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Drivers of lichen species richness at multiple spatial scales in temperate forests

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Abstract

Background: Only few studies analysing lichen diversity have simultaneously considered interactions among drivers that operate at different spatial and temporal scales.

Aims: The aims of this study were to evaluate the relative importance of host tree, and local, landscape and historical factors in explaining lichen diversity in managed temperate forests, and to test the potential interactions among factors acting at different spatial scales.

Methods: Thirty-five stands were selected in the Órség region, western Hungary. Linear models and multi-model inference within an information-theory framework were used to evaluate the role of different variables on lichen species richness.

Results: Drivers at multiple spatial scales contributed to shaping lichen species richness both at the tree and plot levels. Tree level species richness was related to both tree and plot level factors. With increasing relative diffuse light lichen species richness increased; this effect was stronger on higher than on lower part of the trunks. At the plot-scale, species richness was affected by local drivers. Landscape and historical factors had no or only marginal effect.

Conclusions: Lichen conservation in temperate managed forests could be improved if the complex interactions among host tree quality and availability, micro-climatic conditions, and management were taken into consideration.

Key words: conservation; diffuse light; epiphytic lichens; forest management; historical factors; landscape

Introduction

Epiphytic lichens are affected by several environmental factors whose relative importance may depend on the scale of the analysis (Bowker et al. 2006; Will-Wolf et al. 2006; Ellis and Coppins 2009, 2010). Hence, to provide effective conservation strategies to improve lichen diversity the influence of different environmental and management-related factors needs to be evaluated at multiple spatial and temporal scales (Crawley and Harral 2001; Willis and Whittaker 2002). Studies that address the relationships between lichen diversity and forest structure and diversity usually consider three spatial scales: host tree, forest stand, and the surrounding landscape. However, few studies have simultaneously considered interactions between drivers operating at different scales. Similarly, the influence of historical processes has often been overlooked even if ecological continuity and past management are potentially relevant for explaining present patterns of lichen occurrence (e.g. Ranius et al. 2008b).

Tree host species and age are among the main factors that affect lichens (Uliczka and Angelstam 1999). Different tree species may host different lichen communities owing to differences in chemical and physical features of their bark (Jüriado et al. 2009). Crown structure may vary among tree species, providing different conditions for lichen establishment on the stems (Nascimbene et al. 2009b). Increasing tree age benefits lichens as a result of a combined effect of increased surface availability, and more stable substrate conditions (e.g. Edman et al. 2007; Lie et al. 2009; Nascimbene et al. 2009a), providing a longer colonisation time that may favour rare or dispersal limited species (Fritz et al. 2008a). Bark texture and pH also change with tree age and ameliorate conditions for lichen establishment (Gustafsson and Eriksson 1995; Ranius et al. 2008a; Fritz and Heilmann-Clausen 2010).

Host trees do not grow in isolation and bark habitat conditions are also affected by the forest stand structure which modifies light quality and availability, local microclimate, and propagule pressures. In managed forests, most of the ecological factors that affect lichens are related to forest management (e.g. Edman et al. 2007; Nascimbene et al. 2007). Therefore,

studies addressing the impact of forest management on epiphytic lichens have usually been designed at the local (stand)-level. The main factors at the stand level are related to forest age, occurrence of substrate types, and light conditions (e.g. Fritz et al. 2008b). Increasing diversity of tree species and amount of substrate are expected to positively affect lichen richness by increasing habitat heterogeneity and the associated available niches (Lõhmus et al. 2007; Moning et al. 2009; Nascimbene et al. 2009b). Light conditions also play a role in shaping lichen communities (Gustafsson and Eriksson 1995; Jairus et al. 2009). Most lichens of temperate forests have an optimum under intermediate light conditions, avoiding both direct solar radiation (Barkman 1958) and excessive shade (Aude and Poulsen 2000; Humphrey et al. 2002; Moning et al. 2009).

Finally, the importance of the landscape context to local lichen community dynamics is increasingly considered for setting science-based criteria for lichen conservation (Dettki and Esseen 1998; Hedenås and Ericson 2008; Paltto et al. 2010). The landscape context influences large-scale regional processes of lichen metapopulations especially in fragmented and dynamic landscapes, such as managed forests (Caruso et al 2010). In fragmented habitats, local species persistence is the result of extinction-colonisation dynamics which are influenced by the availability of propagules in the surrounding landscape and by habitat connectivity (Scheidegger and Werth 2009). These complex regional dynamics may also depend on past management, since there could be a time delay between the response of organisms and the time elapsed since habitat perturbation (Snäll 2004; Ellis and Coppins 2007; Ranius et al. 2008b; Kussaari et al. 2009). This process is summarised in the concept of ‘extinction debt’, i.e. species may exhibit a time-delayed extinction after habitat perturbation. As lichens are long-lived organisms and have usually long generation times, they are expected to be subjected to this ‘extinction debt’ (Kussaari et al. 2009).

Considering that epiphytic lichen diversity patterns in forests might be the result of several processes acting at different spatial and temporal scales, the aim of this study was to explore the relative importance of host tree characteristics, plot level factors, landscape and

history variables in explaining lichen species richness. Potential interactions between factors acting at different spatial scales were also tested.

We hypothesized that tree level lichen richness is influenced by both tree (e.g. tree species, tree size) and plot-level factors (e.g. light conditions) indicative of local environmental conditions experienced by lichens on the trunks. In this perspective, we assumed that these factors acting at different spatial scales may also interact, i.e. tree with different characteristics can support different lichen communities depending on the average forest stand conditions. Considering species richness at the local scale (i.e. whole stand), we hypothesized that the number of species could be influenced not only by local stand characteristics but also by large-scale processes such as dispersal. For this reason, we further tested the effect of current and historical landscape composition (e.g. tree species proportions in the surrounding of sampling plots) on local lichen communities. We hypothesized that forest continuity and large proportion of forest in the landscape should promote local lichen diversity.

Materials and methods

Study area

The study was carried out in the Órség National Park, western Hungary (46° 51' - 55' N and 16° 07' - 23' W, Figure 1). There is no industry in the region and only traditional, extensive agricultural practices are used. Due to the relatively small extent of the study area (ca. 44,000 ha) any effect of pollution was expected to be similar at the different sampling sites.

The elevation of the study area ranged between 250 and 350 m a.s.l. The mean annual temperature was 9.0-9.5 °C and precipitation 700-800 mm year⁻¹ (Dövényi 2010). The bedrock was alluvial gravel mixed with loess. On hills, the most common soil types were pseudogleyic and lessivage brown forest soils, whilst in valleys mire and meadow soils, the upper layer of which were acidic (pH 4.5-4.7; Szodfridt 1969).

Forests were dominated by beech (*Fagus sylvatica* L.), sessile and pedunculate oak (*Quercus petraea* (Matt.) Liebl. and *Q. robur* L.), hornbeam (*Carpinus betulus* L.), Scots pine

(*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karst.), which occur in both pure and mixed stands. A more detailed description of the studied stands can be found in Tinya et al. (2009) and Márialigeti et al (2009). Since the twelfth century, the area has been characterised by small-scale extensive farming, resulting in a shifting mosaic of arable land, coppice and meadows. Currently, forests cover a large part of the hills of this region, resulting in a continuous forested landscape. State-owned forests are managed by using a shelter wood system with a rotation period of 70-110 years, while in private forests selective logging is used.

Sampling design and data collection

Thirty-five forest stands were selected from the stand structure database of the Forest Management Directorate of the Hungarian Central Agricultural Office by stratified random sampling representing different combinations of the main tree species (pine, oak, hornbeam, beech). Further criteria of site selection included dominant trees older than 70 years, avoiding slopes, absence of ground-water influence. The minimum distance between the stands was 500 m).

We measured various environmental factors at three spatial scales (Figure 2). At the tree scale, circumference and tree species identity of each tree with a diameter at breast height (DBH) > 5 cm were recorded. At the local stand scale, structural variables were measured in 40 m x 40 m plots. The basal area of each plot was calculated and the density of saplings (tree or shrub individuals taller than 0.5 m and < 5 cm DBH) was recorded. Light conditions (photosynthetically active radiation) were measured at 36 points at 1-m height in a systematic design within the plots and on a nearby open field by a LAI-2000 Plant Canopy Analyzer (LICOR Inc. 1992; Tinya et al. 2009) and the mean value of relative diffuse light was calculated for each plot. At the landscape scale, the proportion of different land-cover types (old-growth 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) by using aerial photographs and forest authority data.

At the local and landscape scale, we estimated historical land use, based on the map of the Second Military Survey of the Habsburg Empire from 1853 (Arcanum 2006). At the local scale we retrieved information on the historical land use (forest, arable land, or meadow) of our sample plots. At the landscape level, we quantified the proportion of forest in 1853 around the plots (radius=300 m) (Table 1).

Lichen sampling

Epiphytic lichens were recorded in a 30 m x 30 m plot positioned in the middle of the 40 m x 40 m tree survey plot. In each plot, all live trees with DBH >20 cm were surveyed in two areas on the trunks: from the ground level up to a height of 50 cm, and from 50 cm up to 150 cm. For each position, the occurrence of lichen species was recorded around the whole tree. In further analyses we used as response variable both the number of lichen species per tree and the cumulative number of species per plot. In the 35 plots a total of 1052 trees were sampled. Sampling area differed between low and high position at the tree level and between different plots at the forest level due to the different number of trees. However, the inclusion of tree diameter and basal area as predictors did account for this different sampling effort at either scale of analyses (see below).

Environmental predictors

All of our environmental variables corresponded to ecologically meaningful predictors of lichen species richness patterns, acting at different spatial and temporal scales (Table 1). At the tree level, different tree species with different bark properties are expected to host different lichens. Tree DBH is known to be an important factor affecting lichen richness, which is expected to increase with tree size. Vertical position on the trunks may be important for lichens since it is likely to influence humidity and light conditions (Barkman, 1958; Fritz, 2009).

At the stand level, the Shannon diversity index of tree species is indicative of diversity of substrates available for lichen colonisation. Therefore, a high Shannon tree diversity value is

expected to increase lichen species richness within plots. Shannon diversity was based on the relative volume (log-transformed values) of different tree species (oak, beech, hornbeam, pine, spruce, and other tree species). As the proportion of each substrate may influence lichen colonisation, we also considered the relative volume of the main tree species (oak, pine, and beech) as a predictor. Shrub density (Shrubs) may influence the microclimate on the first metres of the trunks. Light conditions (Relative diffuse light) are important for photosynthetic organisms and lichens are expected to be disadvantaged by canopy closure that causes excessive darkness. Basal area (Basal), an indicator of both substrate amount and tree density, was calculated based on the measured trees (DBH > 5 cm). This parameter was correlated ($r = -0.59$, $P < 0.001$) with light.

At the landscape scale, we considered the proportion of the dominant host trees, hypothesising that this feature could influence lichen richness within plots by controlling propagule pressure. As the importance of forest continuity for lichens is acknowledged to benefit lichen diversity, we included the historical information on the presence of forest in our plots in 1853. Together with this parameter we also considered the proportion of forest in the surrounding of the plots in the same year.

Data analysis

Analysis at the tree scale. We used linear mixed models to test the tree and plot level predictors and their interactions on the number of lichen species at the tree level (number of species found on single trees). In these models we included local variables which are expected to shape the environmental conditions experienced by single trees within plots (basal area, relative diffuse light and shrub density). We did not include local variables related to forest composition and diversity (i.e. proportion of beech, spruce, and pine). We also included three ecologically meaningful interactions: an interaction between light and the sample position on the trunk, interaction between light and host-tree species, and an interaction between position and host tree

(Table 2). At this scale, we did not test the effect of landscape factors as these are expected to be more important for the whole community of lichens at the plot scale.

Analysis at the plot scale. We used linear models to test local, landscape and historical variables on the number of lichen species at the plot level (i.e. sum of all the species found on all the trees for each plot; Table 1). The plot level variables tested were: shrub density, basal area, relative diffuse light, relative volume of beech, oak, and pine. The landscape and historical variables tested were: proportion of beech, oak and pine, proportion of forest in the surroundings of plots in 1853, and continuity of local forest. The mixed model included tree identity and plot as random factors to account for the spatial nestedness of the sampling. In all the models residuals approximated a normal distribution. The log-transformed number of lichen species was used as response variable in all the models.

Multi-model inference

At both scales of analysis, we compared the fit of all the possible candidate models obtained by the combination of the predictors described above by using second-order Akaike's information criterion (AICc). The AICc is a measure of relative model fit, proportional to the likelihood of the model and the number of parameters used to generate it. The best fitting model is the one with the lowest AICc. In a set of n models each model i can be ranked by using its difference in AICc score with the best-fitting model ($\Delta AICc_i = AICc_i - AICc_{\text{minimum}}$). The difference in AICc values indicates the relative support for the different models. A model is usually considered plausible if its $\Delta AICc$ is below 2 (Burnham and Anderson 2002). For each model i we also calculated an Akaike's weight (w_i), which is the probability that model i would be selected as the best fitting model if the data were collected again under identical circumstances (Burnham and Anderson 2002). Akaike's weight should be interpreted as a measure of model selection uncertainty. The multi-model inference analyses were performed using the 'MuMIn' package (Barton 2010) implemented in the R (R Development Core Team 2011).

Results

Diversity of lichens

In the 35 plots 44 lichen species were recorded, including 21 crustose, 16 foliose, and seven fruticose species. Considering the position on the trees, 43 species were found between 50 and 150 cm, while 36 were found between 0-50 cm. The mean number of species per plot and per tree was 10.3 ± 4.9 (SD) and 5.6 ± 1.9 , respectively. The species mainly contained chlorococcoid green algae as photobiont (38 species) while six contained *Trentepohlia*. Twenty-nine species reproduced by vegetative propagules and 15 by spores. The species were mainly adapted to acidic-subacidic substrates, intermediate conditions of light and humidity, avoiding eutrophicated substrates. The most common species were (their frequencies are in brackets): *Lepraria* sp. (35 plots), *Phlyctis argena* (Spreng.) Flot. (33), *Cladonia coniocraea* (Flörke) Spreng. (28), *Dimerella pineti* (Ach.) Vezda (25), *Graphis scripta* (L.) Ach. (24), *Flavoparmelia caperata* (L.) Hale (18), *Melanelixia fuliginosa* (Duby) O. Blanco, A. Crespo, Divakar, Essl., D. Hawksw. & Lumbsch (17), *Hypocenomyce scalaris* (Ach.) M.Choisy (16), *Lecanora expallens* Ach. (15), *Chaenotheca ferruginea* (Sm.) Mig. (13), and *Hypogymnia physodes* (L.) Nyl (13). Eight species were found in only one plot.

Drivers at the tree scale

At the tree scale, we found support for only one plausible model (i.e. $\Delta AICc < 2$) that had a large model weight (Table 2). The model included several predictors at both the tree and plot scales explaining mean tree species richness on the trees. We found strong support for an effect of host tree, position on the trunk, DBH, and relative diffuse light. We found higher species richness on oak and hornbeam and lower on pine and beech. We also found strong support for an interaction between position on the trunk (low vs. high) and host tree (Figure 3), and between position on the trunk and light (Figure 4). In particular, on oak and hornbeam lichen diversity was higher on the higher part of the trunk, while on pine we found an opposite pattern, the

lower part being more diverse. On beech there was no substantial difference between the two positions (Figure 3). Increasing diffuse light benefited lichen diversity in both positions (Figure 4). However, lichen diversity was more enhanced by increasing diffuse light in the high than in the low position.

Drivers at the plot and landscape scales

At the plot scale, we found six plausible models explaining plot species richness, i.e. $\Delta\text{AICc} < 2$ (Table 3). The models mainly included the effect of the proportion of the main tree species, cover of shrubs, and light (Table 3). The cover of oak had a positive effect, while pine and beech had a negative effect on lichen richness. These models explained ca. 70% of the total variation in species richness at the plot level. No landscape or historical variables were included except for a weak negative effect of beech forests which was included in two plausible models.

Discussion

Our study provides clear evidence that drivers at multiple spatial scales contribute to shape lichen species richness on tree trunks both at the tree and local stand levels. A large body of literature supports the view that tree-level factors are fundamental for explaining lichen richness at the scale of single tree (e.g. Lie et al. 2009). However, our results support the idea that at this spatial scale local factors, indicative of environmental conditions, are also influential (see also Jürriado et al. 2009) and interact with tree-level factors.

The pattern of species richness at the tree level was mainly related to tree-level factors and one local factor. The most interesting result is associated with the interaction between tree and plot level factors. Probably, the main drivers underlying the observed pattern of species richness were host tree species and DBH which summarise physico-chemistry and microclimate associated with bark features, tree structure, and age. Amongst the broadleaf trees, oak and hornbeam hosted greater species richness than pine. While oak is a dominant species, hornbeam has a scattered distribution, forming a lower canopy layer under the main canopy provided by

oaks. Our results suggest that the occurrence of hornbeam within stands should be enhanced to promote higher lichen richness, although increasing their abundance may reduce economic value of the forests. Interestingly, DBH was a significant factor even though its range of variation was relatively small. This result suggests that a prolongation in the rotation period and/or the maintenance of large trees in the stand matrix would enhance lichen species richness (see also Dettki and Esseen 1998; Johansson 2008; Nascimbene et al. 2010).

The interaction between position on the trunk and relative diffuse light influenced lichen species richness, causing higher species richness at high than at low position on the trunk, likely because lichens may suffer from competition with bryophytes at the lower portions of the bole. The interaction between host tree and position on the trunk mostly reflected a contrasting response of lichen species richness between oak (and to a less extent hornbeam) and pine. This result may be related to differences both in bark properties and tree structure. The bark of oak and hornbeam constitutes a more stable substrate than the bark of pine. Moreover, while the sympodial structure of oak and hornbeam allows rainwater to flow along the branches to the trunk providing humid conditions adequate for lichen establishment, the monopodial structure of pine causes the intercepted rain fall mainly as drip water from the canopy to the ground, resulting in more dry conditions on the trunk (Nascimbene et al. 2009b).

Considering lichen richness at the plot-scale, we found support for the effect of local drivers related to both substrate type and microclimatic conditions, while in our system landscape and historical factors had no, or only marginal, importance. The relative proportion of the dominant tree species is a key factor for lichen richness which is enhanced by the presence of oak and lowered by pine or beech-dominated stands. Two factors, for which we found strong support in our models, are indicative of microclimatic conditions under the canopy: light availability, and the density of shrubs in the understory. Light conditions play a relevant role in shaping lichen communities, an excessive canopy closure being detrimental to many lichens in temperate forests (Humphrey et al. 2002; Moning et al. 2009). Our results indicated that in these dense forests light is a key limiting factor for lichens, although also excessive canopy openness

has been demonstrated to be detrimental for many species (Gauslaa and Solhaug 2000; Hedman et al. 2007; Jairus et al. 2009). Both excessive canopy closure and openness should be avoided, preferring harvesting strategies which allow maintaining intermediate light conditions (Jairus et al. 2009). This would avoid the negative effects of the shelterwood system which may lead to excessive shading in mature stands and to an abrupt exposure to light at the final harvest. The density of shrubs in the understory was positively associated with lichen species richness. A similar result was obtained for epiphytic bryophytes by Király and Ódor (2010), corroborating the hypothesis that shrubs benefit epiphytes creating a stable and humid microclimate, decreasing the effect of wind and desiccation (Aude and Poulsen 2000). Its positive effect on air humidity can override its potentially negative influence by decreasing light availability for epiphytes in the first metres of the trunks.

The influence of landscape and historical factors was not supported by our models except for a weak negative effect of the proportion of beech forest in the surrounding landscape. This result may be explained by the relatively high forest cover in the landscape, by large habitat connectivity, and by the fact that the most common tree species form a fine-grained mixture within stands. Despite the fact that the historical proportion of forest in the surrounding landscape was quite heterogeneous, several of them being bordered by arable lands, most of them (28 out of 35) were already forested in 1853. Landscape and historical factors are probably more relevant in fragmented landscapes where dispersal limitation of the species and metapopulation processes may influence their spatial distribution (Löbel et al. 2006; Snäll et al. 2003, 2004).

Since patterns of lichen richness within forests are influenced by drivers acting at different spatial scales, management practices should be tailored accordingly. While traditionally forest management acts at the stand-level, effective lichen conservation measures should be also planned at the tree-level. The retention of large trees and maintaining a mixture of different tree species are general criteria to be adopted in management and are already supported in conservation literature. However, our study indicates that the effect of stand

management can have different results depending on the host tree species and the position of the sampling area on the trunks. At the local stand scale, we suggest to increase the proportion of tree species that host the highest number of lichen species, i.e. oak and hornbeam in this case. In particular, the retention of scattered hornbeam trees forming a secondary canopy layer could be an effective strategy. In general, our study indicates that lichen conservation in temperate managed forests could be improved if species diversity is considered the result of complex interactions between host tree quality and availability, micro-climatic conditions, and management. The improvement of lichen richness by a more conservation-oriented management is desirable in protected areas where conservation issues should be prioritised. Increasing lichen richness may also benefit forest function since lichens play an important role in the forest water-cycle (Knops et al. 1996), nutrient cycling (Pike 1978), and are a crucial component in forest food-webs (e.g. Edwards et al. 1960; Flaherty et al. 2010; Gerson and Seaward 1977; Hayward and Rosentreter 1994; Petterson et al. 1995).

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References

Arcanum. 2006. Secondary Military Survey of the Habsburg Empire 1806-1869. DVD-room. Arcanum Kft., Budapest.

- Aude E, Poulsen RS. 2000. Influence of management on the species composition of epiphytic cryptogams in Danish *Fagus* forests. *Applied Vegetation Science* 3: 81–88.
- Barkman JJ. 1958. Phytosociology and ecology of cryptogamic epiphytes. Including a taxonomic survey and description of their vegetation units in Europe. Van Gorcum & Comp. N.V., Assen.
- Barton K. 2010. MuMIn: Multi-model inference R package version [01317].
- Bowker MA, Benlap J, Davison DW, Goldstein H. 2006. Correlates of biological soil crust abundance across a continuum of spatial scales: support for a hierarchical conceptual model. *Journal of Applied Ecology* 46: 152–163.
- Burnham KP, Anderson DR. 2002. Model selection and multimodel inference. A practical information–theoretic approach. Springer, Verlag, Berlin.
- Caruso A, Thor G, Snäll T. 2010. Colonization-extinction dynamics of epixylic lichens along a decay gradient in a dynamic landscape. *Oikos* 119: 1947–1953.
- Crawley M J, Harral J E. 2001. Scale Dependence in Plant Biodiversity. *Science* 291: 864–868.
- Dettki H, Esseen PA. 1998. Epiphytic macrolichens in managed and natural forest landscapes: a comparison at two spatial scales. *Ecography* 21: 613–624.
- Dövényi Z. 2010. Cadastre of Hungarian regions. MTA Földrajtudományi Intézet, Budapest (in Hungarian).
- Edman M, Eriksson AM, Villard MA. 2008. Effects of selection cutting on the abundance and fertility of indicator lichens *Lobaria pulmonaria* and *Lobaria quercizans*. *Journal of Applied Ecology* 45: 26–33.
- Edwards RY, Soos J, Ritcey RW. 1960. Quantitative observation on epidendric lichens used as food by caribou. *Ecology* 41: 425–431.
- Ellis CJ, Coppins BJ. 2007. 19th century woodland structure controls stand-scale epiphyte diversity in present-day Scotland. *Diversity and Distributions* 13: 84–91.

- Ellis CJ, Coppins BJ. 2009. Quantifying the role of multiple landscape-scale drivers controlling epiphyte composition and richness in a conservation priority habitat (juniper scrub). *Biological Conservation* 142: 1291–1301.
- Ellis CJ, Coppins BJ. 2010. Integrating multiple landscape-scale drivers in the lichen epiphyte response: climatic setting, pollution regime and woodland spatial-temporal structure. *Diversity and Distributions* 6: 43–52.
- Flaherty EA, Ben-David M, Smith WP. 2010. Diet and food availability: implications for foraging and dispersal of Prince of Wales northern flying squirrels across managed landscapes. *Journal of Mammalogy* 91: 79–91.
- Fritz Ö. 2009. Vertical distribution of epiphytic bryophytes and lichens emphasizes the importance of old beeches in conservation. *Biodiversity and Conservation* 18: 289–304.
- Fritz Ö, Niklasson M, Churski M. 2008a. Tree age is a key factor for the conservation of epiphytic lichens and bryophytes in beech forests. *Applied Vegetation Science* 12: 93–106.
- Fritz Ö, Gustafsson L, Larsson K. 2008b. Does forest continuity matter in conservation? A study of epiphytic lichens and bryophytes in beech forests of southern Sweden. *Biological Conservation* 141: 655–668.
- Fritz Ö, Heilmann-Clausen J. 2010. Rot holes create key microhabitats for epiphytic lichens and bryophytes on beech (*Fagus sylvatica*). *Biological Conservation* 143: 1008–1016.
- Gauslaa Y, Solhaug KA. 2000. High-light-intensity damage to the foliose lichen *Lobaria pulmonaria* within a natural forest: the applicability of chlorophyll fluorescence methods. *Lichenologist* 32: 271–289.
- Gerson U, Seaward MRD. 1977. Lichen-invertebrate associations. In: Seaward MRD, editor. *Lichen Ecology*. Academic Press, London. pp. 69–119.
- Gustafsson L, Eriksson I. 1995. Factors of importance for the epiphytic vegetation of aspen *Populus tremula* with special emphasis on bark chemistry and soil chemistry. *Journal of Applied Ecology* 32: 412–424.

- Hayward GD, Rosentreter R. 1994. Lichens as nesting material for northern flying squirrels in the northern Rocky Mountains. *Journal of Mammalogy* 75: 663–673.
- Hedenås H, Ericson L. 2008. Species occurrences at stand level cannot be understood without considering the landscape context: Cyanolichens on aspen in boreal Sweden. *Biological Conservation* 141: 710–718.
- Humphrey JW, Davey S, Peace A J, Ferris R, Harding K. 2002. Lichens and bryophyte communities of planted and semi-natural forests in Britain: the influence of site type, stand structure and deadwood. *Biological Conservation* 107: 165–180.
- Jairus K, Lõhmus A, Lõhmus P. 2009. Lichen acclimatization on retention trees: a conservation physiology lesson. *Journal of Applied Ecology* 46: 930–936.
- Johansson P. 2008. Consequences of disturbance on epiphytic lichens in boreal and near boreal forests. *Biological Conservation* 141: 1933–1944.
- Jüriado I, Liira J, Paal J, Suija A. 2009. Tree and stand level variables influencing diversity of lichens on temperate broad-leaved trees in boreo-nemoral floodplain forests. *Biodiversity and Conservation* 18: 105–125.
- 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: 2063–2069.
- Knops JMH, Nash TH, Schlesinger WH. 1996. The influence of epiphytic lichens on the nutrient cycling of an oak woodland. *Ecological Monographs* 66: 159–179.
- Kuussaari M, Bommarco R, Heikkinen RK, Helm A, Krauss J, Lindborg R, Ockinger E, Pärtel M, Pino J, Rodà F, Stefanescu C, Teder T, Zobel M, Steffan-Dewenter I. 2009. Extinction debt: a challenge for biodiversity conservation. *Trends in Ecology & Evolution* 24: 564–571.
- LI-COR Inc. 1992. LAI-2000 Plant Canopy Analyzer Instruction Manual. LI-COR Inc., Lincoln.

- Lie MH, Arup U, Grytnes JA, Ohlson M. 2009. The importance of host tree age, size and growth rate as determinants of epiphytic lichen diversity in boreal spruce forests. *Biodiversity and Conservation* 18: 3579–3596.
- Löbel S, Snäll T, Rydin H. 2006. Metapopulation processes in epiphytes inferred from patterns of regional distribution and local abundance in fragmented forest landscapes. *Journal of Ecology* 94: 856–868.
- Lõhmus A, Lõhmus P, Vellak K. 2007. Substratum diversity explains landscape-scale co-variation in the species-richness of bryophytes and lichens. *Biological Conservation* 135: 405–414.
- Márialigeti S, Németh B, Tinya F, Ódor P. 2009. The effects of stand structure on ground-floor bryophyte assemblages in temperate mixed forests. *Biodiversity and Conservation* 18: 2223–2241.
- Moning C, Werth S, Dziöck F, Bässler C, Bradtka J, Hothorn T, Müller J. 2009. Lichen diversity in temperate montane forests is influenced by forest structure more than climate. *Forest Ecology and Management* 258: 745–751.
- Nascimbene J, Marini L, Nimis PL. 2007. Influence of forest management on epiphytic lichens in a temperate beech forest of northern Italy. *Forest Ecology and Management* 247: 43–47.
- Nascimbene J, Marini L, Motta R, Nimis PL. 2009a. Influence of tree age, tree size and crown structure on lichen communities in mature Alpine spruce forests. *Biodiversity and Conservation* 18: 1519–1522.
- Nascimbene J, Marini L, Nimis PL. 2009b. Influence of tree species on epiphytic macrolichens in temperate mixed forests of northern Italy. *Canadian Journal of Forest Research* 39: 785–791.
- Nascimbene J, Marini L, Nimis PL. 2010. Epiphytic lichen diversity in old-growth and managed *Picea abies* stands in Alpine spruce forests. *Forest Ecology and Management* 260: 603–609.

- Paltto H, Thomasson I, Nordén B. 2010. Multispecies and multiscale conservation planning: setting quantitative targets for red-listed lichens on ancient oaks. *Conservation Biology* 24: 758–768.
- Petterson RB, Ball JP, Renhorn KE, Esseen PA, Sjöberg K. 1995. Invertebrate communities in boreal forest canopies as influenced by forestry and lichens with implications for passerine birds. *Biological Conservation* 74: 57–63.
- Pike LH. 1978. The importance of lichens in mineral cycling. *The Bryologist* 81: 247–257.
- R Development Core Team 2011. R: A language and environment for statistical computing R Foundation for Statistical Computing, Vienna, Austria ISBN 3–900051–07–0, URL <http://www.R-project.org>.
- Ranius T, Johansson P, Niclas B, Niklasson M. 2008a. The influence of tree age and microhabitat quality on the occurrence of crustose lichens associated with old oaks. *Journal of Vegetation Science* 19: 653–662.
- Ranius T, Eliasson P, Johansson P. 2008b. Large-scale occurrence patterns of red-listed lichens and fungi on old oaks are influenced both by current and historical habitat density. *Biodiversity and Conservation* 18: 289–304.
- Scheidegger C, Werth S. 2009. Conservation strategies for lichens: insights from population biology. *Fungal Biology Reviews* 23: 55–66.
- Snäll T, Riberiro PJ, Rydin H. 2003. Spatial occurrence and colonisations in patch-tracking metapopulations: local conditions versus dispersal. *Oikos* 103: 566–578.
- Snäll T, Hagstrom A, Rudolphi J, Rydin H. 2004. Distribution pattern of the epiphyte *Neckera pennata* on three spatial scales - importance of past landscape structure, connectivity and local conditions. *Ecography* 27: 757–766.
- Szodfridt I. 1969. Data to the soil characteristics of the forests of Örség. *Vasi Szemle*, 23, 386–394.
- Will-Wolf S, Geiser LH, Neitlich P, Reis AH. 2006. Forest lichen communities and environment - How consistent are relationships across scales? *Journal of Vegetation*

Science 17: 171–184.

TABLES

Table 1. Predictors of lichen species richness on forest tree trunks in the Órség National Park, Hungary included in the analyses.

Predictor	Unit	Min	Max	Mean
Tree scale (single tree within a forest stand)				
Tree diameter at the breast height (DBH)	cm	5	98	23
Position on the trunk (<0.50 m; 0.5-1.5 m) (Position)	-	-	-	-
Host tree (beech, hornbeam, oak, or pine)	-	-	-	-
Plot scale (forest stand)				
Tree species Shannon-diversity (Tree diversity)	-	0.19	1.95	0.92
Relative volume of oak	%	1	96	36
Relative volume of pine	%	0	79	26
Relative volume of beech	%	0	94	28
Shrub density (Shrubs)	individual ha ⁻¹	0	4706	974
Basal area	m ² ha ⁻¹	48	110	75
Relative diffuse light	%	0.6	10.4	2.9
Landscape scale (buffer around plots with a 300-m radius)				
Proportion of oak	%	0	63.3	5.9
Proportion of pine	%	0	83.8	26.7
Proportion of beech	%	0	71	8.6
Historical factors				
Continuity of local forest (forest or no forest in 1853)	-	-	-	-
Proportion of forest in the surroundings of plots (radius=300 m) in 1853	%	24	100	76.6

Table 2. Plausible model ($\Delta\text{AICc} < 2$) obtained from the general linear mixed models, testing the effect of four tree-level, three plot-level variables, and three interactions on lichen species richness on trees. Only one model was selected that had $\Delta\text{AICc} < 2$. For each variable we also reported the sum of the model weights ($\sum w_i$) of the models in which the variable occurs.

Best model		
k	14	
AIC	1466.74	
AICc	1466.96	
ΔAICc	0.00	
Model weight	0.987	
Estimates		$\sum w_i$
Intercept	0.086	-
Tree factors		
DBH	0.007	1.00
Host tree	*	1.00
Position on the trunk	*	1.00
Plot level factors		
Basal area	-	0.70
Relative diffuse light	0.375	1.00
Shrub density	-	0.45
Tree x local factors		
Relative diffuse light x Position	*	1.00
Relative diffuse light x Host tree	-	0.09
Position x Host tree	*	1.00

* indicates a categorical variable included in the models.

k is higher than the number of model parameters as AICc requires the estimation of sample σ^2 .

In multi-model inference k is equal to the number of parameters estimated in the model plus 1 (for σ^2) (Burnham and Anderson 2002).

Table 3. Plausible general linear models ($\Delta\text{AICc} < 2$), testing the effect of our seven local, three landscape, and two historical predictors on lichen species richness at the plot scale. Models are ordered according to their ΔAICc . For each variable we also reported the sum of the model weights ($\sum w_i$) of the models where the variable occurs.

	Best model	2nd	3rd	4th	5th	6th	
k	6	5	7	7	6	6	
Adj. R^2	0.72	0.693	0.74	0.738	0.71	0.71	
AICc	230.52	252.73	214.02	215.43	239.02	239.15	
ΔAICc	0	0.29	0.55	0.78	1.27	1.29	
Model weight	0.057	0.049	0.043	0.038	0.03	0.03	
	Estimates						$\sum w_i$
Intercept	9.654	4.09	6.652	9.908	7.855	5.036	
Plot level							
Shrubs density	0.002	0.002	0.002	0.002	0.002	0.002	1.00
Tree species Shannon-diversity (Tree-diversity)	-	-	-	-	-	-	0.19
Basal area	-	-	-	-	-0.047	-	0.29
Relative diffuse light	2.845	2.467	2.613	2.859	1.95	2.572	0.90
Relative volume of beech	-5.618	-	-	-4.175	-	-	0.42
Relative volume of oak	-	6.314	3.886	-	7.039	5.109	0.68
Relative volume of pine	-7.633	-	-4.788	-8.252	-	-2.718	0.63
Landscape factors							
Proportion of beech	-	-	-0.057	-0.047	-	-	0.34
Proportion of oak	-	-	-	-	-	-	0.26
Proportion of pine	-	-	-	-	-	-	0.20
Historical factors							
Proportion of forest in the surroundings of plots in 1853	-	-	-	-	-	-	0.16
Continuity of local forest	-	-	-	-	-	-	0.15

k is higher than the number of model parameters as AICc requires the estimation of

sample σ^2 . In multi-model inference k is equal to the number of parameters estimated in the model plus 1 (for σ^2) (Burnham and Anderson 2002).

Figures

Figure 1. Map of the studied area and the position of the plots. AT, Austria; CRO, Croatia; CZ, Czech Republic; HU, Hungary; IT, Italy; SK, Slovakia; SLO, Slovenia.

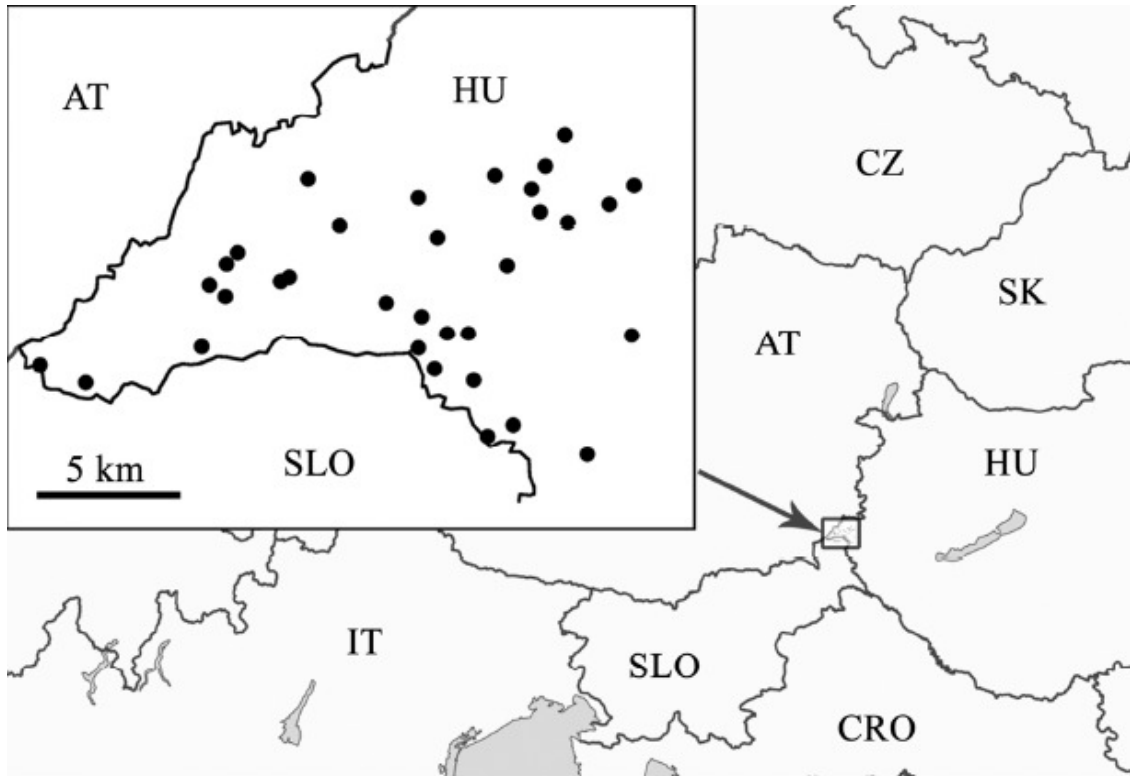


Figure 2. The sampling scheme used to estimate factors that are related to lichen species richness in forest stands. (a) We measured lichen species richness at two positions on the trunk of 1052 trees located in (b) 35 forest stands; (c) we also quantified landscape composition around each forest stand within a 300-m radius. We quantified historical factors (1853) at both the local (forest continuity) and landscape scale (proportion of forest cover in 1853).

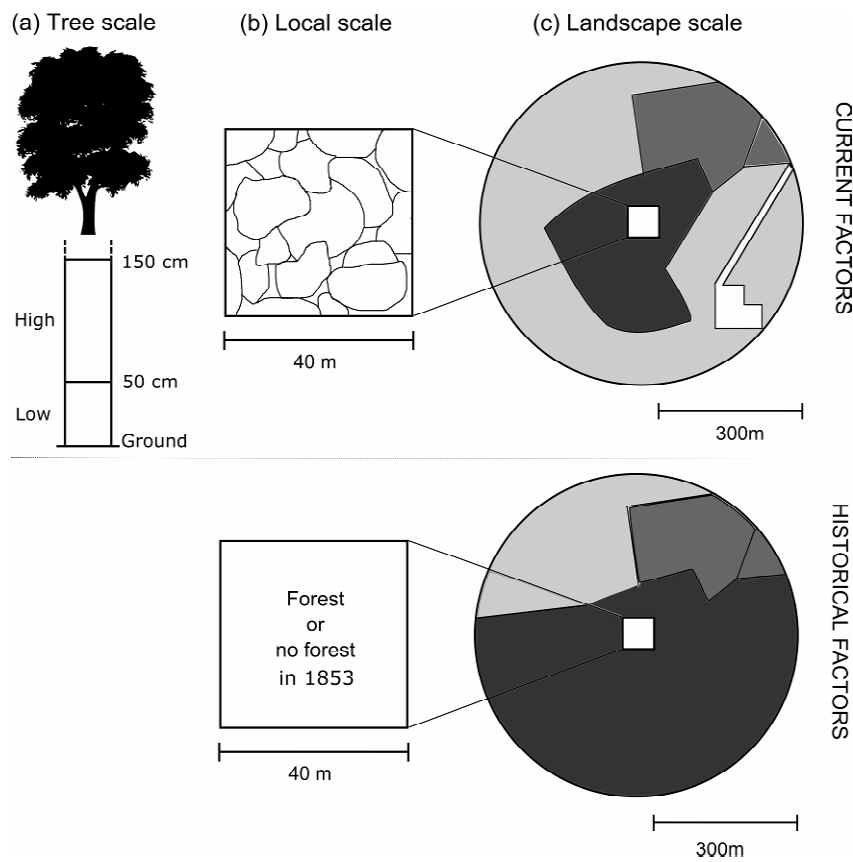


Figure 3. Mean (\pm SE) lichen species richness describing the interaction between host tree and position on the trunk (low: <50 cm; high: 50-150 cm). As the position effect includes also a surface area effect, the effect of interest is the interaction between position and host tree. Both interactions were supported by the high sum of model weights (Table 1).

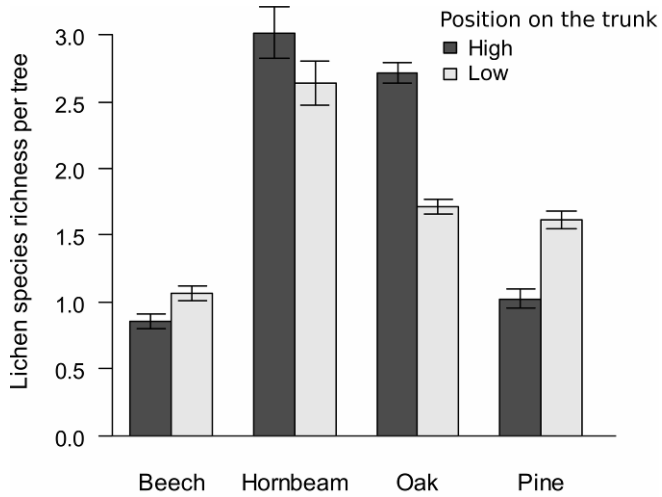


Figure 4. Relationship between mean lichen species richness at the tree level and light conditions separately for the low (<50 cm; ● and solid line) and high position (50-150 cm; ○ and dashed line) on the trunk. Each circle is the average number of lichen species per tree in each position (low and high), in each plot.

