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Title: Factors influencing epiphytic bryophyte and lichen species richness at different spatial scales in managed temperate forests

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Abstract

The effect of management related factors on species richness of epiphytic bryophytes and lichens was studied in managed deciduous-coniferous mixed forests in Western-Hungary. At the stand level, the potential explanatory variables were tree species composition, stand structure, microclimate and light conditions, landscape and historical variables; while at tree level host tree species, tree size and light were studied.

Species richness of the two epiphyte groups was positively correlated. Both for lichen and bryophyte plot level richness, the composition and diversity of tree species and the abundance of shrub layer were the most influential positive factors. Besides, for bryophytes the presence of large trees, while for lichens amount and heterogeneity of light were important. Tree level richness was mainly determined by host tree species for both groups. For bryophytes oaks, while for lichens oaks and hornbeam turned out the most favourable hosts. Tree size generally increased tree level species richness, except on pine for bryophytes and on hornbeam for lichens.

The key variables for epiphytic diversity of the region were directly influenced by recent forest management; historical and landscape variables were not influential. Forest management oriented to the conservation of epiphytes should focus on: (i) the maintenance of tree species diversity in mixed stands; (ii) increment the proportion of deciduous trees (mainly oaks); (iii) conserving large trees within the stands; (iv) providing the presence of shrub and regeneration layer; (v) creating heterogeneous light conditions. For these purposes tree selection and selective cutting management seem more appropriate than shelterwood system.

Keywords: stand structure, tree size, host preference, microclimate, light, diversity.

Abbreviations:

DBH	Diameter at breast height
SD	Standard deviation

Introduction

Forest management considerably influences the diversity and composition of forest dwelling organisms (Bengtsson et al. 2000; Paillet et al. 2010; Peterken 1996) by a direct control on many stand scale conditions such as tree species composition, size distribution of trees, vertical structure, canopy closure, microclimate, dead wood availability and forest continuity. Many studies across different management regimes proved that epiphytic bryophytes and lichens are among the most sensitive components of the forest biota to management induced effects (Aude and Poulsen 2000; Bardat and Aubert 2007; Berg et al. 2002; Nascimbene et al. 2007; Rose 1992; Vanderpoorten et al. 2004). Epiphytic species directly exploit trees as living habitat and therefore tree species composition of stands considerably determines the epiphytic assemblages (McGee and Kimmerer 2002). Many species have preferences to host trees, characterized by different physical and chemical bark conditions (Barkman 1958; Jüriado et al. 2009). More optimal bark conditions of broad-leaved trees (e.g. aspen) explain their importance in the epiphytic diversity of boreal forests (Kuusinen and Penttinen 1999). Tree size and age are also crucial stand level factors for epiphytic diversity (Fritz et al. 2008a; Lie et al. 2009). Over-mature trees host more diverse epiphyte assemblages and many species are significantly associated to them (McGee and Kimmerer 2002; Nascimbene et al. 2009a). Beside the simple area effect, this pattern is also explained by higher habitat (bark) diversity of old trees (Barkman 1958), and by the elongated colonization time, which is crucial for dispersal limited species (Fritz et al. 2008a). During the ageing of trees a directional compositional change (succession) is observed in epiphytic vegetation, which is influenced by deterministic (e.g. changing bark conditions) and stochastic factors (Barkman 1958, Peck and Frehlich 2008). The third important group of stand level variables influenced by management are microclimate (air humidity and temperature) and light conditions, which can considerably modify the host and size related effects (Hauck and Javkhlan 2008; Mazimpaka et al. 2010; Ranius et al. 2008).

However, on coarser spatial and temporal scales, other drivers are crucial in the composition of epiphytic communities, as macro-climatic conditions (Bates et al. 2004; Marini et al. 2011), elevation (Berryman and McCune 2006), landscape level forest continuity (Snäll et al. 2004) and historical factors (Berg et al. 2002; Rose 1992). Unfortunately, the separation of the importance of different factors acting at different spatial levels is not obvious, because most studies focused on one definite spatial scale (as tree, stand, landscape or continent related factors).

Despite the fact that epiphytic bryophytes and lichens occupy the same physical space, interact each other and are potentially limited by the same environmental conditions, only few studies compared their environmental limitations and interactions. Beside the many similarities (host preference, tree size and age effects, fragmentation effects), lichen assemblages are supposed to be more limited by light and less sensitive to desiccation than bryophytes (Gustafsson and Eriksson 1995; Ranius et al. 2008).

This study investigated the influence of potential environmental factors on epiphytic bryophyte and lichen species richness at different spatial scales (stand and tree level) in managed Central-European mixed forests. At stand level, tree species composition, stand structure, light and microclimate conditions, landscape characteristics and management history, while at tree level host species, tree size and light conditions were tested as potential explanatory variables. At stand level, specialist epiphytic bryophytes and forest specialist lichens were distinguished as functional groups. Beside the general exploration of the relationships between environmental factors and epiphyte richness, this study aimed at improving forest biodiversity conservation of the studied region.

Material and methods

Study area

The study area is in Őrség National Park (N 46°51'-55' and W 16°07'-23') at the westernmost part of Hungary (Fig. 1). The annual mean temperature is 9.0–9.5 °C, the precipitation is 700-800 mm. The elevation is between 250-350 m, the landscape is divided into hills and wide valleys (Dövényi 2010). The bedrock consists of alluviated gravel and loess. On hills, the most common soil types are pseudogleyic and lessivage brown forest soils, while in valleys mire and meadow soils with an acidic upper layer can be found. The soil of forests is acidic and nutrient poor (0-30 cm, pH 4.3, carbon 3.09%, nitrogen 0.12%, A. Bidló pers. comm.).

The vegetation 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 mixing tree species (*Betula pendula* Roth., *Populus tremula* L., *Castanea sativa* Mill., *Prunus avium* L., etc.) is relatively high (Tímár et al. 2002).

Most of the original forests of the region were cut in the middle ages and in the secondary stands the proportion of pioneer tree species (such as *Pinus sylvestris* and *Betula pendula*) and the cover of acidofrequent herbs, bryophytes and lichens increased. Special cultivation forms as ridging on arable lands and litter collection in forests contributed to the leaching and acidification of the soil. The landscape is still determined by historical processes, however, the traditional cultivation forms are given up, and this leaded to the increase of deciduous trees and mesophytic herbs in forests. Nowadays, the largest part of the Őrség National Park (as all National Parks in Hungary) is managed harmonizing timber production and conservation purposes. In private forests spontaneous stem selection system resulting in uneven aged stands, while in state forests shelterwood silvicultural system with a rotation period of 70–110 years are applied (Tímár et al. 2002).

Data collection

Thirty-five stands were selected by stratified random sampling from the database of the Hungarian National Forest Service (Fig. 1). Preliminary inclusion 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). Because we wanted to represent the characteristic tree species combinations of the region the compartments of the database were grouped according to tree species combination types and the studied plots were randomly selected within the groups.

Within each stand, a 40 m x 40 m plot was pointed out for stand structural measurements. Geographical position, circumference, species identity, height, height of crown base and crown projection were measured of each tree with DBH (diameter at breast height) larger than 5 cm. Average diameter and length of logs thicker than 5 cm diameter and longer than 0.5 m were recorded. Density of sapling species (tree or shrub individuals taller than 0.5 m and thinner than 5 cm DBH) was recorded. Relative light conditions (percentage of above canopy total light) was modelled in 36 systematically arranged points at 1.3 m height by tRAYcy model (Brunner 1998) using tree position and size data (Tinya et al. 2009a). For tree level analyses, the light conditions in the position of each tree individuals were modelled also by the tRAYcy model predicting relative light values for the position of trees at 1.0 m height. 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). As landscape variables, proportion of forests (stand age older than 20 yr), clearcuts (stand age younger than 20 yr) and non-forested areas (settlements, meadows, arable lands) was estimated around the plots within a circle with 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 was registered (as binary variable) 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 occurrence of bryophyte and lichen species was recorded in every living tree with minimum 20 cm DBH from the base to 1.5 m height. The nomenclature followed Hill et al. (2006) for mosses, Grolle and Long (2000) for liverworts and Nimis and Martellos (2003) for lichens.

Data analyses

At stand level, general linear regression models were built to explore relationships between epiphyte richness and potential explanatory variables (Faraway 2005). As response variables we considered the total number of species of both bryophytes and lichens and the species richness of two functional groups: one including specialist epiphytic bryophytes (Orbán and Vajda 1983; Smith 2004) and one including lichens mainly related to forest habitats (forest specialists) according to their ecological requirements (Nimis and Martellos 2008). Saxicolous bryophytes were ranked among specialist epiphytes, because rocks lack in the region, and saxicolous species occur exclusively on trees (Online Resource Table 2).

The measured and derived explanatory variables are listed in Table 1. The proportion of tree species was expressed based on their volumes. Volumes of trees were calculated by species specific equations from DBH and height variables (Sopp and Kolozs 2000). *Quercus petraea*, *Q. robur* and *Q. cerris* L. were merged as oaks, rare tree species were merged as mixing trees. Tree species diversity was expressed by Shannon index with natural logarithm based on the relative volume of species (Shannon and Weaver 1949). Diversity of landscape elements was calculated in the same way. Plot level light conditions were expressed as the mean and standard deviation of relative light using the 36 measurements. Because these two variables were strongly correlated, a linear regression was used between standard deviation as dependent and mean as explanatory variables. The residuals of standard deviation were used during the modelling as descriptor of light heterogeneity independent from the mean. 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. Some explanatory variables (proportion of tree species, light variables) were ln transformed before the analysis. All variables were standardized (zero mean, one standard deviation).

Before modelling, preliminary selection and data exploration were performed. The dependent variables satisfied the normality condition and were not transformed. Pairwise correlation analyses and graphical explorations were carried out between the dependent variables and potential explanatory variables. Inter-correlations among explanatory variables were also checked. Only those explanatory variables were included to linear model selection that significantly correlated with the dependent variables, had homogenous scatter plots with it, and their inter-correlations with other explanatory variables were low (the absolute values of the correlation coefficients were lower than 0.35). After the preliminary selection, 5-8 explanatory variables got into the selection procedure of regression models. The minimal adequate model was built with backward elimination using deviance analysis with F-test (ANOVA). Second order interactions were also considered. After modelling, the normality and variance homogeneity of residuals were checked.

At tree level, species richness of bryophytes and lichens were analyzed by general linear mixed models (Zuur et al. 2009). The dependent variables were ln transformed. The fixed effects were tree species (beech, pine, hornbeam, oak, mixing species), DBH and tree level relative light; plot was applied as random factor. Full models included all interaction terms. Fixed effect selection was made by maximum likelihood method; random effect was tested by restricted maximum likelihood method (Faraway 2006).

In all the models, trees without lichens or bryophytes were also included. Data analyses were carried out by R 2.14.0 (The R Development Core Team 2011) and by the R package “nlme” (Pinheiro et al. 2011).

Results

Stand level analyses

Sixty bryophyte and forty-four lichen species were recorded in 35 plots on 971 trees (Online Resource). From the 971 studied tree individuals 225 were beech, 344 pine, 324 oak, 56 hornbeam and 22 mixing tree species. 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. Bryophyte and lichen richness were significantly positively correlated to each other (r=0.39, p=0.019, df=34). Twenty-five specialist epiphytic bryophytes (the mean was 6.7±2.5 (SD), the range was 1-11) and twenty forest specialist lichens (the mean was 5.2±2.2 (SD), the range was 2-11) were found. The correlation between the species richness of specialist epiphytic bryophytes and forest specialist lichens was not significant (r=0.08, p=0.627, df=34).

Considering the regression models (Table 2), for bryophyte species richness stand structure was determinant: shrub density and tree species diversity were the most important positive factors, while tree density with a negative effect and big trees with a positive one were far less important; the model explained 54% of the total variance. These variables significantly correlated with bryophyte species richness, the absolute values of correlation coefficients were higher than 0.4 (Fig. 2). Air humidity was also significantly correlated with bryophyte species richness (Fig. 2, r=0.42), however, it was excluded during the model selection. As an alternative model air humidity could be used instead of shrub density, the two variables were slightly inter-correlated (r=0.36, p=0.034). Because of higher R^2 and better model diagnostics, shrub density was used in the final model. For lichens, the proportion of oaks and shrub density were the most determinant factors accounting for 50% of the total variance (Table 2). The interaction between these two factors had a negative influence in the model, so the positive effect of shrub layer was less important in oak dominated stands than in other stand types. High temperature range and the amount and heterogeneity of light also increased lichen species richness. The model had high predictive power, R^2 was 0.68.

The visual interpretation of these relationships showed, that shrub density was a key variable for the species richness of both organism groups (Fig. 2). However, for other variables their responses were different: for epiphytic bryophytes big tree density, tree species diversity and air humidity had higher importance, for lichens oak proportion and light were more determinant (Fig. 2). In the model for specialist bryophytes, mean DBH was the most determinant variable, pine proportion had a negative effect, but the positive effect of DBH was more pronounced in pine dominated stands than in other stand types (positive interaction, Table 2). The model explained 41% of the total variance. Forest specialist lichens were positively determined by the amount and heterogeneity of light and tree species diversity (the model explained 45% of the total variance). Generally, the R^2 of the models for specialist groups were lower than for general species richness.

Tree level analyses

Mean tree level species richness was 2.9±2.1 (SD) for bryophytes and 2.2±1.5 (SD) for lichens. For bryophytes oak, for lichens oak and hornbeam were the most species rich hosts (Fig. 3). Correlation between tree level species richness of bryophytes and lichens was 0.34 ($p<0.001$).

Tree species was the most determinant factor for both bryophytes and lichens (Table 3, Fig. 4). The effect of plot (random factor) was also considerable in both cases. The amount of light and DBH had a quite strong effect for lichens, while in case of bryophytes they were far less important (Table 3). The highest bryophyte species richness was predicted for oaks (between 3 and 5), the lowest (hardly more than 1) for pine (Fig. 4). Tree size effect was strong on every broad-leaved species (the most important on hornbeam), while on conifers size effect was not found. Light effect was strong on beech and mixing tree species, while bryophyte species richness on oak, pine and hornbeam was independent from light conditions. For lichens, hornbeam was the species-richest tree, however contrary to other tree species, its richness was not influenced by tree size and light.

Discussion

In our managed forests epiphytic bryophyte and lichen richness are influenced by similar environmental factors mainly related to tree species composition, stand structure and microclimate. However, while tree species composition is strongly influential for both groups, bryophytes proved to be more sensitive than lichens to forest structure and air humidity and lichens were more to light conditions sensitive than bryophytes. Historical and landscape factors were not influential.

Tree species composition and host tree species

The positive correspondence between the diversity of trees and epiphytes is a general phenomenon in the forests of the temperate zone (McGee and Kimmerer 2002; Nascimbene et al. 2009b). In our stands, tree species diversity greatly improved epiphyte richness. Deciduous trees are generally species richer than coniferous and their presence in conifer dominated stands is a key factor for epiphyte richness (Cleavitt et al. 2009; Gustafsson and Eriksson 1995; Kuusinen and Penttinen 1999).

This result is also corroborated by tree level analyses that emphasize the importance of tree species reflecting the strong host preference of epiphytes (Berg et al. 2002; Király and Ódor 2010; Slack 1976; Szövényi et al. 2004). Host preference is driven by bark texture, chemistry, water and nutrient supply of different tree species (Barkman 1958; Hauk and Javkhlan 2008). The mesotrophic, wrinkle-rich bark of oaks provides wind-proof, moist microhabitats suitable for both epiphyte groups. On this tree species, bryophytes may establish huge populations with high cover values that are often overgrown by large lobed foliose lichens. Epiphytes on the smoother bark of beech and hornbeam are more exposed to hardships of environment (e.g.

stemflows, sun exposure, desiccating winds). However, it is noteworthy that hornbeam is relevant for lichen richness, mainly hosting crustose species that may be favoured because of the lack of competition with bryophytes and foliose lichens (Ranius et al. 2008). Conifers (especially pine) are colonized only by a few species. The bark of pine is very acidic, and its loose flaked surface hinders the establishment and growth of epiphytes. Moreover, pine minimizes the lead of rainwater to the trunk creating very dry conditions unsuitable for bryophytes and lichens (Barkman 1958).

Stand structure and tree size

In general, both bryophytes and lichens are sensitive to stand structure and tree size (Fritz et al. 2008a; McGee and Kimmerer 2002). However, in our study this group of environmental factors was relevant especially for bryophytes, while it had a weaker effect on lichens. In particular, the positive effect of the shrub layer for bryophytes can be explained in term of local humidity (Gustafsson and Eriksson 1995; Ranius et al. 2008), providing shaded conditions that protect bryophytes from wind and desiccation (Thomas et al. 2001). This factor positively influences also lichen richness, although lichen diversity was not clearly related to air humidity. The importance of the shrub layer for lichens is higher under less favourable situations where it may mitigate the dryer condition of the bark. Where light is not a limiting factor the positive effect of the shrub layer may override the potential negative effect of shading (Aude and Poulsen 2000).

Density of big trees was also a significant explanatory variable for bryophyte species richness. Large trees with cracked, decayed bark and deeper bark fissures have a variety of microhabitats, and provide longer colonization and successional time for dispersal limited species (Fritz et al. 2008a; Lie et al. 2009). Moreover, large over-mature trees can create a temporal bridge between the tree generations before and after forest harvest providing the stands with the survived, local source populations of epiphyte species (Moe and Botnen 1997; Rose 1992). However, large, over-mature trees are very rare in the forests of the region (they are practically missing from our dataset), which is probably a major limiting factor of the regional epiphytic diversity. This can also be the explanation that on tree level the effect of tree size was relatively low. However, the effect of tree size is specific to the studied organism groups and hosts. For bryophytes the bark of pine is unfavourable independently from the size of the trees. Hornbeam has a particular assemblage of preferential lichen species, which can occur with similar probability on small as well as on large trees.

Microclimate and light

Microclimate conditions and the amount and heterogeneity of light had considerable importance for lichens, while these factors did not directly influenced the diversity of bryophytes, although shrub layer was correlated with air humidity. In the studied forests terricolous bryophyte species show positive correlations with light, but epiphytes and epixylic species are independent from it (Tinya et al. 2009b). For forest lichens, the heterogeneity of light conditions has the same importance as tree species diversity. The stronger light demand of lichens compared to bryophytes is supported by many studies (Gustafsson and Eriksson 1995; Humphrey et al. 2002). The higher light demand and better desiccation tolerance of lichens is the reason that single, veteran trees as remnants of grazed forests or forested meadows are more important for the conservation of lichens than for bryophytes (Löhmus and Löhmus 2011; Moe and Botnen 1997; Rose 1992). In our study, a mosaic of sunny and shady patches provides enough light for lichens and concurrently they avoid desiccation.

Historical and landscape-scaled factors

Many studies emphasized the importance of historical factors in the diversity of epiphytes. The continuity of the forest stands (Fritz et al. 2008b; Rose 1992) and the permanent presence of over-mature individuals (Hazell and Gustafsson 1999; Moe and Botnen 1997) are crucial for the survival of sensitive and dispersal limited epiphytic species. Epiphytes, especially lichens, are very sensitive to the landscape pattern (fragmentation and isolation) of their potential habitat (Buckley 2011; Löbel et al. 2006a,b; Snäll et al. 2004). Neither historical nor landscape level factors influenced the species richness of epiphytes in this study. The forest cover in the near-by landscape of the plots (circle of 300 m radius) was high (89.8%, Table 1), and it was also relatively high in the end of 19th century (76.6%, Table 1). These values were much lower considering the whole studied region: 56% and 38%, respectively (Gyöngyössy 2008). The secondary stands of the region had been using by humans quite intensively for centuries, over-mature, large trees are very rare in the region. The species pool of the recent epiphyte assemblages mainly contains species adapted to these conditions, species sensitive to fragmentation and forest continuity probably disappeared in the historical past.

Conclusion

Our study suggests that tree species diversity and composition are key factors for the diversity of both epiphyte groups. Especially oaks hosts species rich assemblages, but for lichens hornbeam is also important, while the species richness on pine is very low. However, bryophytes are more influenced by stand structure of the managed forests (high shrub density, presence of large trees), while lichens are more sensitive to light conditions. Bryophytes prefer more humid, shaded forests, while for the current regional species pool of lichens more open conditions are optimal. Most predictors that were included in the models can be directly influenced by management. The main strategy of management focusing on epiphyte diversity should be the maintenance of tree species diversity in mixed stands, increment the proportion of deciduous trees (mainly oaks), conserving large trees within the stands, providing the presence of shrub and regeneration layer, creating heterogeneous light conditions. Even-aged forests with one-layered, closed canopy are adverse for epiphytes. Tree selection system and selective cutting would be the best management to achieve these conditions. Some studies support the usefulness of this management systems for epiphytes (Aude and Poulsen 2000; McGee and Kimmerer 2002), while some others question it preferring shelterwood management (Bardat and Aubert 2007). In forests maintained by shelterwood management system the retention of relatively large patches of older trees is important for the diversity of epiphytes (Hazell and Gustafsson 1999; Löhmus and Löhmus 2011). These patches will provide safe-sites for the survival of epiphytes and mitigate microclimate stress after harvest. In addition, extended rotation and regeneration periods may be applied in shelterwood management to improve the conditions for epiphytic bryophytes and lichens.

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Table 1 Explanatory variables of stand level analyses and their minimum, maximum and mean values based on the 35 studied plots (DBH: diameter at breast height; [1]: the values are the percentage of forests)

Explanatory variable	Minimum	Maximum	Mean
Tree species composition			
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, mixing species)	-	-	-
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)[1]	56.9	100.0	89.8
Diversity of landscape elements	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)	-	-	-

Table 2 Significant explanatory variables in the stand level regression models for species richness. R^2: adjusted coefficient of determination; estimate: the parameter of the variable in the regression equation; variance %: percentage of the explained variance by the explanatory variable within the model; F-statistics were used to estimate the significance of the variables and the models; df: degrees of freedom; significance levels are indicated by stars: *= p < 0.05; **= p < 0.01; *** = p < 0.001; DBH: diameter at breast height

Explanatory variables	Estimate	Variance %	F-values
Bryophytes R^2=0.54, F(4,30)=10.81***			
Shrub density	2.2432	23.43	17.16***
Tree species diversity	1.7725	18.35	13.44***
Tree density	-1.7202	10.52	7.71**
Big tree density	1.0029	6.74	4.94*
Lichens R^2=0.68, F(6,28)=13.06***			
Oak proportion	1.2341	20.05	21.32***
Shrub density	1.0348	19.98	21.25***
Temperature range difference	1.1628	13.1	17.66***
Oak proportion: shrub density	-1.3548	10.99	11.69**
Standard deviation of relative light	0.8006	6.95	7.39*
Mean relative light	1.0029	4.76	5.06*
Specialist bryophytes R^2=0.41, F(3,31)=9.02***			
Mean DBH	1.3174	26.05	26.05***
Pine proportion	-0.0791	8.46	8.46*
DBH: pine proportion	1.0984	12.10	12.10*
Forest specialist lichens R^2=0.45, F(3,31)=10.12***			
Standard deviation of relative light	1.0786	22.67	13.91***
Tree species diversity	1.0307	18.57	11.39**
Mean relative light	0.9593	8.23	5.05*

Table 3 Mixed effect regression models for tree level bryophyte and lichen species richness as dependent variables. Explanatory variables were tree species, DBH (diameter at breast height), relative light and their interactions as fixed factors; and plot as random factor. Fixed effect selection was made by maximum likelihood method (ML), random effect was tested by restricted maximum likelihood method (REML) using the Chi^2 distribution for the estimation of significance. For comparison the log.ratio (log-likelihood ratio) of the explanatory variables within fixed effect was explained as percentage. Significance levels were indicated by stars: *= $p < 0.05$; **= $p < 0.01$; ***= $p < 0.001$

	Log.ratio	
	Bryophytes	Lichens
Fixed effects	364.32*** (100%)	264.94*** (100%)
Tree species	295.94*** (81.2%)	169.18*** (63.9%)
DBH	22.86*** (6.3%)	47.37*** (17.9%)
Relative light	5.19* (1.4%)	60.96*** (23.0%)
Tree species: DBH	14.84** (4.1%)	12.39* (4.7%)
Tree: light	12.60* (3.5%)	9.15^{ns} (3.5%)
Random factor (plot)	347.46***	246.06***

Fig. 1 Geographical position of the studied area (a, grey rectangle) and the studied plots (b) represented by black dots, built-up areas are grey.

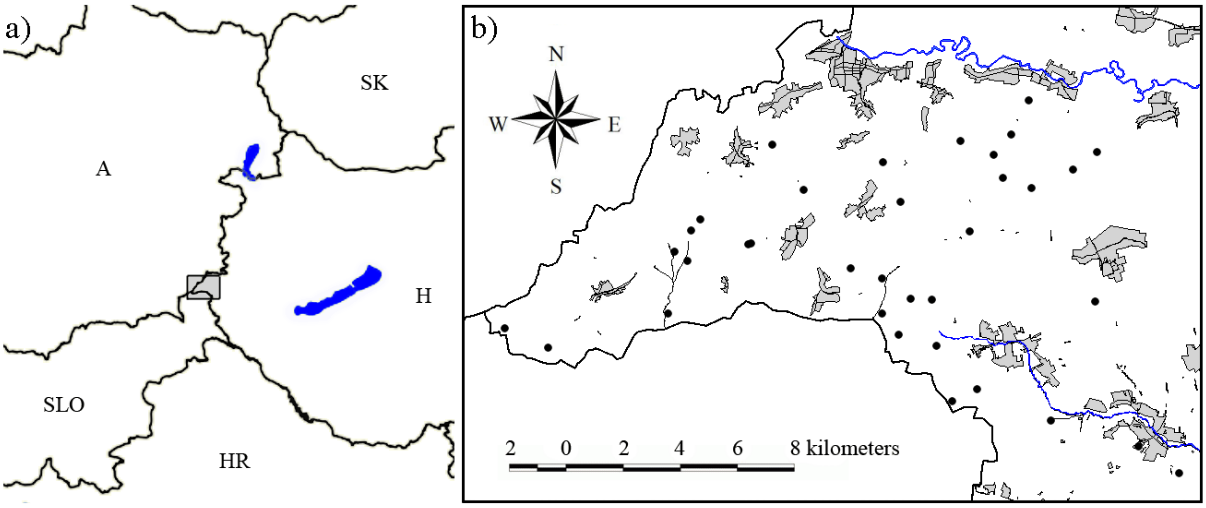

Fig. 2 Correlations of bryophyte (B) and lichen (L) species richness between some selected explanatory variables, indicated as columns. Vertical axes: species richness values; horizontal axes: standardized values of the explanatory variables. 'r=' represents the correlation coefficients (n=35); their significance is indicated by stars: ns= non-significant; *= p<0.05; **= p<0.01; ***= p<0.001

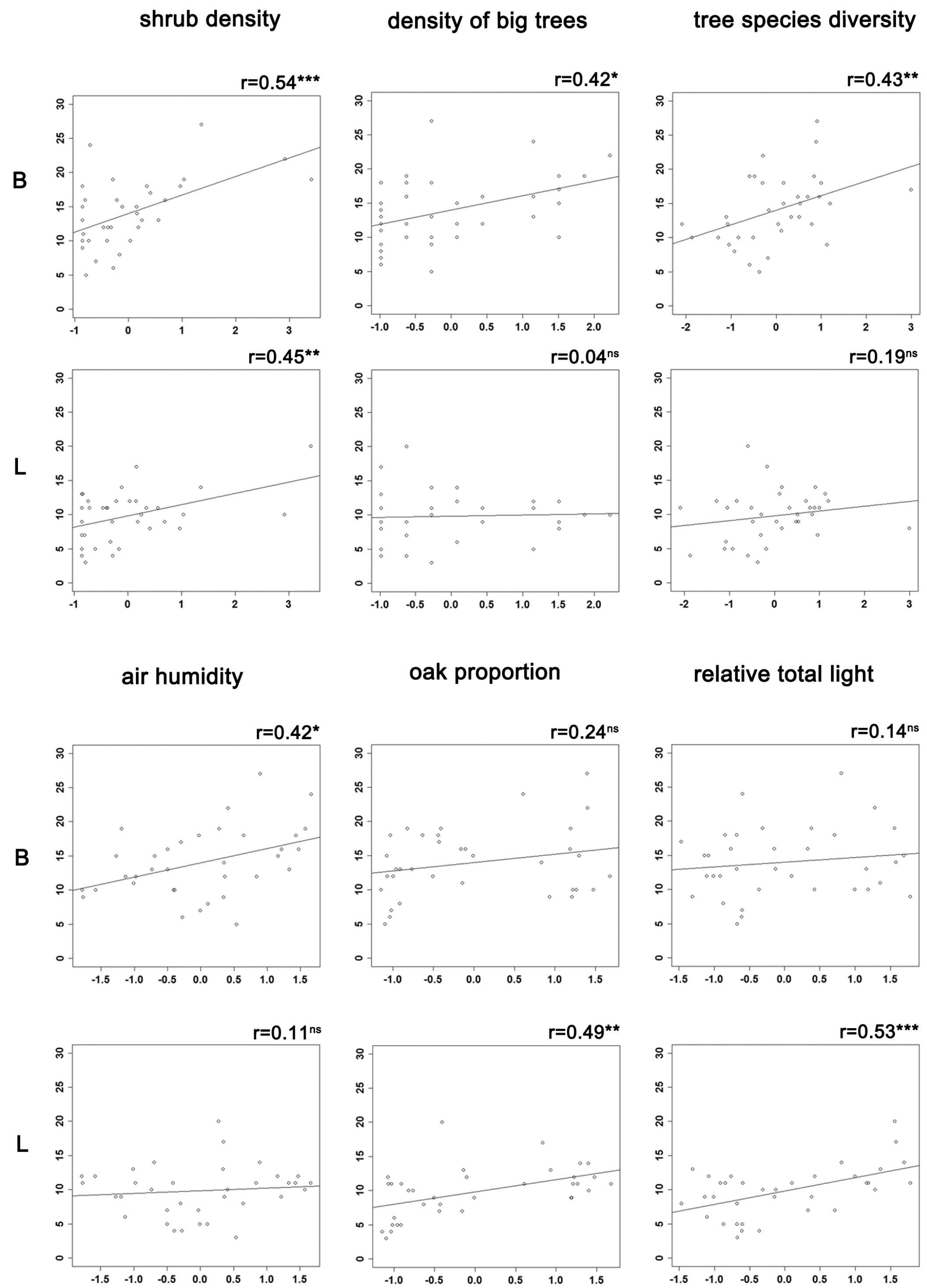

Fig. 3 Tree level species richness of bryophytes and lichens on different tree species. Points are the means, whiskers are the standard deviations. Solid lines are general means, dashed lines are general standard deviations

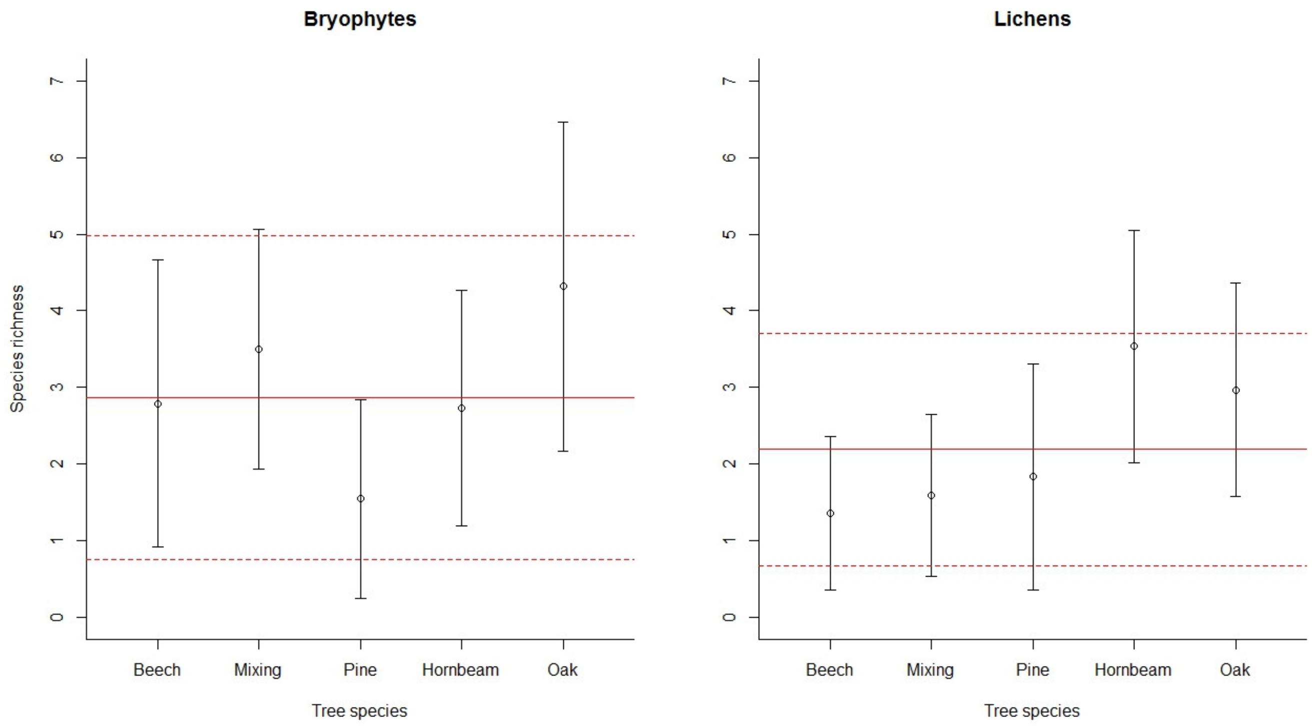

Fig. 4 Predicted tree level species richness values of bryophytes and lichens (in columns) using tree species, DBH (top figures) and relative light (bottom figures) as explanatory variables. For DBH effect light, for light effect DBH was fixed at their median values. Tree species are indicated by different line types and text. For hornbeam and mixing trees the range of diameter was lower than for other trees, because the abundance of larger individuals is low in the studied region