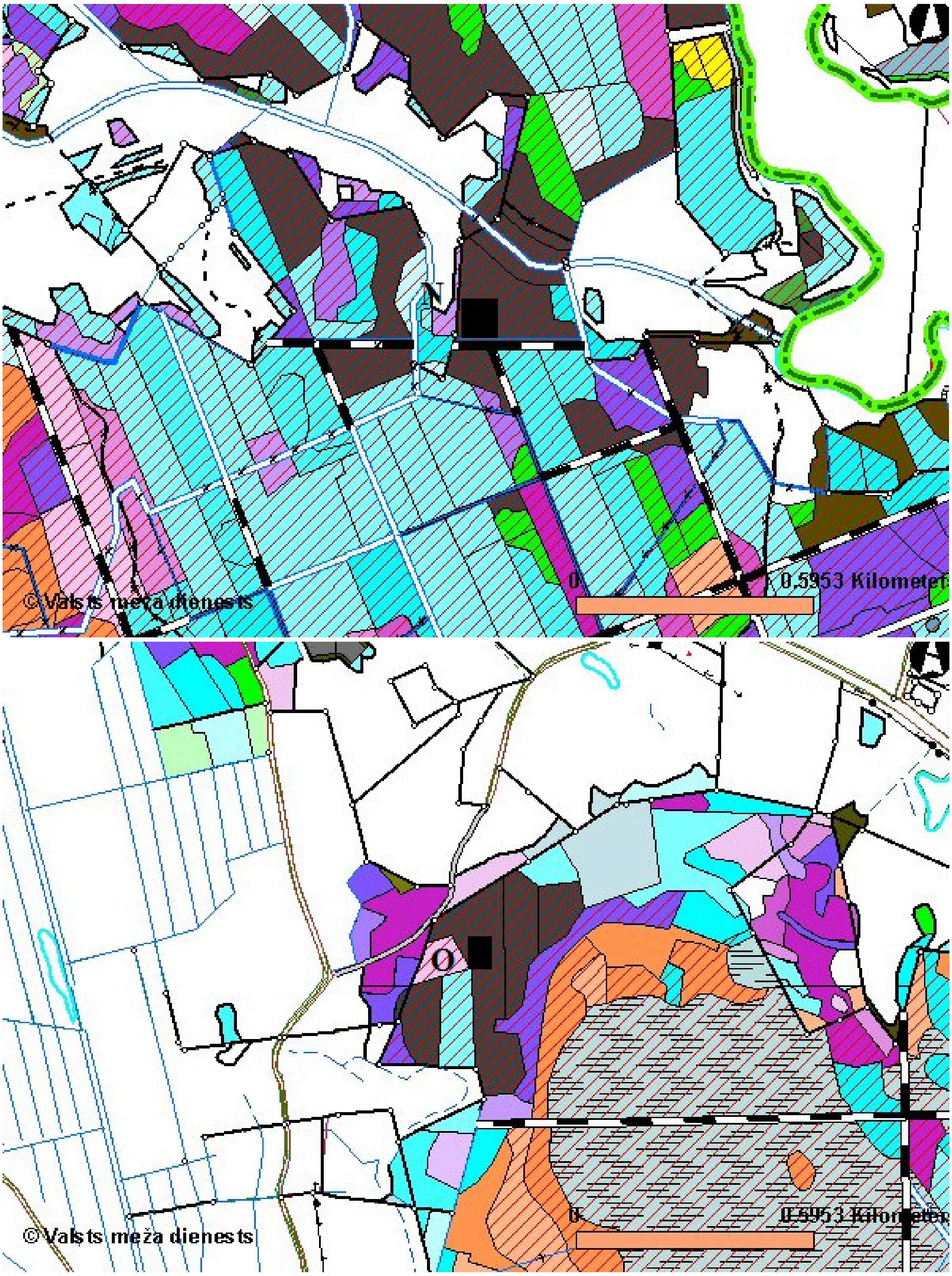
Appendix 2-6

Location of studied stands (stands A – P, Moricsala) shown on forest inventory maps. Scale 1:15000.



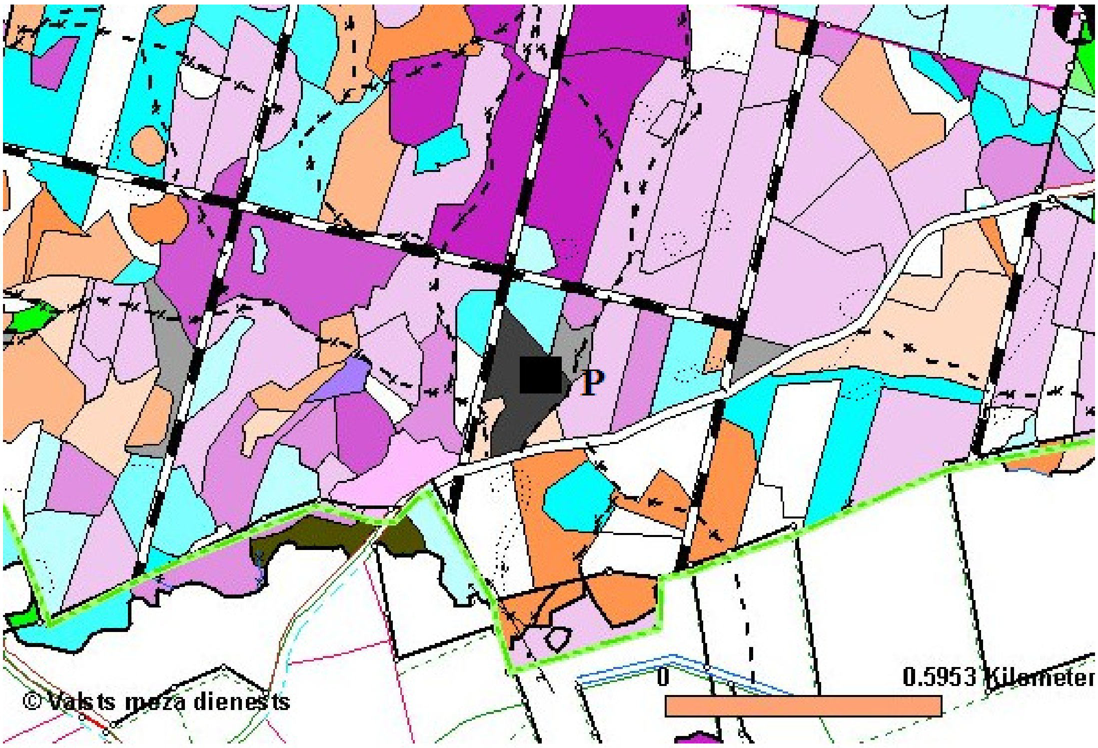
Appendix 2-7

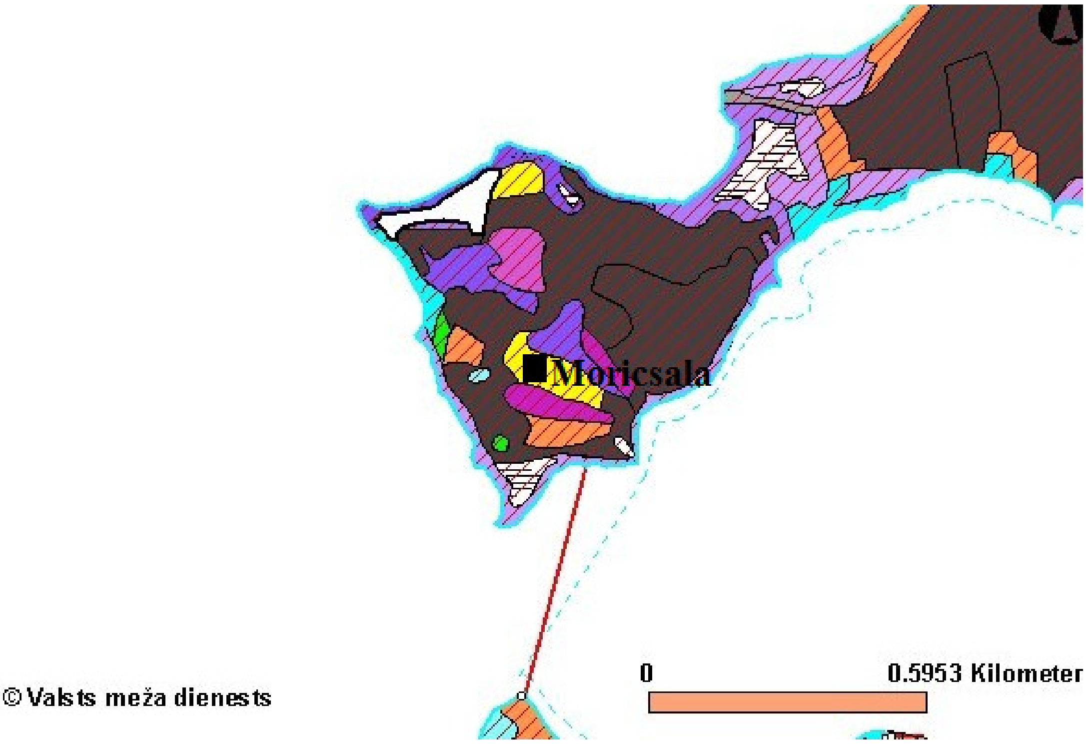
Location of studied stands (stands A – P, Moricsala) shown on forest inventory maps. Scale 1:15000.



Appendix 2-8

Location of studied stands (stands A – P, Moricsala) shown on forest inventory maps. Scale 1:15000.





Appendix 3-1

Logging history of the studied woodland key habitats (WKHs) and *Quercus robur* stands. Mean and maximum tree ages is given for deciduous, coniferous and separately for oak 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; 2011 – mixed black alder, birch, spruce, ash 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; 2011 – mixed black alder, spruce 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; 2011 – black alder, spruce, birch 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; 2011 – mixed spruce, aspen stand.	Selective cut 1941-1960	1(aspen), 4 (unknown)
E	76 (black alder – 99, spruce – 150)	1932 – clearcut; 1982 – young birch stand; 2011 – mixed black alder, spruce, birch stand.	Clearcut 1932	-

Appendix 3-2

Logging history of the studied woodland key habitats (WKHs) and *Quercus robur* stands. Mean and maximum tree ages is given for deciduous, coniferous and separately for oak trees.

Stand	Mean tree age in 2011 (max tree age)	Stand description in records	Time of clearcut/ wood removal	Number of cut stumps (species)
F	77 (black alder – 136, spruce – 110)	1929 – mixed young black alder, 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.		-

Appendix 3-3

Logging history of the studied woodland key habitats (WKHs) and *Quercus robur* stands. Mean and maximum tree ages is given for deciduous, coniferous and separately for oak trees.

Stand	Mean tree age in 2011 (max tree age)	Stand description in records	Time of clearcut/ wood removal	Number of cut stumps (species)
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.		-
M	113 (oak - 199, spruce - 137)	1960 - mature oak stand; 1972 - mixed oak, spruce, pine stand (110 years); 1892 - mature oak stand; 2011 - mixed spruce, oak stand.		
N	86 (oak - 327, spruce - 114)	1952 - mixed oak, ash stand (140 years); 2011 - mixed spruce, oak, black alder, ash, elm stand.		
O	107 (oak - 184, spruce - 144)	1960 - mature oak stand; 1972 - mature oak stand; 1982 - mature oak stand; 2011 - mixed spruce, oak stand.		4 (oak)
P	83 (oak - 92, aspen - 129, spruce - 107)	1961 - spruce stand (60 years); 1971 - mixed spruce, oak, birch and aspen stand (55 years); 2011 - mixed spruce, oak, aspen stand.		2 (unknown species)

Appendix 4-1

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). Also number of plots (n=4) where bryophyte species were recorded in *Quercus robur* stands is shown. Woodland key habitat (WKH) indicator species are indicated in bold.

	Deciduous woodland key habitats						*Quercus robur* stands			
	Substrate				Management		Substrate			
Bryophyte species	Living trees	Downed trees	Dead standing trees	Stumps	Managed	Less-managed	Living trees	Downed trees	Dead standing trees	Stumps
Liverworts										
Blepharostoma trichophyllum	2	5			3	3				
Calypogeia azurea		1				1				
Calypogeia neesiana		1				1				
Calypogeia sp.	1					1				
Calypogeia suecica		4		1	1	3				
Cephalozia bicuspidata	1	2		1	2	2				
Chephalozia connivens		1		1		2				
Chephalozia lunulifolia		2			1	1				
Chephaloziella elachista		1			1					
Chephaloziella spinigera		1				1				
Chiloscyphus pallescens		2				2				
Frullania dilatata	7	1	2		3	4	1			
Jamesoniella autumnalis	10	6		1	5	5				
Frullania tamarisci	1				1					
Lejeunea cavifolia	5		1		3	3	1		1	
Lepidozia reptans	11	7	4	2	5	6		1		1

Appendix 4-2

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). Also number of plots (n=4) where bryophyte species were recorded in *Quercus robur* stands is shown. Woodland key habitat (WKH) indicator species are indicated in bold.

	Deciduous woodland key habitats						*Quercus robur* stands			
	Substrate				Management		Substrate			
Bryophyte species	Living trees	Downed trees	Dead standing trees	Stumps	Managed	Less-managed	Living trees	Downed trees	Dead standing trees	Stumps
Lophocolea heterophylla	12	12	4	1	5	7	1	3		2
Metzgeria furcata	2		1		1	2				
Nowellia curvifolia		8	1		3	5		1		
Plagiochila asplenoides	1	4	2	2	4	6	2			
Ptilidium pulcherrimum	12	8	4		5	7	1			
Radula complanata	12	6	9		5	7	4	2	2	
Ricardia palmata		2				2				
Mosses										
Amblystegium serpens	5	1	1			5	3			
Anomodon attenuatus							1		1	
Atrichum undulaturm	1				1			2		
Aulacomnium androgynum	1				1					
Brachythecium campestre				1		1				
Brachythecium rutabulum	1	1	5		5	7	4	2	2	3
Brachythecium salebrosum	3	7	1		3	5		2		
Bryum subapiculatum	1				1					
Bryum subelegans								1		

Appendix 4-3

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). Also number of plots (n=4) where bryophyte species were recorded in *Quercus robur* stands is shown. Woodland key habitat (WKH) indicator species are indicated in bold.

	Deciduous woodland key habitats						*Quercus robur* stands			
	Substrate				Management		Substrate			
Bryophyte species	Living trees	Downed trees	Dead standing trees	Stumps	Managed	Less-managed	Living trees	Downed trees	Dead standing trees	Stumps
Calliergon cordifolium		3			2	1				
Calliergonella cuspidata	1	1			1	1				
Cirriphyllum piliferum	1				1					
Climacium dendroides	1	2			1	1				
Dicranum montanum	12	9	8	5	5	7	4	2	1	2
Dicranum polysetum	6	4	1	2	3	4				
Dicranum scoparium	12	1	5	6	5	7	3	2		2
Eurhynchium angustirete	12	11	7	6	5	7	3	1		1
Eurhynchium striatum	1				1		1	1		
Fissidens adianthoides	1				1					
Fissidens taxifolius		1				1	1			
Herzogiella seligeri	4	7	1		3	5		2		1
Homalia trichomanoides	9	3	5		4	6	4	2	1	1
Homalothecium sericeum	2		2		2	2	2			
Hylocomnium splendens	8	8	4	3	4	6		2		
Hypnum cupressiforme	12	11	9	3	5	7	4	4	2	3
Isothecium alopecuroides	2				1	1				

Appendix 4-4

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). Also number of plots (n=4) where bryophyte species were recorded in *Quercus robur* stands is shown. Woodland key habitat (WKH) indicator species are indicated in bold.

	Deciduous woodland key habitats						*Quercus robur* stands			
	Substrate				Management		Substrate			
Bryophyte species	Living trees	Downed trees	Dead standing trees	Stumps	Managed	Less-managed	Living trees	Downed trees	Dead standing trees	Stumps
Leucodon sciuroides	1		1		1	1	2			
Mnium hornum	3	2		1	3	2	2			
Neckera complanata	3		1		1	2				
Neckera pennata	7	1	4		2	5	2		1	
Orthotrichum affine	4				2	2				
Orthotrichum speciosum	4				2	2	1			
Oxyrrhynchium hians	4	1			1	3				
Plagiomnium affine	6	1		1	2	4	2	1		1
Plagiomnium cuspidatum	11	9	9	3	5	7	4	3	1	3
Plagiomnium undulatum	6	4	2	1	3	3				
Plagiothecium curvifolium	2				1	1		1		
Plagiothecium denticulatum	1					1				
Plagiothecium laetum	12	2	4	1	5	7	3	1		
Platygyrium repens	4	2		1	2	3	1			
Pleurozium schreberi	8	9	1	3	4	7		2		2
Pohlia cruda	1					1				
Polytrichum juniperinum	1	1		1	2					

Appendix 4-5

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). Also number of plots (n=4) where bryophyte species were recorded in *Quercus robur* stands is shown. Woodland key habitat (WKH) indicator species are indicated in bold.

	Deciduous woodland key habitats						*Quercus robur* stands			
	Substrate				Management		Substrate			
Bryophyte species	Living trees	Downed trees	Dead standing trees	Stumps	Managed	Less-managed	Living trees	Downed trees	Dead standing trees	Stumps
Ptilium crista-castrensis		4				4		1		
Pylaisia polyantha	5				3	2				
Rhizomnium punctatum	4	4			3	3	1			
Rhodobryum roseum	4	2			2	3	2			
Rhytidiadelphus triquetrus	1	1	4	5	5	7		1		
Sanionia uncinata	5	2	1		3	3			1	
Tetraphis pellucida	9	3	1	5	5	4				2
Thuidium delicatulum	6	2			2	4	2			1
Thuidium tamariscinum	6	2			3	4				
Ulota crispa	8	1	3		4	4	1			