

This manuscript is contextually identical with the following published paper:

Király, I., Ódor, P. 2010. The effect of stand structure and tree species composition on epiphytic bryophytes in mixed deciduous– coniferous forests of Western Hungary. *Biological Conservation* 143(9): 2063-2069.

Running head: The effects of stand structure on epiphytic bryophytes

Title: The effect of stand structure and tree species composition on epiphytic bryophytes in mixed deciduous-coniferous forests of Western Hungary

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## **Abstract**

The effect of tree species, stand structure, landscape and historical variables was studied on the species composition, species richness and cover of epiphytic bryophyte assemblages in mixed deciduous-coniferous forests of Western Hungary. Stand and tree level assemblages were analyzed by ordinations and generalized linear modeling in 35 70-110 yr old stands of different management regimes.

Bryophytes showed a considerable preference to different host trees, which resulted that stand level diversity of bryophyte assemblages was determined mainly by tree species diversity, and their composition by tree species composition. Cover and diversity of epiphytic bryophytes were the highest on oaks (*Quercus petraea* and *Q. robur*), and the lowest on Scotch pine (*Pinus sylvestris*). The presence of sapling (shrub) layer increased, whereas a large number of medium sized trees decreased bryophyte species richness in this study. Tree size was much less influential which is explained by the lack of large, veteran trees. Forest management maintaining tree species diversity, structural heterogeneity and temporal continuity of the stands could considerably contribute to the conservation of this organism group. Selective cutting is more appropriate for these conservational purposes than shelterwood management system.

Keywords: bryophyte cover, conservation, species composition, species richness, forest management,

## **1. Introduction**

The ecology of cryptogamic epiphytes has been investigated for long, but their conservation receives increased attention in recent studies.

Up to the 1980's, interest was focused on (1) the effect of host tree species, bark factors and site conditions on epiphyte assemblages (Barkman, 1958; Slack, 1976; Palmer, 1986); (2) the vertical distribution of epiphytes on trees (Barkmann, 1958; Bates and Brown, 1981; Billings and Drew, 1938; Rasmussen, 1975; Slack, 1976; Smith, 1982); (3) the functional role of epiphytic assemblages especially in the Pacific Northwest and

tropical montane rainforests (Pócs, 1982; Pypker et al., 2006a,b); and (4) the phytosociological description of epiphytic communities (Barkman, 1958). The viewpoints expressed in the general discussion “Do mosses see the forest or the trees?” (sensu Palmer, 1986), determined in most cases the spatial scale of the studies. Distinct assemblages were found on different tree species in investigations focused on a relatively small region (like a forest stand) with relatively homogeneous site conditions (Hauck and Javkhlan, 2008; Nascimbene et al., 2009a; Szövényi et al., 2004). The situation is best characterized by Slack (1976): “In the Adirondacks I can almost invariably tell the species of tree by the epiphytes”. This host preference of epiphytes was mainly explained by the different acidity, nutrient content, humidity and physical structure of tree species’ bark (Barkman, 1958; Smith, 1982). However, while tree species identity is a discrete, nominal factor for epiphyte assemblages, the physical and chemical properties of different bark types show continuous transitions on larger spatial and temporal scale. These factors vary considerably even within a species depending on site fertility, humidity, tree age and bark damages (Bates and Brown, 1981; Boudreault et al., 2008; Gustafsson and Eriksson, 1995; Fritz and Heilmann-Clausen, 2010). In studies of different forest types and site conditions at regional and continental scales, the effects of climatic and edaphic factors overwhelm that of host species (McGee and Kimmerer, 2002; Peck, 1997; Slack, 1976; Schmitt and Slack, 1990).

Recent studies have focused more on the conservation of epiphytes and the anthropogenic effects on them at both stand and landscape levels, as the effects of forest management, habitat fragmentation, and deterioration. Many studies comparing old-growth and managed stands found that epiphytes are very sensitive to management factors (Aude and Poulsen, 2000; Holz and Gradstein, 2005; McGee and Kimmerer,

2002). The size and age of the host trees (the presence of large, mature trees) are crucial in the diversity and conservation of epiphytes (Aude and Poulsen, 2000; Hazell et al., 1998; Kuusinen and Penttinen, 1999; McGee and Kimmerer, 2002; Nascimbene et al., 2009b). There are three, not necessarily exclusive explanations for this phenomenon: (1) a simple area effect, (2) the more optimal and diverse conditions of microhabitats with age and size (e.g. changes of bark characteristics), and (3) more time is available for dispersal limited species for colonization.

The effect of management and human land use can manifested also as fragmentation and isolation. The occurrence of specialist species with limited dispersal capacity is hindered by unavailability of the potential substrates (Alvarenga et al., 2007; Kuusinen and Penttinen, 1999; Löbel et al., 2006; Snäll et al., 2003; Söderström and Herben, 1997).

The aim of this study was to disclose the explanatory variables that determine cover, composition and species richness of epiphytic bryophytes at different spatial scales in a region of deciduous-coniferous forests in Western Hungary. Bryophyte assemblages were separately analyzed at the tree and the stand levels. At the stand level, tree species composition, stand structure, site conditions, landscape characteristics and management history, while at the tree level host species and tree size were analyzed as potential explanatory variables. Facultative and obligate epiphytes were distinguished during the analyses. Moreover we present predictive models that are applicable in forestry and nature conservation practice.

## **2. Material and methods**

## 2.1. Study area

The investigation was carried out in the westernmost part of Hungary, called Órség (N 46°51'-55' and W 16°07'-23'). The elevation is 250-350 m above sea level and the landscape consists of hills and wide valleys. The mean annual temperature is 9.0-9.5 °C, precipitation is 700-800 mm per year (Marosi and Somogyi, 1990). The bedrock is alluviated gravel mixed with loess. On hills the most common soil types are pseudogleyic and lessivage brown forest soils, while in valleys mire and meadow soils can be found, the upper layer of which are acidic (pH 4.5-4.7, Szodfridt, 1969).

The forests of the hills are dominated by beech (*Fagus sylvatica*), sessile and pedunculate oak (*Quercus petraea* and *Q. robur*), hornbeam (*Carpinus betulus*), Scotch pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*), which occur in monodominant and mixed stands as well. The proportion of different mixing species (*Betula pendula*, *Populus tremula*, *Castanea sativa*, *Prunus avium*, etc.) is high (Tímár et al., 2002). A more detailed description of the studied stands can be found in Tinya et al. (2009a) and Márialigeti et al. (2009).

Since the 12<sup>th</sup> century, the area has been characterized by extensive farming, resulting in a shifting mosaic of arable lands, young forests and meadows. This management led to considerable changes of forest sites: deterioration of nutrients and acidification. The proportion of trees with pioneer character (such as Scotch pine and weeping birch) increased, and these secondary forests were colonized by acidophytic herbs, shrubs and bryophytes. Currently, two types of forest management are used: spontaneous stem selection system resulting in uneven aged stands in private forests, and shelterwood management system with a rotation period of 70-110 years in state forests.

## *2.2. Data collection*

35 forest stands were selected from the stand structural database of the Hungarian National Forest Service by stratified random sampling representing different tree species composition and stand structure. Further criteria of site selection were as follows: dominant trees older than 70 years, more or less level slope, absence of ground-water influence and spatial independence of sites (the distance was minimum 500 m between the stands).

Stand structural variables were measured in 40 x 40 m<sup>2</sup> plots of the stands. Circumference, species identity and height of each tree with diameter at breast height (DBH) larger than 5 cm were recorded. Average diameter and length of logs thicker than 5 cm diameter and longer than 0.5 m were recorded. Density of saplings (tree or shrub individuals taller than 0.5 m and thinner than 5 cm DBH) was recorded. Absolute cover of different substrates (litter, open soil, dead wood) was visually estimated in dm<sup>2</sup> within the plots. Light conditions were measured in 36 points at one meter height in a systematic design within the plots by LAI-2000 Plant Canopy Analyzer instruments and on a nearby open field (LI-COR Inc., 1992; Tinya et al., 2009a,b). The mean and coefficient of variation of relative diffuse light were calculated. The proportion of different landcover types (old beech, oak, Scotch pine, Norway spruce and mixed forests, young forests, non-forested areas) was estimated around the plots (within a circle with 300 m radius) using maps and data of Hungarian National Forest Service. Historical data were generated based on the map of the Second Military Survey of the Habsburg Empire from 1853 (Arcanum, 2006), the management type of the plots and

the proportion of these in their vicinity (in the circle of 300 m radius) was estimated (Table 1).

Epiphytic bryophytes were recorded in a 30 x 30 m<sup>2</sup> plot positioned in the middle of the 40 x 40 m<sup>2</sup> plot. Every living tree with DBH at minimum 20 cm was sampled from the bottom to 1.5 m height. Cover of bryophyte species were estimated in dm<sup>2</sup>. Nomenclature follows Hill et al. (2006) for mosses and Grolle and Long (2000) for liverworts. Additional information concerning the studied sites and other investigated organism groups are available on the website [http://ramet.elte.hu/~ramet/project/ors\\_erdo/index\\_en.htm](http://ramet.elte.hu/~ramet/project/ors_erdo/index_en.htm).

### 2.3. Data analysis

Relationships between bryophyte species composition and potential explanatory variables were explored by indirect and direct ordination (Podani, 2000). In stand level analysis, the estimated cover of bryophyte species was ln transformed. Species occurring in less than four plots were omitted from the analysis. The examined stand level explanatory variables are listed in Table 1. The proportion of tree species was determined based on their volumes. Tree species diversity was expressed by Shannon index with natural logarithm based on the relative volume of species (Shannon and Weaver, 1949). Diversity of landcover types was calculated in similar way. In these analyses, *Quercus petraea* and *Q. robur* were not distinguished ('oaks' in the following). Redundancy analysis (RDA) was performed as a direct ordination, supposing approximately linear relationships between species performance and explanatory variables (Leps and Smilauer, 2003). The explanatory variables were

standardized by standard deviation before the analysis. In direct ordinations, the explanatory variables were selected by manual forward selection. The effect of explanatory variables was tested by F-statistics via Monte-Carlo simulation, the number of permutations was 1000, the accepted significance level was 0.05 (ter Braak and Smilauer, 2002). The significance of the canonical axes was tested in similar way. Because the longitude coordinate had a significant effect during the selection, it was used as a covariable in the final ordination.

The relationships between some selected biological variables of bryophyte assemblages at the stand level (cover and species richness of the whole assemblage; species richness of specialist and facultative epiphytes) and the potential explanatory variables were analyzed by generalized linear models (Table 1; Faraway, 2005, 2006). These two functional groups were generated based on literature and field experience (Orbán and Vajda, 1983; Smith, 2004). Saxicolous bryophytes were considered as specialist epiphytes, because rocks do not appear in Órség, and saxicolous species occur exclusively on trees (see the electronic supplement). Before building regression models, statistical pre-analyses were performed. The distribution of the dependent and the explanatory variables was tested for normality and if it diverged significantly from the normal, then the data were ln transformed. Correlation matrices were calculated and scatterplots were made to explore the interrelationships among the explanatory variables and between the dependent and the explanatory variables. During the pre-analysis 5-6 explanatory factors were applied to the selection procedure of regression models. The minimal adequate model was built with backward selection. During the selection procedure, deviance analysis with F-test (ANOVA) was applied.

Tree level species composition was analyzed by canonical correspondence analysis as direct ordination using ln transformed cover data of bryophyte species. Species with frequency lower than six and trees with bryophyte species richness lower than three were omitted from the analysis. Because the frequency of Norway spruce trees became very low after this reduction, Scotch pine and Norway spruce were treated together as conifers. The explained variance by tree species, DBH and plot was analyzed by variation partitioning (Leps and Smilauer, 2003). The significance of the environmental variables and the whole model was tested similarly to the plot level ordination. In the final model, the effects of DBH and tree species on bryophyte composition were used as explanatory variables and plot as covariable.

Bryophyte cover and species richness at the tree level were analyzed by generalized mixed models, where DBH, tree species and their interaction were used as fixed factors and plot as random factor (Faraway, 2006). Both bryophyte cover and species richness were ln transformed before the analysis. The significance of the models was tested by the maximum likelihood ratio method.

Multivariate analyses were carried out with Canoco for Windows 4.5 (ter Braak and Smilauer, 2002), regression models with R 2.6.2., for general mixed models the R package „lmer” were used (The R Development Core Team, 2008; Bates, 2005). Statistica 8.0 (Statsoft, 2008) was used for descriptive statistics and correlation analysis.

### **3. Results**

#### *3.1. Stand level analyses*

The canonical axes of RDA explained 38.8% of total variance. The effect of the relative volume of oaks surpassed the other explanatory variables, explaining 13.6% of total variance (Table 2). The first axis (explained variance 17.1%) correlated negatively with the relative volume of oaks and positively with the density of all trees (Fig. 1). Among the bryophytes, the two dominant facultative epiphyte species (*Hypnum cupressiforme* and *Platygyrium repens*) had positive correlation with relative oak volume, and some frequent specialist epiphyte species (*Frullania dilatata*, *Radula complanata*, *Homalia trichomanoides*, *Ulota crispa*, *Metzgeria furcata*, *Isothecium alopecuroides*, and *Dicranum montanum*) had a similar pattern. The second axis (explained variance 10.7%) positively correlated with the density of saplings, the average of diffuse light and the diversity of tree species. Acidophytic facultative epiphytes had high positive scores on the second axis (*Dicranum scoparium*, *Polytrichum formosum*, *Plagiothecium laetum*, *Pleurozium schreberi*, and *Lophocolea heterophylla*), they were affected mainly by the density of saplings and the diversity of tree species. Some facultative epiphytes with intermediate cover (*Plagiomnium affine*, *Brachytheciastrum velutinum*, *Thuidium delicatulum*, and *Amblystegium serpens*) correlated positively with the average of diffuse light.

Considering the regression models (Table 3), the cover of bryophytes increased mainly with the relative volume of oaks, which explained 65.0% of total variance. The density of all trees showed a far less important, negative effect. The model explained 70.6% of the total variance. Species richness increased with density of saplings and diversity of tree species, but decreased with density of all trees. All the three explanatory factors had almost the same importance in the model, which explained 51.6% of total variance. Considering species richness of specialist epiphytes, only two significant explanatory

factors were found: the relative volume of Scotch pine had a large negative effect, while all trees density had a marginally significant negative effect. The model explained 35.4% of the total variance. Species richness of facultative epiphytes was raised by two significant factors with the same importance: density of saplings and diversity of tree species (model explaining 51.3% of the total variance).

### 3.2. Tree level analyses

Among the surveyed trees (1052), 514 fulfilled the criteria of ordinations. The three tree level explanatory variables (plot, tree species and DBH) explained 27.1% of the variance ( $F=4.65$ ,  $p<0.001$ , Fig. 2). Although all factors were significant, plot explained the largest part of the variance (16.4%,  $F=3.25$ ,  $p<0.001$ ), the effect of tree species was intermediate (5.8%,  $F=9.47$ ,  $p<0.001$ ), while the variance explained by DBH was marginal (0.4%,  $F=2.49$ ,  $p<0.001$ ). The interactions between variables were weak, except the tree species – plot interaction (4.1%).

Using plot as a covariable, the general effect of tree species and tree size explained 6.2% of the total variance (Fig. 3,  $F=8.09$ ,  $p<0.001$ ). Most of the species preferred oaks, especially large oaks. This tree maintained a species-rich bryophyte assemblage including facultative (e.g. *Brachytheciastrum velutinum*, *Plagiomnium affine*, and *Platygyrium repens*) and specialist (e.g. *Homalia trichomanoides*, *Metzgeria furcata*, *Isothecium alopecuriodes*, *Radula complanata*, and *Frullania dilatata*) epiphytes. Most of the species avoided coniferous trees except the epixylic *Lophocolea heterophylla*. Some small cushion forming specialist epiphytic mosses such as *Orthotrichum spp.*, and *Ulota crispa* preferred beech and hornbeam to other host tree species.

Considering the regression models, the tree species was the most determinant factor for tree level bryophyte cover, overwhelming the effect of tree size and plots (Table 4). There was a relatively high cover on oak trees (between 30-50%, depending on tree size), while the cover on coniferous trees was practically zero (Fig. 4a). The modeled cover on beech was 5-8%, a bit lower than on hornbeam and other mixing species.

Similarly to cover, tree level species richness of bryophytes was also determined mainly by the tree species, although the effects of tree size and plot were more considerable than for cover (Table 4). Species richness on conifers was low (about 1.2) independently of the size of the trees (Fig. 4b). Species richness was higher on oak (between 3 and 5) than on beech and other mixing species (between 2 and 3.5). DBH had a more important effect on hornbeam than on other species.

#### **4. Discussion**

Species composition, cover and diversity of epiphytic bryophytes at both stand and tree levels were determined mainly by the host species; especially oaks were influential on the diversity of epiphytes. A possible interpretation of this is that the mesotrophic, wrinkle-rich bark structure of oaks offers many shady, windproof and moist microhabitats, where bryophyte propagules can easily adhere to, while they are washed off by the rainfall from the trees of smooth bark (Barkman, 1958; Ranius et al., 2008). Furthermore, soil granules can adhere to wrinkles, which promote the colonisation of facultative epiphytes such as *Plagiothecium spp.* and *Plagiomnium spp.* (Billings and Drew, 1938). Besides, oaks have a relatively open canopy system which allows much light of forest floor, which is also important for epiphytes. On the contrary, on Scotch

pine a similarly emergent, but negative preference occurred, especially in the tree-level analysis. Scotch pine has dry, acidic, oligotrophic bark with loose flaked surface that is not appropriate for a permanent bryophyte cover (Barkman, 1958).

Tree species diversity significantly increased stand level species richness of epiphytes. This result seems to be related to the high host specificity of bryophytes. Therefore, stands with diverse tree species composition support variable epiphytic assemblages (Szövényi et al., 2004; Peck, 1997; Peck et al., 1995; McGee and Kimmerer, 2002; Berg et al., 2002; Cleavitt et al., 2009). In the studied region, the bryophyte diversity on beech was lower than on oaks, however, it had a characteristic species composition because many specialist epiphytes (*Ulota crispa*, many *Orthotrichum* species) preferred beech. Therefore, the co-occurrence of large oak and beech trees within a stand can considerably increase the stand-level diversity of epiphytes (Berg et al. 2002).

Several studies agreed that among the stand structural characteristics the occurrence of old, big trees is one of the most determinant variables in the diversity of epiphyte assemblages (Aude and Poulsen, 2000; Rose, 1992; Moe and Botnen, 1997; Fritz et al., 2008; Lie et al., 2009). The relatively low impact of tree size in this study does not question its biological importance; it can be explained more readily by data structure (95% of the studied trees belonged to the 20-50 cm DBH range) and the lack of veteran trees because of the intensive management. We can suppose that if more extremely large, veteran trees occur in these forests the stand level diversity of epiphytic bryophytes would considerably increase.

Density of all trees had a considerable negative effect at the stand level species composition, richness and cover. It could have many complex indirect effect on epiphytic assemblages, however, its practical advantage is that it is very simple to

measure or estimate. The high values of this variable mean that the proportion of small trees (DBH larger than 5 cm) is high. The most common species in this size category is hornbeam whose secondary canopy layer can create very shaded conditions in the studied zone of epiphytes (on trunks below 1.5 m), without increasing air humidity (compared with sapling density, see below). In many forest types, light turned out to be an important factor for epiphytic bryophytes (Aude and Poulsen, 2000; Bardat and Aubert, 2007; Coote et al., 2007; Hosokawa and Odani, 1957; Moe and Botnen, 1997). In this region terrestrial bryophytes showed much stronger positive correlations with light than epixylic and epiphytic ones, light proved more determinant factor for ground floor assemblages than for epiphytes (Márialigeti et al., 2009; Tinya et al., 2009a).

Density of saplings raised epiphytic species richness, and had a considerable effect on species composition. Many studies emphasized the importance of shrub and sapling layer for epiphytic bryophytes, which can create a stable and humid microclimate by decreasing the effect of wind and desiccation (Aude and Poulsen, 2000; Gustafsson et al., 1992). Its positive effect on air humidity can overwhelm its negative influence by decreasing light for epiphytic and terrestrial bryophytes.

Although landscape and historical factors were analyzed in the model selections, they did not turn out as significant factors for epiphytic bryophytes. The forest cover in the studied region is high, the stands are not isolated, and the most common tree species show a fine grained mixture within the stands. It is supposed that dispersal limitation of the species influences their spatial distribution in the studied region less than in more fragmented landscapes of Western and Northern Europe (Löbel et al., 2006; Snäll et al., 2003, 2004; Rose, 1992). Temporal forest continuity is heterogeneous in the studied region. Based on a military map from 1853, a considerable part of the studied stands

was arable land or meadow at that time, while others had longer continuity. However, based on studies of Fritz et al. (2008) and Rose (1992), epiphytic bryophytes seem to be less sensitive to forest continuity than lichens.

## **5. Conclusions**

In the studied region, epiphytic bryophytes showed considerable preference to different host trees, which resulted that plot level diversity of this assemblage is determined mainly by tree species diversity; especially oaks had emergent importance of the species richness and cover of epiphytes. Besides, stand structural heterogeneity, presence of sapling (shrub) layer increased, while large number of medium sized trees decreased the diversity of this organism group. On this basis, tree selection management, which is traditionally applied by local farmers in this region, can maintain more optimal conditions for epiphytic bryophytes, than the shelterwood management of state forest companies. The latter management type decreases both tree species diversity and structural complexity of the stands.

## **Acknowledgements**

The authors thank Dóra Király, Gábor Lengyel, Zsuzsa Mag, Sára Márialigeti, István Mazál, Balázs Németh, Ildikó Pados, Flóra Tinya for field assistance and János Podani for useful comments on the manuscript. The study was supported by Hungarian Science Foundation (OTKA 68218, 79158). Péter Ódor is a grantee of the János Bolyai Scholarship.

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**Table 1**

Examined explanatory variables in stand level analyses. Minimum, maximum and mean values of the variables based on the 35 studied stands.

| <b>Explanatory variable</b>   | <b>Minimum</b> | <b>Maximum</b> | <b>Mean</b> |
|---|----------------|----------------|-------------|
| <b>Tree species composition</b>   |                |                |             |
| Tree species richness   | 2.0            | 10.0           | 5.6         |
| Tree species diversity (species-volume, Shannon-diversity)  | 0.19           | 1.95           | 0.92        |
| Relative volume of tree species (beech, hornbeam, oaks, Scotch pine, Norway spruce, mixing species)   | -              | -              | -           |
| <b>Stand structure</b>  |                |                |             |
| Mean DBH (cm)   | 13.6           | 40.6           | 26.3        |
| Coefficient of variation of DBH   | 0.17           | 0.98           | 0.49        |
| Density of all trees (stems/ha)   | 218            | 1318           | 591         |
| Sapling density (stems/ha)  | 0              | 4706           | 952         |
| Density of large trees (DBH>50 cm) (stems/ha)   | 0              | 56             | 17          |
| Timber volume (m <sup>3</sup> /ha)?   |                |                |             |
| Snag volume (m <sup>3</sup> /ha)  | 0              | 65             | 12          |
| Log volume (m <sup>3</sup> /ha)   | 1              | 36             | 11          |
| <b>Substratum types</b>   |                |                |             |
| Cover of dead wood (m <sup>2</sup> /ha)   | 79             | 730            | 261         |
| Cover of litter (m <sup>2</sup> /ha)  | 7815           | 9834           | 9367        |
| Cover of mineral soil (m <sup>2</sup> /ha)  | 9              | 472            | 147         |
| <b>Light conditions</b>   |                |                |             |
| Relative diffuse light (mean)   | 0.6            | 10.3           | 2.9         |
| Relative diffuse light (coefficient of variation)   | 0.12           | 1.23           | 0.51        |
| <b>Geographical position</b>  |                |                |             |
| Geographical coordinates of longitude   | -              | -              | -           |
| Geographical coordinates of latitude  | -              | -              | -           |
| <b>Landscape variables</b>  |                |                |             |
| Proportion of landcover types in the surroundings (radius=300 m) of the plots (old beech, oak, Scotch pine, Norway spruce and mixed forests, young forests, non-forested areas) | -              | -              | -           |
| Diversity of landcover types (Area of landcover types, Shannon diversity)   | 0.11           | 1.86           | 1.11        |
| <b>Management history</b>   |                |                |             |
| Proportion of management types in the surroundings of plots (radius=300 m) in 1853 (forest, meadow, arable land)  | -              | -              | -           |
| Management type of the plots in 1853 (forest, meadow, arable land)  | -              | -              | -           |

**Table 2**

Significant explanatory variables of the redundancy analysis at the stand level. 38.8% of the total variance was explained. Variance %: percentage of the explained variance by the explanatory factors within the RDA. (Test: F-statistics; \*:  $p < 0.05$ , \*\*:  $p < 0.01$ , \*\*\*:  $p < 0.001$ .)

| Explanatory variables  | Variance % | F-value, significance |
|------------------------|------------|-----------------------|
| Relative oak volume    | 13.6       | 5.19***               |
| All trees density      | 8.8        | 3.62***               |
| Sapling density        | 7.6        | 3.35***               |
| Light average          | 5.1        | 2.34**                |
| Tree species diversity | 4.0        | 1.91*                 |

**Table 3**

Significant explanatory variables in the stand level regression models.  $R^2$ : adjusted coefficient of determination, it showed the explained proportion of total variance by the model. Estimate: the parameter of the variable in the regression equation. Variance %: percentage of the explained variance by the explanatory factor within the model. For the estimation of the significance of the variables and the models F-statistics were used. \*:  $p < 0.05$ , \*\*:  $p < 0.01$ , \*\*\*:  $p < 0.001$ .

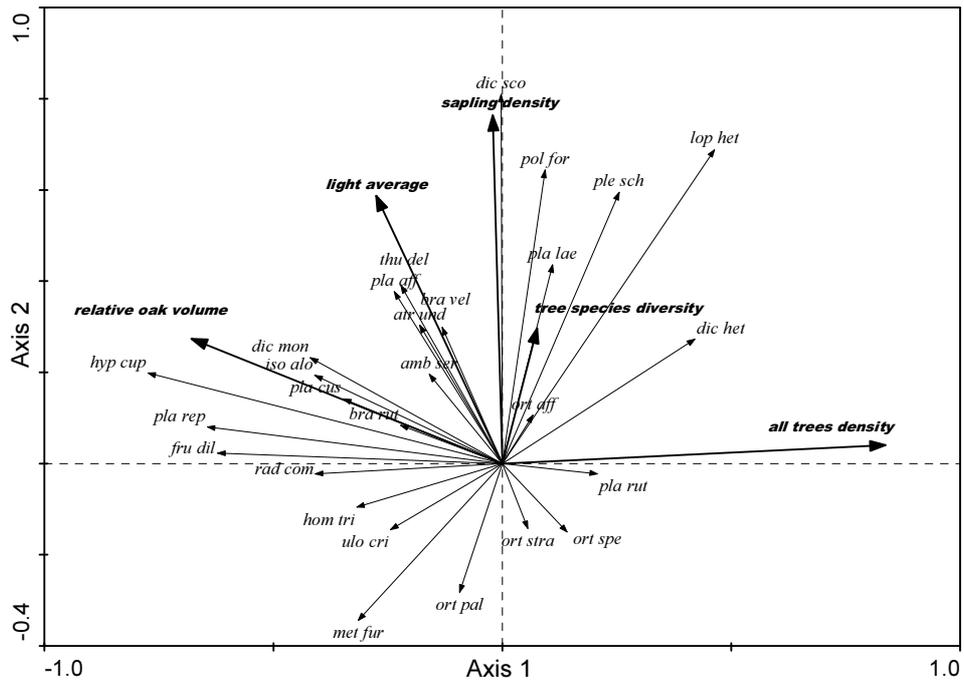
| Explanatory variables                                  | Estimate | Variance % | F-values, significance |
|--|----------|------------|------------------------|
| Cover of bryophytes; $R^2=0.706$                       |          |            |                        |
| Relative oak volume                                    | +67.128  | 65.0       | 75.45***               |
| All trees density                                      | -25.281  | 7.4        | 8.54**                 |
| Species richness of bryophytes; $R^2=0.516$            |          |            |                        |
| Sapling density  | +2.378   | 22.9       | 16.06***               |
| Tree species diversity                                 | +1.820   | 18.1       | 12.70**                |
| All trees density                                      | -1.927   | 15.0       | 10.54**                |
| Species richness of specialist epiphytes; $R^2=0.354$  |          |            |                        |
| Scotch pine relative volume                            | -0.599   | 26.3       | 13.60***               |
| All trees density                                      | -1.095   | 11.8       | 6.09*                  |
| Species richness of facultative epiphytes; $R^2=0.513$ |          |            |                        |
| Sapling density  | +0.272   | 28.9       | 20.23***               |
| Tree species diversity                                 | +0.213   | 25.3       | 17.66***               |

**Table 4**

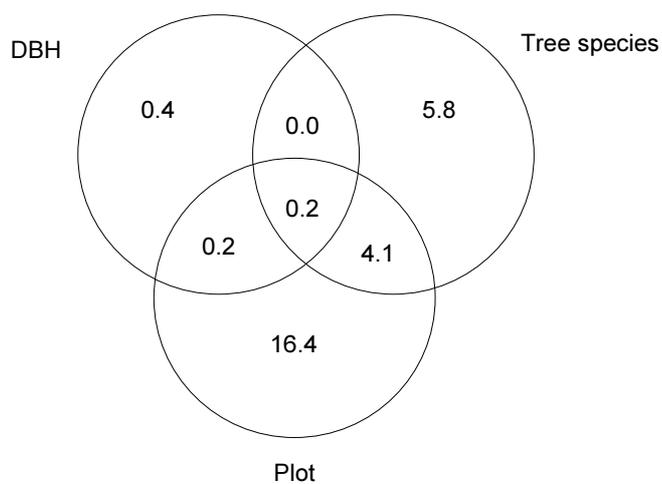
Mixed effect regression models for tree level bryophyte cover and species richness as dependent variables; tree species, diameter at breast height (DBH) and their interaction as fixed factors; and plot as random factor. The effect of the factors was tested by maximum likelihood ratio method using the Chi<sup>2</sup> distribution for the estimation of significance. \*\*\*: p<0.001; df: degrees of freedom.

|                                | Log ratio | df | p   |
|--------------------------------|-----------|----|-----|
| Cover of bryophytes            |           |    |     |
| fixed factors                  | 1228.2    | 9  | *** |
| tree species                   | 1201.5    | 4  | *** |
| DBH                            | 17.0      | 1  | *** |
| interaction                    | 19.8      | 4  | *** |
| random factor                  |           |    |     |
| plot                           | 205.9     | 1  | *** |
| Species richness of bryophytes |           |    |     |
| fixed factors                  | 392.1     | 9  | *** |
| tree species                   | 342.3     | 4  | *** |
| DBH                            | 32.7      | 1  | *** |
| interaction                    | 19.6      | 4  | *** |
| random factor                  |           |    |     |
| plot                           | 281.3     | 1  | *** |

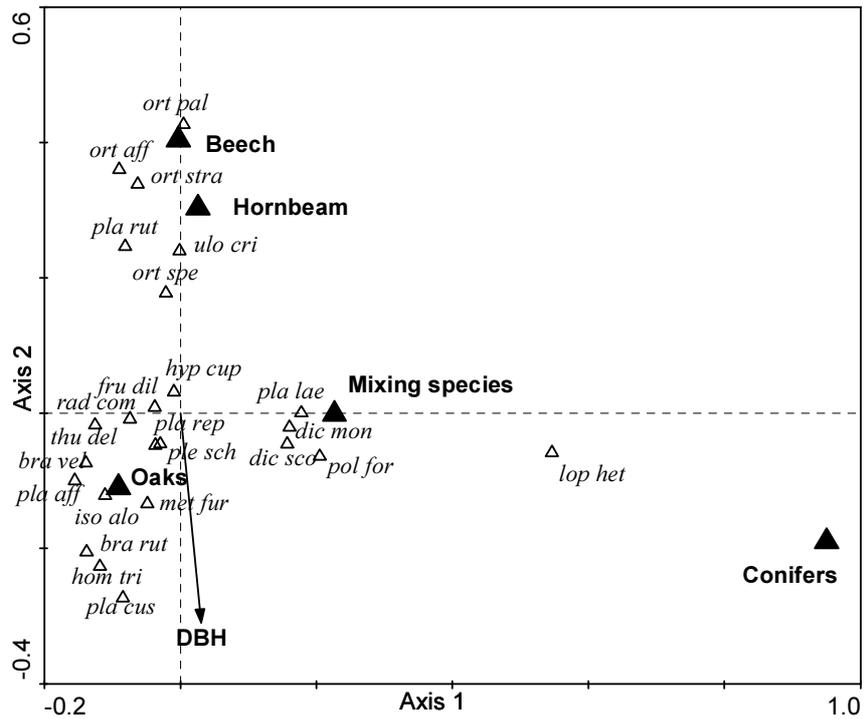
**Fig. 1.** Redundancy analysis of species composition at the stand level, the first and second axes are indicated. Explained variance of the canonical axes was 39.1% (first 17.1%, second 10.7%). Codes of bryophyte species consist of the first three letters of the genus and the species names (see electronic supplement). For explanatory variables, see Table 1.



**Fig. 2.** Result of variation partitioning at the tree level explanatory variables. 27.1% of the total variance was explained (canonical correspondence analysis; Test: F-statistics  $F=4.20$ ;  $p<0.001$ ). Numbers on figure mean the percentage of the explained variance by the explanatory variables and their interactions. DBH: diameter at breast height.



**Fig. 3.** Canonical correspondence analysis of species at the tree level. Tree species (as a factor of five levels) and DBH (diameter at breast height) were applied as explanatory variables and plots as covariables. Explained variance of the model was 6.2% (first axis 3.4%, second 1.8%). Codes of bryophyte species consist of the first three letters of the genus and the species names (see electronic supplement).



**Fig. 4.** Model estimation of tree level bryophyte cover (a) and species richness (b) depending on diameter at breast height (DBH as X axis) and tree species (marked by different lines and letters). C: conifers (including Scotch pine and Norway spruce), B: beech, H: hornbeam, M: other mixing tree species, O: oaks (including sessile and pedunculate oak).

