



Lichen diversity in temperate montane forests is influenced by forest structure more than climate

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ABSTRACT

Although the effect of forest management on lichens in temperate forests has been widely examined, little is known about the influence of management-related factors on their biodiversity relative to factors that cannot be altered by management. Here we determined whether forest structure or climate determines lichen diversity in the Bavarian Forest National Park in southeastern Germany, taking spatial variables into account. We investigated 517 single tree stems along 4 transects in 113 pre-stratified plots (8 m in diameter) in this montane forest. We grouped environmental variables into three sets: climate (macroclimate, non-manageable), forest structure (manageable), and space. The explanatory powers of these sets of variables for lichen diversity were compared using variance partitioning for the lichen community, species density, and threatened species density. The relationships of single characteristics of forest structure with lichen species diversity were analyzed using generalized linear models (GLM). Lichen diversity was better explained by stand structures than by climate. Spatial effects influenced the number of species per plot. Among the structural features, the availability of dead wood and sycamore maple as well as forest continuity were most important for the enhancement of lichen diversity. Open canopy structures affected the total diversity positively. Although the availability of large trees was not an influential factor in the GLM at the plot level, high diversity levels were generally associated with large stem diameters at the level of single stems. We provide recommendations for sustainable forest-management practices that aim at specifically enhancing lichen diversity in temperate areas experiencing low levels of air pollution.

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1. Introduction

One aim of modern sustainable forest management is the preservation of management-sensitive species. Therefore, a detailed knowledge of the influence of management-related factors on biodiversity as compared to factors that cannot be altered via management is essential. One of the major taxonomical groups sensitive to management are lichens, which are thus important indicators of forests that are close to natural conditions (Ulikzka and Angelstam, 2000). Three major threats are known to have the potential to alter lichen diversity: forest management, air pollution, and climate change (Wirth et al., 1996; Thor, 1998; Ellis et al., 2007a,b).

Temperate forest management influences forest structures, which in turn determine habitat qualities and affect lichen species (Uliczka and Angelstam, 1999; Price and Hochachka, 2001; Gustafsson et al., 2004). Modern forestry has created tree stands with an even age distribution (Gunnarsson et al., 2004). This change in forest continuity through management affects lichen species density, especially the density of threatened species (Tibell, 1992). Especially the conversion of old-growth forest into young, managed stands leads to a significant reduction in the epiphytic lichen biomass (Esseen et al., 1996) and species diversity (Uliczka and Angelstam, 1999). In many managed areas, the rate of disappearance of lichen populations significantly exceeds the rate of establishment of new populations (e.g., Pykälä, 2004).

Epiphytic lichen diversity in temperate forests throughout the northern hemisphere increases with stand age (Neitlich and McCune, 1997; Kuusinen and Siitonen, 1998; Price and Hochachka, 2001; Gustafsson et al., 2004; Nascimbene et al., 2007), which is

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due to limitations in the dispersal and establishment of lichens (Hilmo, 2002; Hilmo and Sastad, 2001; Werth et al., 2006) and slow biomass accumulations of epiphytic lichens (Sillet et al., 2000). Thus, mainly time, i.e. habitat age, comes to the fore as an ecologically effective dimension, especially for threatened lichen species (Tibell, 1992; Goward, 1994; Crites and Dale, 1998; Thor, 1998; Uliczka and Angelstam, 1999). In this context, it is easy to understand why lichen biomass is strongly related to the mass, diameter, and age of branches: many lichen species need long periods to colonize a suitable habitat (Esseen et al., 1996). Thus, the diameter of the substrate is related to the lichen species composition (Esseen et al., 1996), species richness (Humphrey et al., 2002), and especially the abundance of threatened species, which are often weak colonizers (Caruso et al., 2008).

Large stem diameters are a surrogate for various factors, including an obvious species–area effect, i.e., the larger the diameter, the larger the area that may be colonized and the more species that may be expected on the single stem. This species–area effect is well known in ecology (Arrhenius, 1921; Preston, 1962; Rosenzweig, 1995) and may not be clearly separated from other effects that may positively influence lichen diversity on large stems. These other effects include long periods of exposure to large stems and the rough surface of large stems, which may aid lichen colonization (Crites and Dale, 1998; Uliczka and Angelstam, 1999). However, an experimental approach suggests that young bark surfaces are not less favorable for lichen colonization, but old forest stands have a higher propagule density and thus lichen dispersal is more efficient (Hilmo and Sastad, 2001). Nonetheless, as stem size is adequate as a general proxy for compound factors, large stem diameters are a suitable target variable in a forest management that aims at increasing lichen diversity, regardless of how the diversity increase is caused.

Forest management causes a reduction in certain forest structures, such as coarse woody debris (Gibb et al., 2005). This greatly alters the habitat quantity and quality for lichens (Caruso et al., 2008). The substrate volume, e.g., the amount of dead wood, and the type of substrate, e.g., tree species, are among the most important driving environmental factors to explain the density of red-listed lichen species (Ohlson et al., 1997; Löhmus and Löhmus, 2001; Gustafsson et al., 2004). Certain tree species are highly preferred because of their specific chemical attributes and bark roughness (Degelius, 1954; Kuusinen, 1996b; Hauck et al., 2001; Uliczka and Angelstam, 1999; Pykälä et al., 2006). Sycamore maple is specifically known to hold high diversity levels in lichens (Macher, 1992). Forest management also influences the cover of the forest canopy layer. This in turn affects the availability of light, which positively affects the growth of lichens (e.g., Ahmadjian, 1993; Uliczka and Angelstam, 1999; Svensson et al., 2005).

The impact of climate change on lichens is a relatively recent issue; however, long-term monitoring suggests that lichens respond to global warming (Insarov et al., 1999; Cezanne et al., 2008). In the Netherlands, arctic-alpine/boreo-montane species appear to be declining, while (sub)tropical species are invading, independent of nutrient demands and decreasing SO₂ emissions (van Herk et al., 2002). In western Europe, more epiphytic species appear to be increasing rather than declining, as a result of global warming (Aptroot and van Herk, 2007). Model predictions indicate major shifts in the distribution of lichen species (Ellis et al., 2007b; Giordani and Incerti, 2008). However, these studies did not separate the influence of climate from the influence of structural and historical variables (Ellis and Coppins, 2007; Ellis et al., 2009). Also these previous lichen bioclimatic studies have focused on target species only, which are expected (a priori) to be responsive to climate change. Such bioclimatic modeling does not pretend to explain ‘diversity’ at a plot-scale, and has been carried out previously only at a countrywide scale beyond the influence of

local forest management. In contrast, our study aims on the assessment of the relative importance of local climate compared to stand structure for characteristics of the whole epiphytic lichen community at a finer local scale that is relevant to forest-management-decisions, and at which the species will most likely respond to climate change. However climate–habitat interactions at the landscape-scale are potentially important and the relative importance of their separate effects has not previously been quantified.

Our goal here was to find out whether forest structure variables determine lichen diversity when climate variables are also considered in the same analysis. We chose an area free of air pollution to isolate climatic and stand-structure effects. The following two questions are specifically addressed:

1. To what extent does forest management influence lichen diversity (community, species density, threatened species density) compared to local climatic variation?
2. Which of the forest structure variables included in a multivariate analysis play a key role for lichen diversity among forest structures (i) at the plot (0.1 ha) level and (ii) at the single stem level?

We hypothesized that forest structure variables are the major driving factors for lichen diversity in temperate montane forests. Based on the current knowledge, we assume that among forest structures, (a) old forests retain higher lichen diversity levels than young forests, (b) forests with large amounts of dead wood have higher lichen diversity levels than forests with small amounts of dead wood, (c) an open canopy layer causes higher diversity levels than a closed canopy layer, and (d) high tree species numbers increase lichen diversity.

At the level of a single stem, we tested whether (a) a deciduous substrate has a higher lichen diversity than a coniferous substrate, (b) sycamore maple has a higher lichen diversity than beech, spruce, and fir, (c) dead substrates have a higher lichen diversity than living substrates, and (d) thick stems have a higher lichen diversity than thin stems.

We discuss the results in the context of sustainable forest-management practices, and we suggest management strategies that maximize lichen diversity in temperate forests in areas with little air pollution.

2. Methods

2.1. Study area and lichen sampling

Our study site is within the Bavarian Forest National Park, situated in southeastern Germany along the Czech Republic border. This unmanaged montane forest area contains an altitudinal gradient with a high variety of structures distributed almost independently from elevation and a broad tree age gradient. The rich structural diversity is caused by heavy infestation with bark beetles, mainly *Ips typographus*, since the 1990s (Müller et al., 2008). The study site includes areas that were managed up to a few decades ago, but also remnant primeval forest areas that have never been managed, thereby increasing the length of the management gradient. We established sampling plots every 100 m along four 29.3-km transects from the bottom (650 m a.s.l.) to the top of the mountains (1420 m a.s.l.). From these we selected 113 pre-stratified (randomly within altitude classes) plots to sample all types of forest stands with an equal distribution along the altitudinal gradient. For details, see Bässler et al. (2008) and Müller et al. (2009).

At each plot, all epiphytic lichens were recorded from August to November 2007 within a radius of 8 m and up to a height of 2 m,

including all trees and dead wood stems and logs (hereafter referred to as stems, total: 517 stems) by an experienced lichenologist (J. Bradtka). At each plot, 1–10 single stems were investigated (average: 5.0 stems per plot), depending on the availability of stems. Lichens growing on the ground and on rocks were not considered in our analysis.

Red lists are widely accepted to present a summary of the status of rare and declining species (Gustafsson et al., 2004) and thus are used here to form the response variable “number of threatened species per sample”, where samples refers to plots or single stems. Since no red list has been published for lichens of Bavaria, we used the German red list (Wirth et al., 1996).

Environmental data for all plots were sampled in autumn 2006 and in summer 2007 (Table 1; for details, see Bässler et al., 2008). The variable “altitude” was left out in the data processing in favor of physiologically effective climate variables, such as temperature or precipitation, since the surrogate altitude and these physiologically effective variables were highly correlated along our climatic gradient (Körner, 2007; Müller et al., 2009).

2.2. Statistical analyses

All statistical analyses were conducted in the framework of R, version 2.8.0 (R Development Core Team, 2008). We grouped environmental variables into three basic sets: climate (macroclimate, non-manageable), forest structure (manageable), and space. Our selection of the forest structure variables is an a priori determination based on current knowledge of environmental factors that are known to influence lichen diversity in temperate forests as presented in the introduction. To represent lichen diversity, we chose two univariate response variables (species density and threatened species density) and one multivariate response variable (species community composition). Space was considered to quantify the spatial effects routed in our sampling design and was represented by a second-order trend surface based on the coordinates (compare Table 1 with introduction). Forty-five climate variables were available for all plots. These were subjected to a principal-components analysis (PCA) to maintain full environmental space but avoid colinearity. The first four axes

explained 89% of all variance. For the further analyses, the projected axis scores of the first four axes were used to represent the variable ‘climate’ (Schweiger et al., 2008). The analysis of the main components (PCA) showed that the first four axes represent temperature and precipitation (annual average [°C], means of the vegetation periods [days], extreme temperatures [°C], global radiation [J/(cm² days)], and extreme radiation [J/(cm² days)] and thus correspond to macro-climatic factors that are effective for lichens (Cezanne et al., 2008). An overview of the investigated variables and their data ranges is given in Table 1.

Species density refers to the number of species per plot or stem (Gotelli and Colwell, 2001). All explanatory variables were standardized to zero mean and unit variance (Oksanen et al., 2006). We used log-transformed density data. Species data for the community matrix were square-root transformed, in order to adjust the high numbers of common species.

To compare the explanatory power of the different environmental variable sets, we partitioned the variation of response table Y with respect to the three explanatory tables using the function *varpart* in *vegan*. This application uses partial redundancy analysis (RDA) for community matrixes as independent variables and partial multiple regression analysis for vector-independent variables. We calculated adjusted *R* square values because this is the only unbiased method (Peres-Neto et al., 2006). Preliminary detrended correspondence analyses (DCA) revealed the length of the first axis gradient as 3.9, which is within the range (2.0–4.0) in which one can select unimodal ordination, such as canonical correspondence analysis (CCA), or linear ordination, such as RDA (Økland, 1990). The same results were obtained with a partial CCA. As only RDA supports adjusted *R* square values for community variance partitioning, we present only the results of RDA.

To test the significance of the influence of our independent fractions on lichen data, we applied a permutation test with 1000 permutations using the function *anova* in *varpart*. This shows whether the particular independent fraction exhibits a significant explanatory power to the corresponding lichen variable (community, species density, threatened species density). To determine the errors of our independent fractions, we used a bootstrapping of the variance partitioning, which allowed us to construct 95%

Table 1

Investigated environmental variables and their variance within the dataset, as well as response variables and their variance.

Environmental variable sets	Data range	Mean
Space		
X	–	–
Y	–	–
X × Y	–	–
X × X	–	–
Y × Y	–	–
Climate (non-manageable factors): projected axis scores of the first four axes of a PCA, based on 45 climate variables		
Forest structure (manageable factors)		
Average stand age from forest inventory grid with 0.1 ha plots [years]. Determined by drill samples.	35–400 years	159 years
Dead wood volume [m ³ /0.1 ha] estimated on 0.1 ha plots	0–70.9 m ³ /0.1 ha	13.5 m ³ /0.1 ha
Maximum diameter at breast height (1.3 m) diameter on 0.1 ha plot [cm]	0–130 cm	53.4 cm
Laser penetration rate (LiDAR measurement) in the space between 2 and 50 m above ground on 0.1 ha plots [%]	0–92.2%	29.4%
Number of tree species on 0.1 ha plots [species]	0–7 species	2.2 species
Diameter of the substrate (stem) [cm]	2–150 cm	37.4 cm
Response variables		
Species density: number of lichen species per 0.1 ha plot per single stem		
	Plot: 1–58 species	Plot: 20 species
	Stem: 1–23 species	Stem: 4.2 species
Threatened species density: number of threatened lichen species per 0.1 ha plot per single stem (German Red List data; Wirth et al., 1996)		
	Plot: 0–39 species	Plot: 6.7 species
	Stem: 0–14 species	Stem: 1.4 species
Community: number of encounters per lichen species per 0.1 ha plot		
	–	–

confidence bands for our independent effects. The bootstrapping was conducted with 2000 replicates according to Roff (2006).

To analyze the relationships of single characteristics of lichen species diversity with the forest structure variables, we applied generalized linear models (GLM). As our raw data are count data, we selected Poisson error structures (Quinn and Keough, 2002).

When the GLM considered the species or threatened species density on single stems, the dataset consisted of continuous and categorical variables with several classes within the variable “tree species”. However, a GLM does not provide a decent insight into the influence of the category variables, although these would be of major interest for practical applications. Therefore, we calculated multiplicity-adjusted Wald-Intervals (following Hothorn et al., 2008a; implemented in the package *multcomp*, Hothorn et al., 2008b) and the corresponding multiplicity-adjusted *p*-values (Fig. 3). Using these inference measures, we restricted the probability of erroneously declaring at least one predictor as influential to $\alpha = 0.05$. This procedure allowed us to fulfil all requirements in multiple testing of the hypothesis even in complex predictor sets (Quinn and Keough, 2002).

Owing to our survey design, spatial autocorrelation needed to be addressed, as one of the key assumptions in statistical models in the present context is the spatial independence of residuals (Dormann et al., 2007). Therefore, in the variance partitioning process, we considered space as a separate environmental variable set (see Table 1). Finally, we checked the residuals of our GLM models for spatial independence using spline (cross)-correlograms (package *ncf*, Dormann et al., 2007).

3. Results

We found 138 lichen species on our plots (see Supplementary table). On our study plots, variance partitioning resulted in a total explained variance of 23.3% for lichen community composition, 36.8% for species density, and 20.6% for threatened species density. The independent explained variance extracted from the data sets for climatic, forest structural, and spatial variances showed that forest structure had the greatest effect and climate had the lowest effect (Fig. 1). This was most apparent for the threatened species density. Spatial correlations for species density had a higher independent effect than for community and threatened species density.

The GLM of the single structural variables at the plot level resulted in similar patterns of significance for both the number of species and the number of threatened species per sample (Table 2). Variables that significantly correlated to both species numbers and threatened species numbers per sample were related to forest continuity (age) and substrate availability (dead wood volume). Open canopy (laser penetration rate) positively affected the total species number per sample at a highly significant level, but did not

Table 2

Results of the generalized linear model of the forest structural variables at the plot level (0.1 ha). The estimators of the standardized predictors are given. Significant *p*-values are indicated in parentheses; n.s. not significant. For details regarding the variables, see Table 1.

Response variable	No. of species per sample	No. of threatened species per sample
Age	0.089 (**)	0.256 (***)
Dead wood volume	0.200 (***)	0.228 (***)
Maximum diameter at breast height	0.022 (n.s.)	−0.054 (n.s.)
Laser penetration rate	0.218 (***)	0.086 (n.s.)
No. of tree species	0.044 (n.s.)	0.185 (***)

** $p < 0.01$.

*** $p < 0.001$.

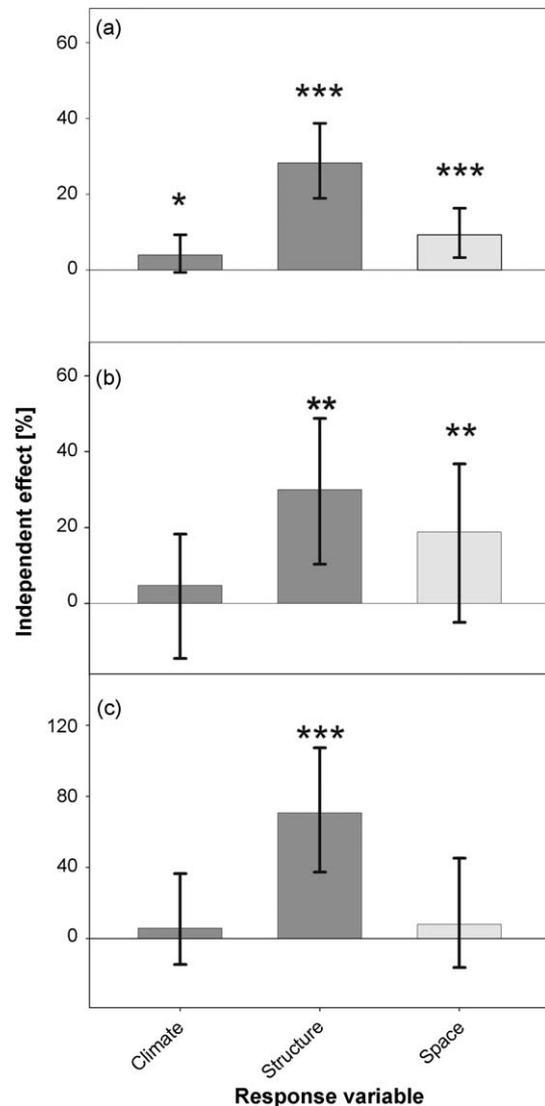


Fig. 1. Exclusive explanatory contribution of climatic, forest-structural, and spatial variable sets of the total explained variance for each dataset based on variance partitioning (function *varpart* in *vegan*, Oksanen et al., 2006). (a) Lichen community composition, (b) species density, and (c) threatened species density, all at the 0.1 ha plot level. To test the significant influence of each independent fraction on the independent variables, a permutation test was applied (function *anova* in *vegan*); significant *p*-values are indicated by asterisks: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. To display the variability of our independent fractions, a bootstrapping of variance partitioning was additionally applied, and the 95% confidence interval is shown in the box plots by whiskers. Note that the significance by permutation and the confidence bands shown by the whiskers are not related to each other. Also note that the target variables differ significantly from each other (vector, community matrix); they cannot be compared quantitatively among each other.

significantly affect the threatened species number per sample. Tree species diversity (number of tree species) was highly significantly correlated to threatened species number per sample but not to species number per sample. Our assessment of the spatial autocorrelation for residuals of the GLMs by inspection of spline (cross)-correlograms (Fig. 2), indicated no spatial dependence of the residuals for threatened species per sample, but some dependence for the total number species on a scale of around 1 km, which is in agreement with the results shown in Fig. 1.

Also the GLM of the environmental variables at the level of single stems resulted in similar patterns of significance for both the number of species and the number of threatened species per sample (Fig. 3). The tree species was crucial for both numbers;

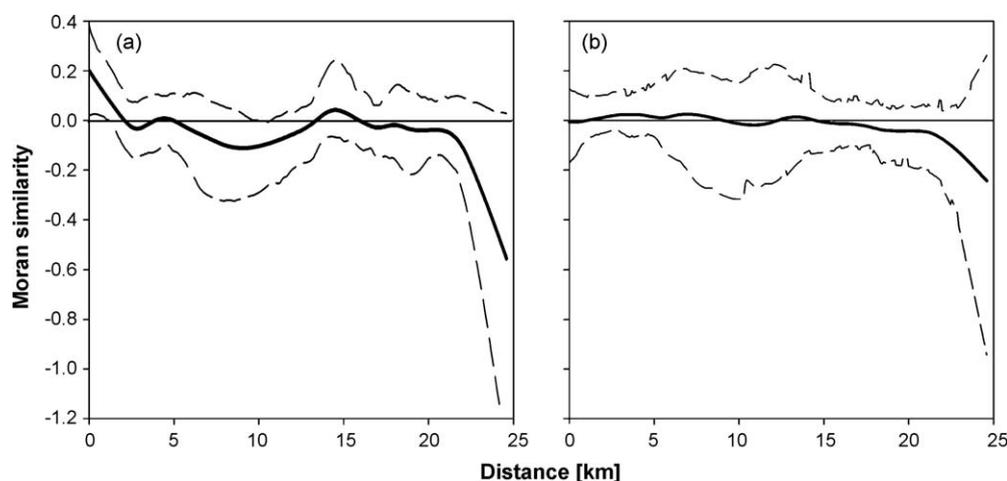


Fig. 2. Spline (cross)-correlogram (Bjørnstad et al., 1999; Bjørnstad and Falck, 2000) of the GLM residuals of (a) the number of all species per sample and (b) the number of threatened species per sample. Both analyses were performed at the plot level (0.1 ha). The non-centered correlogram provides estimates of the spatial correlation for discrete distance classes and is based on Moran's I.

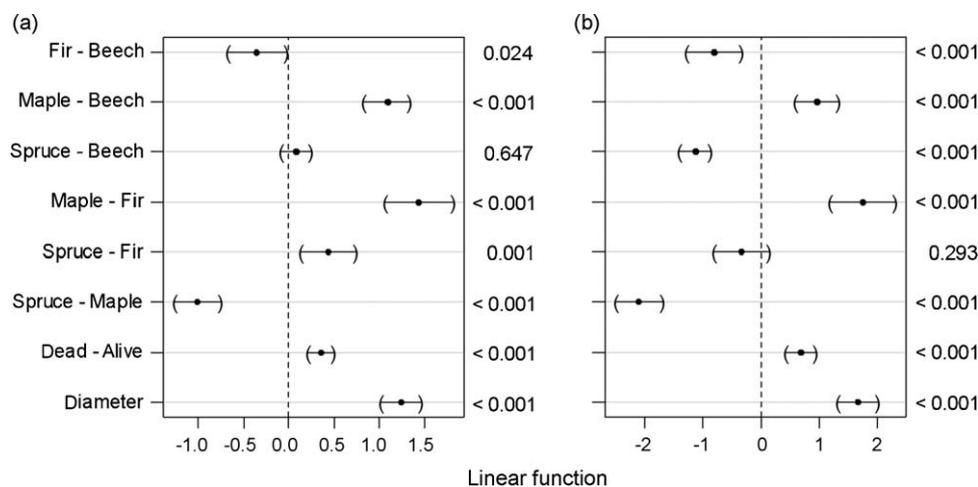


Fig. 3. Generalized linear models with post hoc performance considering (a) the number of species per sample and (b) the number of threatened species per sample, both at the level of single stems ($n = 517$). Multiplicity-adjusted Wald intervals (Laplace, 1812; Landauer, 1997) and the corresponding multiplicity-adjusted p -values are displayed. Fir $n = 23$, maple $n = 14$, beech $n = 177$, spruce $n = 304$, alive $n = 330$, dead $n = 224$. The graphs show the size of the estimators and the confidence intervals. If the confidence interval encloses the zero line, the influence of the environmental variable is not significant. If the value of one category variable is greater than another, the confidence interval lies to the right of the zero line. For example, with maple vs. fir, the confidence interval lies to the right and maple is therefore of higher importance for lichen diversity than fir.

especially sycamore maple (*Acer pseudoplatanus*) was of high importance for lichen diversity. At the single stem level, the substrate diameter and dead wood as the substrate were highly significant for both the number of species and the number of threatened species per sample.

4. Discussion

We did not consider the influence of long-range atmospheric pollution (Hawksworth and Rose, 1970; Ferry et al., 1973) because in the past the influence of SO_2 emissions on lichen diversity in the Bavarian Forest has been rated as low, especially in comparison to northeastern Bavaria (Macher, 1992; Windisch and Vorbeck, 1996). This is exemplified by the wide distribution of SO_2 -sensitive species, such as *Alectoria sarmentosa*, *Bryoria nadvornikiana*, *Gyalecta ulmi*, and *Loxospora cisonica*, within the Bavarian Forest National Park and their rarity or uncommonness elsewhere in Bavaria. These species are characteristic for permanent clean air with low SO_2 concentrations, which rate the highest index of atmospheric purity (IAP) values (Ellenberg et al., 1992). Never-

theless, it is important to note that forest management aimed at maintaining or enhancing lichen diversity will only be efficient in places where air pollution levels are sufficiently low, such as in our study area. Large areas of Central Europe still receive considerable amounts of air pollution (van Herk et al., 2007), which is particularly detrimental in dry climates. However, SO_2 emissions have generally decreased in the past decades, and in some areas, lichens have re-invaded "lichen deserts", i.e., areas formerly free of lichens because of intense air pollution (Kandler and Poelt, 1984; van Dobben, 1996). Thus, in contrast to a few decades ago, the influence of forestry on lichen diversity has increased.

Nitrogen depositions have been identified as an important factor that favor nitrophilous lichen species, such as *Xanthoria parietina*, *Xanthoria candelaria*, and *Phaeophyscia orbicularis* (van Herk et al., 2007; Frati et al., 2008). However, since nitrophytes were locally rare among the lichen species we studied, we do not believe that N deposition is a major issue in our study area.

In our study, both the diversity of threatened lichen species and the diversity of total lichen species were mainly affected by forest structure, whereas macroclimatic factors were far less important,

despite the steep elevational gradient investigated. The investigated gradient in the Bavarian Forest National Park ranges from 4.2 °C to 7.8 °C average annual temperature, which also represents a broader regional scale (BayFORKLIM, 1996). Since all of the forest structure variables investigated can be actively influenced by forest management, our results demonstrate that forest management exerts a great effect on the diversity of epiphytic lichens. Our results also indicate the potential for sustainable forest-management strategies, which could actively enhance lichen diversity in temperate forests.

Our results differ from those of a study in northern Norway, where climate as well as forest structure were found to be highly relevant for macrolichen communities (Werth et al., 2005). Climate was likely significant in the Norwegian study because a particularly long gradient comprising humid oceanic and dry inland sites was investigated (Werth et al., 2005). In studies in Great Britain using bioclimatic envelopes, lichen communities had a large potential to react to climate change (Ellis and Coppins, 2008; Ellis et al., 2007a,b), but in these and several other studies, the effects of forest structure as a habitat-defining feature were not considered. Such an approach may lead to an incomplete interpretation of the occurrence patterns of lichens, which are highly forest-structure-dependent organisms. Moreover, the climate warming that started in the last decades is proceeding faster than past climate changes, which means that even if the temperature at a specific altitude increases by +2.0 K within 100 years (IPCC, 2007; Spekat et al., 2007), the creation of dead wood structures, such as those of large broadleaf trees, will not follow at the same pace. This underlines the superior role of forest structures as a decisive influencing factor for lichen species density and community composition within the next decades.

Spatial autocorrelation was detected for the number of species per sample at the plot level, at a scale of up to 1 km. This result indicates that whole mountain slopes are developing characteristic structural features owing to large-scale natural dynamics, such as bark beetle infestations, that cause similar lichen diversity and community patterns to evolve on a scale of a few kilometres (Müller et al., 2008). However, the analysis clearly showed that forest structure results in the greatest exclusive explanatory contribution, which is in line with numerous other studies (Lesica et al., 1991; Hyvärinen et al., 1992; Uliczka and Angelstam, 1999; Cameron, 2002). This was true for community composition, species numbers per sample, and in particular for the number of threatened lichen species per sample. In the majority of European forests, structures are determined directly by forest management. This implies that lichen diversity, including density of threatened species, can be actively managed, and even enhanced, if adequate silvicultural methods are utilized.

In our study, we found a clearly positive influence of sycamore maple on lichen species densities for both the total number of species and the number of threatened species per sample. This effect is probably caused by more than one factor. First, the chemical attributes of the bark play an important role (e.g., Kuusinen, 1996b; Hauck et al., 2001), as shown for the bark of *Populus tremula*, which offers favorable conditions for cyanobacterial lichens in boreal forests (Kuusinen, 1994, 1996a; Uliczka and Angelstam, 1999). Second, the bark of sycamore maple is rough even in younger trees and thus may be colonized more easily even at an early age.

Regarding to the biogeographic scope and consequently the wider relevance of the results, the findings of other studies of temperate forests all over the northern hemisphere suggest, that the effect of forest structure on forest lichen epiphytes is outstanding (Crites and Dale, 1998; Gustafsson et al., 2004; Hyvärinen et al., 1992; Kuusinen and Siitonen, 1998). Forest

structure obviously shapes epiphyte lichen diversity and communities beyond the influence of climate in many montane forests all over the northern hemisphere.

4.1. Management recommendations

From our analyses, we identified those forest structure variables that play a key role for lichen diversity. Thus, we strongly recommend that the amount of dead wood be generally increased by conserving enough veteran trees within a stand, and that along the whole elevation gradient a considerable number of stands should be created with a canopy cover less than 50%, which is typical for all high mountain spruce forests in our study area. To specifically support red-listed species, the portion of native broad-leaved tree species characteristic of a given locality should be enhanced; in low mountain ranges of Central Europe, this is mainly *A. pseudoplatanus*. Additionally, these broad-leaved trees should be allowed to grow to maturity and beyond.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2009.05.015.

References

- Ahmadjian, V., 1993. The Lichen Symbiosis. John Wiley and Sons, New York.
- Aptroot, A., van Herk, C.M., 2007. Further evidence of the effects of global warming on lichens, particularly those with *Trentepohlia* phycobionts. *Environ. Pollut.* 146 (2), 293–298.
- Arrhenius, O., 1921. Species and area. *J. Ecol.* 9, 95–99.
- Bässler, C., Förster, B., Moning, C., Müller, J., 2008. The BIODIVERSITY-Project: biodiversity research between climate change and wilding in a temperate montane forest. The conceptual framework. *Waldökologie, Landschaftsforschung und Naturschutz* 7, 21–33.
- Bayerischer Klimaforschungsverbund (BayFORKLIM, 1996): Bayerischer Klima-Atlas. Meteorological Institute University of Munich, Munich.
- Bjørnstad, O.N., Falck, W., 2000. Nonparametric spatial covariance functions: estimation and testing. *Environ. Ecol. Stat.* 8, 53–70.
- Bjørnstad, O.N., Ims, R.A., Lambin, X., 1999. Spatial population dynamics: analysing patterns and processes of population synchrony. *Trends Ecol. Evol.* 11, 427–431.
- Cameron, R.P., 2002. Habitat associations of epiphytic lichens in managed and unmanaged forest stands in Nova Scotia. *Northeastern Nat.* 27–46.
- Caruso, A., Rudolphi, J., Thor, G., 2008. Lichen species diversity and substrate amounts in young planted boreal forests: a comparison between slash and stumps of *Picea abies*. *Biol. Conserv.* 141 (1), 47–55.
- Cezanne, R., Eichler, M., Kirschbaum, U., Windisch, U., 2008. Flechten als Anzeiger des Klimawandels/Lichens as indicators of climate change. *Sauteria* 15, 159–174.
- Crites, S., Dale, M.R.T., 1998. Diversity and abundance of bryophytes, lichens, and fungi in relation to woody substrate and successional stage in aspen mixed-wood boreal forests. *Can. J. Bot.* 76 (4), 641–651.
- Degelius, G., 1954. The Lichen Genus *Collema* in Europe: Morphology, Taxonomy and Ecology. *Inst. of Botany, Univ. of Uppsala, Sweden*.
- Dormann, C.F., McPherson, J.M., Araújo, M.B., Bivand, R., Bolliger, J., Carl, G., Davies, R.G., Hirzel, A., Jetz, W., Kissling, W.D., Kühn, I., Ohlemüller, R., Peres-Neto, P.R., Reineking, B., Schröder, B., Schurr, F.M., Wilson, R., 2007. Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography* 30, 609–628.
- Ellenberg, H., Weber, H., Düll, R., Wirth, V., Werner, W., Paulißen, D., 1992. Zeigerwerte der Pflanzen Mitteleuropas. *Scripta Geobot.* 18, 1–258.
- Ellis, C.J., Coppins, B.J., Dawson, T.P., Seaward, M.R.D., 2007a. Response of British lichens to climate change scenarios: trends and uncertainties in the projected impact for contrasting biogeographic groups. *Biol. Conserv.* 140, 217–235.
- Ellis, C.J., Coppins, B.J., Dawson, T.P., 2007b. Predicted response of the lichen epiphyte *Lecanora populicola* to climate change scenarios in a clean-air region of Northern Britain. *Biol. Conserv.* 135, 396–404.
- Ellis, C.J., Coppins, B.J., 2007. Changing climate and historic-woodland structure interact to control species diversity of the 'Lobarion' epiphyte community in Scotland. *J. Vegetation Sci.* 18 (5), 725–734.
- Ellis, C.J., Coppins, B.J., 2008. Contrasting functional traits maintain lichen epiphyte diversity in response to climate and autogenic succession. *J. Biogeogr.* 33, 1643–1656.
- Ellis, C.J., Yahr, R., Coppins, B.J., 2009. Local extent of old-growth woodland modifies epiphyte response to climate change. *J. Biogeogr.* 36 (2), 302–313.
- Esseen, P.-A., Renhorn, K.-E., Pettersson, R.B., 1996. Epiphytic lichen biomass in managed and old-growth boreal forests: effect of branch quality. *Ecol. Appl.* 6 (1), 228–238.

- Ferry, B.W., Baddeley, M.S., Hawksworth, D.L. (Eds.), 1973. Air Pollution and Lichens. Athlone Press, University of London.
- Frati, L., Brunialti, G., Loppi, S., 2008. Effects of reduced nitrogen compounds on epiphytic lichen communities in Mediterranean Italy. *Sci. Total Environ.* 407 (1), 630–637.
- Gibb, H., Ball, J.B., Johansson, T., Atlegrim, O., Hjalten, J., Danell, K., 2005. Effects of management on coarse woody debris volume and composition in boreal forests in northern Sweden. *Scand. J. Forest Res.* 20 (3), 213–222.
- Giordani, P., Incerti, G., 2008. The influence of climate on the distribution of lichens: a case study in a borderline area (Liguria, NW Italy). *Plant Ecol.* 195 (2), 257–272.
- Gotelli, N.J., Colwell, R.K., 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecol. Lett.* 4, 379–391.
- Goward, T., 1994. Notes on old growth-dependent epiphytic macrolichens in inland British Columbia, Canada. *Ann. Bot. Fennica* 150, 31–38.
- Gunnarsson, B., Hake, M., Hultengren, S., 2004. A functional relationship between species richness of spiders and lichens in spruce. *Biodivers. Conserv.* 13 (4), 685–693.
- Gustafsson, L., Appelgren, L., Jonsson, F., Nordin, U., Persson, A., Weslien, J.-O., 2004. High occurrence of red-listed bryophytes and lichens in mature managed forests in boreal Sweden. *Basic Appl. Ecol.* 5 (2), 123–129.
- Hauck, M., Jung, R., Runge, M., 2001. Relevance of element content of bark for the distribution of epiphytic lichens in a montane spruce forest affected by forest dieback. *Environ. Pollut.* 112, 221–227.
- Hawksworth, D.L., Rose, F., 1970. Qualitative scale for estimating sulphur dioxide air pollution in England and Wales using epiphytic lichens. *Nature* 227, 145–148.
- Hilmo, O., Sastad, S.M., 2001. Colonization of old-forest lichens in a young and an old boreal *Picea abies* forest: an experimental approach. *Biol. Conserv.* 102 (3), 251–259.
- Hilmo, O., 2002. Growth and morphological response of old-forest lichens transplanted into a young and an old *Picea abies* forest. *Ecography* 25 (3), 329–335.
- Hothorn, T., Bretz, F., Westfall, P., 2008a. Simultaneous inference in general parametric models. *Biometrical J.* 50 (3), 346–363.
- Hothorn, T., Bretz, F., Westfall, P., 2008b. Multcomp: simultaneous inference for general linear hypotheses. R Package Version 1.0-3, <http://CRAN.R-project.org>.
- Humphrey, J.W., 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. *Biol. Conserv.* 107 (2), 165–180.
- Hyvärinen, M., Halonen, P., Kauppi, M., 1992. Influence of stand age and structure on the epiphytic lichen vegetation in the middle-boreal forests of Finland. *Lichenologist* 24, 165–180.
- Inсарov, G.E., Semenov, S.M., Inсарova, I.D., 1999. A system to monitor climate change with epilithic lichens. *Environ. Monit. Assess.* 55 (2), 279–298.
- IPCC, 2007. Climate Change 2007—The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the IPCC. Cambridge University Press, Cambridge, New York.
- Kandler, O., Poelt, J., 1984. Wiederbesiedlung der Innenstadt von München durch Flechten. *Naturwissenschaftliche Rundschau* 37, 90–95.
- Körner, C., 2007. The use of 'altitude' in ecological research. *Trends Ecol. Evol.* 22 (11), 569–574.
- Kuusinen, M., Siitonen, J., 1998. Epiphytic lichen diversity in old-growth and managed *Picea abies* stands in southern Finland. *J. Vegetation Sci.* 9 (2), 283–292.
- Kuusinen, M., 1994. Epiphytic lichen flora and diversity on *Populus tremula* in old-growth and managed forests of southern and middle boreal Finland. *Ann. Bot. Fennica* 31, 245–260.
- Kuusinen, M., 1996a. Cyanobacterial macrolichens on *Populus tremula* as indicators of forest continuity in Finland. *Biol. Conserv.* 75, 43–49.
- Kuusinen, M., 1996b. Epiphyte flora and diversity of basal trunks of six old-growth forest tree species in southern and middle boreal Finland. *Lichenologist* 28, 443–463.
- Landauer, T. K., 1997. Behavioral research methods in human-computer interaction. In: Helander, M., Landauer, T.K., Prabhu, P. (Eds.), *Handbook of Human-Computer Interaction*. Amsterdam, Netherlands, pp. 203–227.
- Laplace, P.S., 1812. *Theorie Analytique des Probabilités*. Paris, France.
- Lesica, P., McCune, B., Cooper, S.V., Hong, W.S., 1991. Differences in lichen and bryophyte communities between old-growth and managed second-growth forests in the Swan Valley, Montana. *Can. J. Bot.* 69, 1745–1755.
- Lõhmus, P., Lõhmus, A., 2001. Snags, and their lichen flora in old Estonian peatland forests. *Ann. Bot. Fennica* 38, 265–280.
- Macher, M., 1992. Epiphytische Flechten im Nationalpark Bayerischer Wald. *Schriftenreihe des Bayerischen Staatsministeriums für Ernährung, Landwirtschaft und Forsten* 13, Grafenau.
- Müller, J., Bässler, C., Strätz, C., Klöcking, B., Brandl, R., 2009. Molluscs and climate warming in a low mountain range national park. *Malacologia* 51 (1–2), 133–153.
- Müller, J., Bußler, H., Goßner, M., Rettelbach, T., Duelli, P., 2008. The European spruce bark beetle *Ips typographus* (L.) in a national park—from pest to keystone species. *Biodivers. Conserv.* 17, 2979–3001.
- Nascimbene, J., Marini, L., Nimis, P.L., 2007. Influence of forest management on epiphytic lichens in a temperate beech forest of northern Italy. *Forest Ecol. Manag.* 247 (1–3), 43–47.
- Neitlich, P.N., McCune, B., 1997. Hotspots of epiphytic diversity in two young managed forests. *Conserv. Biol.* 11, 172–182.
- Ohlson, M., Söderström, L., Hörnberg, G., Zackrisson, O., Harmansson, J., 1997. Habitat qualities versus long-term continuity as determinants of biodiversity in boreal old-growth swamp forests. *Biol. Conserv.* 81, 221–231.
- Økland, R.H., 1990. Vegetation ecology: theory, methods and applications with reference to Fennoscandia. *Sommerfeltia Suppl.* 1, 1–233.
- Oksanen, J., Kindt, R., Legendre, P., O'Hara, R.B., 2006. *Vegan: Community Ecology Package Version 1.8*. R Package.
- Peres-Neto, P., Legendre, P., Dray, S., Borcard, D., 2006. Variation partitioning of species data matrices: estimation and comparison of fractions. *Ecology* 87, 2614–2625.
- Preston, F.W., 1962. The canonical distribution of commonness and rarity: Part I. *Ecology* 43, 185–215.
- Price, K., Hochachka, G., 2001. Epiphytic lichen abundance: effects of stand age and composition in coastal British Columbia. *Ecol. Appl.* 11 (3), 904–913.
- Pykälä, J., 2004. Effects of new forestry practices on rare epiphytic macrolichens. *Conserv. Biol.* 18 (3), 831–838.
- Pykälä, J., Heikkinen, R.K., Toivonen, H., Jääskeläinen, K., 2006. Importance of forest act habitats for epiphytic lichens in Finnish managed forests. *Forest Ecol. Manag.* 223 (1–3), 84–92.
- Quinn, G.P., Keough, M.J., 2002. *Experimental Design and Data Analysis for Biologists*. Cambridge University Press, Cambridge.
- R Development Core Team, 2008. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria available at: www.r-project.org/
- Roff, D.A., 2006. *Introduction to Computer-Intensive Methods of Data Analysis in Biology*. Cambridge University Press, New York, USA.
- Rosenzweig, M.L., 1995. *Species Diversity in Space and Time*. Cambridge University Press, Cambridge.
- Schweiger, O., Settele, J., Kudrna, O., Klotz, S., Kühn, I., 2008. Climate change can cause spatial mismatch of trophically interacting species. *Ecology* 89, 3472–3479.
- Sillet, S.C., McCune, B., Peck, J.E., Rambo, T.R., Ruchty, A., 2000. Dispersal limitations of epiphytic lichens result in species dependent on old-growth forests. *Ecol. Appl.* 10 (3), 789–799.
- Spekat, A., Enke, W., Kreienkamp, F., 2007. Neuentwicklung von regional hoch aufgelösten Wetterlagen für Deutschland und Bereitstellung regionaler Klimaszenarios auf der Basis von globalen Klimasimulationen mit dem Regionalisierungsmodell WETTREG auf der Basis von globalen Klimasimulationen mit ECHAM5/MPI-OM T63L31 2010 bis 2100 für die SRES-Szenarios B1, A1B und A2. *Publikationen des Umweltbundesamtes* 1–149.
- Svensson, M., Johansson, P., Thor, G., 2005. Lichens of wooden barns and *Pinus sylvestris* snags in Dalarna, Sweden. *Ann. Bot. Fennica* 42, 351–363.
- Thor, G., 1998. Red-listed lichens in Sweden: habitats, threats, protection, and indicator value in boreal coniferous forests. *Biodivers. Conserv.* 7, 59–72.
- Tibell, L., 1992. Crustose lichens as indicators of forest continuity in boreal coniferous forests. *Nordic J. Bot.* 12, 427–450.
- Uliczka, H., Angelstam, P., 1999. Occurrence of epiphytic macrolichens in relation to tree species and age in managed boreal forests. *Ecography* 22, 396–405.
- Uliczka, H., Angelstam, P., 2000. Assessing conservation values of forest stands based on specialised lichens and birds. *Biol. Conserv.* 95, 343–351.
- van Dobben, H.F., 1996. Decline and recovery of epiphytic lichens in an agricultural area in The Netherlands (1900–1988). *Nova Hedwigia* 62, 477–485.
- van Herk, C.M., Aptroot, A., van Dobben, H.F., 2002. Long-term monitoring in the Netherlands suggests that lichens respond to global warming. *Lichenologist* 34, 141–154.
- van Herk, C.M., Mathijssen, E.A.M., de Zwart, D., 2007. Long distance nitrogen air pollution effects on lichens in Europe. *Lichenologist* 35, 247–359.
- Werth, S., Tømmervik, H., Elvebakk, A., 2005. Epiphytic macrolichen communities along regional gradients in northern Norway. *J. Vegetation Sci.* 16, 199–208.
- Werth, S., Wagner, H.H., Gugerli, F., Holderegger, R., Csencsics, D., Kalwij, J.M., Scheidegger, C., 2006. Quantifying dispersal and establishment limitation in a population of an epiphytic lichen. *Ecology* 87 (8), 2037–2046.
- Windisch, U., Vorbeck, A., 1996. Flechten als Bioindikatoren der Luftgüte in Bayern. *Bayerisches Landesamt für Umweltschutz*.
- Wirth, V., Schöller, H., Scholz, P., Ernst, G., Feuerer, G., Gnüchtel, T., Hauck, A., Jacobsen, M., John, V., Litterski, B., 1996. *Rote Liste der Flechten (Lichenes) der Bundesrepublik Deutschland*. *Schriftenreihe für Vegetationskunde* 28, 307–368.