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# Title: Patterns and drivers of species composition of epiphytic bryophytes and lichens in managed temperate forests

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Abstract:

Epiphytic bryophytes and lichens are an important component of the endangered forest biota in temperate forests, their diversity and composition patterns being regulated by tree, stand and landscape scale factors. The aim of this study is to improve ecological understanding of such factors in managed coniferous-deciduous mixed forests of Hungary in the context of forest management. In particular, this study investigate the effect of tree species composition, stand structure (tree size distribution, shrub layer, dead wood), microclimate (light, temperature, air humidity), landscape and historical factors on the stand level and tree level composition of epiphytic bryophytes and lichens. The relationships were explored by multivariate methods (redundancy analysis, canonical correspondence analysis, variation partitioning) and indicator species analysis. Tree species is among the most important driver of species composition in both organism groups. For bryophytes, the continuity of forest microclimate and the presence of shrub layer are also important, while lichen assemblages are influenced by light availability. Landscape and historical variables were less influential than stand scale factors. On the basis of our results, the main strategy of management focusing on epiphyte diversity conservation should include: 1) the maintenance of tree species diversity in mixed stands; 2) increasing the proportion of deciduous trees (mainly oaks and hornbeam); 3) the maintenance of large trees within the stands; 4) the presence of shrub and regeneration layer; 5) the creation of heterogeneous light conditions.

Keywords: mosses, lichenized fungi, tree species composition, microclimate, light conditions

Abbreviations: CCA – canonical correspondence analysis; DBH – diameter at breast height; DCA – detrended correspondence analysis; ISA – indicator species analysis; RDA – redundancy analysis; SD – standard deviation.

## 1. Introduction

Epiphytic bryophytes and lichens comprise a considerable part of the forest biota in the temperate and boreal zone (Barkman, 1958; Ellis, 2012; Smith, 1982). In moist boreal coniferous forests they play an important role in ecosystem processes, influencing water balance and nutrient accumulation (McCune, 1993; Pike, 1978; Pypker, et al. 2006a, 2006b). In deciduous and mixed forests their biomass is smaller, but they largely contribute to forest biodiversity (Coppins and Coppins, 2005; Slack, 1977).

Their diversity and composition patterns are regulated by tree, stand and landscape scale factors (Barkman, 1958; Bartels and Chen, 2012; Ellis, 2012; Hauck, 2011; Marini et al., 2011; Nascimbene et al., 2012). Many studies focused on tree level patterns have emphasized that different tree species in the same locality maintain diverse epiphytic assemblages (Mezaka et al., 2012; Slack, 1976; Szövényi et al., 2004) as an effect of different chemical-physical features of the bark (Bates and Brown, 1981; Fritz and Heilmann-Clausen 2010; Gustafsson and Eriksson, 1995). Tree size and age are also relevant determinants of epiphyte diversity; larger and older trees maintain more diverse assemblages than younger ones, with many associated species (Fritz et al., 2008a; Lie et al., 2009; Nascimbene et al., 2009a). This phenomenon has a complex explanation: big trees provide larger colonization surface (area effect), and old trees ensure longer time for the establishment and growth of local populations, also providing higher microhabitat diversity. On a tree, a clear vertical zonation of epiphytes is observed, which appears in the vertical distribution of different growth forms, and functional traits (Fritz, 2009; McCune, 1993). This is influenced mainly by microclimatic factors as light availability and air humidity (Hosokawa and Odani, 1957; Peck et al., 1995). At the stand scale, the importance of tree species diversity in driving epiphytic assemblages reflects the host preferences of many epiphytes (Mezaka et al., 2012; Palmer, 1986). However, at this spatial scale also microclimatic factors (light, air humidity, temperature), and structural elements modifying microclimate (canopy openness, shrub layer, vertical structure of the canopy) are very influential for epiphytes (Király et al., 2013; Song et al., 2012). Moreover, old-growth unmanaged stands maintain more diverse epiphytic communities than managed forests (Lesica et al., 1991), providing higher microhabitat and substrate diversity (e.g. higher tree species richness, tree size heterogeneity and presence of veteran trees, quantity and quality of dead wood). The continuity of the forest stands and the available substrates is determinant for many dispersal limited species (Fritz et al., 2008b; Rose, 1992).

At the landscape scale, many epiphytic species are regulated by metapopulation dynamics (Johansson et al., 2012; Löbel et al. 2006; Snäll et al. 2003). The mortality of the local populations is regulated mainly by deterministic factors, as the cessation of the host trees, while the colonization of new areas is influenced by stochastic factors (Löbel et al., 2006; Roberge et al., 2011). The landscape scale distribution of many epiphyte species is limited by their dispersal ability, especially for asexual species with high substrate specificity (Johansson et al., 2012; Löbel and Rydin, 2009), particularly where potential microhabitats have very isolated distributions across the landscape. These species are very sensitive to past and recent habitat fragmentation, and the longevity of the available substrates (Snäll et al., 2004).

Tree, stand and landscape scale factors are considerably modified by human activities which have made cryptogamic epiphytes a threatened group in temperate forests (Paillet et al. 2010). Supported by historical and archeobotanical evidences, 30-80% of these species disappeared from the Atlantic region of Europe before the 18th century (Rose, 1992; Ellis et al., 2011). Recent land use, especially forest management (including timber production and conservation purposes), has considerable influence on survival and local population size of these organisms (Nascimbene et al., 2013a). For this reason, it is necessary to explore the most important regulating factors acting at different spatial scales across regions. While the effect of host species is relatively widely studied for epiphytes there is a lack of information concerning the effect microclimate and stand structure that in our study are accounted for with a set of directly measured variables. The separation of stand level and tree level composition and the comparison of the effects of environmental constraints between epiphytic bryophytes and lichens are also novel to this study.

This study aimed to investigate the effect of potentially relevant factors in determining the bryophyte and lichen diversity of coniferous-deciduous mixed forests in Hungary. In particular, it will explore the effect of tree species composition, stand structure (tree size distribution, shrub layer, dead wood), microclimate (light, temperature, air humidity), and landscape and historical factors on the stand level composition of epiphytic bryophytes and lichens. A similar analysis was also conducted at the tree level, assessing the effect of tree species, tree size and light conditions on epiphytic assemblages on individual trees. Preferences of individual epiphyte species to different tree species were also tested. This study is closely related to Király et al. (2013), which investigated species richness patterns of epiphytes utilising the same dataset.

## 2. Material and methods

### *2.1. Study area*

The study area is located in Őrség National Park (N 46°51'-55' and W 16°07'-23'), West Hungary (Fig. 1). The elevation is 250-350 m, the mean annual temperature is 9.0–9.5 °C and the precipitation is 700-800 mm (Dövényi, 2010). The bedrock consists of alluviated gravel and loess, the most common soil types are pseudogleyic and lessivage brown forest soils, which are nutrient poor and slightly acidic (pH of the 0-30 cm layer is 4.0-4.8, Bidló pers. comm.).

The study area is dominated by beech (*Fagus sylvatica* L.), sessile and pedunculate oak (*Quercus petraea* L. and *Q. robur* L.), hornbeam (*Carpinus betulus* L.), Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karst.), forming monodominant and mixed stands as well. The proportion of different subordinate tree species (*Betula pendula* Roth., *Populus tremula* L., *Castanea sativa* Mill., *Prunus avium* L., etc.) is relatively high (Tímár et al., 2002). The main forest habitat types of the region are sessile oak-hornbeam woodlands (Hungarian habitat code: K2), acidofrequent beech woodlands (Hungarian habitat code: K7a), and acidofrequent mixed coniferous forests (Hungarian habitat code: N13) (Bölöni et al., 2008).

Most of the original forests of the region were cut in the middle ages and in the regrown secondary forest the proportion of pioneer tree species (such as *Pinus sylvestris* and *Betula pendula*) and the cover of acidofrequent herbs, bryophytes and lichens increased (Gyöngyössy 2008, Tímár et al. 2002). Today, the mixed forests with natural tree species composition are increasingly managed harmonizing timber production and conservation purposes. In private forests, stem selection is applied by local farmers without real management planning, while state forests are managed by shelterwood silvicultural systems with a rotation period of 70–110 years (Tímár et al., 2002).

### *2.2. Data collection*

Thirty-five 2-10 ha sized stands were selected by stratified random sampling from the database of the Hungarian National Forest Service (Fig. 1). In all studied stands the age of the dominant trees was between 70 and 110 years. The topography was more or less flat and the top-soil was not influenced by ground-water. The forest stand compartments of the database were grouped according to tree species combination types and the studied plots (5-10 per type) were randomly selected within the groups. In this way the sample represented the main tree species combinations of the region, including a continuous gradient in the proportion of the main tree species. The distance between selected stands was a minimum of 500 m.

Within each stand, a 40 m x 40 m plot was established for stand structure measurements. For each tree with DBH larger than 5 cm geographical position, circumference, species identity, height, height of crown base, and crown projection were recorded. Average diameter and length of logs thicker than 5 cm diameter and longer than 0.5 m were also recorded as well as density of sapling species (tree or shrub individuals taller than 0.5 m and thinner than 5 cm DBH). Relative light conditions (percentage of above canopy total light) were modelled by the tRAYci model (Brunner, 1998) using the position, size and canopy data of the trees (see details in Tinya et al., 2009). For stand level conditions, light values were predicted in 36 systematically arranged points at 1.3 m height using a grid of 5 m intervals. For tree level analyses, relative light values were predicted in the position of each individual tree. Air humidity and temperature were measured in the middle of the plots at 1.3 m height using Voltcraft DL-120 TH data loggers in 24 hours measurements with 5 minutes recording frequency. The measurements of all plots were carried out within a five days period. During this period two reference plots were measured permanently. Eight temperature and air humidity measurements were carried out during three vegetation periods (2009 June, October; 2010 June, August, September, October; 2011 March, May). Geographical position of the plots was given in meters based on the Hungarian Geographical Projection (EOV).

Landscape variables including proportion of forests (stand age older than 20 yr), clearcuts (stand age younger than 20 yr) and non-forested areas (settlements, meadows, arable lands) were estimated around the plots within a circle of 300 m radius, using maps and data of the Hungarian National Forest Service. Data on management history were generated based on the map of the Second Military Survey of the Habsburg Empire from 1853 (Arcanum, 2006). The existence of forest in the plots (as a presence/absence variable) was recorded and the proportion of forested area in the historical landscape (in the circle of 300 m radius) was calculated.

Epiphytic bryophytes and lichens were recorded in 30 m x 30 m plots positioned in the middle of the 40 m x 40 m plots. The absolute cover of bryophyte and lichen species (in $dm^2$) was estimated on every living tree with minimum 20 cm DBH, surveying the whole trunk from the base to 1.5 m height. Nomenclature of bryophytes followed Hill et al. (2006) and Grolle and Long (2000), while ecological requirements follow Király et al.(2013). For bryophytes, specialist and facultative epiphytes were separated, species belonging to the first group occur exclusively on bark in the region, while facultative epiphytes can also live on soil or decayed wood; the categorisation of each species is included in Király et al. (2013). Nomenclature and ecological information on lichens are based on Nimis and Martellos (2008).

### *2.3. Data analysis*

The relationships between species composition of the two epiphyte groups and environmental variables were explored by ordination techniques both at stand and tree level. For both taxon groups, principal component analysis and Detrended Correspondence Analysis (DCA) were used as indirect preliminary analysis. At stand level, the DCA revealed relatively short gradient lengths along the ordination axes for both organism groups (1.7-2.4 SD units), which presume a linear response between species and explanatory variables (ter Braak and Smilauer, 2002). Therefore, the relationships between species composition and environmental variables were further explored by variation partitioning (Peres-Neto et al. 2006) and Redundancy Analysis (RDA, Leps and Smilauer, 2003; Podani, 2000). At tree level, the gradient length of the DCA axes were longer (5.2-7.4 SD units) presuming a unimodal species-environmental gradient response (ter Braak and Smilauer, 2002). For this reason, Canonical Correspondence Analysis (CCA) was used as direct ordination techniques. At tree level, the association of epiphytic species to tree species were evaluated by Indicator Species Analysis (ISA, Dufrene and Legendre, 1997; Legendre and Legendre, 1998). In all cases, bryophytes and lichens were analysed separately. In stand level ordinations, the performance of each epiphyte species was expressed as total cover (in dm$^2$) within each plot. Cover values were ln transformed before the analysis and species occurring in less than four plots were excluded.

The measured and derived explanatory variables used for RDA are listed in Table 1. The proportion of tree species (beech, hornbeam, oak, Scots pine, Norway spruce, subordinate trees) was expressed based on their volumes. Volume of trees was calculated by species specific equations from DBH and tree height (Sopp and Kolozs, 2000). *Quercus petraea*, *Q. robur* and *Q. cerris* L. were merged as oaks, rare tree species were merged as subordinate trees. Tree species diversity was expressed by Shannon index with natural logarithm based on the relative volume of species (Shannon and Weaver, 1949). The Shannon index with natural logarithm was also used for the expression of landscape diversity using the relative cover of the landscape elements. Stand level light conditions were expressed as the mean and standard deviation of relative light using 36 measurements. Since these two variables were strongly correlated, a linear regression was performed between standard deviation as dependent and mean values as explanatory variable. The residuals of standard deviation were then used as independent descriptor of light heterogeneity. For air humidity and temperature, differences were calculated from the two reference plots. Relative daily mean and range values were expressed for both variables and averaged over the eight measurements.

For fulfilling normality conditions, some explanatory variables (proportion of tree species, light variables) were ln transformed before the analyses. All variables were standardized (zero mean, one standard deviation). Variation partitioning was carried out to explore the amount of variance in the species assemblages accounted for by the main groups of explanatory variables (Leps and Smilauer 2003, Peres-Neto et al. 2006). The studied groups of explanatory variables were tree species composition, stand structure, microclimate (including light conditions) and landscape-historical variables (Table 1). For the final RDA model individual explanatory variables were used (Table 1). The significant explanatory variables were selected by manual forward selection. Before the statistical selection, collinearity between the explanatory variables was checked by pairwise correlations. Strongly correlated variables ($r>0.6$) were excluded from the selection. The effect of explanatory variables was tested by F-statistics via Monte-Carlo simulation with 499 permutations. The accepted significance level was 0.05 (Leps and Smilauer, 2003; ter Braak and Smilauer, 2002). The significance of the first and all canonical axes was tested in a similar way. Because the longitude geographical position had a significant effect in the RDA of lichens it was used in the final model as covariable.

For tree level ordinations, species occurring on less than 5 trees and trees bearing less than 3 epiphytic species were eliminated from the analysis. Tree level cover values of the epiphytic species were ln transformed before the analysis. In CCA, the explanatory variables included were tree species identity, DBH and light conditions. Tree species identity was used as a factor (beech, hornbeam, oak, pine and subordinate species) and plot identity was treated as covariable. The effects of the explanatory variables, as well as the effect of the canonical axes (first and all axes) were tested with the same method used for stand level analysis. The permutations were restricted to the blocks of the covariable (plots). In all direct ordinations, the scaling of biplots was focused on species correlations (Leps and Smilauer, 2003; ter Braak and Smilauer, 2003).

For ISA, the preference of each epiphytic species to tree species was analysed separately considering only species occurring on minimum 10 trees. Trees without epiphytes were included in this analysis, considering beech, hornbeam, oak, and pine. The indicator values of the epiphytic species were tested via Monte-Carlo simulation using 1000 permutations. The accepted significance level was lower than 0.01.

Multivariate analyses were carried out with Canoco for Windows 4.5 (ter Braak and Smilauer, 2002), the ISA was performed in R 2.14.0 environment (The R Development Core Team, 2011) using the labdsv package (Roberts, 2012), for variation partitioning the vegan package were used (Oksanen et al., 2011).

## 3. Results

### *3.1. Descriptive statistics*

60 bryophyte and 44 lichen species were recorded in 35 plots on 971 trees (225 beeches, 344 pines, 324 oaks, 56 hornbeams, and 22 subordinate trees). For bryophytes the mean stand level species richness was 14.0±5.0 (SD, standard deviation), the range was 5-27, while for lichens the mean was 9.8±3.7 (SD), the range was 3-20. Mean tree level species richness was 2.9±2.1 (SD) for bryophytes and 2.2±1.5 (SD) for lichens. Details of species richness patterns can be found in Király et al. (2013). In the stand level ordinations, 27 bryophytes and 26 lichens were included. In the tree level ordinations, 27 species and 492 trees were included for bryophytes and 30 species and 349 trees for lichens. For ISA, 22 bryophytes and 22 lichens occurring on 949 trees were considered. The species and their authorities, their stand level frequencies, abbreviations and inclusions in different analyses are listed in the Appendix.

### *3.2. Stand level species composition*

For bryophytes, variables related to tree species composition and stand structure explained the largest part of the species variance, while for lichens tree species composition and microclimate were the most important (Fig. 2). The effect of landscape-historical variables was less influential for both organism groups than stand level explanatory variables.

After forward selection, six explanatory variables were significant in the RDA model of bryophytes, oak proportion being the most important and only one variable was related to landscape (Table 2).The first two canonical axes of the RDA explained 30.3% of the species variance, both the first and all canonical axes were significant (F=7.12, P<0.002 and F=3.65, P<0.002, respectively). The first RDA axis (explained variance 20.3%) expressed a tree species composition gradient (pine-oak), but tree size and forest cover also influence it (Fig. 3). The second RDA axis (explained variance 10.1%) was mainly a shrub layer – forest microclimate gradient. The most common epiphytic species (*Hypnum cupressiforme, Platygyrium repens, Isothecium alopecuroides, Radula complanata, Frullania dilatata*) were related to oak. Beside their oak preference, some specialist epiphytic species (*Metzgeria furcata, Ulota crispa, Homalia trichomanoides*) were also related to larger trees. Species enhanced by shrub layer, and cooler microclimate were facultative epiphytes (*Polytrichastrum formosum, Dicranum scoparium, Pleurozium schreberi, Plagiothecium laetum, Brachytheciastrum velutinum, Plagiomnium affine*), mainly occurring on the bottom of the trunks. These species can establish also on soil and dead wood. Most epiphytic bryophytes avoided pine dominated stands, exceptions were the epixylic *Lophocolea heterophylla* and *Dicranella heteromalla* living mainly on bare soil.

For lichens, five significant explanatory variables were included in the RDA model, from which light was the most important, and three variables represented tree species composition (Table 2). Landscape-historical variables were not selected for the model. The first two canonical axes of the RDA explained 51.9% of the species variance, both the first and all canonical axes were significant (F=12.71, P<0.002 and F=8.00, P<0.002, respectively). The first RDA axis was positively correlated with mean relative light and oak proportion and negatively correlated with basal area and hornbeam proportion (Fig. 4). The second RDA axis represented a pine proportion gradient. Species associated with pine (e.g. *Dimerella pineti, Chaenotheca ferruginea, Hypocenomyce scalaris*) were acidophytic lichens which typically establish on the bark of conifers. Species associated with hornbeam and positively correlated with basal area (e.g. *Graphis scripta, Lecanora expallens*) are typical of sub-acidic smooth barked trees, mostly in deciduous forests. *Pertusaria amara* has a wide ecological range and it often behaves as an aggressive competitor, being able to overgrow other crustose lichens and even bryophytes. *Phlyctis argena*, which was abundant on hornbeam, beech and oak is an aggressive colonizer with optimum in deciduous forests.

The other species associated to oak were mainly large-lobed foliose lichens (e.g. *Parmelia sulcata, Flavoparmelia caperata*) with a relatively wide ecological range, preferring open forest sites.

### *3.3. Tree level species composition*

The canonical axes of bryophyte CCA explained 8.15% of the species variance (6.2% for the first two axes) and both the first and all canonical axes were significant (F=18.97, P<0.002 and F=6.69, P<0.002, respectively). All the explanatory variables were significant, but host tree species was the most important, while the effects of DBH and light were less influential (Table 3). The first CCA axis represented an oak-pine gradient (Fig. 5), similarly to stand level results. Very few species preferred pine (positive side of the first axis), most of them were terricolous bryophytes. Only the epihytic-epixylic species *Lophocolea heterophylla* occurred often on pine. The weft and mat forming pleurocarpic species preferred oak. Some of them were specialists (e.g. *Homalia trichomanoides*, *Isothecium alopecuroides*), but most of them were facultative epiphytes, like *Brachythecium* and *Plagiothecium* species. The second CCA axis was associated with beech and hornbeam. Some small cushion-forming specialists (*Orthotrichum* species, *Ulota crispa*) preferred the smooth bark of these trees. These bryophytes were less related to large trees than pleurocarpic mosses preferring oak. The ISA corroborated the associations found by CCA (Table 4). Many species were significantly associated with oak, most of them were pleurocarpic, weft-forming bryophyte, but some liverworts (*Metzgeria furcata, Radula complanata*) also occurred among them. Cushion-forming *Orthotrichum* species and *Plagiothecium denticulatum* var. *undulatum* were associated with beech. The only species related to pine was *Lophocolea heterophylla*.

For lichens, the canonical CCA axes explained 13.6% of the species variance (10.8% the first two axes). Similarly to bryophytes, the most important factors for lichens were related to host tree species (Table 3). The first CCA axis mainly represented a pine-oak gradient (Fig. 6). Species associated with pine were typical and common acidofrequent lichens mainly occurring on conifers (*Hypocenomyce scalaris, Hypogymnia physodes*). The most typical species on oak were parmelioid sub-acidofrequent lichens such as *Flavoparmelia caperata* and *Parmelia sulcata*, but also *Cladonia coniocraea* was frequent, mainly at the base of the trunks. This oak-related assemblage was potentially noteworthy for conservation since it is locally enriched by sensitive and rare species as *Cetrelia olivetorum* or *Parmotrema perlatum*. The second CCA axis was positively related to hornbeam and negatively to DBH and light conditions. Hornbeam mainly hosted crustose species that usually establish on smooth bark in relatively shaded conditions such in the case of *Graphis scripta, Plyctis argena*, and *Pyrenula nitida*. The results of ISA confirmed those of CCA (Table 5). Hornbeam had the highest number of associated species. Although hornbeam had a similar smooth bark as beech, beech had much less associated species (only *Lecanora expallens*). Species related to oak and pine are the same of those highlighted in the CCA section above.

## 4. Discussion

In our managed forests, tree species composition, stand structure, and microclimate influenced species composition of both epiphytic bryophytes and lichens. Their patterns are mainly driven by similar factors. However, some differences were found that should be accounted for in management practices to enhance the conservation of these important groups.

### *4.1. Tree species*

Tree species was the most important factor driving the composition of both epiphyte groups. In general, this study supports results of other stand scale studies indicating that epiphytic diversity is closely related to tree species richness, especially in mixed coniferous-deciduous forests, because of the different epiphytic assemblages hosted by different tree species (Berg et al., 2002; McGee and Kimmerer, 2002; Mezaka et al., 2012; Nascimbene et al., 2009b; Schmitt and Slack, 1990). Only at higher spatial scales this effect is likely to be overridden by factors operating at regional scale such in the case of climate, air condition, and landscape types (Bates et al., 1997, 2004; Frisvoll and Presto, 1997; Marini et al., 2011).

Many epiphytic bryophytes, mainly weft-forming mosses and mat-forming liverworts, are related to oaks as well as lichen assemblages dominated by large foliose species that are enhanced by the wrinkle rich bark of this tree providing a humid microhabitat. In these favourable conditions large epiphytes outcompete smaller species, occupying the available surface. On smooth barked trees, epiphytes are likely to experience more stressful conditions (e.g. more exposed to desiccation). Species associated with these trees have more stress-tolerant and pioneer traits. However, these species can be also replaced by weft-forming large species along with tree aging (Boudreault et al., 2000, Cobb et al. 2001, Sillett et al. 2000). Bryophytes and lichens have contrasting species richness pattern on these trees. Bryophyte assemblages are species poor both on beech and hornbeam, including only a few cushion-forming specialists (e.g. *Orthotrichum spp.*). On hornbeam, lichens form species rich assemblages, dominated by crustose species that otherwise are outcompeted by bryophytes and foliose lichens on oak (Aptroot, 2012; John and Dale, 1995; Ranius et al., 2008). The relevance of hornbeam as lichen substrate in European temperate forests was recently highlighted also by Hauck et al. (2013). Interestingly, that study provided evidence for a dramatic impoverishment of lichen assemblages on beech as a consequence of centuries of forest management for timber production. Our results corroborate this view since on beech we found species poor lichen communities composed by common species (see also Nascimbene et al., 2012).

Pine hosts species poor bryophyte assemblages, which is explained by its loose flacked unstable acidic bark (Barkman, 1958; Hauck and Javkhlan, 2008). However, some acidofrequent lichens are strongly related to this tree species, mainly establishing at the base of the trunks where the bark is more stable.

Tree species richness is a key element for forest biodiversity in this region. It was the most important variable for the diversity and composition of many other organism groups (herbs, seedlings, spiders, terricolous bryophytes, Ódor unpubl.). Compared to other regions of Hungary, fine scale tree species diversity of this region is extremely high. Conservation oriented forest management should maintain this high tree species richness in mixed stands. Silvicultural systems based on natural regeneration process could easily sustain this diversity. Some tree species not favoured for timer production could be relevant for biodiversity, as hornbeam for lichens.

### *4.2. Tree size*

Large and old trees considerably influence the composition of epiphytes with many threatened species and high epiphyte diversity in old-growth forests (Lie et al., 2009; Mazdule et al. 2012; McGee and Kimmerer, 2002; Nascimbene et al., 2009a). However, in our study tree size has a small effect on the composition of bryophyte and no effect on lichen assemblages. This result is probably related to the fact that our forests are managed with relatively short rotation cycles and old, large trees are virtually absent. The age range of our trees was accordingly small even if the range of DBH was probably enough (20-50 cm) to determine an area effect that is however more influential for bryophytes than for lichens (Fritz et al., 2008a). Since forests have a long history of management for timber production it is supposed that dispersal limited species, sensitive to the longevity of the substrate, already disappeared from this region (Hauck et al., 2013).

However, creating set aside areas (like core zones of forest reserves), leaving high density of retention trees after clearcuts, and sparing veteran trees in tree selection silvicultural system could contribute to increase the density of old, large trees of the region. Higher density of these trees could enable the recolonization of the sensitive epiphytic species in the area.

### *4.3. Microclimate and shrub layer*

Light was among the main drivers of lichen composition, while it had scarce effect on bryophytes. It is a general phenomenon that the composition of epiphytic lichens is related to light conditions, determining high diversity of lichens in open forests and on solitary trees (Aptroot, 2012; Coote et al., 2007; Moe and Botnen, 1997; Nascimbene et al., 2013b; Norden et al., 2012). Bryophytes generally prefer more shaded conditions and higher air humidity (Hosokawa and Odani, 1957; Humphrey et al., 2002; Lesica et al., 1991; Ranius et al., 2008). However, some studies emphasize that many specialist epiphytic bryophytes prefer more open conditions as forest edges and solitary trees (Moe and Botnen, 2000, Vanderporten et al., 2004). Studies supporting the positive effect of shaded conditions were carried out in forested regions, as in our case, while studies supporting the positive effect of open conditions were focused on areas where forest cover was low in the landscape. In our forests, only terricolous bryophytes are enhanced by increasing light availability, while epixylic and epiphytic species are related to shaded conditions (Tinya et al., 2009). Many facultative epiphytes are sensitive to microclimatic conditions, preferring relative cool and humid stands (Király et al. 2013). In this perspective, the relevance of the shrub layer in driving bryophytes assemblages could be related to the fact that it enhances local air humidity (Aude and Poulsen, 2000; Brunialti et al., 2010). In our study region, this structural factor was influential also for the species richness of epiphytic (Király et al., 2013) and ground-floor bryophyte assemblages (Márialigeti et al., 2009). The continuity of forest microclimate, heterogeneous light conditions, and permanent presence of shrub layer could be more easily maintained using tree selection silvicultural system and continuous forest cover forestry methods than in the framework of shelterwood system.

### *4.4. Landscape and historical factors*

Many dispersal limited epiphytic species are sensitive to the fragmentation of their habitat. Both recent (Kuusinen and Penttinen, 1999; Snäll et al., 2003) and historical (Berglund and Jonsson, 2005; Snäll et al., 2004) landscape patterns can determine the spatial distribution of these organisms. However, in our study the effect of these factors was far less important than that of stand level drivers. Landscape and historical factors had no effect on lichen composition, while recent forest cover had a marginal effect on bryophytes. These forests had been managed for centuries, and the forest cover was lower in the past than today (Gyöngyössy, 2008). It is supposed that dispersal limited, specialist species disappeared from the region in the past (Ellis et al., 2011), and the current species pools are adapted to more closed and disturbed conditions. This interpretation is also corroborated by Hauck et al. (2013) that relate the pauperization of the epiphytic lichen flora in temperate forests of north-western Germany with the long lasting human disturbance that caused the replacement of native stands, mainly composed of beech, with oak-hornbeam dominated secondary stands.

## 5. Conclusions, implications for management

In our study region, forest management aims to harmonize timber production with biodiversity conservation to accomplish the policies of nature protection of the National Park, fitting to the general concept of sustainable forest management. In this perspective, this study proved that the most determinant factors influencing the composition of epiphytes primarily reflect on trends in recent forest management (tree species richness and composition, light and microclimate conditions, shrub layer, presence of large trees) giving a real opportunity to improve forest biodiversity conservation.

The maintenance of mixed stands including oaks, beech and pine as dominant trees considerably increases the diversity of epiphytic assemblages because of the host preferences of the species. The presence of subordinate trees (thus stands with higher overall tree species richness) is also very important. In particular, hornbeam is a highly suitable host for several lichen species. This tree species is usually not favoured by management practices focused on timber production, but its enhancement should be included in more conservation-oriented practices.

For bryophytes, the continuity of forest microclimate (high and balanced air humidity) is very important. This habitat condition could be provided by enhancing continuous forest cover forestry, presence of shrub layer and heterogeneous vertical structure (Aude and Poulsen, 2000; Király and Ódor, 2010). Lichen assemblages are limited by light availability and the optimal light conditions could be provided by small scale thinning and gap creation (Nordén et al., 2012).

On the basis of our results, the main strategy of management focusing on epiphyte diversity conservation should include: 1) the maintenance of tree species diversity in mixed stands; 2) the increase of the proportion of deciduous trees (mainly oaks and hornbeam); 3) the maintenance of large trees within the stands; 4) the presence of shrub and regeneration layer; 5) the creation of heterogeneous light conditions. In this perspective, tree selection silvicultural systems and the approaches of continuous forest cover forestry are likely to be more appropriate for the conservation of epiphytes than shelterwood systems (Aude and

Poulsen, 2000; McGee and Kimmerer, 2002; Nascimbene et al., 2013a), even if Bardat and Aubert (2007) emphasized that shelterwood system could provide better conditions for epiphytes at higher spatial scales. In the framework of shelterwood system, the extension of rotation and regeneration periods and the maintenance of a large proportion of retention trees after harvest are widely supported measures to enhance forest epiphytes (Caners et al. 2013; Hannerz and Hanell, 1997; Hazzell and Gustafsson, 1999; Löhmus and Löhmus, 2011).

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**Table 1** Explanatory variables used in stand level analyses. Their minimum, maximum and mean values are given where appropriate from the 35 studied plots

| Explanatory variable | Minimum | Maximum | Mean |
|---|---|---|---|
| Tree species composition | | | |
| Tree species richness | 2.0 | 10.0 | 5.6 |
| Tree species diversity[1] | 0.19 | 1.95 | 0.92 |
| Proportion of tree species (beech, hornbeam, oaks, Scots pine, subordinate trees) | - | - | - |
| Stand structure | | | |
| Mean DBH (cm) | 13.6 | 40.6 | 26.3 |
| Coefficient of variation of DBH | 0.2 | 1.0 | 0.5 |
| Tree density (stems/ha) | 218.7 | 1318.7 | 591.2 |
| Shrub density (stems/ha) | 0.00 | 4706.2 | 952.2 |
| Big tree density (DBH>50 cm, stems/ha) | 0.0 | 56.2 | 17.3 |
| Basal area ($m^2$/ha) | 24.1 | 49.7 | 34.2 |
| Snag volume ($m^3$/ha) | 0.0 | 64.6 | 12.1 |
| Log volume ($m^3$/ha) | 1.2 | 35.6 | 10.8 |
| Light conditions | | | |
| Mean relative light (%) | 4.8 | 40.3 | 16.0 |
| Standard deviation of relative light | 0.7 | 15.2 | 3.9 |
| Microclimate | | | |
| Temperature difference (K) | -0.9 | 0.7 | -0.1 |
| Temperature range difference (K) | -0.4 | 2.5 | 0.9 |
| Air humidity difference (%) | -1.8 | 3.3 | 0.8 |
| Air humidity range difference (%) | -2.3 | 6.6 | 1.9 |
| Geographical position | | | |
| EOV (Hungarian Geographical Projection) coordinates of longitude and latitude (m) | - | - | - |
| Landscape variables | | | |
| Proportion of landscape elements (%, forests, clearcuts, non-forested areas)[2] | 56.9 | 100.0 | 89.8 |
| Diversity of landscape elements[1] | 0.11 | 1.86 | 1.11 |
| Management history (in the 19th century) | | | |
| Proportion of forest in the landscape (%) | 24.0 | 100.0 | 76.6 |
| Plot was a forest (binary) | - | - | - |

*DBH* diameter at breast height

[1] Shannon diversity

[2] the values are the percentage of forests

**Table 2** Explained variance of the significant explanatory variables used in the stand level Redundancy Analysis (RDA)

| Variables | Variance (%) | F-value | P |
|---|---|---|---|
| Bryophytes | | | |
| Oak proportion | 14 | 5.5 | 0.002 |
| Temperature difference | 8 | 3.2 | 0.002 |
| Mean DBH | 8 | 3.4 | 0.002 |
| Pine proportion | 5 | 2.5 | 0.002 |
| Recent forest cover | 5 | 2.4 | 0.014 |
| Shrub density | 4 | 1.9 | 0.042 |
| Lichens | | | |
| Mean relative light | 22 | 9.5 | 0.002 |
| Pine proportion | 20 | 11.2 | 0.002 |
| Oak proportion | 7 | 4.7 | 0.002 |
| Hornbeam proportion | 4 | 2.8 | 0.004 |
| Basal area | 4 | 2.3 | 0.008 |

**Table 3** Explained variance (conditional effect) of the significant explanatory variables in tree level Canonical Correspondence Analysis (CCA)

| Variables | Variance (%) | F-value | P |
|---|---|---|---|
| Bryophytes | | | |
| Tree species | 7.2 | 16.7 | 0.002 |
| DBH | 0.6 | 2.8 | 0.026 |
| Relative light | 0.4 | 2.0 | 0.006 |
| Lichens | | | |
| Tree species | 12.6 | 18.2 | 0.002 |
| Relative light | 0.5 | 1.9 | 0.034 |
| DBH | 0.5 | 1.7 | 0.012 |

**Table 4** Indicator Species Analysis of bryophytes related to tree species. Only bryophyte species which were significantly (P<0.01) related to a tree species are listed,. Values represent the number of occurrences (frequency) on different tree species

| Species | Beech | Hornbeam | Oak | Pine | Total | Indtree | Indval | P |
|---|---|---|---|---|---|---|---|---|
| Number of trees | 225 | 56 | 324 | 344 | 949 | | | |
| *Orthotrichum pallens* | 24 | 4 | 1 | 0 | 29 | Beech | 0.0917 | 0.001 |
| *Orthotrichum stramineum* | 41 | 0 | 6 | 0 | 47 | Beech | 0.1751 | 0.001 |
| *Plagiothecium denticulatum var. undulatum* | 1 | 3 | 6 | 1 | 11 | Hornbeam | 0.0405 | 0.006 |
| *Brachytheciastrum velutinum* | 20 | 5 | 85 | 5 | 115 | Oak | 0.1791 | 0.001 |
| *Dicranum montanum* | 68 | 6 | 121 | 136 | 331 | Oak | 0.1973 | 0.001 |
| *Homalia trichomanoides* | 0 | 1 | 20 | 0 | 21 | Oak | 0.0542 | 0.005 |
| *Hypnum cupressiforme* | 203 | 56 | 324 | 108 | 691 | Oak | 0.428 | 0.001 |
| *Isothecium alopecuroides* | 6 | 6 | 46 | 0 | 58 | Oak | 0.0775 | 0.004 |
| *Metzgeria furcata* | 22 | 6 | 65 | 0 | 93 | Oak | 0.1395 | 0.001 |
| *Plagiomnium affine* | 0 | 1 | 20 | 1 | 22 | Oak | 0.0571 | 0.004 |
| *Plagiomnium cuspidatum* | 0 | 0 | 13 | 0 | 13 | Oak | 0.0401 | 0.009 |
| *Platygyrium repens* | 8 | 3 | 162 | 2 | 175 | Oak | 0.4533 | 0.001 |
| *Radula complanata* | 77 | 21 | 160 | 0 | 258 | Oak | 0.2248 | 0.001 |
| *Chiloscyphus profundus* | 22 | 8 | 40 | 186 | 256 | Pine | 0.4059 | 0.001 |

*Total* Summed number of occurrences (frequencies)

*Indtree* Tree species with the highest indicator values

*Indval* Indicator value related to the tree species

*P* significance of the indicator value

**Table 5** Indicator species analysis of lichens related to tree species. Only lichen species which were significantly ($P<0.001$) related to a tree species are listed. Values represent the number of occurrences (frequency) on different tree species.

| Species | Beech | Hornbeam | Oak | Pine | Total | Indtree | Indval | P |
|---|---|---|---|---|---|---|---|---|
| Number of trees | 225 | 56 | 324 | 344 | 949 | | | |
| *Lecanora expallens* | 32 | 1 | 2 | 0 | 35 | Beech | 0.1164 | 0.001 |
| *Arthonia radiata* | 1 | 16 | 0 | 0 | 17 | Hornbeam | 0.2849 | 0.001 |
| *Graphis scripta* | 92 | 49 | 3 | 0 | 144 | Hornbeam | 0.698 | 0.001 |
| *Lecanora carpinea* | 1 | 8 | 2 | 0 | 11 | Hornbeam | 0.1372 | 0.001 |
| *Lecanora chlarotera* | 2 | 18 | 0 | 0 | 20 | Hornbeam | 0.313 | 0.001 |
| *Pertusaria amara* | 0 | 7 | 8 | 0 | 15 | Hornbeam | 0.1201 | 0.001 |
| *Phlyctis argena* | 104 | 47 | 216 | 1 | 368 | Hornbeam | 0.4552 | 0.001 |
| *Pyrenula nitida* | 0 | 12 | 0 | 0 | 12 | Hornbeam | 0.2143 | 0.001 |
| *Cladonia coniocraea* | 2 | 0 | 145 | 66 | 213 | Oak | 0.3132 | 0.001 |
| *Flavoparmelia caperata* | 2 | 0 | 166 | 1 | 169 | Oak | 0.5114 | 0.001 |
| *Lepraria sp.* | 46 | 16 | 257 | 65 | 384 | Oak | 0.5885 | 0.001 |
| *Parmelia sulcata* | 2 | 1 | 41 | 1 | 45 | Oak | 0.1148 | 0.001 |
| *Chaenotheca ferruginea* | 0 | 0 | 2 | 32 | 34 | Pine | 0.0814 | 0.002 |
| *Dimerella pineti* | 1 | 1 | 7 | 246 | 255 | Pine | 0.6918 | 0.001 |
| *Hypogymnia physodes* | 0 | 0 | 13 | 81 | 94 | Pine | 0.2201 | 0.001 |
| *Hypocenomyce scalaris* | 0 | 0 | 1 | 86 | 87 | Pine | 0.2477 | 0.001 |

*Total* Summed number of occurrences (frequencies)

*Indtree* Tree species with the highest indicator values

*Indval* Indicator value related to the tree species

*P* significance of the indicator value

**Fig. 1.** Location of the study area (a, grey rectangle) and the geographical positions of the 35 plots (b, black dots), built-up areas are shown by grey. A = Austria; SLO = Slovenia; HR = Croatia; H = Hungary; SK = Slovakia.

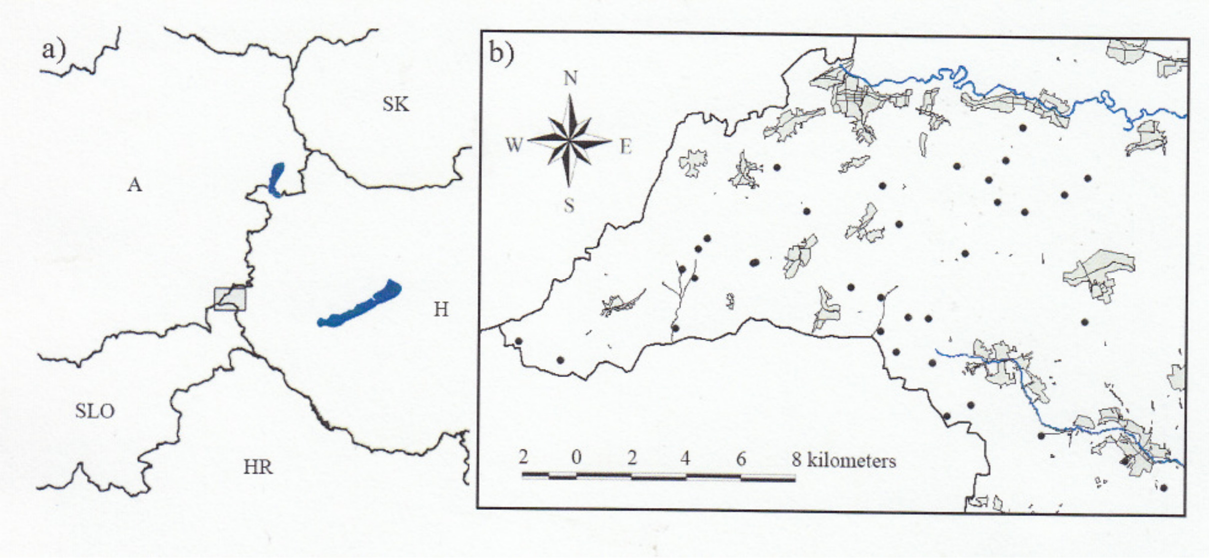

**Fig. 2.** Variation partitioning of bryophyte (a) and lichen (b) assemblages among the following groups of explanatory variables: tree species composition, stand structure, microclimate (including light) and landscape-historical variables (boxes).

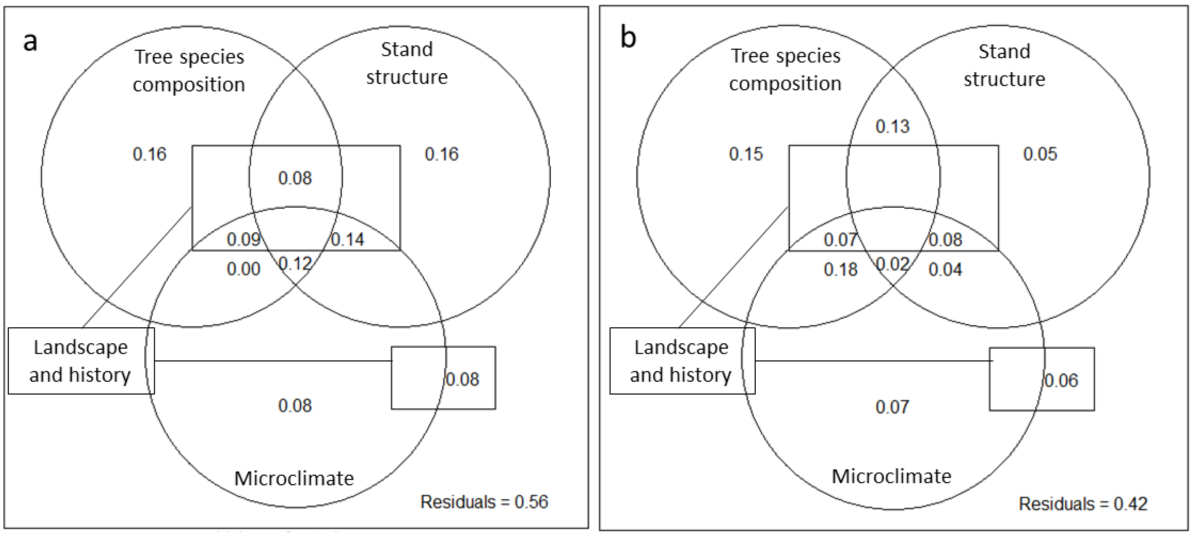

**Fig. 3.** Ordination biplot of the stand level Redundancy Analysis of bryophytes. Species are indicated by blue arrows, labelled by the six letter codes (three letters from genus and three from species names, see Table A.1). Explanatory variables are represented by red arrows. Explained variances (%) of the axes are indicated. DBH: diameter at breast height

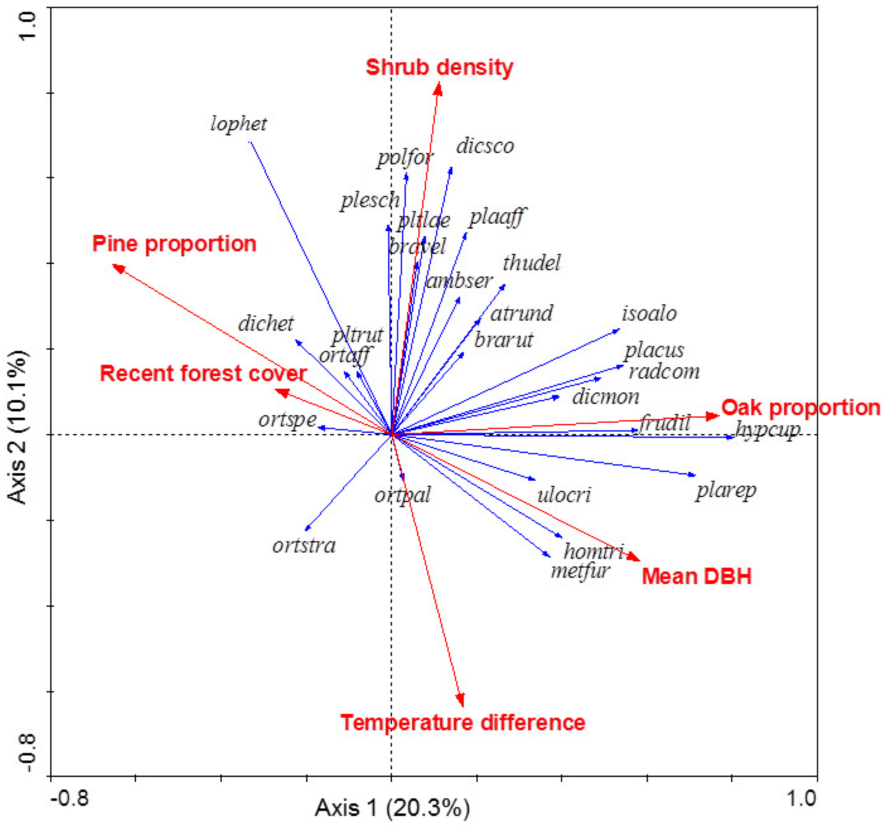

**Fig. 4.** Ordination biplot of the stand level Redundancy Analysis of lichens. Species are indicated by blue arrows, labelled by the six letter codes (three letters from genus and three from species names, see Table A.2). Explanatory variables are represented by red arrows. Explained variances (%) of the axes are indicated.

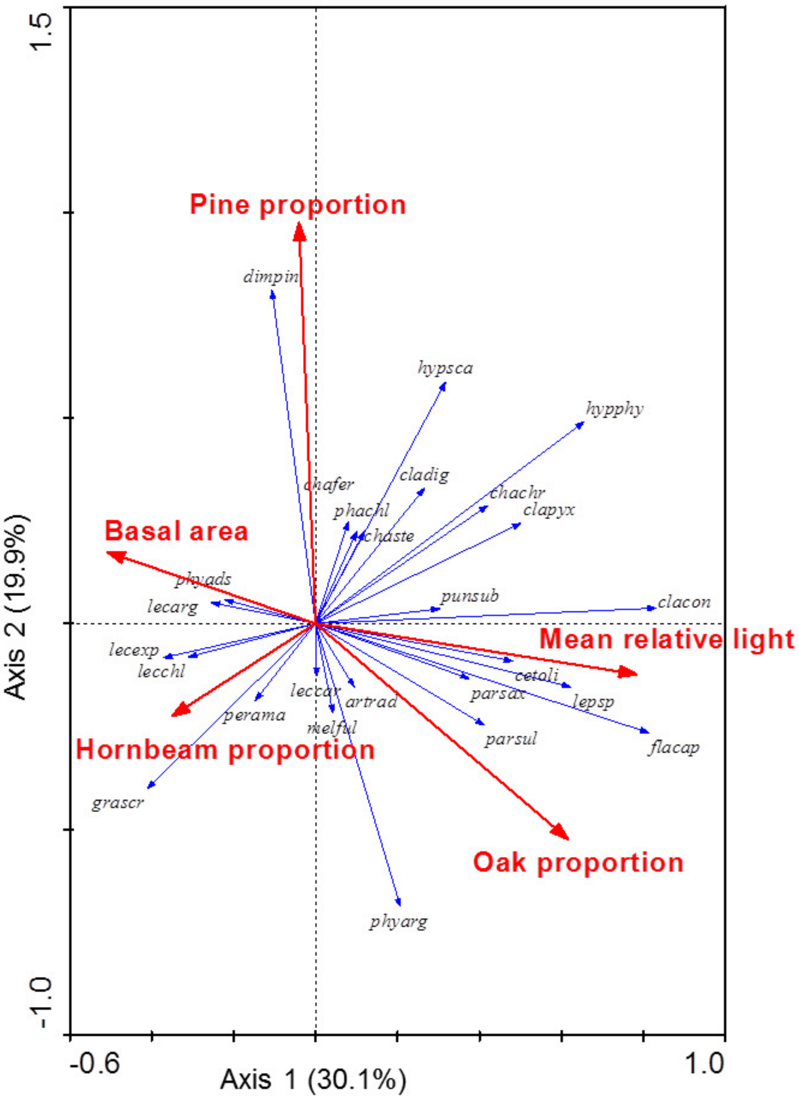

**Fig. 5.** Ordination biplot of tree level canonical correspondence analysis of bryophytes. Species are indicated by blue triangles, labelled by the six letter codes (three letters from genus and three from species names, see Table A.1). Explanatory variables are represented by red triangles (factors) or red arrows (numeric variables). Explained variances (%) of the axes are indicated. DBH: diameter at breast height

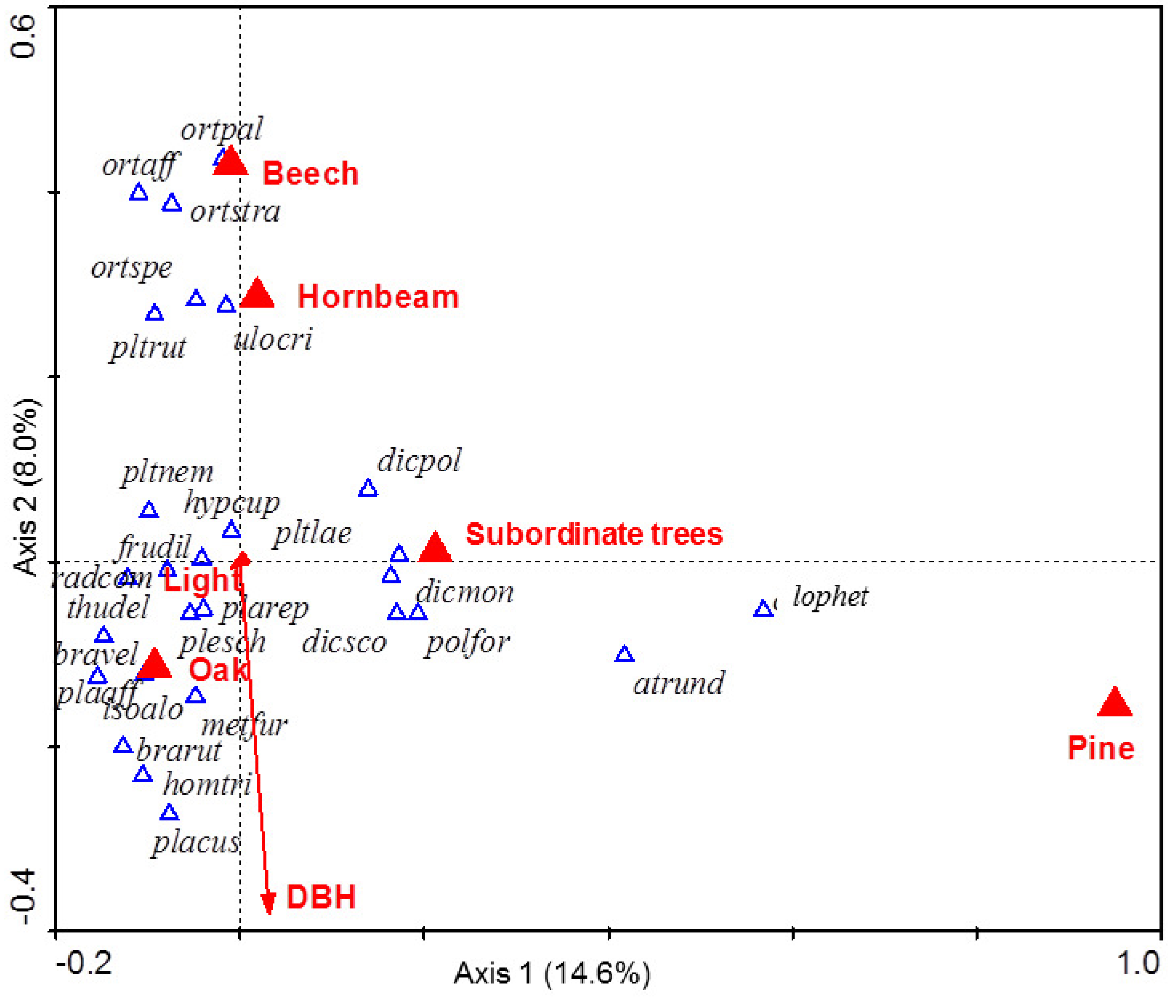

**Fig. 6.** Ordination biplot of tree level canonical correspondence analysis of lichens. Species are indicated by blue triangles, labelled by the six letter codes (three letters from genus and three from species names, see Table A.2). Explanatory variables are represented by red triangles (factors) or red arrows (numeric variables). Explained variances (%) of the axes are indicated. DBH: diameter at breast height