UNIVERSITY OF LATVIA
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# EPIPHYTIC BRYOPHYTE AND LICHEN ECOLOGY IN LATVIAN DECIDUOUS FORESTS

**For Doctor of Biology Degree**
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**PhD Thesis**

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# Annotation

Epiphytic bryophytes and lichens are important components of global biodiversity. Nature protection and long-term forestry become more important due to the increase of modern forestry in forest ecosystems. Ecological studies about epiphytes are needed and are still insufficient in Latvia. The aim of the present study is to provide an overview of the epiphytic bryophyte and lichen flora and the main ecological characters in Latvian deciduous forests.

In total 148 epiphyte (73 bryophyte and 75 lichens) species were found in the present study. Overall 14 species were red-listed in Latvia and 21 were Woodland Key Habitat (WKH) indicator species. One bryophyte species *Dicranum viride* is protected in the European Union. The study on epiphyte biodiversity was conducted in 34 territories in Latvia including five WKH and five European Union protected habitats. A transplantation experiment was performed in two territories.

Epiphytic bryophytes were studied on 1060 trees. For 1020 trees were analyzed tree species, height, diameter at brEast height, inclination, bark crevice depth, bark pH, but tree age was evaluated for 137 trees in tree level. Forest type, stand age, area and connectivity as forest stand variables were evaluated for the 34 studied territories. All studied variables were analyzed in relation to each epiphytic species group. Epiphytic bryophyte vertical and horizontal spatial distribution was determined on each of 1020 tree stems. Transplantation experiments were conducted in deciduous managed forest and old-growth forest for *Neckera pennata* and *Lobaria pulmonaria* (overall on 40 trees). Differences in epiphyte geographical distribution were found. Epiphytic bryophyte and lichen distribution was influenced significantly ($p<0.05$) by tree level as well as by forest stand level variables. However, differences were found in factor significance among the studied epiphytic species groups. Tree species, forest stand type and area were the most important variables influencing epiphytic species distribution in Latvian deciduous forests. Epiphytic vertical spatial distribution was more important than horizontal spatial distribution. Microclimate conditions may be more important for *Neckera pennata*, but dispersal limitations could be crucial for *Lobaria pulmonaria*.

The PhD thesis is written on 77 pages. In total 184 references are cited. The PhD Thesis consist of the sections: Annotation, Anotācija, Literature, Materials and Methods, Results, Discussion, Conclusions, Main thesis, Acknowledgements, References, Appendix. The Thesis was prepared in the University of Latvia, Faculty of Biology, Department of Botany and Ecology from 2006 to 2009.

# Anotācija

**Promocijas darba nosaukums latviski: "Epifītisko sūnu un ķērpju ekoloģija lapu koku mežos Latvijā".**

Epifītiskās sūnas un ķērpji ir nozīmīgas bioloģiskās daudzveidības sastāvdaļas. Dabas aizsardzība un ilglaicīga mežsaimniecība kļūst aizvien aktuālākas palielinoties mūsdienu mežsaimniecības aktivitātēm meža ekosistēmās. Ekoloģisku pētījumu par epifītiem trūkst un ir nepieciešami lapu koku mežos Latvijā.

Kopumā pētījumā konstatētas 148 epifītu (73 sūnu un 75 ķērpju) sugas, no kurām 14 ir Sarkanās grāmatas sugas Latvijā un 21 – Dabisko meža biotopu (DMB) indikatorsuga. Viena sūnu suga – *Dicranum viride* ir Eiropas nozīmes aizsargājama suga. Pētījums par epifītu daudveidību veikts 34 Latvijas teritorijās ietverot piecus DMB un piecus Eiropas nozīmes aizsargājamus biotopus. Transplantācijas eksperiments veikts divās teritorijās.

Epifītiskās sūnas pētītas kopumā uz 1060 kokiem. Koka suga, augstums, diametrs krūšu augstumā, noliekums, mizas rievas dziļums, mizas pH noteikts 1020 kokiem, bet koka vecums – 137 kokiem koka mērogā. Meža tips, mežaudzes vecums, platība un nepārtrauktība kā mežaudzes mēroga faktori noteikti 34 teritorijām. Visi pētītie faktori analizēti saistībā ar epifītu sugu skaitu deviņām epifītu sugu grupām. Epifītu vertikālā un horizontālā telpiskā izplatība analizēta uz 1020 kokiem. Transplantācijas eksperimenti veikti ar *Neckera pennata* un *Lobaria pulmonaria* apsaimniekotā lapu koku mežā un dabiskā lapu koku mežā (kopā uz 40 kokiem). Vērojamas atšķirības epifītu ģeogrāfiskajā izplatībā. Epifītisko sūnu un ķērpju izplatību ietekmēja būtiski ($p<0.05$) gan koka mēroga, gan mežaudzes mēroga faktori. Vērojamas atšķirības faktoru būtiskumā starp pētītajām epifītu sugu grupām. Koka suga, mežaudzes meža tips un mežaudzes platība novērtēti kā vieni no svarīgākajiem faktoriem epifītu izplatībā lapu koku mežos Latvijā. Epifītu vertikālā izplatība nozīmīgāka par horizontālo telpisko izplatību. Mikroklimatiskie apstākļi ir būtiski *Neckera pennata* izplatībā, bet izplatīšanās ierobežojumi ietekmē *Lobaria pulmonaria*.

Promocijas darba apjoms ir 77 lapas. Citētas 184 atsauces. Promocijas darbs sastāv no Annotation, Anotācija, Introduction, Literature, Materials and Methods, Results, Discussion, Conclusions, Main thesis, Acknowledgements, References, Appendix. Promocijas darbs izstrādāts Latvijas Universitātē, Bioloģijas fakultātē, Botānikas un ekoloģijas katedrā no 2006. līdz 2009. gadam.

# Introduction

Epiphytes are plants growing on other plants without deriving substances from their living tissues. Trees (phorophytes) support diverse epiphytic flora (Bates 2000).

The loss and fragmentation of natural habitats by agriculture, forestry and urbanization are the main causes of decreasing biodiversity at local, regional and global scales (Hanski 2005). Due to increase of forest management intensity, there is decline of areas where natural structures, processes and species are characteristic. Biodiversity still is much more higher in Latvia in comparison with other Nordic and Central European states (Priedītis 2000) giving potential for new approaches and opportunities for studies in deciduous forests.

Epiphytic bryophytes and lichens of forest ecosystems are widely used as indicators of forest continuity and naturalness (Ek et al. 2002, Frego 2007). They are also part of the forest biodiversity supporting existence of other forest dwelling organisms as well as ensuring the moisture regime and forest ecosystem stability (Glime 2007).

Epiphytes are important organisms regulating humidity of the habitat. They increase the content of vapour in the air, promote growth, as well as protect the trunk from damages and frost. Epiphytes participate in all processes in forest ecosystems (Cieśliński et al. 1996a).

The aim of the present dissertation is to provide an overview of the epiphytic bryophyte and lichen flora and the main ecological characters of epihytic bryophytes and lichens in Latvian dry deciduous forests. The hypotheses of the present study are – 1) Latvian deciduous forests ensure rich potential for long-term-existence of epiphytic bryophytes and lichens, 2) tree level variables as well as stand level variables affect epiphytic bryophyte and lichen distribution. The following objectives were defined:

1) evaluate the distribution of epiphytic bryophyte and lichen species in Latvian dry deciduous forests,
2) characterize the role of tree and forest stand level variables affecting epiphytic bryophyte and lichen species distribution,
3) evaluate dispersal demands of *Neckera pennata* and *Lobaria pulmonaria* with transplantation experiment.

# 1. Literature

## 1.2. Deciduous forests

### 1.2.1.Distribution history

Deciduous forests began to expand about 7400 years ago in the Atlantic period, when *Ulmus laevis* and *Alnus* spp. expanded on a warming climate. The distribution of *Betula* spp. gradually increased while that of broad-leaved tree species decreased. The broad-leaved forests reached their optimum about 6000 years ago (Zunde 1999). Due to increase of agriculture pressure the deciduous forests have become fragmentary (McNeeley et al. 1995, Dumpe 1999, Hanski 2005). Latvia is located in the hemiboreal vegetation zone at the ecotone between two biomes: boreal and mixed forest zone. Both boreal and nemoral forests are recognized in the hemiboreal zone (Hytteborn et al. 2005).

### 1.2.2. Characteristics of deciduous forests

Deciduous forests are distributed in the northern part of this vegetation type in Latvia and are included in European summergreen vegetation class (Krüssman 1968). Deciduous forests cover 45% of the whole forest cover (coverage of the stands with a deciduous species as the dominant) in Latvia (VMD 2009).

*Carpinus betulus* has a Central European distribution extending also in southern Russia and in Latvia reaches it northern range (Miller 1924). *Alnus glutinosa* is distributed in most of Europe including West Siberia (McVean 1953), *Betula pendula*, *Populus tremula*, *Salix caprea*, *Sorbus aucuparia* are located in the central part of the species distribution ranges covering also partly Russia. *Alnus incana* is near its southern distribution border in Latvia, but remnant patches exist in Central Europe. Broad-leaved tree species like *Tilia cordata*, *Quercus robur*, *Acer platanoides*, *Ulmus glabra*, *Ulmus laevis* and *Fraxinus excelsior* cover Southern Europe, Eastern Europe and the southern part of Scandinavia (Krüssman 1968). Broad-leaved forests are distributed in river valleys, slopes, lake Islands and plains in the previous distribution range of broad-leaved tree species in Latvia. Forests dominated by broad-leaved tree species cover 1 % of the total Latvian forest area (VMD 2009).

Nutrient rich soils are characteristic in deciduous forests. Common tree species are *Fraxinus excelsior* and *Quercus robur*. The understory is typically dominated by shrubs *Padus avium, Lonicera xylosteum, Viburnum opulus* and herb layer plants such as *Mercurialis perennis, Polygonatum multiflorum, Gagea lutea, Hepatica nobilis* (Kabucis (ed.) 2001). A dense cover of epiphytic bryophytes is favoured on tree trunks in nutrient rich forests – where there is high transpiration of plant leaves (Аболинь 1968). Creation of gaps by mortality of one or small groups of trees is the most common natural disturbance in deciduous forests. Forests in alluvial plains are affected by fluctuation of water level. Species are adapted to seasonal rhythms reflecting change in microclimatic conditions (Priedītis 1999).

The main natural disturbance in deciduous forests is windthrow, initiating gap dynamics (Rackham 2003). Fires are less common in deciduous forests due to lack of a moss layer on the forest floor and resistant trees impede crown fire (Kuuluvainen 2002).

Deciduous forests ensure rich plant diversity. In this forest type a spring aspect, when vascular plants are most visible by flowering, is the most emphasized. Lichen and bryophyte cover is not clearly visible on the forest floor, but it is more dominant on tree trunks. In boreo-nemoral forests epiphytic bryophytes and lichens are distributed on deciduous trees and this habitat is dynamic and declining (Löbel et al. 2006a).

## 1.3. Factors predicting epiphyte distribution

### 1.3.1. Habitat type, continuity, connectivity, area and age

**Habitat** in relation to local environment and geography are important in determining epiphyte distribution (Barkman 1958, Аболинь 1968, Slack 1976). Some epiphytes are limited to certain forest types (Barkman 1958, Sõmermaa 1972). The epiphytic bryophyte flora is most diverse in moist habitats in cloud forests (Pòcs 1982).

Hoffman (1971) and Slack (1976) found that bryophyte species richness on trees is higher in mesic sites and greatest for lichens in xeric sites, but species diversity was much higher in xeric sites.  However, Rose (1976) observed that sheltered ravines have richer lichen flora than exposed sites.

The distribution of a specific epiphyte or any other organism in a specific habitat is highly dependent on the degree of adaptation to the ecological conditions in the habitat (Mazimpaka, Lara 1995). Habitat diversity between stands is important in epiphyte distribution (Slack 1976). Obligate epiphytes show greater dependence with types of the broad-leaved forests and less to the habitat humidity (Cieśliński 1996a). Bryophyte habitats are generally more humid, compared with lichen habitats in Central Europe (Frahm 2003). Tilio-Carpinetum forests are among the richest in mosses, while Pino-Quercetum are poorest (Cieśliński et al. 1996a). The richest in lichens are oak-linden-hornbeam forest and black alder bog forests (Cieśliński et al. 1996a).

Bryophytes are more sensitive to microclimate conditioned by the habitat type. However strong differences in epiphyte species composition among broad-leaved forest habitats have not found and only a few species showed a significant relation with a particular habitat type (Cieśliński et al.1996a). Broad-leaved forests as well as separate deciduous trees in fragmented landscape are an important habitat for obligate epiphytic bryophyte species distribution in Belgium and France (Vanderpoorten et al. 2004).

**Continuity** involving various microhabitats, ecological responses, temporal aspect may be crucial for the existence of forest dwelling organisms (Frego 2007). Lack of forest stand continuity could be one of the causes of poor epiphytic lichen species richness in forests (Straupe 2008). Continuity of forest area was the most important factor explaining epiphytic community distribution in Danish *Fagus* forests (Aude, Poulsen 2000). In an other study Fritz et al. (2008) found a significant relationship with forest continuity and epiphytic species distribution in Swedish *Fagus sylvatica* forests. However, also microlimate, tree canopy and big trees play an important role for several species distribution (Aude, Poulsen 2000). On the other hand, in study on *Lobaria pulmonaria,* ecological continuity was not found to be important (Kalwij et al. 2005).

Continuity was important for *Neckera pennata* distribution in broad-leaved forest (Snäll et al. 2004). Forest continuity is important feature for forest biodiversity (Nilsson et al. 2001). Lichens were used as indicators of woodland continuity in Great Britain (Rose 1976). Fritz et al. (2008) found, that forest continuity was significant for red-listed bryophyte species, all lichen species, lichen indicator species and red-listed lichen species richenss.

Old isolated forest stands surrounded by monoculture forests are inhospitable for species specialised on old deciduous trees. Therefore, continuum of patches should be maintained in managed forest landscape for long-term dispersal of epiphytic lichens (Kuusinen 1996a). Distributions of several threatened epiphytic lichen species are related with specific forest stand with big trees, ensuring **continuity** (Nilsson et al. 1995). Connectivity of phorophytes was associated with *Neckera pennata* metapopulation dynamics after Snäll et al. (2005a). Forest stand connectivity was associated with occurrence probability of epiphytes (Boudreault et al. 2000, Löbel et al. 2006a). Red listed species prefer more continuous habitats and small, fragmented patches are not suitable for their distribution (Paltto et al. 2006).

Forest stand **area** is mentioned as a significant factor influencing epiphytic species distribution (Berglund, Jonsson 2003, Ojala et al. 2000). Habitat size was found as one of the most important factors influencing long-term population existence (Hanski, Ovaskainen 2001, Löbel et al. 2006a). For example, epiphytic lichen species richness increased with an area in Scotland woodlands (Ellis, Coppins 2007) as well es epiphytic bryophyte species richness in Swedish deciduous forests (Löbel et al. 2006a). Forest fragment size influences significantly bryophyte (Baldwin, Bradfield 2007) and lichen species diversity in various habitat types (Gignac, Dale 2005).

Forest **age** was not related to red-listed species richness in a study by Gustafsson et al. (2003). In another study Red data book species richness was positively related with suitable habitat surroundings, but this trend was not observed for indicator species (Paltto et al. 2006).

### 1.3.2. Phoropyte characteristics

Tree level variables were found to be the most important stand level variables for epiphytic lichen species distribution in Estonian old-growth forests (Jüriado et al. 2009a). **Tree species** is mentioned as one of the most important factors influencing epiphytic bryophyte and lichen species distribution in various studies (Billings, Drew 1938, Barkman 1958, Аболинь 1968, Tapper 1976, Trynoski, Glime 1982, Bates 1992, Peck et al. 1995, Uliczka, Angelstam 1999, Boudreault et al. 2000, Mežaka et al. 2008). Variation patterns of the lichen assemblages on trees were mostly explained by the phorophyte species in Estonian deciduous forests (Jüriado et al. 2009b). Epiphyte and phorophyte relationships are changing systems, rather than static associations. Host trees initially are empty dynamic islands, gradually colonised by epiphytes. Differences are observed in host specificity suitable for particular epiphyte species. When a tree island falls, most of the epiphytes are replaced with non-epiphytic species. All bryophyte and lichen propagules land with equal frequency on trees, but establishment could be determined by bark characteristics, leaf canopy of tree as these factors affect light and moisture (Slack 1976).

Several bryophyte species prefer specific tree species (Barkman 1958, Āboliņa 1978). Bryophyte species richness can be higher on certain tree species and lichen species richness – on other tree species (Barkman 1958).

Higher epiphytic bryophyte and lichen richness is more common on *Fraxinus excelsior, Acer platanoides, Tilia cordata, Ulmus* spp. (Аболинь 1968), *Populus tremula* (Āboliņa 1978), *Sorbus aucuparia, Quercus robur, Alnus incana, Alnus glutinosa* (Straupe 2008), *Carpinus betulus* in Latvia (Piterāns 2001, Mežaka et al. 2008).

New trees and flaking bark offer virgin areas to epiphytes. Highest epiphytic species richness was found on trees distributed in various habitat types. Betulin is a characteristic substance in *Betula pendula* and *Alnus glutinosa*, which may be the reason of poor epiphytic vegetation on this tree species (Barkman 1958). Suija et al. (2007) found a difference in epiphytic lichen distribution on tree species among different forest habitats. *Populus tremula*, *Betula pendula* and *Alnus incana* hosted the highest lichen species richness (Suija et al. 2007). Epiphytic bryophyte communities varied among tree species in Adirondack Northern hardwood forests (McGee, Kimmerer 2002).

**Tree inclination** is an important factor affecting epiphyte distribution, but has not been widely discussed (Barkman 1958, Smith 1982, Kuusinen 1994a). Different humidity regimes exist in various trunk parts of inclined trees. Comparatively more bryophytes were found on the upper part of inclined trees (Strazdiņa 2005). In the upper part rainwater flows on the lower part of the tree trunk promote bryophyte growth on all directions of exposure until a thick bryophyte cover forms, afterwards the tree base receives low amounts of water and overgrow with the lichen *Lepraria* (Olsen 1917). A decrease of tree inclination leads to reduced flow of water and epiphytes obtain more water resources (Barkman 1958). Kuusinen (1994a) found that bryophyte distribution was higher on inclined *Salix caprea* in Southern and Middle boreal areas in Finland. On the other hand, Snäll et al. (2005a) found that *Neckera pennata* avoids leaning trees.

Tree inclination 5-15$^{o}$ showed a high relationship with epiphytic bryophyte diversity among *Fraxinus excelsior* and on more slanting trees a lower diversity trend was found (Rasmussen 1975).

**Tree diameter** is significant factor especially regarding rare epiphytic species distribution (Barkman 1958, Trynoski, Glime 1982, Aude, Poulsen 2000, Hedenås, Ericson 2000, Friedel et al. 2006, Znotiņa 2003, McGee, Kimmerer 2002, Snäll et al. 2004). Tree diameter was significant for lichen species richness (Kuusinen 1994a, Hedenås, Ericson 2000) and bryophyte species richness (Ojala et al. 2000).

Relatively few publications exist about the relationship of epiphyte species and **tree height**. In most of cases tree height is highly correlated with tree diameter. However, in other studies tree height was found also as a significant factor influencing epiphyte species richness as separate factor (Mežaka, Znotiņa 2006, Belinchòn et al. 2007).

**Bark roughness** showed a significant influence in epiphytic bryophyte and lichen distribution in several studies (Barkman 1958, Bates 1992, Friedel et al. 2006). Fissured bark on the basal part of *Salix caprea* ensures additional microhabitats for epiphytes

(Kuusinen 1994a). Owing to secondary growth, bark is flaking with epiphytes. Tree bark commonly has a relief offering a variety of microclimates in small areas (Barkman 1958).

The bark of older trees is more cracked, thick and humus accumulates, ensuring the establishment of epiphytes (Аболинь 1968). Bark roughness involves a factor complex. Tree bark is rougher on basal part of tree trunks and it is favourable for epiphytic bryophyte distribution in contrast to the smoother upper part. The greatest richness of epiphytes is found on cracked bark. (John, Dale 1995, Znotiņa 2003). However, in other studies the highest epiphyte species richness was observed on smooth bark compared with cracked bark (Barkman 1958). Bark fissures influence negatively total species richness and lichen species richness (Löbel et al. 2006b). The cleavages, lateral surfaces of cracks create a specific microclimate favourable for the occurrence of rare species characteristic to primeval forests (Cieśliński et al. 1996a).

Different opinions exist about **tree bark pH** influence on epiphyte distribution. Some authors (Loppi, Frati 2004) did not find any relation with tree bark pH and epiphytic lichen species richness, but others found tree bark pH as one of the most intrinsic parameters influencing epiphytic species composition on trees (Barkman 1958, Bates, Brown 1981, Bates 1992, Kuusinen 1996b, Hobohm 1998, Weibull 2001, Znotiņa 2003, Weibull, Rydin 2005, Larsen et al. 2006). Substrate pH amplitudes of various substrates were detected previously for hepatics in Latvia by Apinis, Diogucs (1935) and mosses in Latvia and Estonia by Apinis, Lācis (1936).

Bark wounds, bird excrements, dusts and sea salt neutralize tree bark. *Betula* spp. bark pH can be in the range from 3.80 to 4.30. Acidity of bark can also be influenced by 1) epiphytes, 2) accumulating dusts and sand making humus, 3) increased respiration decreases pH, 4) acidic influence from lichen acids. Lichens can alter pH by about 0.70-1.30 units (Barkman 1958).

A high correlation was observed between tree bark pH of *Fraxinus excelsior* and *Quercus petraea* and epiphyte community variation, which was related with differences between *Fraxinus excelsior* and *Quercus petrae* (Bates 1992).

Tree species can be divided into two groups depending on tree acidity – *Betula pendula* pH 4.00-5.00, *Alnus* spp., *Salix caprea*, *Populus tremula* pH>5.00. Du Rietz (1945) divided trees in three groups depending on bark pH – 1) rich bark (pH 5.00-7.00), 2) medium rich (pH 4.00-5.00), 3) poor (pH<4.00). The lowest tree bark pH was found for *Quercus* spp. (pH 2.90), the highest for *Acer* spp. (pH 7.70) (Barkman 1958).

A correlation between epiphyte species richness and **tree age** has been reported in several studies about bryophytes (Slack 1976, Аболинь 1968) and lichens (Uliczka, Angelstam 1999, Johansson et al. 2007, Ranius et al. 2008). Trees becoming older ensure not only time for epiphyte establishment, but also change in bark structure (Slack 1976).

Tree age is a significant factor influencing lichen species richness on *Populus tremula* and *Betula pendula* (Uliczka, Angelstam 1999). Straupe (2008) found that the highest epiphytic lichen species richness was in older *Alnus glutinosa* forest stands in Latvian forest with high biological value.

### 1.3.3. Horizontal and vertical spatial distribution

Tree exposure has been mentioned as a significant factor influencing epiphyte distribution in several studies (Billings, Drew 1938, Slack 1976, Trynoski, Glime 1982, Jüriado et al. 2009a).

Microclimate varies in different directions of exposure on tree trunks. In addition microclimate differences may be less pronounced in dense forests and ravine forests. Epiphytic vegetation zones on phorophytes has been observed to be higher on the North direction of exposure. Light intensity, temperature commonly are higher on the South direction of exposure in Europe. On the other hand, a different trend can be found on inclined trees. Differences in daily temperature are lowest in the North direction of exposure on tree trunks influenced mostly by evaporation and not by wind. West winds are most rainy, and hence trees often are wet on this side. A South-West direction of exposure is the driest (Barkman 1958).

Less correlation in epiphyte distribution depending on direction of exposure was found on straight trees in dense forests or shaded ravines, where there is an absence of direct sunlight or wind (Barkman 1958). The South direction of exposure is shadowed more in summer, not in the East and West directions of exposures (Lüdi, Zoller 1953). In study by Trynoski and Glime (1982) significantly higher bryophyte cover was found in the North direction of exposure on trees than on the South and East directions. Straupe (2008) found significant differencies of lichen species richness in various directions of exposures and heights on *Quercus robur* trunks.

The eastern direction of exposure is affected by winds coming from the West. Higher evaporation and transpiration on the West side of trees is more pronounced in winter, when tree leaves are absent to decrease the wind velocity (Trynoski, Glime 1982).

The epiphytic flora differs between higher (0.50-1.50m) and lower (until 0.50m) zones on trees (Slack 1976, Bates 1992, Franks, Bergström 2000, Mežaka, Znotiņa 2006). Straupe (2008) found that lichen species richness varied at different heights and exposures on *Quercus robur* in Latvia. Light intensity, wind, and evaporation increases with height on tree trunk (Barkman 1958).

Humidity is higher at the tree base as it is relatively protected from wind-induced desiccation effects (Trynoski, Glime 1982). The tree basal part has the most favourable microclimte for bryophytes due to favourable hydric conditions (Mazimpaka, Lara 1995). The highest humidity occurs on the basal part of tree trunks and decreases with tree height (Ochsner 1933). Humidity is buffered from desiccation at tree base due to the moisture-holding humus and plants of the forest floor. The tree base also is protected by snow cover from extremly low temperature in winter (Trynoski, Glime 1982). Species found on the basal part of *Fraxinus excelsior* trunks in Norway were facultative epiphytes or epigeic species (Moe, Botnen 1997).

Upper zones on tree trunks are occupied by desiccation-tolerant taxa such as Orthotrichaceae, *Frullania*, Lejeuneaceae, and the tree basal parts – by Brachytheciaceae and Hypnaceae. Obligate epiphytes are mostly early successional species, which are followed by facultative epiphytes on the stem base (Smith 1982).

### 1.3.4. Transplantation experiments

Transplantation experiments are needed to better predict factors influencing epiphytic species distribution. This information is needed to select the best methods for forest long-term managament. *Lobaria pulmonaria* is a characteristic species of old-growth forests (Lesica et al. 1991). Gauslaa et al. (2001) conducted an experiment with *Lobaria pulmonaria* on wooden blocks, and found that the growth of lichen was correlated with rainfall during the studied time period and *Lobaria pulmonaria* was also susceptible to light after transplantation. Edman et al. (2007) concluded that selective cutting affected negatively the abundance and frequency of *Lobaria pulmonaria*. Branches with transplanted *Lobaria pulmonaria* grew comparatively better in old-growth forest with higher light compared with managed forest (Coxson, Stevenson 2007). In contradiction Hilmo (2002) did not find a difference in lichen *Lobaria scrobiculata* growth after transplantation experiments in old-growth forest and young planted forest confirming the hypothesis that dispersal limitation could be more important than microclimate conditions in particular forest stand for lichen distribution. Hazell and Gustafsson (1999) found that survival and vitality of *Antitrichia curtipendula* was significantly higher in forest than in a clearcut. Highest survival of *Lobaria pulmonaria* was found in clustered trees on the clear felled sites and the survival was similar between the scattered trees and on the clearcuts and in the forests. The vitality of *Lobaria pulmonaria* was highest on clustered trees on the clearcut and lowest in the forest.

Different methods have been used for transplantation experiments. Rosso et al. (2001) used plastic net transplants in bags for biommass study with *Antitrichia curtipendula*. Hazell and Gustafsson (1999) used plastic nets with metal staples for *Lobaria pulmonaria* and *Antitrichia curtipendula* transplantation. Gauslaa et al. (2006) used frames for transplantation experiments with *Lobaria pulmonaria* on *Picea abies* in Norway. Ingerpuu et al. (2007) made successful transplantation experiment with *Neckera pennata* in Estonian boreo-nemoral forests by pressing bryophyte into bark crevices.

## 1.4. Conservation of old-growth deciduous forests

### 1.4.1. Impacts and current condition

Protected territories are geographically determined areas under special state conservation. The main aim of protected territories is conserve and maintain nature diversity as rare ecosystems, habitats for protected species, unique and characteristic landscapes of Latvia, geological and geomorphological formations (VMD 2009).

In total 19 conservation categories are defined for forest habitat protection by the government of Latvia (Tab. 1). National Parks and Nature Reserves comprise the biggest area under forest protection in Latvia. Differences are observed in conservation status and amount of protected forests among forest owners. The highest area of protected forests is found in National Parks and in the Protected Landscape Regions in private forests. Forests are protected more as Nature Reserves in State forests. More than 1/5 of Latvian forests are protected. It is important to note, that a large part of the protected territories mentioned in Table 1 are divided in several zones, where forest management as cutting is not forbidden and both coniferous and deciduous forests are included. Also, that in total 2607836 ha or 88.10% of Latvian forests are without any forest management restriction (VMD 2009).

Several administrative categories have been used for evaluation and protection of old-growth forests in Latvia. However dicrepancies exist as Latvia located in hemiboreal vegetation zone, where different classifications of forest types have been used and they did not reflect each other completely.

Table 1

Different protection catogories in Latvia.

| Categories of protected territories | Private forests (ha) | State forests (ha) | Municipality forests (ha) | Total forest area (ha) |
|---|---|---|---|---|
| Total Latvian forest area | 1388403.50 | 1492897.00 | 79901.30 | 2961201.80 |
| National Parks | 50622.50 | 50655.60 | 964.20 | 102242.30 |
| Nature Reserves | 14593.30 | 82148.70 | 1210.00 | 97952.00 |
| North Vidzeme Biosphere Reserve (Nature Reserve) | 493.90 | 2451.30 | 0.40 | 2945.60 |
| Nature Parks | 28026.80 | 31280.50 | 2270.30 | 61577.60 |
| Protected landscape regions | 41994.40 | 30831.70 | 556.90 | 73383.00 |
| Protected dendrological plantations | 71.50 | 504.70 | 26.60 | 602.80 |
| Geological and geomorphological Nature Monuments | 694.70 | 629.70 | 32.30 | 1356.70 |
| Local meaning Nature Reserves and parks (two categories) | 173.40 | 392.40 | 11.40 | 576.90 |
| Microreserves and buffer belts around microreserves | 1089.80 | 26965.30 | 185.00 | 28240.10 |
| Buffer belts around microreserves | 514.10 | 27800.50 | 76.40 | 28391.00 |
| Baltic sea coast dune protective zone | 1783.00 | 5517.70 | 992.20 | 8292.90 |
| Baltic sea restricted management belt | 18937.50 | 45586.40 | 2298.60 | 66822.50 |
| Watercourse, along waters, wetlands, around cities protective zones (three categories) | 34425.90 | 48318.2 | 15008 | 97752.1 |
| Forests in administrative borders of cities | 1142.10 | 3032.00 | 5626.30 | 9800.40 |
| Specially protected forest districts | 1711.70 | 20226.70 | 2336.80 | 24275.20 |
| Total protected territories | 196274.60 | 376341.40 | 31595.40 | 604211.40 |
| Without management restrictions | 1301829.00 | 1250816.00 | 55191.30 | 2607836.30 |

### 1.4.2. Deciduous forests under European Union and Latvian legislations

In total five types of dry decidous forests are protected in the European Union (EU) and also in Latvia (LRMK 2000a, Tab. 2). Under Latvian legislation deciduous forests with *Carpinus betulus* are also a protected habitat type (LRMK 2000a) including similar habitat characteristics as Sub-Atlantic and medio-European oak or oak-hornbeam forests of the Carpinion betuli 9160. All these forests are multilayered, different age forest stands with diameter of deciduous trees more than 0.30 m. There is a shrub-rich layer and understory tree layer and key elements such as trees with hollows, snags, dead wood in different decay stages (Priedītis 1999, Kabucis (ed.) 2004, EU 2007). Several red-listed forest species are distributed in deciduous forests (Berg et al.1995).

Western Taïga (9010*) are natural old-growth forests and young forest stages naturally developing after fire (Tab. 2). Old-growth forests represent climax or late succession stages with slight human impact or without any human impact, being habitats for many threatened species, especially, bryophytes, lichens, fungi, and invertebrates. Some of the present old natural forests have human impact, but in spite of that they maintain many characteristics of the natural forests. Characteristic tree species distributed as *Betula spp*, *Populus tremula*, *Picea abies*, vascular plants – *Dechampsia flexuosa*, *Vaccinium myrtillus*, bryophytes – *Dicranum scoparium*, *Pleurozium schreberi*, *Hylocomium splendens*. Western taïga forests are common in the whole territory of Latvia (Kabucis (ed.) 2004, EU 2007, VMD 2009).

Fennoscandian hemiboreal natural old broad–leaved deciduous forests (Quercus, Tilia, Acer, Fraxinus or Ulmus) rich in epiphytes (9020*) are old mixed tree forests outside of river alluvial land (Tab. 2). Epigeic bryophytes are poor in cover. More abundant are epixylic and epiphytic bryophytes (*Homalia trichomanoides*, *Orthotrichum* spp.) and lichens (*Arthonia vinosa*, *Lobaria pulmonaria*, *Phlyctis agelaea*) on trees. Similar characteristics are found in riparian mixed forests of Quercus robur, Ulmus laevis and U. minor, Fraxinus excelsior or F. angustifolia, along the large rivers (Ulmenion minoris) (91 F0), but differences are more related with moisture regime and habitat geographical location in Latvia (Priedītis, 1999, Kabucis (ed.) 2004, EU 2007).

Sub-Atlantic and medio-European oak or oak-hornbeam forests of the Carpinion betuli (9160) are forests with *Quercus robur*, as well as mixed forests with *Quercus robur*, *Carpinus betulus*, *Tilia cordata*, *Fraxinus excelsior* and *Picea abies* (Tab. 2). This type is rare in Latvia: more in South-western, western, but on lake Islands more in eastern Latvia (Priedītis 1999, Kabucis (ed.) 2004, EU 2007).

Tilio-Acerion forests of slopes, screees and ravines (9180*) are rarely found in Latvia, most are in river valleys as well as in ancient ravines (Tab. 2). Epixylic and epiphytic bryophytes are more common than epigeic flora. The habitat is shaded and plants are characteristic of humid and fertile soils. This habitat is fragmentary, more in the eastern part in Latvia on lake Islands (Priedītis, 1999, Kabucis (ed.) 2004, EU 2007).

Table 2.

Protected deciduous forest habitats in European Union.

| Forest type | Tree species | Herb layer | Shrub layer | Characteristics | Distribution in Latvia |
|---|---|---|---|---|---|
| Western Taïga (9010*) | *Betula spp., Populus tremula* | *Deschampsia flexuosa, Vaccinium myrtillus, Equisetum* | | | common |
| Fennoscandian hemiboreal natural old broad–leaved forests (Quercus, Tilia, Acer, Fraxinus or Ulmus) rich in epiphytes 9020* | *Fraxinus excelsior, Tilia cordata, Acer platanoides* | *Mercurialis perenne, Lathyrus vernus, Hepatica nobilis, Pulmonaria obscura* | *Corylus avellana* | dead wood, epiphytic bryophytes and lichens | rare |
| Sub-Alantic and medio-European oak or oak-hornbeam forests of the Carpinion betuli 9160 | *Quercus robur, Carpinus betulus, Tilia cordata* | *Stellaria holostea,Me-lica nutans, Mercurialis perenne, Anemone nemorosa* | *Corylus avellana, Lonicera xylosteum* | soils with medium humidity, humid sandy loam or loam soils | rare in Latvia; more on south-western, western, in lake Islands in eastern part of Latvia |
| Tilio-Acerion forests of slopes, screes and ravines 9180* | *Fraxinus excelsior, Tilia cordata, Ulmus glabra* | *Actaea spicata, Anemone nemorosa, Ficaria verna, Lunularia rediviva* | *Corylus avellana* | calcareous or sandy soils | rare in Latvia, river valleys, ancient ravines |
| Riparian mixed forests of Quercus robur, Ulmus laevis and U. minor, Fraxinus excelsior or F. angustifolia, along the great rivers (Ulmenion minoris) 91F0 | *Fraxinus excelsior, Ulmus* spp., *Quercus robur, Populus tremula, Alnus glutinosa* | *Ficaria verna, Gagea lutea, Humulus lupulus* | *Ribes pubescens* | in high water level conditions forests could be flooded | rare in Latvia, more in banks of Gauja, Pededze, Ogre rivers |

Explanations: after Kabucis (ed.) 2004, EU 2007, VMD 2009.

### 1.4.3. Deciduous forest Woodland Key Habitats

A natural forest is spatially heterogeneous in vegetation composition at different spatial scales due to abiotic factors, past history of disturbance and stochastic factors

(Kuuluvainen 2002). Generalist species are found in a broad range of conditions, but specialist species have narrow ecological amplitude (Priedītis 2000).

A Woodland Key Habitat (WKH) is an area which contains habitat specialists that cannot sustainably survive in stands managed for timber production. The definitions of WKH specialist species and indicator species are specially adapted to Latvian WKH inventory defined by Ek et al. (2002). In total there are 40001 ha of WKH area in Latvia after inventory data (VMD 2009).

A well-founded expectation that a habitat specialist exists within an area is a sufficient criteria for designating the area as WKH. Habitat specialists are species that are specialised for a certain habitat. Within the framework of this project the definition is narrower: a habitat specialist is a threatened species that is dependent on a certain level of quality in specific WKH and will become extinct if these habitats are subjected to forest cutting (Ek et al. 2002). WKH ensure higher red-listed plant species richness compare to productive forests (Gustafsson 2002, Perhans et al. 2007).

Indicator species are species that have rather high demands on their living conditions but not as high as those of a habitat specialist.  These are  rather specialised species and show a certain forest quality by their very existence. They are mostly found in WKH, sometimes in large numbers, but may occasionally be found outside them, mostly in small numbers. The existence of an indicator species is one indication that an area is a WKH (Ek et al. 2002). Indicator species should be easily distinguished in the field, susceptible to habitat changes, not rare in a suitable microhabitat in a forest. The best indicator species are organisms characterized by low reproduction ability and after changing of habitat quality can not emmigrate (Priedītis 2000, Nilsson 2001, Frego 2007). Characteristic bryophyte  indicators in deciduous forests are *Homalia trichomanoides, Neckera pennata,* bryophyte habitat specialist species – *Geocalyx graveolens, Trichocolea tomentella,* lichen indicator species – *Bacidia rubella, Graphis scripta,* lichen habitat specialist species – *Lobaria pulmonaria, Thelotrema lepadinum* (Ek et al. 2002).

The existence and quantities of different indicator species and key elements determine whether an area is a WKH. The indicator species are not a threatened species in Latvia. There is, of course, no clear boundary between threatened habitat specialists and non-threatened indicator species. Indicator species are used because they are not as rare or difficult to find as habitat specialists. Key elements are features of the forest that are important for habitat specialists. Examples are different kinds of woody debris and old trees of different species (Ek et al. 2002).

Within the WKH inventory, forests were classified into artificial categories, such as broad-leaved WKH, aspen WKH, ravine WKH, slope WKH and riparian WKH (Ek et al. 2002). These categories have little similarity to growth condition types used in forest management, and can be only partly overlap the EU habitat classification. To a certain extent, this impedes using the categories for research as comparison with other studies is hindered.

Several forest structure features are used to define the WKHs, as criteria for their identification. Dead wood in different decay stages (Jönsson, Jonsson 2007), old living trees, standing natural snags, uprooted stems are important key elements in WKHs (Ek et al. 2002, Siitonen et al. 2009). Forest stands disturbed by storms, broken stems and wind-thrown trees with uprooted stems are additional valuable features (Berg et al. 2002).

**Broad-leaved WKH** is naturally regenerated stand with at least 50% of stand volume consisting of broad-leaved trees (Tab. 3). *Betula* spp, *Populus* spp., *Alnus* spp. can make a natural mixture in tree layer. *Corylus avellana* is common in the shrub layer. Tree continuity is shown by the occurrence of indicator species red-listed species and protected species (Thor 1998, Gustafsson et al. 1999, Snäll et al. 2004, Ek et al. 2002, Paltto et al. 2006, Suija et al. 2007). Stems of old broad-leaved trees extensively covered with epiphytic mosses are  typical feature (Ek et al. 2002, EU 2007). Total inventoried area of broad-leaved forest WKH is 1888 ha in Latvia (VMD 2009).

**Aspen WKH** is a naturally regenerated stand where at least 50% of the stand volume consists of *Populus tremula* (Tab. 3). It has often been exposed to a major natural disturbance (wind-throw, fire) or, more often, human disturbance (clear-felling) which is followed by a natural succession favouring deciduous trees. The WKH is often a naturally regenerated left-over of previously broad-leaved or mixed coniferous-deciduous forests cut during the starting period of modern forestry. The forest may have been subjected to natural disturbances and processes under some period of time, primarily storms. Stands rich in aspen are highly prone to wind disturbance (Ek et al. 2002). Apen forests ensure species rich flora and fauna (Hedenås, Ericson 2000, Pykälä et al. 2006). Stems of broad-leaved trees and aspen extensively covered with epiphytic mosses are a typical feature, which also indicates a long continuity (Ek et al. 2002). In total 2025 ha of aspen WKH have been inventoried in Latvian forests (VMD 2009).

A ravine, valley or brook formation is typical for **ravine WKH** (Tab. 3). The width of ravine should exceed 10 m and depth must be at least 5 m. The width of stream does not exceed 15 m. A stream must be active all year round or only during some seasons. The valley ensures a stable microclimate with continuous shade and humidity and it is also protected from fire and wind. Ground water seepage ensures a moist microclimate. Ravine forests can be corridors for habitat specialist species or ensure a refugia for them surrounding if ecological conditions have deteriorated (Ek et al. 2002). In total 296 ha of ravine WKH was inventoried in Latvian forests (VMD 2009).

Table 3.

Main features of deciduous Woodland Key Habitats in Latvia.

| WKH type | Characteristics | Bryophyte indicator species | Lichen indicator species | Bryophyte habitat specialist species | Lichen habitat specialist species |
|---|---|---|---|---|---|
| Broad-leaved | at least 50% of broad-leaved tree species, epiphytic mosses | *Anomodon sp., Homalia trichomanoides, Jamesoniella autumnalis, Jungermannia leiantha, Lejeunea cavifolia, Metzgeria furcata, Neckera complanata, Neckera pennata, Odontoschisma denudatum,* | *Acrocordia gemmata, Arthonia leucopellea, Arthonia spadicea, Arthonia vinosa, Bacidia rubella, Chaenotheca brachypoda, Graphis scripta, Lecanactis abietina, Leptogium saturninum, Peltigera collina, Pertusaria pertusa* | *Frullania tamarisci, Lophozia ascendens, Scapania apiculata, Anastrophyllum hellerianum, Geocalyx graveolens, Scapania nemorea, Trichocolea tomentella* | *Arthonia byssacea, Arthonia cinereopruinosa, Arthonia cinnabarina, Bacidia rosella, Caloplaca lucifuga, Cetrelia cetrarioides, Chaenotheca chlorella, Cybebe gracilenta, Cyphelium sessile, Evernia divaricata, Gyalecta ulmi, Bactrospora* spp., *Calicium adspersum, Chaenotheca phaeocephala, Collema* spp., *Lobaria pulmonaria, Lobaria scrobiculata, Nephroma* spp., *Opegrapha vermicellifera, Parmelia acetabulum, Parmelia tiliacea, Pertusaria flavida, Pertusaria hemisphaerica, Phlyctis agelaea, Ramalina thrausta*, *Sclerophora* spp., *Thelotrema lepadinum, Usnea florida* |
| Aspen | at least 50% *Populus tremula*, succession forest, epiphytic mosses | | | | |
| Ravine | shade and humidity | | | | |
| Slope | height of slope > 10 m | | | | |
| Riparian | periodic flooding, permanently moist microclimate | | | | |

**Slope WKH** have a slope that may facing in any direction, but most of cases towards on a watercourse, lake, located on the side of a moraine hill, or on a coastal or continental dune (Tab. 3). The height of slope should exceed 10 m. Slope might have a ground water seepage, or the river below the slope provides a moist microclimate. North facing slopes can be crucial for species having poor dispersal ability and which require a stable moist microclimate. South-facing slopes can provide necessary conditions for thermophylic species (Ek et al. 2002). In total 318 ha of slope forests were inventoried in Latvian forests (VMD 2009).

Due to difficulties in forest harvest in ravine and on slopes, these forest types have been preserved. Soil erosion and the constant presence of bare soil are typical features providing additional ecological niches (Ek et al. 2002).

**Riparian WKH** is forested, commonly fertile, riparian zone at the water edge of rivers, streams and lakes (Tab. 3). They are subjected to wind, ice, sun and in many cases periodic flooding. The terrain may be flat or sloping, at times with running ground water. Riparian forests are a transitional zone between two complex ecosystems, ensuring ecological conditions for species depending on both ecosystems. A permanently moist microclimate is characteristic for this habitat. Soil erosion along the river bank in some places as well as deposition of soil in other places can be pronounced in riparian forests (Ek et al. 2002, Prieditis 2002). In total 480 ha of riparian WKH were inventoried in Latvian forests (VMD 2009).

## 1.5. Bryophyte and lichen protection in Latvia

A total of 508 bryophyte species (Āboliņa 2003) and 503 lichen species (Piterāns 2003) have been found in Latvia, of which 203 bryophyte (Āboliņa 1994) and 34 lichen species (Piterāns, Vimba 1996) are red-listed in Latvia. However, in Latvia the red-list is not associated with protection of the species, but rather serves as an informative data base.

A total of 134 bryophyte and 66 lichen species are specially protected in Latvia (LRMK 2000b). In total 23 bryopyte and 42 lichen species are microhabitat species in Latvia (LRMK 2001).

A total of 16 bryophyte species are included in the WKH indicator species list (e.g. *Homalia trichomanoides, Neckera pennata*) and 14 bryophyte species (e.g. *Neckera crispa, Plagiothecium latebricola*) are WKH specialist species. A total of 19 lichen species are WKH indicators (e.g. *Bacidia rubella, Graphis scripta*) and 36 are specialist species (e.g. *Thelotrema lepadinum, Lobaria pulmonaria*) in WKH (Ek at al. 2002). In total 22 WKH lichen and 12 bryophyte WKH specialist species and two WKH lichen and three WKH bryophyte indicator species are microhabitat species in Latvia (LRMK 2001). Specially protected are 27 lichen and 13 bryophyte specialist species and eight lichen indicator species and four bryophyte indicator species (LRMK 2000b) in Latvia.

# 2. Materials and methods

## 2.1. Studied territories

Overall 34 territories in the epiphytic bryophyte and lichen species diversity (diversity) study part were studied in eight geographically different Latvian geobotanical regions (Fig. 1). Summarized information about studied territories in different geobotanical regions compiled in Appendix 1 and in Table 4.

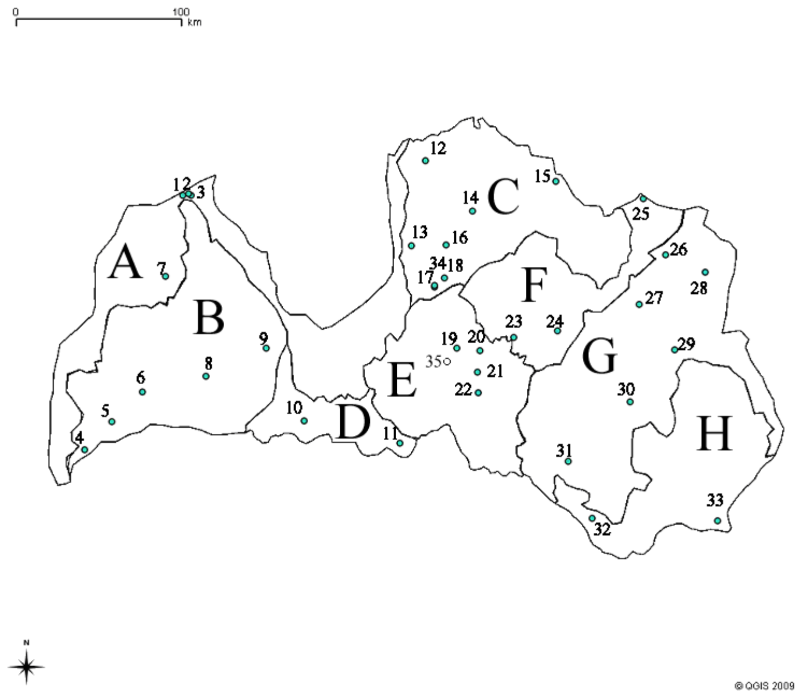



Figure 1. Studied territories. 1 – Cirsti 2 – Šlīteres bāka, 3 – WKH in Slītere National Park, 4 – Dunika nature Reserve, 5 – Ruņupe valley nature Reserve, 6 – Venta un Šķervelis nature Reserve, 7 - Moricsala Nature Reserve, 8 – Ciecere lake island Nature Reserve, 9 – WKH in Lestene pagasts, 10 – Vilce valley Nature Park, 11 – Paņemūnes meži Nature Reserve, 12 – Staicele, 13 – WKH in Vidriži pagasts, 14 – Zilaiskalns Nature Reserve, 15 – Pirtslīcis-Līkā atteka Nature Reserve, 16 – WKH in Straupe pagasts, 17 – Kaķīškalns, 18 – Velnala, 34 – Nurmiži Reserve, 19 – WKH in Laubere pagasts, 20 – Vērenes gobu un vīksnu audze Nature Reserve, 21 – Aizkraukles purvs un meži Nature Reserve, 22 – Korkuļu sausgultne un pazemes upe, 23 – Ērgļi, 24 – Dārznīcas pilskalns, 25 - Korneti-Peļļi Nature Reserve, 26 – Jaunanna, 27 – Pededze, 28 – Vjada, 29 – Maziča, 30 – WKH in Varakļāni pahasts, 31 – Tadenava Microreserve, 32 – Egļu kalns, 33 – Starinas mežs nature Reserve, 35 – Zīļu pļavas (transplantation experiment). Geobotanical regions: A – Coastal, B – West Latvian, C – North Livland, D – Zemgale, E – Mid Latvian, F – Central Livland, G – North-Eastern Latvian, H – South-Eastern. Full names of the studied territories in Appendix 1.

Table 4.

Characteristics of geobotanical regions.

| Geobotanical regions | Studied territories | Absolute altitude (m) and soil characteristics | Annual rainfall (mm) | Average temparature in January (°C) | Average temparature in July (°C) | Forest characteristics | Forest cover (%) or approximate of geobotanical region and soil characteristics |
|---|---|---|---|---|---|---|---|
| Coastal | Šlīteres bāka, Cirsti, WKH in Slītere National Park, Moricsala Nature Reserve | 47 | 600-650 | -3, -5 | +16.5 | *Pinus sylvestris, Quercus robur, Tilia cordata, Picea abies* | >50, sandy and loamy soils |
| West Latvian | Ruņupe valley Nature Reserve, Venta un Šķervelis Nature Reserve, Ciecere lake Island Nature Reserve, Dunika Nature Reserve, WKH in Lestene pagasts | 184 | 550-700 | -4 | +17.5 | *Picea abies,Tilia cordata, Ulmus glabra* | ~35, carbonate rich soils |
| Zemgale | Paņemūnes meži Nature Reserve, Vilce valley Nature Park | 40 | 550 | -5 | +17, +17.5 | *Fraxinus excelsior, Quercus robur, Betula pendula, Populus tremula* | forest cover fragmentary, loamy soils |
| Mid Latvian | Aizkraukles purvs un meži Nature Reserve, WKH in Laubere pagasts, Korkuļu sausgultne un pazemes upe Geological and Geomorphological Nature Monument | 200 | 500-700 | -6, -5 | +16.5, +17 | Deciduous forests and randomly with *Picea abies* | forest cover fragmentary, dolomite, carbonate rich soils |
| Central Livland | Dārznīcas pilskalns, Ērgļi, Korneti - Peļļi Nature Reserve | 312 | 650-750 | -4 | +17, +17.5 | coniferous forests | ~25, sandy-loamy soils |
| North Livland | Kaķīškalns, Nurmiži Reserve, Velnala, Zilais kalns Nature Reserve, Staicele, WKH in Straupe pagasts, WKH in Vidriži pagasts, Pirtslīcis - Līkā atteka Nature Reserve | 127 | 450-550 | -5.5 | +16.5, +17 | coniferous and decidous - coniferou forests | ~30, sandy and loamy soils |
| North-Eastern Latvian | Jaunanna Nature Reserve, Vjada forests Nature Reserve, Pededzes lejtece Nature Reserve, Tadenava, Maziča | 145 | 530-650 | -7.4 | +17.0 | broad-leaved-coniferous forests | forest cover fragmentary, sandy and loamy soils |
| South-Eastern | Egļu kalns WKH, Starinas mežs Nature Reserve | 220 | 575 | -7 | +17.0 | *Populus tremula, Betula pendula* | <25, sandy and loamy soils |

Explanations: All data in table after, Ramans (1975), Klane (1975), Jaunputniņš (1975), Klane, Ramans (1975), Temņikova (1975), Kabucis (1998), Kabucis ed. (2001), Kabucis ed. (2004), WWF (1992), Лайвиньш (1983), Биркмане (1974), Табака (1974), Табака (1977), Табака (1979), Табака, Биркмане (1982), Табака и др. (1985), Табака (1987), Табака (1990), Full names of territories in Appendix 1.

Differences in climatic conditions are observed among geobotanical regions. The highest topography and highest amount of annual rainfall is found in Central Livland, the lowest point in the Zemgale geobotanical region and the smallest amount of rainfall in the North Livland. The coldest winter is assumed to be in the North-Eastern geobotanical region.

Coastal, Westlatvian and Central Livland are the warmest geobotanical regions in winter. West Latvian, Zemgale and Central Livland are the most warmest geobotanical regions in summer, while the Coastal geobotanical region are the coolest (Tab. 4).

## 2.2. Field work

### 2.2.1. Tree and forest stand level

Data were collected from 2006 to 2008 in different deciduous forest types and geobotanical regions in Latvia. The studied territories were selected based on WKH inventory data. Mostly of the studied territories were dry broad-leaved WKHs, but also aspen WKHs were included due to the high biological value of these forests. GPS coordinates were recorded for each studied territory. Sample plots were selected randomly.

The number of sample plots (20x20m) varied among the studied territories. In total 30 trees (minimal DBH 0.05m) were selected in each sample plot. If in one sample plot the number of trees was less than 30, other sample plot(s) was made next to the previous sample plot. If more than 30 trees were found in a selected sample plot, trees with larger DBH were sampled. Tree species, height (m), DBH (m), inclination (degrees, direction of exposure), bark pH, bark crevice depth (mm) were measured for each tree (Tab. 5).

Due to the time limit, tree age was determined only in five territories for 137 trees. Tree bark was cored by a Prestlera corer and tree rings were counted afterwards for determination of tree age. Tree inclination was measured at 0.50 m height on tree. Inclination up to 0.50–2.00 m height was measured if tree stem was straight at 0.50 m height. If tree was straight overall until 2.00 m height, tree was evaluated as straight. Tree height was measured with Sunto relascope. In total 0.50 g tree bark samples until 3.00 mm depth of tree bark were collected from the North direction of exposure up to 1.30 m height on tree trunk for pH measurements in the laboratory. Tree inclination was measured with a surveying compass. Bark crevice depth was measured with metal ruler in North direction of exposure at 1.20 m height on tree.

Forest stand area, age and connectivity were evaluated based on digital forest stand maps and inventory data (VMD 2009). Connectivity existed, if the adjacent forest stand in the same age and forest type bordered with the studied forest stand (Tab. 5).

Table 5.

Studied variables.

| Variable | Description |
|---|---|
| Tree level | |
| Tree species | *Acer platanoides, Alnus glutinosa, Alnus incana, Betula pendula, Carpinus betulus, Fraxinus excelsior, Populus tremula, Tilia cordata, Ulmus glabra, Ulmus laevis, Salix caprea, Sorbus aucuparia*, *Quercus robur* |
| Tree diamater at breast height | Amplitude 0.05 - 1.32 m |
| Tree age | Amplitude 27-201 years |
| Tee height | Amplitude 3.00-49.40 m |
| Bark crevice depth | Amplitude 0.00 (smoth bark) - 35.00 mm |
| Bark pH | Amplitude 2.77-7.55 |
| Tree inclination (degrees) | Amplitude 0-30.50$^{o}$ |
| Tree inclination (exposure) | E (east), SE (south-eastern), W (west), N (north), NW (north-western), NE (north-eastern) S (south), SW (south-western) |
| Stand level | |
| WKH type | Aspen WKH, broad-leaved WKH, ravine WKH, slope WKH, riparian WKH |
| Protected habitats under EU and Latvian legislation | Western Taïga (9010*)<br>Fennoscandian hemiboreal natural old broad–leaved deciduous forests (Quercus, Tilia, Acer, Fraxinus or Ulmus) rich in epiphytes (9020*) |
| Forest stand area | Taken from forest stand maps and forest inventory data. Amplitude 0.50-12.60 ha |
| Forest stand age | Taken from forest stand maps and forest inventory data. Amplitude 40-210 years |
| Connectivity | Taken from forest stand maps and forest inventory data. Values - 1 - connectivity exist, 0 - no connectivity |

Epiphytic bryophyte and lichen species occurrence was detected on each tree (in total 1020 trees) and cover was evaluated in two heights (until 0.50m and 0.50-2.00m) and in four directions of exposures (North, South, East, West) on each tree stem. Epiphyte cover was evaluated as a following gradation: 1 – less than 5 $cm^2$, 2 – 5-25 $cm^2$, 3 – 25-50 $cm^2$, 4 – 50-100 $cm^2$, 2 – more than 100 $cm^2$, modified after Löbel et al. (2006b). Epiphytes were studied in eight subpatches on tree stem. Some subpatches were without epiphytic species and in total 8148 subpatches were studied. Bryophyte and lichen species were identified in the field. Unknown specimens were collected for further identification in laboratory.

Bryophyte species nomanclature follows Grolle, Long (2000), Hill et al. (2006), Āboliņa (2001), Smith (2004), and lichen species nomenclature follows Wirth (1995a, 1995b), Piterāns (2001).

### 2.2.2. Transplantation of *Neckera pennata* and *Lobaria pulmonaria*

Transplantation experiments were started in November 2006 in Zīļu pļavas (Fig. 1), Aizkraukles rajons, Skrīveri pagasts, Mid Latvian Geobotanical region in broad-leaved WKH (56°40'07"N, 25°03'07"E) and a managed forest stand (56°40'14''N, 25°03'07"E). The WKH forest stand was 130 years old with *Fraxinus excelsior* dominating, but recent cuttings had been made in managed forest stand, where isolated *Fraxinus excelsior* were left.

The territory in transplantation experiment was selected based on WKH inventory data and convenient distance for transportation. *Lobaria pulmonaria* and *Neckera pennata* transplants were taken from an adjacent big diameter (DBH=1.14 m) *Fraxinus* e*xcelsior* (donor phorophyte) located between the managed forest and the WKH. All recipient *Fraxinus excelsior* were selected randomly with similar diameter. Tree diameter varied among these trees in WKH 0.24–0.41m and in the managed forest 0.29–0.40m. Bark crevice depth varied from 2.00 to 8.00 mm in WKH and from 2.00 to 5.00 mm in the managed forest. Tree bark pH varied 4.59–6.21 in WKH and 4.08–5.63 in the managed forest.

Transplants with *Neckera pennata* were removed at 1.20 m height on *Fraxinus excelsior*. Four donor phorophytes were selected also in the WKH as *Neckera pennata* material was not sufficient on the previously selected donor tree. *Neckera pennata* transplants varied from 6.00 to 8.30 cm. The size of *Lobaria pulmonaria* transplants was $9cm^2$. All *Neckera pennata* transplants were put at 1.20 m height in North direction, but *Lobaria pulmonaria* at 1.30 m height on North direction of exposure on recieving *Fraxinus excelsior*. All transplantation experiments were conducted on the same day when they were collected.

Transplantation was started in the November 2006 with 10 transplants in managed forest and 10 transplants in WKH. Transplants were attached with neylon thread at November 2006. Each transplant was pulverized with destilled water for decreasing physiological stress. A digital photo was made for each transplant at each inspection time. Transplants were photographing with a Powershot SX100 IS Canon digital photocamera with 8.0 mega pixels, Canon zoom lens 10xIS, operture 6.0-60.0 mm 1:2.8–4.3.

Transplant vitality was evaluated on a four grade scale based on digital photo subjectively: 1) high vitality; moist transplant is greenish, without damaged patches or margins, 2) medium vitality; transplant are still greenish, but some damaged patches occur, 3) low vitality; more than half of transplant area is damaged, remnant green patches left, 4) transplant was died; transplant is brown, without living tissues.

Checking of transplants was made in April 2007. Two receiving trees in the WKH and one in the managed forest had fallen down. Two lichen transplants in WKH and three lichen transplants in the managed forest had fallen down.

New additional trees were selected for lost transplants to supplement the experiment as well as 10 new trees in the WKH and managed forest were selected for continuing the experiment in May 2007. As several transplants had fallen down the medical sling was used as a more appropriate method for attaching transplants. New additional trees (10 receptor trees in each territory were selected to make the experiment more objective). In total 20 reciving trees in each selected forest stand were studied.

The next observations were made in August 2007, December 2007, March 2008, August 2008, December 2008. In total transplantation experiment was made on 40 trees (20 in managed forest and 20 in WKH). Data were analyzed from spring 2007 and spring 2008.

## 2.3. Laboratory work

Bryophytes and lichens initially were removed from tree bark samples before pH measurement. Samples of tree bark were cut (medium size 0.001g). Each sample weighed approximately 0.5 g. Several samples weighed less than 0.50 g due to difficulty of bark removal from *Populus tremula*. Each bark sample was shaken in a 20-ml 1 M KCl solution for 1 h and pH value was determined with a pH-meter (GPH 014, Greisinger Electronic).

For identification of bryophyte and lichen species light microscope and stereomicroscope were used. Several methods as ‘spot tests’, UV light, thin-layer chromatography (TLC) were used for identification of lichen species in the present study.

Lichen samples have been extracted with acetone and the extract into glass plates with silica gel using **TLC** method. The plate was placed in a sealed tank and the base of the plate was immersed in a shallow layer of a mixture of organic solvents (A – toluene/1,4-dioxane/acetic acid 180:45:5, B – hexane/methyl tert-butyl ether/formic acid 140:72:18, C – toluene/acetic acid. Different lichen substances present in the sample in each plate after a passage of solvent through the silica gel layer and later made visible by the sulphuric acid and other reagents. The resulting spots were visible in different colors or positions on the plate (Orange et al. 2001).

Some *Lepraria* samples were identified to genus level due to small insufficient material. *Lepraria* identification was conducted in Charles University, Prague and Senckenberg (Forschungsinstitut un Naturmuseum), Frankfurt am Main.

## 2.4. Data analysis

Initially data about epiphytic bryophyte and lichen species richness were analyzed depending on studied tree level variables (*Acer platanoides, Alnus glutinosa, Alnus incana, Betula pendula, Carpinus betulus, Fraxinus excelsior, Populus tremula, Quercus robur, Ulmus glabra, Ulmus laevis, Tilia cordata, Salix caprea, Sorbus aucuparia,* tree height, DBH, bark crevice depth, bark pH, intensity of tree inclination, direction of exposure of tree inclination, tree age) and forest stand level variables (forest stand area, age, connectivity with adjacent forest stand, broad-leaved WKH, aspen WKH, riparian WKH, other WKH, slope forest WKH, ravine forest WKH, Fennoscandian hemiboreal natural old broad–leaved deciduous forests, Sub-Atlantic and medio-European oak or oak-hornbeam forests of the Carpinion betuli, Tilio-Acerion forests of slopes, screees and ravines, riparian mixed forests of Quercus robur, Ulmus laevis and U. minor, Fraxinus excelsior or F. angustifolia, along big rivers (Ulmenion minoris)). Tree age was determined for 137 trees. Altogether data for 1020 trees were analyzed. Relationship with response variables and total epiphytic species richness (epiphytic bryophytes and lichens), total red-listed species richness (bryophytes and lichens), total WKH indicator species richness (bryophytes and lichens), bryophyte species richness, WKH bryophyte indicator species richness, bryophyte red-listed species richness, lichen species richness, WKH lichen indicator species richness, lichen red-listed species richness were analyzed. Data did not reflect a normal distribution also after transformations and Generalized linear model (GLM) with Gaussian family was used for selecting significant factors ($p<0.05$) influencing response variables. Stepwise selection was used for the evaluation of significant factors. The GLM method was selected based on distribution of residuals and model significance. Interactions were tested among studied continuous variables and continuous variables and tree species. Spearman's rank correlation was used for determining of significant and tight correlation among studied variables. The R programme package 2.7.2. version was used in the analysis (http://www.r-project.org/, Venables et al. 2008).

GLM (Canoco for Windows 4.7) with logit function with binomial distribution was selected for evaluating epiphytic bryophyte and lichen species occurrence probability depend on continuous variables (tree inclination in degrees, DBH, tree age, bark crevice depth, tree height, bark pH, forest stand age, forest stand area). Species with at least occurrence on 30 trees were selected for this analysis.

Epiphytic bryophyte and lichen (overall 110 species) distribution on 1020 trees was analysed by Canonical Correspondence Analysis (CCA) ordination, where tree (tree species, tree inclination (degrees and direction of exposure), DBH, bark crevice depth, tree height, tree bark pH) and stand variables (forest stand age, forest stand area, geobotanical region, WKH type, EU habitat type) were selected after stepwise selection (Braak, Šmilauer 2002). Tree age and species with less than four records were removed from CCA analysis. Epiphytic bryophyte and lichen cover data were used in vertical (until 0.50 m and 0.50-1.50 m) and horizontal (North, South, East, West) spatial structure analysis with CCA ordination method (Canoco for Windows 4.7), and indicator species analysis (after Dufrene M. & Legendre P., PCord 4, McCune B., Mefford M.J. 1999, Multivariate Analysis of Ecological data, Version 4.17, MjM Software, Gleneden Beach, Oregon U.S.A.). In total data on 8148 samples and 129 (71 bryophytes and 58 lichen) species were included in indicator species analysis. Monte Carlo Permutation tests were used for identifying the significant variables in CCA and GLM in Canoco for Windows 4.7 programme package.

The Bonferroni test was used for multiple comparisons of all studied 13 tree species depending on nine epiphytic species richness groups. The Bonferroni test is freely available in the Past programme package (Hammer et al. 2001).

Transplantation data were analysed with Wilcoxon rank test in the R programme package 2.7.2. version to test differences in initial and final transplant vitality. In total 28 *Neckera pennata* and 28 *Lobaria pulmonaria* transplants were analyzed from April 2007 and March 2008.

# 3. Results

## 3.1. Epiphytic bryophyte and lichen species richness

In total 148 (73 bryophyte and 75 lichen) epiphytic species were found in the present study, including 60 bryophytes of Bryopsida and 13 bryophytes of Hepaticopsida. In total 56 crustose, 15 foliose and four fruticose lichens were found.

Overall 14 red-listed species (nine bryophyte and five lichen species), 21 WKH indicator species (12 bryophyte and nine lichen species) and eight WKH specialist (four bryophyte and four lichen) species were found (Ek et al. 2002, Appendix 3).

In total 18 (eight bryophyte and ten lichen) species were specially protected and ten (five bryophyte and five lichen) species were Microreserve species in Latvia (LRMK 2000b, LRMK 2001). One of the recorded bryophyte species (*Dicranum viride*) is an European Habitat Directive species (EU 1992).

The most common bryophyte species were *Hypnum cupressiforme* (on 737 trees), *Radula complanata* (on 681 trees) and the WKH indicator species *Homalia trichom*anoides (on 548 trees). The most common lichen species were *Phlyctis argena* (on 768 trees), *Lepraria lobificans* (on 617 trees) and WKH indicator species – *Graphis scripta* (on 325 trees). *Metzgeria furcata* (on 228 trees) and *Lobaria pulmonaria* (on 14 trees) were the most common red-listed species (Appendix 2).

A significant correlation was found between WKH indicator species richness and red-listed species for total species richness ($p<0.05$, $r=0.64$), bryophyte richness ($p<0.05$, $r=0.74$) and weakly for lichen richness ($p<0.05$, $r=0.17$).

Differences were found in the species distribution among the studied geobotanical regions. Only species with occurrence at least on 10 trees were selected for the evaluation of geographical distribution. Several epiphytic bryophyte and lichen species showed differences in distribution among geobotanical regions or geography in Latvia. *Anomodon attenuatus* was found in the Mid Latvian, North Livland and in North-Eastern Latvian geobotanical regions only, but was absent in South-eastern and western parts of Latvia. A similar distribution trend was found for *Pseudoleskeella nervosa* which had an eastern and central distribution in Latvia: Central Livland, North-Eastern Latvian, Zemgale, North Livland, South-Eastern and Midlatvian geobotanical region. *Dicranum viride* showed distribution in Coastal, Northlivland and North-Eastern Latvia geobotanical regions suggesting a northern distribution in Latvia. *Lejeunea cavifolia* was found in North Livland, North-Eastern Latvia and Mid Latvian gebotanical regions and showed an

Table 6.

Epiphytic bryophyte and lichen species richness among studied forest habitat types.

| Forest type | Species richness: Bryophytes Total | Bryophytes WKH indicators | Bryophytes Red-listed | Lichens Total | Lichens WKH indicators | Lichens Red-listed | Total |
|---|---|---|---|---|---|---|---|
| WKH | | | | | | | |
| Broad-leaved WKH (11 territories) | 60 | 12 | 7 | 57 | 8 | 4 | 117 |
| Aspen WKH (four territories) | 48 | 7 | 3 | 24 | 4 | - | 72 |
| Ravine WKH (two territories) | 38 | 8 | 4 | 24 | 6 | 2 | 62 |
| Slope WKH (13 territories) | 63 | 11 | 8 | 52 | 8 | 4 | 115 |
| Riparian WKH (three territories) | 40 | 7 | 3 | 34 | 5 | 2 | 74 |
| EU | | | | | | | |
| Fennoscandian natural old broad-leaved forest 9020* (eight territories) | 55 | 12 | 6 | 57 | 8 | 4 | 112 |
| Sub–Atlantic and medio-European oak or oak-hornbeam forests of the Carpinion betuli 9160* (two territories) | 41 | 8 | 4 | 26 | 5 | - | 67 |
| Tilio-Acerion forests of slopes, screes and ravines 9180* (14 territories) | 63 | 10 | 8 | 55 | 8 | 4 | 118 |
| Riaprian mixed forests of Quercus robur, Ulmus laevis, U. glabra and U. minor, Fraxinus excelsior or F. angustifolia, along the great rivers (Ulmenion minoris) 91F0 (four territories) | 40 | 6 | 3 | 34 | 5 | 2 | 74 |
| Western Taïga 9010* (one territory) | 47 | 7 | 3 | 17 | 4 | - | 64 |

Explanations: WKH – Woodland key habitat types (Ek et al. 2002), EU – protected habitat types in the European Union (EU 2007). Number of studied territories in the brackets.

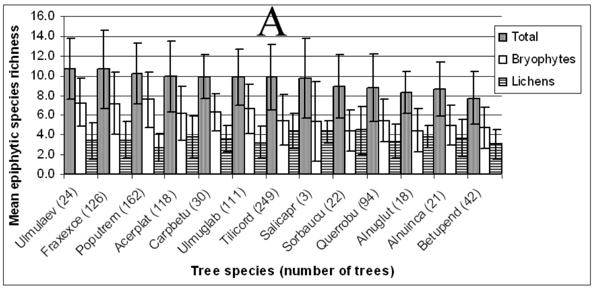
eastern distribution in Latvia. Also lichen *Lecanora carpinea* was not found in Coastal and West Latvian geobotanical regions, but was present in all other five geobotanical regions of Latvia. *Pertusaria albescens* was found in Mid Latvian, Central Latvian and North Livland geobotanical regions showing a northern and central distribution in Latvia. *Antitrichia curtipendula* and *Brachythecium reflexum* were found in the West Latvian geobotanical region only. Lichen *Lecanora glabrata* was found only in West Latvian and Coastal geobotanic regions showing a Western distribution in Latvia. Toyal species richness was the highest in broad-leaved WKH (117 species) as well as in the EU protected habitat Tilio-Acerion forests of slopes, screes and ravines (118 species) (Tab. 6).

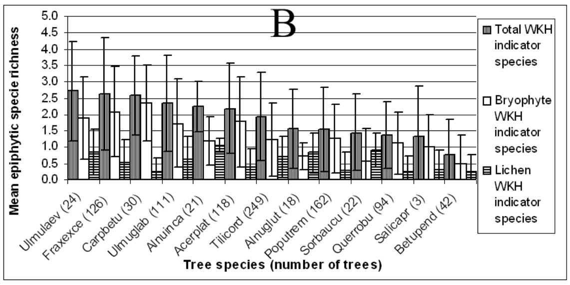
Table 7.

Epiphytic bryophyte and lichen species richness among the studied territories.

| Territory | Species richness | | | | | | |
|---|---|---|---|---|---|---|---|
| | Bryophytes | | | Lichens | | | Total |
| | Total | WKH indicators | Red-listed | Total | WKH indicators | Red-listed | |
| Aizkraukles purvs un meži Nature Reserve | 12 | 7 | 4 | 33 | 1 | - | 45 |
| Ciecere lake Island Nature Reserve | 19 | 3 | 1 | 9 | - | 2 | 28 |
| Cirsti in Slītere National Park | 31 | 8 | 3 | 19 | 4 | - | 50 |
| Dārznīcas pilskalns in Vestiena Protected Landscape Region | 21 | 3 | 1 | 22 | 2 | 1 | 43 |
| Dunika Nature Reserve | 26 | 6 | 4 | 13 | 2 | 1 | 39 |
| Egļu kalns in Svente Nature Park, Augšzeme Protected Landscape Region | 31 | 3 | 1 | 11 | 3 | - | 42 |
| Ērgļi in Ogre valley Nature Park | 25 | 2 | 2 | 19 | 2 | | 44 |
| Jaunanna Nature Reserve | 26 | 7 | 3 | 21 | 3 | 1 | 47 |
| Kaķīškalns in Gauja National Park | 26 | 5 | 3 | 15 | 1 | | 41 |
| Korkuļu sausgultne un pazemes upe Geological and Geomorphological Nature Monument | 19 | 4 | 1 | 18 | 2 | | 37 |
| Korneti-Peļļi in Nature Reserve, Veclaicene Protected Landscape Region | 12 | 1 | - | 19 | 2 | 1 | 31 |
| Maziča Oaks Microreserve | 16 | 2 | 1 | 15 | 3 | - | 31 |
| Moricsala Nature Reserve | 29 | 12 | 4 | 25 | 8 | 4 | 54 |
| Nurmiži Reserve in Gauja National Park | 29 | 7 | 4 | 11 | 3 | 1 | 40 |
| Paņemūnes meži Nature Reserve | 20 | 1 | 1 | 15 | 4 | - | 35 |
| Pededzes lejtece Nature Reserve | 26 | 5 | 2 | 15 | 3 | - | 41 |
| Pirtslīcis – Līkā atteka Nature Reserve in Ziemeļgauja Specially Protected Landscape Region | 23 | 5 | 2 | 20 | 4 | 2 | 43 |
| Ruņupe valley Nature Reserve | 36 | 7 | 3 | 17 | 2 | - | 53 |
| Staicele in Salaca valley Nature Park, North Livland Biosphere Reserve | 27 | 6 | 3 | 12 | 2 | - | 39 |
| Starinas mežs Nature Reserve | 22 | 4 | - | 12 | 3 | - | 34 |
| Šlīteres bāka in Slītere National Park | 30 | 5 | 3 | 23 | 4 | 1 | 53 |
| Tadenava Microreserve | 32 | 7 | 4 | 19 | 3 | - | 51 |
| Velnala in Gauja National Park | 21 | 6 | 2 | 21 | 4 | 2 | 42 |
| Venta un Šķervelis Nature Reserve | 26 | 3 | | 19 | 1 | | 45 |
| Vērenes gobu un vīksnu audze Nature Reserve in Ogre valley Nature Park | 21 | 5 | 1 | 25 | 2 | - | 46 |
| Vilce valley Nature Park | 28 | 6 | 3 | 18 | 5 | - | 46 |
| Vjada forest Nature Reserve | 33 | 7 | 3 | 22 | 4 | 3 | 55 |
| WKH in Laubere pagasts | 35 | 7 | 2 | 21 | 2 | 1 | 56 |
| WKH in Lestene pagasts | 34 | 3 | 1 | 7 | 2 | - | 41 |
| WKH in Slītere National Park | 32 | 7 | 3 | 17 | 6 | 2 | 49 |
| WKH in Straupe pagasts | 22 | 5 | 1 | 16 | 4 | - | 38 |
| WKH in Varakļāni pagasts | 39 | 6 | 3 | 12 | 2 | - | 51 |
| WKH in Vidriži pagasts | 31 | 5 | 2 | 20 | 4 | - | 51 |
| Zilais kalns Nature Reserve in North Livland Biosphere Reserve | 29 | 5 | 3 | 17 | 3 | 2 | 46 |

Epiphytic bryophyte and lichen species richness varied among the studied territories (Tab. 7). Total species richness was the highest in the WKH in Laubere pagasts (56 epiphyte species), bryophyte species richness (39 species) was the highest in WKH in Varakļāni pagasts. Moricsala Nature Reserve had the highest number of bryophyte (12 species) and lichen (eight species) WKH indicator species, lichen red-listed species (four species) as well as total number of WKH indicator species (20 species) and total number of red-listed species (eight species). A similar number of bryophyte red-listed species (four species) was found among the territories Aizkraukles purvs un meži Nature Reserve, Nurmižu Reserve, Tadenava Nature Reserve and Moricsala Nature Reserve (Tab. 7).



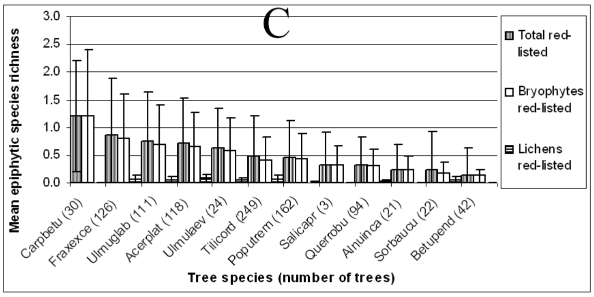




Figure 2. Epiphytic bryophyte and lichen species richness on studied tree species. Total epiphytic species richness (A), WKH indicator species richness (B), total red-listed species richness (C). Number of tree individuals in brackets. *Alnus glutinosa* was removed from the red-listed species graph (C) due to lack of them. Tree species abbreviations in Appendix 2.

Overall 32 epiphytic bryophyte and lichen species were found only once in one studied territory (of 16 studied trritories). For example, *Porina aenea* was found only in Dunika Nature Reserve and *Brachythecium reflexum* in Ciecere lake Island Nature Reserve.

Epiphytic bryophytes and lichens were studied on 13 tree species (Fig. 2). In general epiphytic species richness was similar among the studied tree species as the standart deviations overlaped. However, differences in species richnesss mean values were found. *Ulmus laevis* hosted the highest total epiphytic species richness (10.67±3.09), total WKH indicator species richness (2.71±1.52). Total bryophyte species richness was the highest on *Populus tremula* (7.53±2.78) and lichen species on *Sorbus aucuparia* (4.45±2.48). *Carpinus betulus* hosted the highest WKH bryophyte indicator species richness (2.33±1.15) as well as total (1.20±1.00) and bryophyte (1.20±1.00) red-listed species richness. The highest WKH lichen indicator species richness was found on *Alnus incana* (1.05±0.22) and lichen red-listed species – on *Tilia cordata* (0.07±0.27).

### 3.2. Variables explaining epiphytic species richness on a tree level

Epiphytic bryophytes and lichens were divided into nine groups (total epiphytic bryophyte and lichen, bryophyte, lichen, total WKH indicator, total red-listed, WKH bryophyte indicator, bryophyte red-listed, WKH lichen indicator, lichen red-listed species richness) for determining significant variables (continuous – tree DBH, bark crevice depth, height, inclination, pH, nominal variables – tree species, direction of inclination) affecting composition for each group (Appendix 3). GLM showed that total epiphytic species

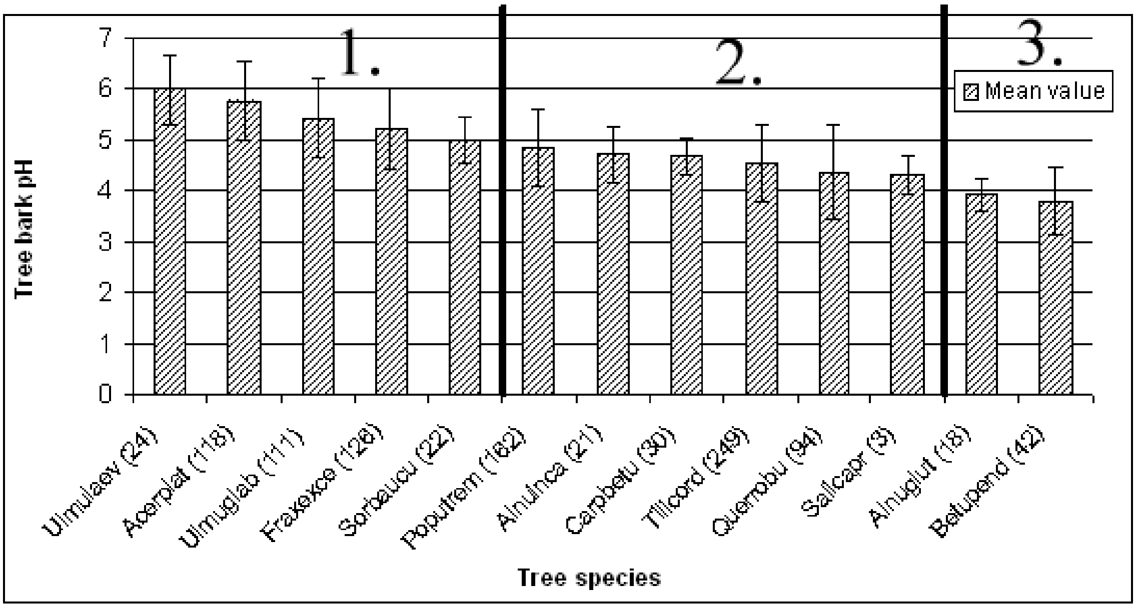



Figure. 3. Tree bark pH among studied tree species. 1. – first pH value group (5.00-6.00), 2. – second pH value group (4.00-<5.00), 3. – third pH value group (3.00-<4.00). Species abbreviations in Appendix 2.

richness was influenced significantly ($p<0.05$) by North inclination of trees, *Betula pendula*, *Quercus robur*, tree height and the interactions – diameter x bark crevice depth, pH x bark crevice depth and *Ulmus glabra* x pH. Tree species, bark pH, tree height and interactions among tree species and pH, pH and inclination in degrees, diameter and bark crevice depth, tree age and pH influenced bryophyte species richness significantly. Similar relationships were found in lichen species richness, but interactions among tree species and pH were more pronounced.

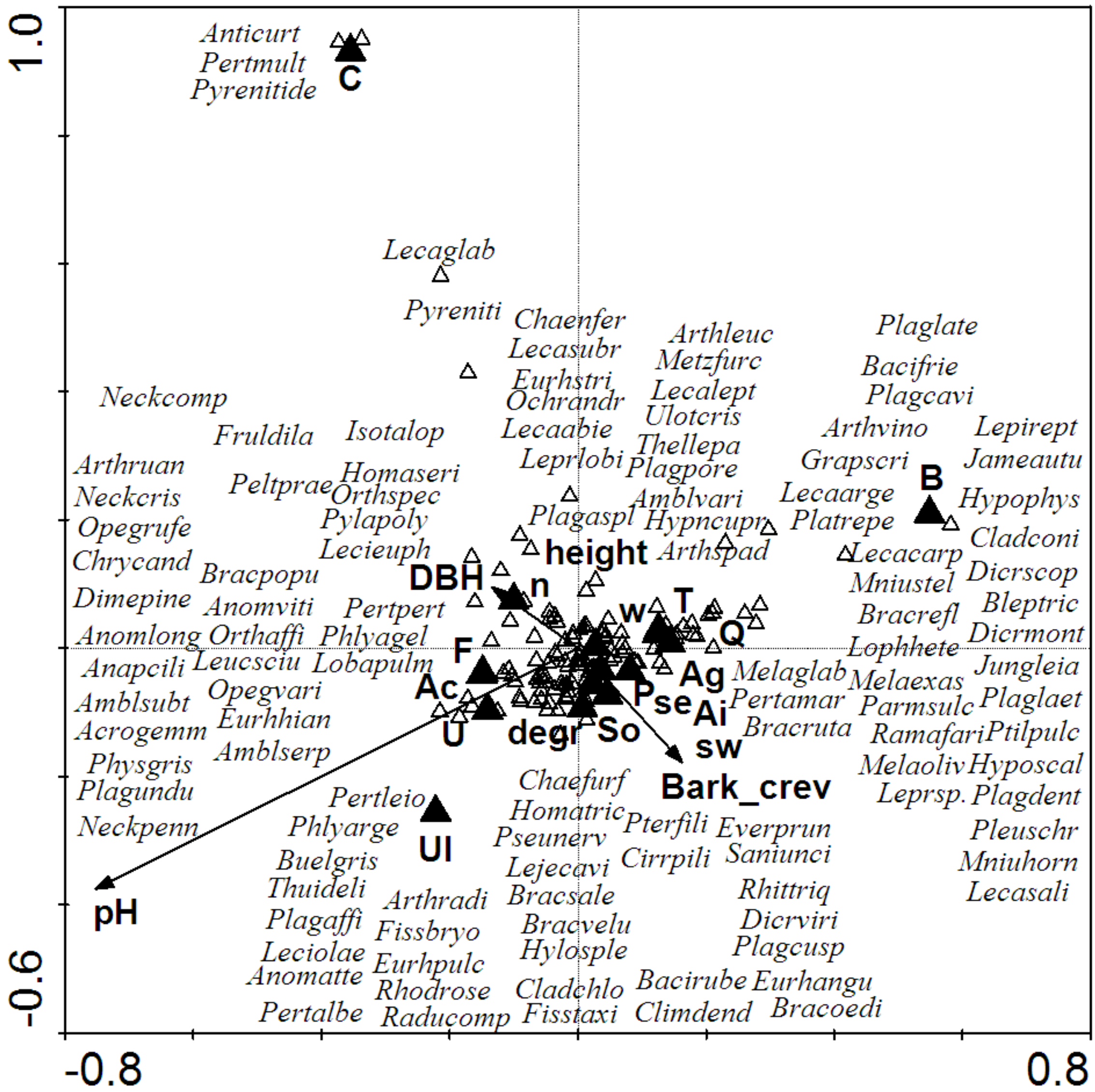



Figure 4. Epiphytic bryophyte and lichen species distribution in relation to tree level variables (CCA ordination). Only significant variables ($p<0.05$) were included in analysis. Epiphyte occurrence data on trees were analyzed. Ac – *Acer platanoides* (r=-0.220 with axis 1), Ag – *Alnus glutinosa* (r=0.047, with axis 1) Ai – *Alnus incana* (r=0.020 with axis 2), B – *Betula pendula* (r=0.385 with axis 1), F – *Fraxinus excelsior* (r=-0.218 with axis 1), C – *Carpinus betulus* (r=0.660 with axis 2), Ul – *Ulmus laevis* (r=-0.188 with axis 2), U – *Ulmus glabra* (r=-0.200 with axis 1) , P – *Populus tremula* (r=-0.168 with axis 2), T – *Tilia cordata* (r=0.295 with axis 1), Q – *Quercus robur* (r=0.153 with axis 1), bark_crev – bark crevice depth (r=-0.138 with axis 1), height – tree height (r=0.039 with axis 2), degr – degrees of tree inclination (r=-0.058 with axis 2), n – tree inclination on North direction (r=-0.135 with axis 1), w – tree inclination on West direction (r=-0.026 with axis 1), sw – tree inclination on South-western direction (r=-0.081 with axis 2), DBH – tree diameter at breast height (r=-0.105 with axis 1), pH – tree bark pH (r=-0.587 with axis 1), $p<0.05$. Species abbreviations in Appendix 4.

Total red-listed species and WKH indicator species richness were more influenced significantly by tree species and tree age. None of the studied factors influenced red-listed lichen species richness significantly, except interactions among tree species with bark crevice depth and tree height. Bryophyte indicator species richness was mostly influenced by tree species and interactions among tree species, pH and tree age. WKH lichen indicator species richness was more influenced by tree species and interactions among tree species and pH as well as tree species and bark crevice depth (Appendix 3).

Tree species showed differences in mean tree bark pH value (Fig. 3). Tree species were divided into three groups according to mean tree bark pH value: trees with higher bark pH (**first group** 5.00-6.00) – *Ulmus laevis, Acer platanoides, Ulmus glabra, Fraxinus excelsior* and *Sorbus aucuparia*, trees with medium acidic bark pH (**second group** 4.00-<5.00) – *Populus tremula, Alnus incana*, *Carpinus betulus, Tilia cordata, Quercus robur, Salix caprea*, trees with acidic bark pH (**third group** 3.00-<4.00) – *Alnus glutinosa* and *Betula pendula*.

A CCA ordination was used to identify the factors driving species composition gradients (Fig. 4). The highest correlation was found between axis 1 and tree bark pH, tree species and bark crevice depth. The axis 2 was correlated mainly with *Carpinus betulus*. Other studied variables – DBH, tree height, inclination showed a relatively low correlation with axis 1 and axis 2. Epiphytic species such as *Brachythecium populeum, Neckera crispa* were located more on the ordination in relation to a higher bark pH while species such as *Brachythecium reflexum, Evernia prunastri, Hypogymnia physodes* were associated with lower pH in the ordination. Other species such as *Antitrichia curtipendula*, *Pyrenula nitidella* were more related with axis 2 associated by *Carpinus betulus*.

Multiple comparisons among the epiphytic species groups and tree species were analysed (Tab. 8). The most significant differences in species composition were affected by *Fraxinus excelsior* and *Betula pendula, Quercus robur, Tilia cordata* as well as *Betula pendula* and *Ulmus glabra, Acer platanoides, Carpinus betulus*. Also *Quercus robur* and *Ulmus glabra* showed significant differences in the four studied epihytic species groups.

Positive and negative relationships were found between the studied tree continuous variables and epiphytic species (Fig. 5). Tree inclination was positively related to occurrence probability of *Lepraria lobificans, Pseudoleskeella nervosa* and *Anomodon attenuatus*, but a negative linear relationship was found with *Homalia trichomanoides* (Fig. 5 A, B). Tree DBH was significantly positively affected probability occurrence of *Hypnum*

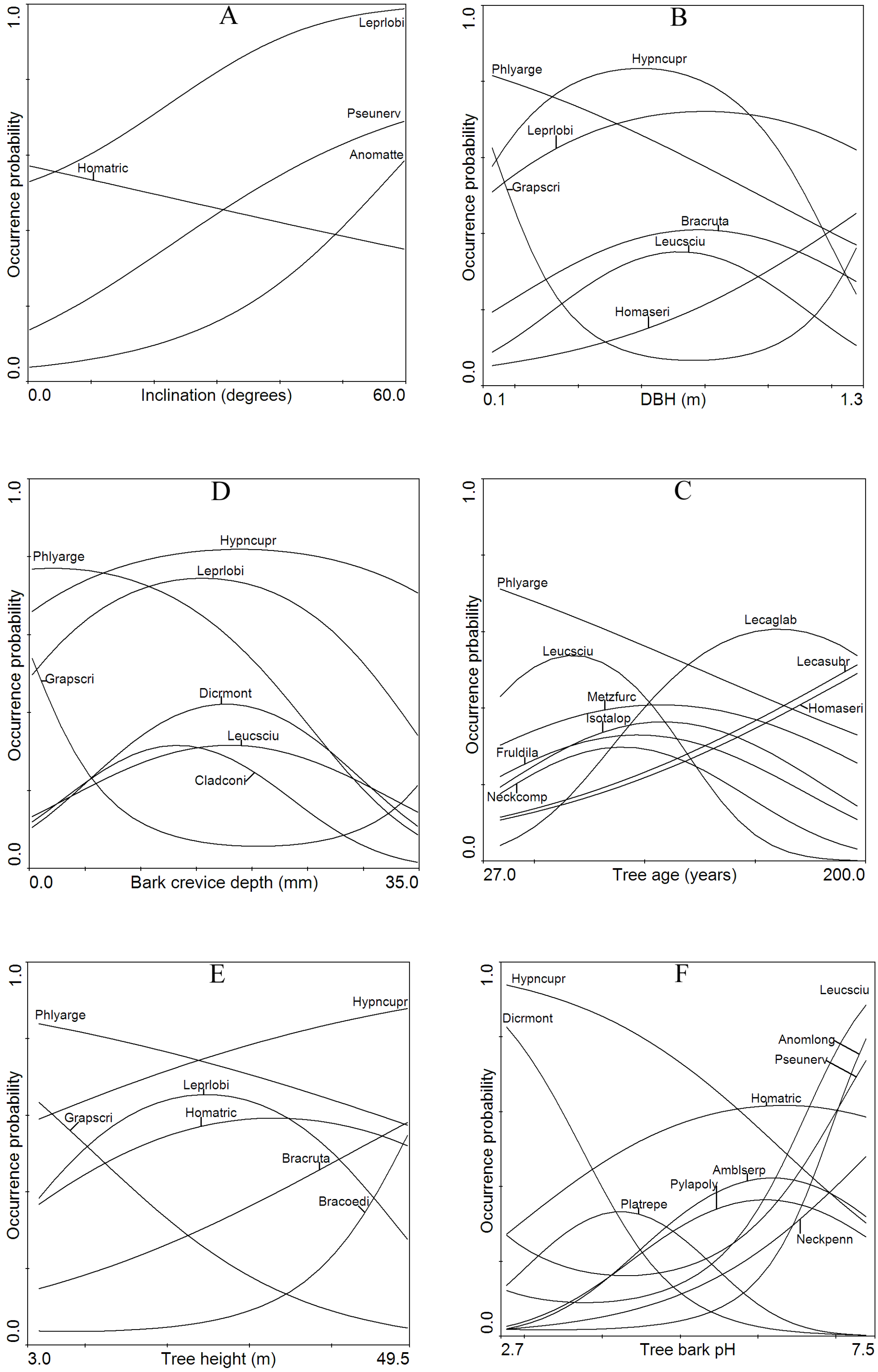
Table 8.

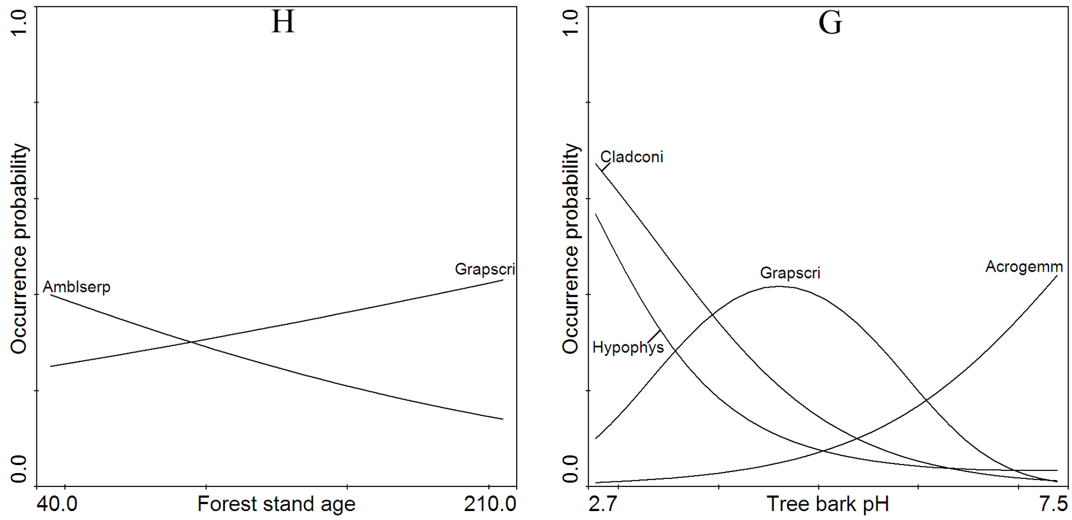
Epiphytic species richness multiple comparisons among tree species after Bonferroni test.

| | Tree species | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Ac | B | C | F | P | Q | So | T |
| Ai | LI | I,LI | LI | - | LI | LI | - | - |
| Ag | - | - | ToR,BrR | - | Br | LI | - | - |
| B | ToR,I,BrR | - | ToR,I,BrR | To,Br,ToR ,I,BrR | To,Br | - | LI | L,I,LI |
| P | Br,L,I | - | ToR,I,BrR | L,ToR,I | - | - | - | - |
| Q | ToR,I | - | ToR,I,BrR | To,Br,ToR ,I | Br | - | - | - |
| So | LI | - | LI | Br | Br,L,LI | LI | - | - |
| T | LI | - | ToR,BrR,L I | Br,L,ToR,I | Br,L,LI | L,LI | - | - |
| U | - | To,Br,ToR ,I,BrR, | - | BrR | I,LI | ToR,I,BrR, LI | - | L |
| Ul | - | Br,I | - | - | I,LI | I,LI | Br | - |

Explanations: LI – lichen indicator species richness, ToR – total red-listed species richness, I – total indicator species richness, BrR – bryophyte red-listed species richness, Br – bryophyte species richness, L – lichen species richness, Br – bryophyte species richness, To – total species richness. Ac – *Acer platanoides*, Ai – *Alnus incana*, Ag – *Alnus glutinosa*, B – *Betula pendula*, C – *Carpinus betulus*, F – *Fraxinus excelsior*, P – *Populus tremula*, Q – *Quercus robur*, So – *Sorbus aucuparia*, T – *Tilia cordata*, U – *Ulmus glabra*, Ul – *Ulmus laevis*, - no significant difference found.

*cupressiforme, Lepraria lobificans, Leucodon sciuroides, Brachythecium rutabulum, Homalothecium sericeum*. Occurrence probability of *Hypnum cupressiforme* until approximately 0.60m, when it started decreasing increasing DBH. Similar response to DBH were found for *Brachythecium rutabulum, Lepraria lobificans* and *Leucodon sciuroides*, when occurrence probability increased until 0.70 m of DBH. Occurrence of *Graphis scripta* was lowest at mid DBH. Clear negative trend between DBH and *Phlyctis argena* was found (Fig. 5 B). *Phlyctis argena* showed a clear linear negative relationship


A
Occurrence probability
1.0
0.0
0.0
Inclination (degrees)
60.0
Leprlobi
Pseunerv
Anomatte
Homatric
B
Occurrence probability
1.0
0.0
0.1
DBH (m)
1.3
Phlyarge
Hypncupr
Leprlobi
Grapscri
Bracruta
Leucsciu
Homaseri
D
Occurrence probability
1.0
0.0
0.0
Bark crevice depth (mm)
35.0
Phlyarge
Hypncupr
Leprlobi
Grapscri
Dicrmont
Leucsciu
Cladconi
C
Occurrence prbability
1.0
0.0
27.0
Tree age (years)
200.0
Phlyarge
Lecaglab
Leucsciu
Lecasubr
Homaseri
Metzfurc
Isotalop
Fruldila
Neckcomp
E
Occurrence probability
1.0
0.0
3.0
Tree height (m)
49.5
Phlyarge
Hypncupr
Leprlobi
Grapscri
Homatric
Bracruta
Bracoedi
F
Occurrence probability
1.0
0.0
2.7
Tree bark pH
7.5
Hypncupr
Dicrmont
Leucsciu
Anomlong
Pseunerv
Homatric
Amblserp
Pylapoly
Platrepe
Neckpenn



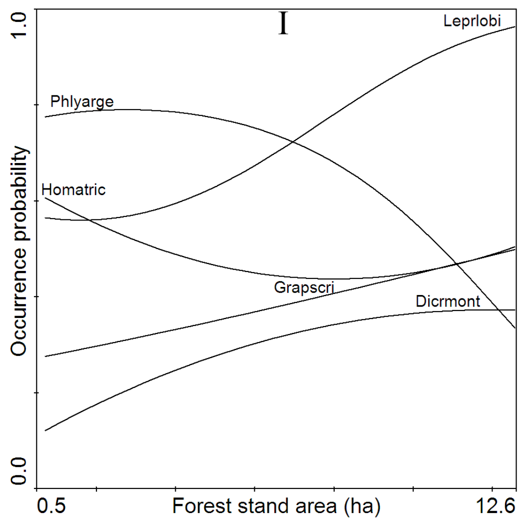




Figure 5. Epiphytic bryophyte and lichen species occurrence probability based on studied variables (GLM). A – tree inclination, B – tree DBH, C – tree age, D – bark crevice depth, E – tree height, F – tree bark pH in relation with bryophytes, G – tree bark pH in relation with lichens, H – forest stand age, I – forest stand area (only significant occurrence probability for each species were included $p<0.05$). Binomial distribution with quadratic degree (except Homatric in A, Phlyarge in B, C, E, Hypncupr, Bracruta in E, Amblserp in H, Grapscri in H and I with linear degree) and logit function were used. Species abbrevations in Appendix 4.

with tree age, while *Lecanora subrugosa* and *Homalothecium sericeum* occurrence probability increased with tree age. Similar trends were found for *Metzgeria furcata, Isothecium alopecuroides, Frullania dilata,* and *Neckera complanata,* where maximum occurrence probability was at 100 years of tree age. Occurrence of *Leucodon sciuroides* rapidly decreased at about 50 years tree age. *Lecanora glabrata* reaches maximum occurrence in 150 old trees (Fig. 5 C). Similar species response to bark crevice depth and DBH was found (Fig. 5 B, D). *Dicranum montanum, Leucodon sciuroides* and *Cladonia coniocraea* showed similar trends. *Phlyctis argena* and *Graphis scripta* showed negative relationship with tree height, while clear positive trends were found for *Hypnum cupressiforma, Brachythecium rutabulum* and *Brachythecium oedipodium. Lepraria lobificans* and *Homalia trichomanoides* showed a similar trend, however, *Homalia trichomanoides* occurred more on taller trees compared with *Lepraria lobificans* (Fig. 5 E). Most of the bryophyte species showed a positive occurrence probability with increasing tree bark pH, while *Hypnum cupressiforme* and *Dicranum montanum* occurrence decreased with increasing pH value (Fig. 5, F). *Cladonia coniocraea* and *Hypogymnia physodes* occurrence probability decreased with increasing pH value, while *Acrocordia gemmata* showed a clear positive relationship with tree bark pH (Fig. 5 G). The optimum pH value for *Graphis scripta* occurrence probability varied between 4.00 and 5.00. Forest stand age influenced positively *Graphis scripta* and negatively *Amblystegium serpens* occurrence probability (Fig. 5 H).

A well pronounced positive trend between tree age and *Lecanora glabrata* was found (Fig. 5 C). A positive relationship were found also between tree age and *Isothecium alopecuroides, Leucodon sciuroides, Metzgeria furcata, Neckera complanata, Frullania dilatata, Lecanora subrugosa and Homalothecium sericeum*. A negative linear relationship was found between *Phlyctis argena* and tree age.

Tree bark crevice depth (Fig. 5 D) was significantly associated positively with occurrence probability of *Hypnum cupressiforme, Lepraria lobificans, Dicranum montanum, Cladonia coniocraea* and *Leucodon sciuroides*, but negatively with *Graphis scripta*.

The higher tree bark pH was associated positively with the occurrence probability of *Homalia trichomanoides, Leucodon sciuroides, Amblystegium serpens, Anomodon longifolius, Pylaisia polyantha, Neckera pennata*, *Pseudoleskeella nervosa* and *Acrocordia gemmata*, but negatively with *Hypnum cupressiforme*, *Dicranum montanum, Platygyrium repens*, *Cladonia coniocraea*, *Graphis scripta* and *Hypogymnia physodes*.

## 3.3. Variables explaining epiphytic species richness on a forest stand level

Continuous variables (forest stand age, area) and nominal variables (WKH and EU forest habitat types, connectivity) were used to test relationships with epiphytic species richness.

Total species richness was affected significantly by forest stand area, connectivity, riparian forest WKH and Fennoscandian natural old broad-leaved forest. Aspen WKH was associated significantly with bryophyte and WKH indicator species richness. Ravine WKH affected significantly bryophyte, lichen, total red-listed, red-listed bryophyte and WKH bryophyte indicator species richness. Slope WKH was associated with bryophyte, total red-listed, WkH indicator species, red-listed bryophyte and WKH bryophyte indicator species richness. Sub-Atlantic and medio-european oak or oak-hornbeam forests of the Carpinion betuli was

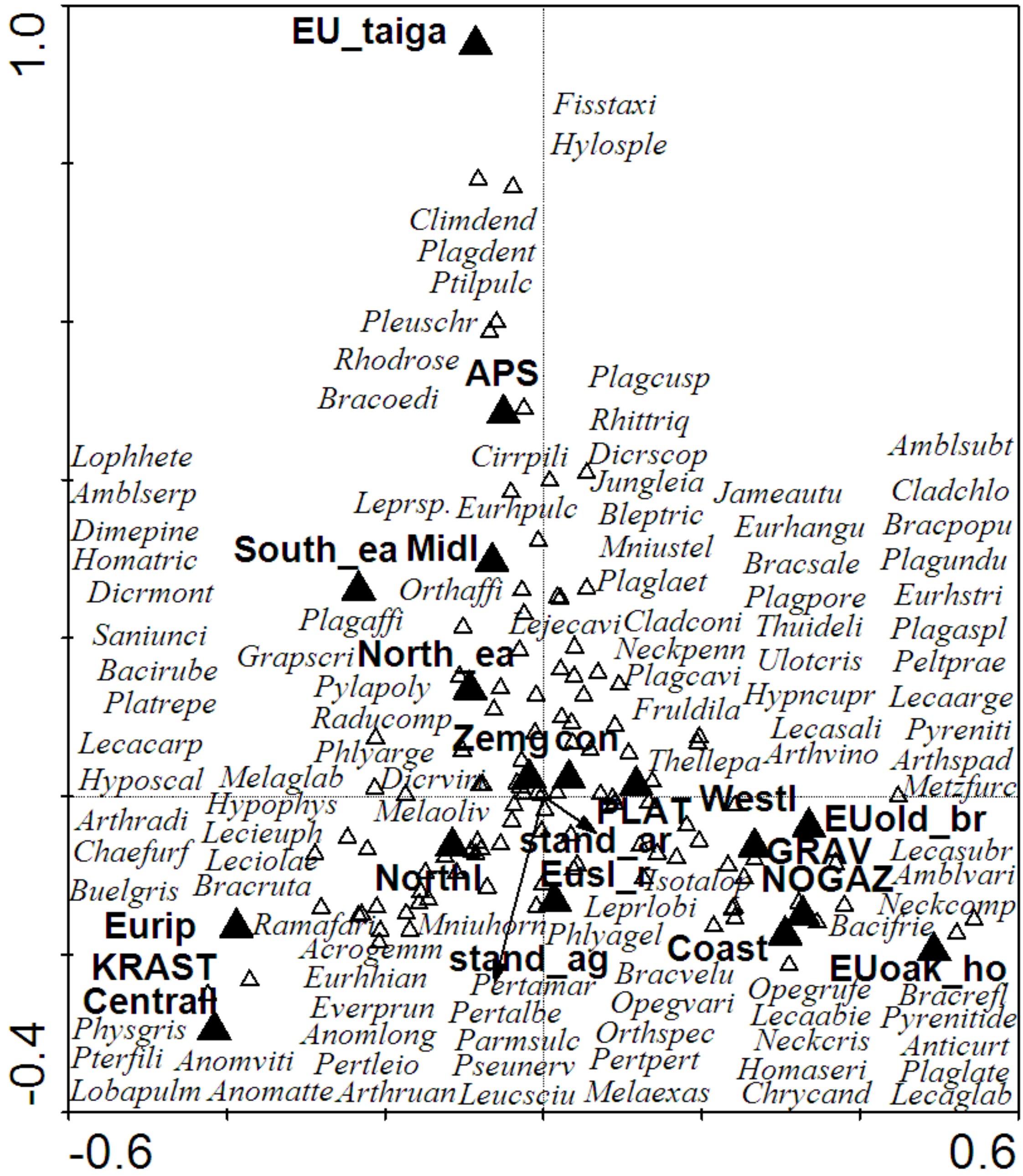



Figure 6. Epiphytic bryophyte and lichen species composition in relation to forest stand level variables (CCA ordination). Epiphyte occurrence data on trees were analyzed. South_ea – South – Eastern geobotanical region (r=0.190 with axis 2), Midl – Mid Latvian geobotanical region (r=0.351 with axis 2), North_ea – North-Eastern Latvian geobotanical region (r=0.170 with axis 2), Zemg – Zemgale geobotanical region (r=0.017 with axis 2), Westl – West Latvian geobotanical region (r=0.410 with axis 1), Coastal – Coastal geobotanical region (r=0.403 with axis 1), Northl – North Livland geobotanical region (r=-0.195 with axis 1), Centrall – Central Livland geobotanical region (r=-0.371 with axis 1), APS – aspen forest WKH (r=0.615 with axis 2) , PLAT – broad-leaved forest WKH (r=0.237 with axis 1), KRAST – riparian forest WKH (r=-0.370 with axis 1), NOGAZ – slope forest WKH (r=0.245 with axis 1), GRAV – ravine forest WKH (r=0.206 with axis 1), EU_taiga – Western Taïga (r=0.579 with axis 2), Eu-rip – riparian mixed forests of *Quercus robur*, *Ulmus laevis*, *U. glabra* and *U. minor*, *Fraxinus excelsior* or *F. angustifolia*, along the great rivers (*Ulmenion minoris*) (r=-0.370 with axis 1), Eusl_r – Tilio-Acerion forests of slopes, screes and ravines (r=-0.371 with axis 2), Euold_br –

Fennoscandian natural old broad-leaved forest (r=0.245 with axis 1), Euoak_ho – Sub–Atlantic and medio-European oak or oak-hornbeam forests of the *Carpinion betuli* (r=0.295 with axis 1), stand_ag – forest stand age (r=-0.191 with axis 2), stand_ar – forest stand area (r=0.053 with axis 1), con – connectivity (r=0.123 with axis 1), p<0.05. Species abbreviations in Appendix 4.

significant habitat for bryophyte, lichen, total red-listed, red-listed bryophyte and WKH indicator species richness. Forests of slopes, screes and ravines was an important significant habitat for all lichen species groups. Riparian mixed forest of Quercus robur, Ulmus laevis and U. minor, Fraxinus excelsior or Fraxinus angustifolia, along the great rivers (Ulmenion minoris) was important for WKH lichen indicator species richness. Forest stand age was significant for WKH indicator species and WKH lichen indicator species richness. Significant relationships were found for forest stand area and stand age for total red-listed, WKH indicator species, red-listed bryophyte, WKH bryophyte indicator species and WKH lichen indicator species richness (Appendix 3).

In a CCA ordination (Fig. 6) the first ordination axis showed the highest correlation with Coastal, West Latvian Central Livland geobotanical regions, Sub–Atlantic and medio-European oak or oak-hornbeam forests of the *Carpinion betuli*, Fennoscandian natural old broad-leaved forest, riparian mixed forests of Quercus robur, Ulmus laevis, U. glabra and U. minor, Fraxinus excelsior or F. angustifolia, along the great rivers (Ulmenion minoris), riparian WKH, slope forest WKH. Species associated with axis 1 in the CCA ordination as *Antitrichia curtipendula, Pyrenula nitidella, Lecanora saligna*, which were found more on the Western part of Latvia and located close to Sub–Atlantic and medio-European oak or oak-hornbeam forests of the Carpinion betuli, Fennoscandian natural old broad-leaved forest and slope forest WKH. In the left part of the axis 1 were located species found more in central Latvia such as *Anomodon viticulosus, Pseudoleskeella nervosa, Pterigynandrum filiforme, Lobaria pulmonaria* found in riparian mixed forests of Quercus robur, Ulmus laevis, U. glabra and U. minor, Fraxinus excelsior or F. angustifolia, great rivers (Ulmenion minoris), riparian forest WKH and Central Livland geobotanical region.

Western Taïga, Aspen WKH, Mid Latvian geobotanical region (upper part of axis 2), Tilio-Acerion forests of slopes, screes and ravines, forest stand age (lower part of axis 2) showed the highest correlation with the second ordination axis. *Fissidens taxifolius, Plagiothecium denticulatum* was associated with the Western Taïga. Other species such as *Ptilidium pulcherrrimum* and *Brachythecium oedipodium* were associated with aspen WKH.

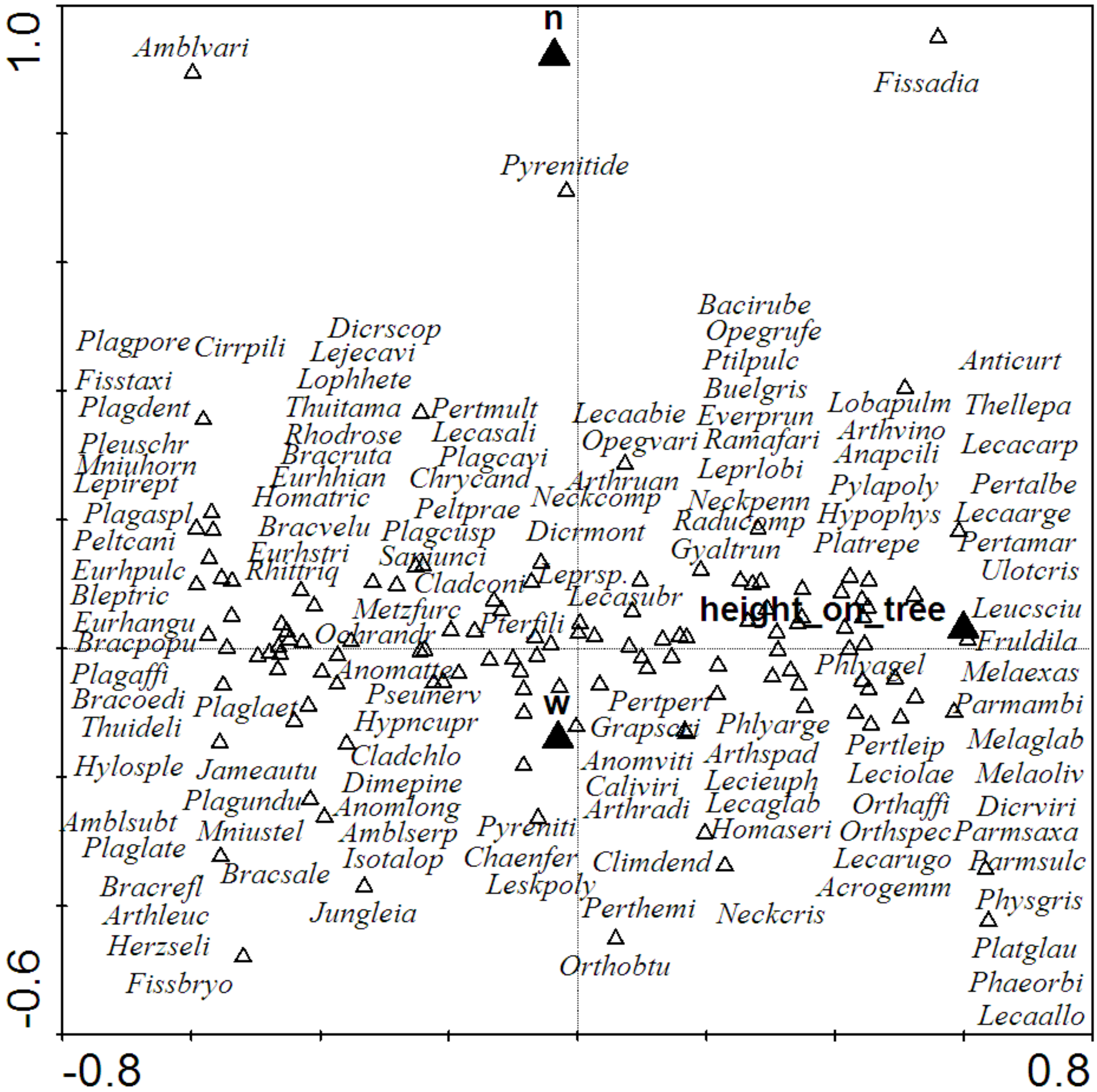



Figure 7. Epiphytic bryophyte and lichen relation to vertical and horizontal spatial distribution (CCA ordination). Epiphyte cover data on tree subplots were analyzed. Height – height on tree trunk (r=0.649 with axis 1), n – North direction of exposure (r=0.156 with axis 2), w – West direction of exposure (r=0.140 with axis 3), Significant variables included only (p<0.05). Species abbreviations after Appendix 4.

Species such as *Homalothecium sericeum*, *Leucodon sciuroides*, *Chrysotrix candelaris* were related to forest stand age and Tilio-Acerion forests of slopes, screes and ravines. Occurrence of *Amblystegium serpens* were influenced negatively, while *Graphis scripta* showed positive relationship with forest stand age (Fig. 5 H). Forest stand area influenced positively occurrence of *Lepraria lobificans, Graphis scripta, Dicranum montanum*, but negatively *Phlyctis argena*. An unclear relationship observed between *Homalia trichomanoides* and forest stand area as cover decreased until 11 ha and then started to increasing (Fig. 5 I).

## 3.4. Epiphytic bryophyte and lichen vertical and horizontal spatial distribution

Epiphytic species richness was similar on tree stem in different directions of exposures. In the North, South, and East directions presented 66 bryophyte species were found for each, the West direction hosted 67 bryophyte species. Lichen species richness in the North direction was 54 species, South – 55 species, East – 53 species, West – 51 species.

Height on tree, North and West directions of exposures were significant variables explaining epiphytic bryophyte and lichen species gradients in the CCA ordination (Fig. 7). The first axis was correlated with height on tree or vertical spatial distribution of epiphytic species. Species as *Orthotrichum speciosum, Frullania dilatata, Melanelia olivacea, Pertusaria amara*, *Phlyctis agelaea*, were associated with height in the ordination being more common at 0.50-2.00 m on tree stem. Other species such as *Plagiochila porelloides*, *Plagiomnium affine*, *Plagiothecium laetum*, *Peltigera canina* prefered the tree base (until 0.50 m).

The second ordination axis was correlated with the North direction of exposure of the tree stem (Fig. 7). Some species (*Fissidens adianthoides, Amblystegium varium, Pyrenula nitidella*) prefered the North direction of exposure. The West direction of exposure was correlated with the third ordination axis as well as species – *Anomodon longifolius, Anomodon viticulosus* and *Pyrenula nitida*.

The highest number of epiphytic indicator species were found up to 0.50m and 0.50-2.00 m height on North direction of tree stem (Tab. 9). Three epiphytic species were indicators on a particular height and direction on tree stem. *Amblystegium serpens* was an indicator species up to 0.50 m height for the South direction, *Phlyctis argena* up to 0.50 m on the East direction and *Radula complanata* at a 0.50-2.00 m height in the North direction.

Table 9.

Epiphytic bryophyte and lichen indicator species in relation to vertical and horizontal spatial distribution.

| Epiphytic species | Height on tree until 0.50m | | | | Height on tree 0.50-2.00m | | |
|---|---|---|---|---|---|---|---|
| | n | s | e | w | n | s | w |
| Bryophytes | | | | | | | |
| *Amblystegium serpens* | | 0.014 | - | - | - | - | - |
| *Brachythecium rutabulum* | 0.034 | - | - | - | - | - | - |
| *Cirriphyllum piliferum* | 0.004 | - | - | - | - | - | - |
| *Homalia trichomanoides* | 0.001 | - | - | - | 0.001 | 0.02 | - |
| *Hypnum cupressiforme* | - | - | - | - | 0.003 | - | 0.031 |
| *Plagiochila asplenioides* | 0.011 | - | - | - | - | - | - |
| *Plagiochila porelloides* | 0.005 | - | - | - | - | - | - |
| *Pylaisia polyantha* | - | - | - | - | 0.028 | - | - |
| *Radula complanata* | | | | | 0.002 | - | - |
| Lichens | | | | | | | |
| *Lepraria lobificans* | 0.031 | - | 0.024 | - | 0.005 | - | - |
| *Lepraria spp.* | 0.001 | 0.043 | - | 0.019 | 0.003 | - | - |
| *Opegrapha rufescens* | 0.025 | - | - | - | - | - | - |
| *Pertusaria amara* | 0.018 | - | - | - | 0.012 | - | - |
| *Phlyctis argena* | - | - | 0.045 | - | - | - | - |

Explanations: n – North, s – South, e – East, w – West directions of exposures on tree trunk. Only indicator species with indicator value>5 selected in the table. Significance values ($p<0.05$) pounted in the table. Epiphyte cover data were analyzed.

## 3.5. Transplantation experiments with *Neckera pennata* and *Lobaria pulmonaria*

The most durable method for transplantation experiments was medical sling. *Neckera pennata* and *Lobaria pulmonaria* vitality were compared between WKH and managed forest. Differences were found in studied transplant vitality comparing data from springs in 2007 and in 2008 using the Wilcoxon Rank Sum test. Transplants with *Neckera pennata* differed significantly between WKH and managed forest ($W=136$, $p=0.048$). No differences were found between *Lobaria pulmonaria* transplant vitality in WKH and managed forest ($W=133$, $p=0.120$).

# 4. Discussion
## 4.1. Species richness

The bryophyte species *Hypnum cupressiforme* and *Radula complanata* were the most common in the present study, as also described previously in Latvia (Āboliņa 2001, Mežaka, Znotiņa 2006, Mežaka et al. 2008). *Hypnum cupressiforme* is an ubiquitous species found on various substrates (Аболинь 1968). *Radula complanata* is common epiphyte also in Western Europe Russian nemoral forests (Шестакова 2004) and in Scandinavia (Hazell et al. 1998).

Of the most frequent lichens *Phlyctis argena* and *Graphis scripta* are common in Latvia (Piterāns 2001, Mežaka et al. 2008) and Estonian forests (Lõhmus 2004). *Lepraria lobificans* was common in the present study, but previously described only once on sandstone in Latvia (Piterāns 2007). However, this species is one of the most common *Lepraria* species in Estonian deciduous forests (Saag 2007). As *Lepraria* species determination requires TLC analysis and can not be solely based on morphology, probably *Lepraria lobificans* is more common in Latvia as previously considered (Orange et al. 2001).

*Homalia trichomanoides* is common in Latvia (Āboliņa 2001, Anonymous 2003, Mežaka et al. 2008), Russian nemoral forests (Шестакова 2004) and Polish nemoral forests (Cieśliński et al.1996b). *Metzgeria furcata* is the most common of epiphytic red-listed species (Anonymous 2003, Mežaka, Znotiņa 2006, Mežaka et al. 2008). *Metzgeria furcata* is a pioneer species colonizing the most xeric habitats and may also cover other species. It has similar ecological characteristics as *Hypnum cupressiforme*, but the latter needs humus for successful establishment while the former can colonize even smooth bark (Rasmussen 1975).

Biogeographical distribution of many species has been described (Jüriado et al. 2009b). Some of the studied species showed a relation with one or several geobotanical regions. Lichen diversity in forest can be influenced by regional climatic differences (Rose 1976). However, it is necessary to evaluate these trends in epiphytic species richness critically as only a small sample of deciduous forests in each geobotanical region were selected for the present study. *Anomodon attenuatus*, *Lecanora carpinea*, *Lejeunea cavifolia* and *Pseudoleskeella nervosa* were not found in West Latvia and were more common in central and eastern parts of Latvia (Fig. 6). *Antitrichia curtipendula*, *Lecanora glabrata* and *Brachythecium reflexum* were found only in the western part of Latvia. These trends partly agree with Аболинь (1968). In the present study *B. reflexum* was found only in one territory on *Quercus robur*, but this species has been found also in Livland on the basal part of *Picea abies* (Аболинь 1968). The average temperature in January is lower in western Latvia in comparison with other studied territories, which may explain the observed differences in distribution, but also habitat characteristics could be important as there are fewer broad-leaved forest WKHs in western Latvia. The higher number of epiphytic species is usually found in coastal regions with prevailing sea winds and higher average temperatures and mild winters (Barkman 1958).

A significant correlation was observed between total WKH indicator species richness and total red-listed species richness in the present study. A similar relationship was found between bryophyte WKH indicator species richness and red-listed species richness in Sweden (Gustafsson et al. 2004). These results confirm the usefulness of the WKH indicator species evaluation of WKHs in Latvia. Paltto et al. (2006) did not find a significant correlation between WKH indicator species richness and red-listed species richness in Swedish broad-leaved forests, but they included also fungi and vascular plants in the analysis, which was not studied in the present work.

Broad-leaved WKH, and Tilio – Acerion forests of slopes, screes and ravines had the highest epiphytic species richness (Fig. 6). These forest types were also the most common among the studied forest types and might be more representative of natural broad-leaved forests (Priedītis 1999). Habitat influenced bryophyte species occurrence in a study by Berg et al. (2002) in Swedish WKHs, and also lichen species richness in Estonia (Jüriado et al. 2003). Forests with larger amounts of structural elements and topography can provide additional ecological niches for species existence. Moist forests, near lakes, falls and marshes are most favourable for epiphytic species distribution (Barkman 1958).

The present results agrees with Heylen et al. (2005), who found that lichens prefered more dryer habitats compared with bryophytes, which grow in more humid habitats. In addition, also the study scale is important. The present study was conducted in different forest habitats, with many microhabitats, while Heylen et al. (2005) was studying more local microclimate in a valley habitat. Red-listed bryophyte species richness was greater in forest habitats with higher humidity. This partly agrees with Bambe, Lārmanis (2001), who found that habitat humidity crucial for bryophyte species composition in the Pirtslīcis-Līkā atteka Nature Reserve in Latvia. Humidity was found to be the most important variable affecting epiphytic bryophyte species distribution (Bates et al. 2004). Location, history and local conditions of forest stand causes lower diversity of lichen species and determine species composition (Johansson et al. 2007). Light conditions could be important as lighting was mentioned as one of the important features influencing trees in a particular forest type in relation to lichen species distribution (Sõmermaa 1972).

The highest total species richness was found in Laubere pagasts, which has a large coverage of broad-leaved WKH. This forest stand was not the oldest among the studied territories, but was in a less fragmented area compared with the other studied territories. Also, the aspen WKH in Varakļāni pagasts, which was not isolated from similar forest stands and urban areas were not pronounced in the surroundings, had the highest bryophyte species richness. However, the total species richness did not reflect accurately the red-listed and indicator species richness. The highest red-listed and indicator species richness was found in Moricsala Nature Reserve, which has been protected since 1912 (Лайвиньш 1983), ensuring little human impact since this time. Several bryophyte and lichen species were found only in one of the studied territories, which might be due to existing specific microclimatic conditions in these territories.

## 4.2. Tree level variables

Similar species richness was found among the studied deciduous **tree species** (Fig. 2). However, tree species was the one of the most significant separate factor influencing epiphytic species richness, also as interactions (Appendix 3). Tree species was found to be an important factor influencing epiphytic bryophyte and lichen species composition in many studies (Barkman 1958, Аболинь 1968, Sõmermaa 1972, Uliczka, Angelstam 1999, Kuusinen 1996b, Mežaka, Znotiņa 2006, Löbel et al. 2006b, Straupe 2008, Mežaka et al. 2009, Jüriado 2009b).

There is a large difference in epiphytic species richness between coniferous and deciduous tree species, but not between deciduous tree species (Barkman 1958, Mežaka, Znotiņa 2006). However, differences were found in the mean values of species richness in studied species groups. *Ulmus laevis* was rich in epiphytes as observed in previous studies (Barkman 1958, Аболинь 1968). *Populus tremula* is known to host the high numbers of bryophyte species (Āboliņa 1978, Kuusinen 1994b, Hazell et al. 1998, Jüriado et al. 2003, Mežaka, Znotiņa 2006, Mežaka et al. 2008). *Sorbus aucuparia* hosted the highest lichen species richness as observed previously in a study of Latvian old-growth broad-leaved forests (Mežaka et al. 2008), in Central Europe (Barkman 1958) and in Finland (Pykälä et al. 2006). However, *Sorbus aucuparia* was poor in lichens in comparison with other studied tree species in Estonian natural forests (Jüriado et al. 2003), where only 22 *Sorbus aucuparia* trees were examined and coniferous forests were also included. *Carpinus* *betulus* hosted the highest total and bryophyte red-listed species richness in the present study. Similar results were obtained by Mežaka et al. (2008) regarding old-growth broad-leaved forests in Latvia, but this was not observed by Szövényi, Tóth (2004) in a study of a stream valley in the Carpathian Basin. *Carpinus betulus* reaches the northern distribution range in Latvia (Mauriņš, Zvirgzds 2006), which might explain the differences in epiphyte composition on this tree species. Also habitat characteristics could be important.

*Alnus incana* hosted the highest WKH lichen indicator species richness in the present study. The highest lichen species richness was found on *Alnus incana* in a Finnish old-growth forest (Kuusinen 1996b). *Alnus incana* is a pioneer tree species as it grows relatively fast, and it rapidly obtains specific bark characteristics suitable for WKH indicator species existence. The highest lichen red-listed species richness was found on *Tilia cordata*, which is supported by previous work in Estonian boreo-nemoral forests (Jüriado et al. 2009b) and in Latvian old-growth broad-leaved forests (Mežaka et al. 2008).

The mean number of lichen species was higher on *Quercus robur* in Estonian broad-leaved forests (Jüriado et al. 2009a). *Fraxinus excelsior* and *Tilia cordata* hosted the highest number of lichen species in Estonia (Jüriado et al. 2009b). *Fraxinus excelsior* was described as an important host tree for epiphytic bryophyte distribution in a valley forest in Denmark (Rasmussen 1975).

Differences of studied epiphytic species richness groups were found between following pairs of tree species – *Fraxinus excelsior* and *Betula pendula, Quercus robur, Tilia cordata* as well as between *Betula pendula* and *Ulmus glabra*, *Acer platanoides*, *Carpinus betulus*, in common with *Quercus robur* and *Ulmus glabra*. *Fraxinus excelsior, Ulmus glabra,* and *Acer platanoides* have a comparatively higher tree bark pH in comparison to *Betula pendula, Quercus robur* and *Tilia cordata* (Fig. 3). Jüriado et al. (2009a) found a similar relationship between *Ulmus glabra* and *Ulmus laevis* in contrast to *Tilia cordata* and *Quercus robur* in Estonian floodplain forests. More specific habitat conditions such as humidity, microclimate might affect species occurrence on *Carpinus betulus*. Similar communities were found between *Alnus* spp. and *Quercus* spp., as well as *Fraxinus* spp. and *Ulmus* spp., *Populus tremula* in Central Europe (Barkman 1958). Epiphytic flora of mosses is similar on *Fraxinus excelsior* and *Acer platanoides* (high similarity), *Tilia cordata* and *Populus tremula* (the highestt similarity) and *Quercus robur* and *Carpinus betulus* in Polish nemoral forests (Cieśliński et al. 1996a). Similar epiphyte floristic patterns on tree species are explained by the similar tree bark physical and chemical properties.

Differences were found in species group response to tree species (Appendix 3). Broad-leaved tree species was one of the most significant factors explaining epiphytic species composition. Total species richness and lichen species richness are known to be strongly related to phorophyte species in the boreo-nemoral region (Löbel et al. 2006b).

**Tree inclination** in degrees did not influence significantly any epiphytic species group as a separate factor. However, significant influence of inclination in degrees was found in interaction with other factors. Tree bark pH interaction with tree inclination in degrees was significant for bryophyte, total red-listed and red-listed bryophyte species richness (Appendix 3). Inclination x tree species interaction affected significantly ($p<0.05$) bryophyte, lichen, total red-listed, red-listed bryophyte and WKH bryophyte indicator species richness. This indicates the importance of factor interactions, inclination was an important factor only for particular tree species and in relation with bark pH. However only particular epiphytic species groups were associated with these interactions. Epiphyte occurrence decreases with tree inclination (Snäll et al. 2004, Löbel et al. 2006b). In the present study the occurrence probability of *Homalia trichomanoides* decreased, while *Lepraria lobificans*, *Pseudoleskeella nervosa* and *Anomodon attenuatus* – increased with inclination (Fig. 5 A). Snäll et al. (2005a) found that decreasing risk of diaspore flush-off could explain species occurrence on moderately inclined trees, but this positive effect can decrease with increasing inclination. Highly inclined trees have lower substrate quality and more competitive species can be common. When thick bryophyte cover has developed on the upper part of inclined tree, lack of water supply promotes *Lepraria* spp. occurrence (Olsen 1917, Barkman 1958). Direction of exposure of inclined trees was a significant factor for the six studied epihytic species groups and the most significant was North exposure. North direction of exposure showed significant correlation with epiphytic species distibution in ordination graph (Fig. 7). This tendency can be explained by higher species richness on the upper part of inclined trees as described by Barkman (1958).

**Tree age** influenced significantly total indicator and WKH bryophyte indicator species richness. The influence of tree age was reflected as interaction with tree species among the studied epiphytic species groups (Appendix 3). Snäll et al. (2005b) found a relation between tree age and occurrence of red-listed lichen *Lobaria pulmonaria*. Tree age was an important explanatory factor for lichen species diversity on *Fraxinus excelsior* in South Sweden forests (Johansson et al. 2007), but tree age class showed only a weak relationship with epiphyte species richness in a river valley (Heylen et al. 2005). *Phlyctis argena* was found more on younger trees and was absent on older trees. *Lecanora* *subrugosa* showed higher occurrence probability with tree age and probably is a competitive species when trees become older. *Leucodon sciuroides* showed higher occurrence probability on younger trees and probably is competitive with *Neckera complanata, Metzgeria furcata, Isothecium myosuroides* and *Frullania dilatata* (Fig. 5 C). Doignon (1949) studied succession of epiphytes in Central Europe and found that *Frullania dilatata* was more common on younger trees, followed by *Neckera* spp. and after that by *L. sciuroides*. *L. sciuroides* occurrence probability on younger trees is higher in comparison with *Frullania dilatata* and *Neckera complanata*, which both showed a similar trend. *Frullania dilatata* was the first epiphytic bryophyte colonizing deciduous trees in Amsterdam (Reynders 1955). Crustose lichens were found as colonizers after foliose lichens on tree stems in Europe (Tyszkiewicz 1935), while Satô (1936) found crustose lichens as initial colonizers in Japanese beech forests. These differences in succesion among epiphytes show, that geographical location of the present study is also important.

**Tree DBH** was not found to be significant as a separate variable for species richness among groups. Tree DBH x bark crevice depth was a better explanatory interaction for several epiphytic species groups (Appendix 3) as well as epiphytic species composition (Fig. 4). *Phlyctis argena* and *Graphis scripta* occurrence rapidly decreased with DBH. However *G. scripta* occurrence probability increased in the largest DBH classes. This might be explained by a decrease of competition or bark flaking, when new colonization is possible. *Lepraria lobificans* showed the highest amplitude showing a similar trend as described by Jüriado et al. (2009b). Tree diameter influenced significantly particular bryophyte species occurrence in other studies (Snäll et al. 2003, Hazell et al. 1998, Ojala et al. 2000), lichen distribution (Hedenås, Ericson 2000, Belinchòn et al. 2007) and overall epiphyte distribution (Barkman 1958, Aude, Poulsen 2000, Löbel et al. 2006b, Ranius et al. 2008), but tree diameter was not found to be an important factor explaining epiphytic bryophyte distribution in stream valley forests (Szövényi, Tóth 2004).

There is rather poor information regarding **tree height** as most of studies do not include this factor as it is covariable with DBH and tree age (Barkman 1958, Mežaka, Znotiņa 2006, Belinchòn et al. 2007). Only a weak relation was found between tree height and DBH in the present study. Tree height influenced a number of the studied epiphytic species groups as separate and interaction factor (Appendix 3). *Hypnum cupressiforme* and *Brachythecium oedipodium* showed a positive relation to tree height. When a tree increases in height, there is a greater substrate area for colonization of *Hypnum cupressiforme* as this epiphyte has a vertical growth form.

**Bark crevice depth** was more pronounced in a factor interactions influencing epiphytic species groups (Appendix 3). Species occurrence probability trends are similar as for DBH graph (Fig. 5 D). Bark roughness has been found to be a significant variable for epiphyte distribution in several studies (Aude, Poulsen 2000, Snäll et al. 2004). Bark crevice depth as a separate factor was significant only for lichen species richness in the present study which partly agrees with Stringer, Stringer (1974), who found bark roughness to be more important for lichen species distribution than bryophyte species. Bark crevice depth was found as a significant factor influencing crustose lichen occurrence on a tree level in Swedish *Quercus robur* forests (Ranius et al. 2008).

In experimental studies *Hypogymnia physodes* soredia survival was higher on rough bark compared with smooth bark (Armstrong 1990) confirming its significance for lichens. The suitable microclimate on bark crevices promotes the establishment of epiphyte propagules (Barkman 1958) due to accumulation of dust as well as humidity and creates better conditions for attachment of diaspores in bark fissures. Changes of bark quality of epiphytes differs among tree species. When trees become older the physical and chemical characteristics become similar among trees species (Sõmermaa 1972). Bark, being a substrate for epiphytes, is characteristic of a great variability of habitat conditions. The oldest and thickest tree specimens, especially *Quercus* spp., *Tilia* spp. and *Fraxinus excelsior* have deep cracks, which are favourable for spread of epiphytes. Physiochemical qualities of the bark are important in epiphyte colonization and more pronounced in lichens (Cieśliński et al. 1996a).

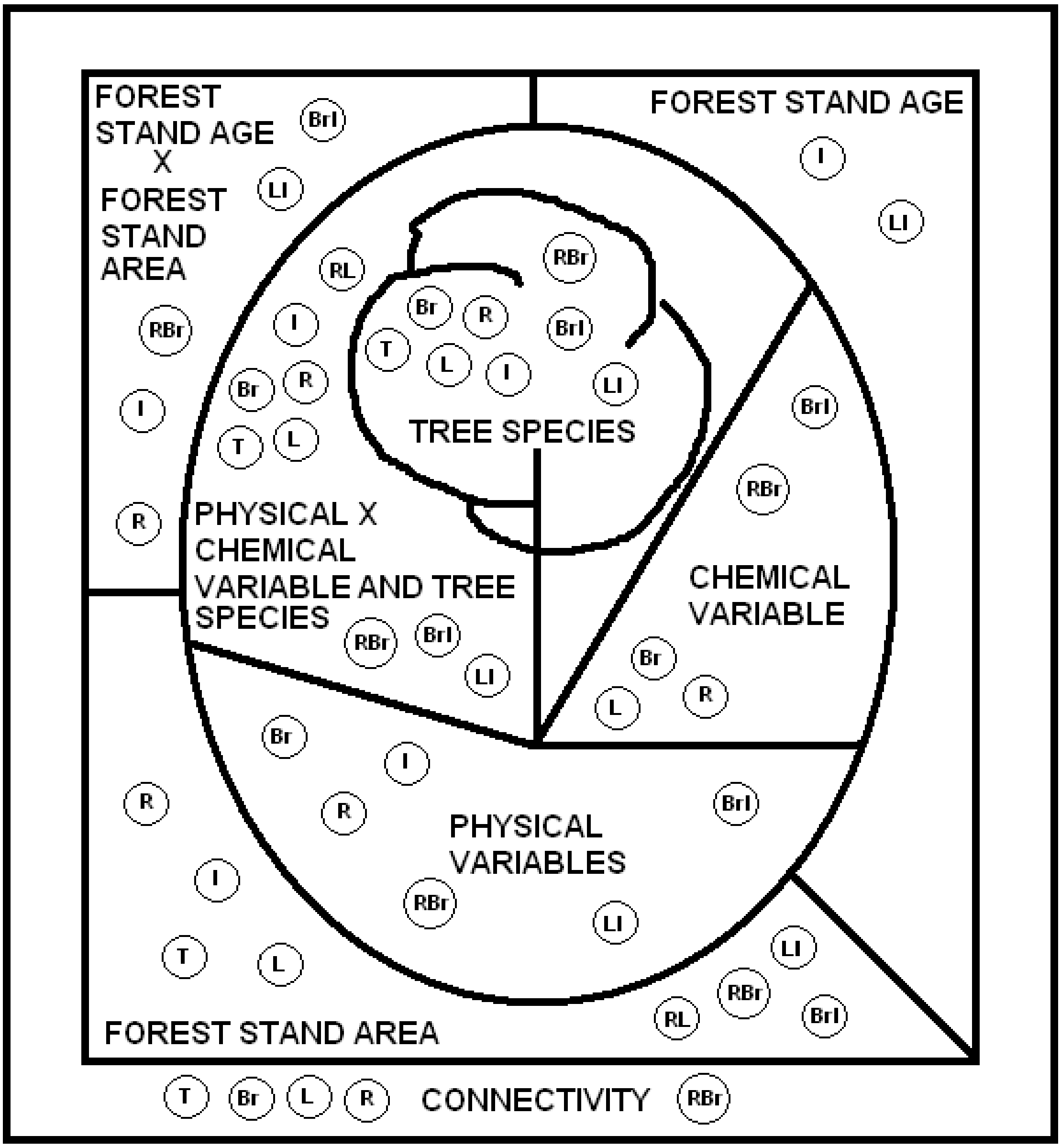
**Tree bark pH** was found to be one of the most important variables, in relation to tree species (Fig. 3). Tree bark pH influenced significantly most of the epiphytic species groups as separate or interaction variables (Appendix 3). Most species showed positive occurrence probability with tree bark pH (Fig. 5 F) including the WKH indicator species *Homalia trichomanoides, Anomodon longifolius, Accrocordia gemmata* and red-listed species *Neckera pennata*. A negative relation with tree bark pH was found for *Hypnum cupresssiforme, Dicranum montanum, Cladonia coniocraea* and *Hypogymnia physodes*. Similar trends for these species have been found in other studies (Apinis, Diogucs 1935, Apinis, Lācis 1936, Hällingback 1995, Hällingback 1996, Dierßen 2001, Löbel et al. 2006b, Jüriado et al. 2009a).

Tree bark pH is one of the most important factors influencing epiphytic flora in boreal (Gustafsson, Eriksson 1995), boreo-nemoral (Löbel et al. 2006b) as well as in nemoral vegetation zones (Cieśliński et al. 1996a). Tree bark pH was the most important for bryophyte species richness. The presence of soil raises bark pH at the tree base (Barkman 1958).

## 4.3. Forest stand age, area and connectivity

**Forest stand age** as a separate factor influenced significantly only total WKH indicator and lichen WKH indicator species richness groups (Appendix 3). *Graphis scripta* occurrence was affected positively by stand age, while *Amblystegium serpens* – negatively (Fig. 5 H). Also, species composition in the ordination was affected significantly by forest stand age (Fig. 6). Forest stand age was significantly related to lichen species diversity in Estonian forests (Jüriado et al. 2003, Jüriado et al. 2009a). Jüriado et al. (2009a) found that stand age affects composition of lichens, but not lichen species richness. Forest stand age did not explain lichen species richness in *Populus tremuloides* forests of North America (Rogers, Ryel 2008). Threatened and vulnerable species did not show any relatioship with forest stand age in coniferous forests (Holien 1996). The present study agrees with the results of Baldwin and Bradfield (2007), who did not find significant relationship between forest patch age and bryophyte species richness in temperate coastal rainforests. These different results emphasize the significance of division of lichens and bryophytes into separate groups to obtain more objective conclusions about species group requirements.

**Forest stand area** was a significant factor for seven studied epiphytic species richness groups (Appendix 3) as a separate variable. Interaction between forest stand area and forest stand age significantly influenced five species richness groups. Forest stand area was positively related to occurrence of *Lepraria lobificans*, *Graphis scripta* and *Dicranum montanum*, while negatively with *Phlyctis argena* and *Homalia trichomanoides* (Fig. 5 I). *Phlyctis argena* is a pioneer species that can not survive in late successional stages of the forest, while *Lepraria lobificans* can survive and disperse with high ability in a wide area. Probably, when the forest stand area is larger, there is a larger chance that part is disturbed. As trees in clear-cut borders and small forest patches could be influenced by windfall, colonizing trees can be suitable for *Phlyctis argena*. Also Ojala et al. (2000) found that epiphytic bryophyte species richness depends on a forest stand area in old-growth *Populus tremula* forests in Finland. The present study reflect the results of Paltto et




Fig

Figure 8. Scheme of studied variable relation with epiphytic species groups in forest stand. tree bark crevice depth, tree height, tree age, DBH, inclination, direction of inclination, height on tree. Chemical variable – tree bark pH. Forest stand variables – age, area. I – total indicator species richness, T – total species richness, R – red-listed species richness, B – bryophyte species richness, L – lichen species richness, RBr – bryophyte red-listed species richness, RL – lichen red- listed species richness, BrI – bryophyte indicator species richness, LI – lichen indicator species richness.

al. (2006), who found that stand area was found to be significant for WKH indicator and lichen species occurrence, but not for bryophyte species distribution. A similar trend was observed also by Lõhmus et al. (2007) in Estonia.

Stand area was significantly related to total red-listed species richness, in contrast with Gustafsson et al. (2003), who found an opposite trend. However, it is important to note that larger habitat patches have larger populations decreasing the risk of stochastic extinctions (Kruys, Jonsson 1997).

**Habitat connectivity** influenced significantly the main studied epiphytic species groups such as total, bryophyte, lichen, total red-listed and bryophyte red-listed species richness. The present study agrees with a recent study by Paltto et al. (2006), who found that red-listed species were more related with suitable habitat in the surrounding landscape, while no such relationship was found for WKH indicator species. Similar results were obtained by Johansson, Ehrlén (2003), who found that lichen species presence on deciduous trees increased with patch connectivity. Connectivity to occupied aspens increased occurrence probability of *Orthotrichum obtusifolium* (Snäll et al. 2003) in Scandinavian forests as well as for *Lobaria pulmonaria* in Finland (Gu et al. 2001). Baldwin, Bradfield (2007) found a significant relationship between bryophyte species richness and distance to nearest old-growth forest stand in temperate coastal rainforests.

Different opinions exist among the importance of scale in epiphytic species distribution. The forest stand was more important for determining epiphytic bryophyte species communitiy distribution than particular tree species in forests of North Carolina (Palmer 1986). Factors at the tree level are more important than factors in stand level for lichen species distribution (Jüriado et al. 2009a). On the other hand, in such comparisons is necessary to take into account all factors, which most of cases is not possible. To explain epiphytic bryophyte and lichen species distribution, is necessary to take account different scales and factor groups as they all are interacting and important components in forest ecosystems (Fig. 8). Mostly, in testing of factor significance in forests, too many generalizations have been accepted and better results might be to determine the habitat requirements for each species separately. The present results are important in nature protection and long-term forestry planning in deciduous forests.

## 4.4. The role of vertical and horizontal spatial distribution

Epiphytic bryophyte and lichen species indicating about the characteristic of a particular height or direction on tree were found in indicator species analysis (Tab. 9) and CCA ordination (Fig. 7). The most pronounced gradient in composition was related to vertical distribution and North direction of exposures, but some species showed specific requirements. North exposure exhibited the greatest bryophyte cover (Trynoski, Glime 1982). Direction of tree stem was not significant for the most of studied epiphytic species.

The present study partly agrees with Straupe (2008), who found that epiphytic lichen species richness did not differ significantly in different directions of exposures and heights on tree trunks in *Alnus glutinosa* WKH. However, the present study contradicts Straupe (2008) as more lichen species was found in the South, South-East direction of exposure up to 0.50 m and in North, North-West direction of exposure at 1.50 m height in that study. Straupe (2008) studied epiphytic lichens in coniferous, *Alnus glutinosa* and *Quercus robur* forests, while dry deciduous forests were studied in the present study.

Lichen communities differed between South and North directions on tree stems in Estonian forests (Jüriado et al. 2009a). Hydrophilous species colonize the North side of the phorophyte stem and photophilous and xerophilous on the South side of tree stem (Sõmeramaa 1972). Epiphytic species vertical distribution are more important than horizontal. For example, *Evernia* spp. and *Ramalina* spp. observed to be found more on the upper part, but *Cladonia* spp. was found at tree base (John, Dale 1995). Species occurring more on higher parts on the tree stem were *Frullania dilatata, Orthotrichum affine, Pertusaria amara,* while on tree base – *Plagiochila asplenoides, Plagiothecium laetum, Peltigera canina* (Fig. 7). *Hypnum cupressiforme* showed a significant relation with North and West directions of exposures higher on the tree stem, while *Phlyctis argena* was an indicator species of the South direction on the basal part of the tree stem. Dust accumulation is highest in the West direction of exposure on tree stems in Europe (Barkman 1958) fascilitating epiphyte establishment.

*Lepraria lobificans* was an indicator species at various heights and exposures on the tree stem due to wide distribution of this species on the studied trees, while *Pertusaria amara* was an indicator of the North direction and *Phlyctis argena* was indicator of East direction both on the tree base in the present study. *Pertusaria amara* was found exclusively on North direction of exposure on *Pinus* spp., but *Phlyctis argena* was found more on North and North-West direction on tree stems in the main Estonian forest types (Sõmermaa 1972).

*Amblystegium serpens* was an indicator of the South direction on tree base. *Hypnum cupressiforme* and *A. serpens* were distributed in a wide range of habitats, as they are sciophytic and also xerophytic species (Аболинь, 1968, Dierßen 2001). The present study only partly agree with Sõmeramaa (1972), who did not find large differences in lichen species richness on tree base and the upper tree stem. The present study agrees with (Horikawa, Nakanishi 1954), who observed greater cover and richness of bryophytes on the basal part of tree stems. High humidity allows the establishment of soil bryophytes.

The lower tree base is a refugia for taxa requiring rather long hydroperiods (Mazimpaka, Lara 1995).

On the upper part of tree trunk were more cushion like forms, such as *Ulota* spp., *Orthotrichum* spp. as this growth form helps to retain humidity and protect from desiccation (Horikawa, Nakanishi 1954). Bryophytes more tolerant to drought are found in the upper basal part and on different heights, such as *Frullania dilatata* and *Orthotrichum* spp. (Mazimpaka, Lara 1995). Obligate epiphytes like *Ulota* spp. and *Orthotrichum* spp. grow on the upper part of the stem and are less common on the basal part (Moe, Botnen 1997). Facultative epiphytes like *Dicranum spp., Isothecium myosoruoides, Hypnum cupressiforme*, *Metzgeria* spp., *Plagiochila* spp., *Frullania* spp. commonly colonized the tree base, while upper tree stem is colonized with obligate or facultative epiphytes (Barkman 1958).

The results of the present study are similar to Голубкова (1959), who found *Hypogymnia physodes* with *Evernia prunastri, Platismatia glauca, Parmelia sulcata, Ramalina* spp. were typically in Russian broad-leaved forests on the upper part of tree stem. The basal part of *Populus tremula* is commonly colonized by bryophytes covered by *Cladonia coniocraea* and *Peltigera canina*. *Lecanora allophana* occurred at height 0.30-0.40 m and *Anaptychia ciliaris* was found from 0.70 m upwards (Голубкова 1959).

The results of the present study are contradiction with Trynoski, Glime (1982), who found that *Pylaisa polyantha, Radula complanata, Ptilidium pulcherrimum* occurrence was not correlated with height on tree stem of *Populus tremula*. The one tree species studied in that study probably does not reflect the trend in the present study, where epiphytes are described on 13 tree species. In the different forest habitats studied the various characteristics of microclimate were more important than particular direction on the tree stem (Tab. 9., Fig. 7-8).

## 4.5. Transplantation

Transplant vitality for *Neckera pennata* in managed forest and WKH differed significantly in the present study. The results could indicate the significance of a particular microclimate, which is crucial for *Neckera pennata* establishment in a managed forest. The present result disagrees with Ingerpuu et al. (2007), who found that dispersal limitation is important for *Neckera pennata* distribution, but not microlimatic conditions. Wiklund, Rydin (2004) found that yearly precipitation was the most important for *Neckera pennata* colony growth, indicating the importance of microclimate.

No significant difference was observed in vitality of *Lobaria pulmonaria* transplantated to a managed and WKH forest stand. The reason for such result could therefore be dispersal limitation. The present study is in contradiction with other studies by Edman et al. (2007), who found selective cutting affected negatively the abundance and frequency of *Lobaria pulmonaria*. *Lobaria pulmonaria* was found to be sensitive to light after transplantation experiments (Gauslaa et al. 2001).

*Lobaria pulmonaria* transplants of branches grew comparatively better in old-growth forest with higher light compared with managed forests (Coxson, Stevenson 2007).

Other studies support the results of the present study as a limited dispersal was found for *Lobaria oregana* (Sillett et al. 2000). Werth et al. (2006) hypothesized that ecological conditions are crucial for establishment of *Lobaria pulmonaria* instead of dispersal limitation.

Based on the results of the present study, the selected transplantation method with a medical sling appears promising for transplantation experiments in the future as well as a plastic net with metal staples, applied for *Antitrichia curtipendula* and *Lobaria pulmonaria* transplantation on 280 *Populus tremula* in Sweden (Hazell, Gustafsson 1999). More replication of experimental transplants with bryophytes and lichens for objectivity are advisible in future research in Latvian forests.

# 5. Conclusions

1. In total 148 epiphytic bryophytes (73 species) and lichens (75 species) were found in the studied Latvian deciduous forests on 13 tree species. Nine bryophyte and five lichen species were Red listed species in Latvia. WKH indicator species compiled 12 bryophyte and nine lichen species. Eight bryophyte and ten lichen species are specially protected in Latvia and five bryophyte and five lichen species are Microreserve species. One bryophyte species – *Dicranum viride* is protected in Council Directive 92/43/EEC on the Conservation of natural habitats and of wild fauna and flora.
2. A significant correlation exists between WKH indicator species richness and red-listed species richness in total, bryophyte and lichen species richness groups.
3. Differences were found in epiphytic species occurrence among the studied geobotanical regions. The greatest difference in epiphytic flora was found between Coastal, West Latvian and other studied geobotanical regions in Latvia.
4. The highest epiphytic species richness was found in broad-leaved WKH, among WKHs and in Tilio-Acerion forests of slopes, screes and ravines among European Union protected forest habitats.
5. Epiphytic species richness mean value varied among studied tree species. Total and WKH indicator species richness was highest on *Ulmus laevis*. The highest bryophyte species richness was on *Populus tremula*, but lichen species richness on *Sorbus aucuparia*. *Carpinus betulus* hosted the highest WKH bryophyte indicator species richness, total and bryophyte red-listed species richness. *Alnus incana* hosted the highest lichen WKH indicator species richness, but the highest lichen red-listed species richness was on *Tilia cordata*.
6. Tree species was one of the most important factors influencing epiphytic species richness in Latvian deciduous forests at the tree level. Tree bark pH more significant ($p<0.05$) relationships with bryophyte species richness and with WKH lichen indicator species richness. The significant differences between epiphytic species group richness among studied tree species were explained with bark physical and chemical characteristics for the particular tree species.
7. The significant interaction between tree age and other studied variables was observed mostly in lichen, total red-listed, red-listed bryophyte and WKH bryophyte indicator species richness. Bark crevice depth showed the highest relationship with lichen indicator species richness.

8. Forest stand area, WKH and European Union forest type were among the most important factors at forest stand level influencing epiphytic species richness. Connectivity was significant ($p<0.05$) for total, bryophyte, lichen, total red-listed species richness. Forest stand age showed significant relationship with WKH indicator and WKH lichen indicator species richness, but in interaction with forest stand area also in red-listed, red-listed bryophytes and WKH bryophyte indicator species richness.
9. Studied epiphytic bryophyte and lichen species showed significant ($p<0.05$) positive and negative relationships with species occurrence probability and studied continuous variables in tree (inclination, diameter at breast height, tree age, bark crevice depth, tree height, tree bark pH) and forest stand level (stand age, area).
10. Height on tree stem, West and North directions on tree stem explained significantly ($p<0.05$) epiphytic species vertical and horizontal spatial distribution on tree stem, but greater influence showed vertical distribution.
11. Significant ($p<0.05$) differences in transplant vitality were found for *Neckera pennata* between deciduous WKH and managed deciduous forest, while no significant differences were found for *Lobaria pulmonaria* transplants between deciduous WKH and managed deciduous forest. Microclimatic conditions could be the most important for the establishment of *Neckera pennata*, while dispersal limitations could exist for *Lobaria pulmonaria*.
12. Epiphytic bryophyte and lichen species distribution was affected by numerous factors, and than interaction at tree and forest stand levels in Latvian deciduous forests. Different epiphytic species groups and particular species have specific habitat demands in forests, what is necessary to take into account in nature protection and long-term forestry in deciduous forests.

# 6. Main thesis

1. The highest epiphytic species richness is related with broad-leaved WKH, and Tilio-Acerion forests of slopes, screes and ravines due to specific ecological niches and microclimate varing in the relatively small scale.
2. Combination and interaction of variables in the present study are the main influences affecting significantly epiphytic bryophyte and lichen distribution in the Latvian deciduous forests in tree and forest stand scale.
3. Transplantation results give the significant knowledge in studies about epiphytic bryophyte and lichen dispersal.

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# Appendix