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Species diversity and species composition of epiphytic bryophytes and lichens – a comparison of managed and unmanaged beech forests in NE Germany

With one Figure and 7 Tables

Summary

The impact of forest management on the species diversity and species composition of epiphytic bryophytes and lichens in beech forests (*Fagus sylvatica*) of NE Germany was analysed. The investigations were carried out in one unmanaged and in one managed forest, with 45 sample plots of 400 m^2 each. In the sample plots, the presence of the epiphytes on 2–4 randomly chosen trees (100 trees per forest) and seven environmental variables were recorded. The total number of species and the mean lichen density per mantle area was higher in the unmanaged forest than in the managed forest. Regression analyses and DCA revealed the diameter at breast height (dbh) as the most important factor affecting the species diversity and species composition in both forest types. The dbh was positively correlated with the number of growth anomalies and with the bark roughness of the phorophytes and thus a good indicator for the habitat quality. Moreover, the light conditions had a significant impact on the species composition in both forests types and on the species diversity in the managed forest. In particular, epiphytes demanding shady conditions and a consistent humidity may suffer from the abrupt exposition to radiation and the lower humidity after logging. Species typical for the unmanaged forest and most rare species must be considered as stenoecious as they demand the shady and humid conditions of the forest interior and grow on old, large trees. With the aim of sustaining the diversity of epiphytic bryophytes and lichens, forest management should ensure the continuous occurrence of big trees above the target diameter. In addition, a single tree selection felling method should be applied to minimise strong changes in the microclimate.

Zusammenfassung

Artenvielfalt und Artenzusammensetzung epiphytischer Moose und Flechten – ein Vergleich zwischen bewirtschafteten und unbewirtschafteten Buchenwäldern in Nordostdeutschland

Der Einfluss der Bewirtschaftung auf die Artenvielfalt und Artenzusammensetzung epiphytischer Moose und Flechten in Buchenwäldern Nordostdeutschlands wurde analysiert. Die Untersuchungen erfolgten in einem unbewirtschafteten und einem benachbarten, bewirtschafteten Waldgebiet in jeweils 45 Untersuchungsflächen à 400 m^2. In den Untersuchungsflächen wurden die Stetigkeit der Epiphyten an jeweils zwei bis vier zufällig ausgewählten Trägerbäumen (100 Bäume je Waldtyp) sowie sieben Umweltvariablen aufgenommen. Im Naturwald waren die Gesamtartenzahl sowie die mittlere Artendichte der Flechten bezogen auf die Mantelfläche höher als im Wirtschaftswald. Die Regressionsanalysen und die DCA wiesen den Brusthöhendurchmesser (BHD) als den für die Artenvielfalt und Artenzusammensetzung bedeutsamsten Faktor aus. Der BHD korrelierte positiv mit der Anzahl an Wuchsanomalien und der Rindenrauigkeit der Trägerbäume und ist deshalb ein guter Indikator für die Habitatqualität. Weiterhin zeigten die Lichtverhältnisse einen signifikanten Einfluss auf die Artenzusammensetzung in beiden Waldtypen sowie auf die Artenvielfalt im Wirtschaftswald. Insbesondere schattentolerante und austrocknungsempfindliche Arten können durch die plötzliche Lichtstellung und Veränderung des Mikroklimas infolge forstlicher Eingriffe geschädigt werden. Die Arten mit deutlich höherer Stetigkeit im Naturwald sowie die meisten seltenen Arten gelten als stenök, da sie die schattigen und luftfeuchten Bedingungen eines geschlossenen Waldinnenklimas benötigen und überwiegend an alten, starken Bäu-

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men siedeln. Zur Erhaltung der Artenvielfalt epiphytischer Moose und Flechten sollten daher im Rahmen forstlichen Managements starke Bäume über den Zieldurchmesser hinaus erhalten werden. Weiterhin ist eine einzelstammweise Nutzung anzustreben, um Schwankungen im Mikroklima zu minimieren.

Introduction

Epiphytic bryophytes and lichens are an integral component of forest ecosystems and represent a characteristic part of the plant species diversity (LESICA et al. 1991). Moreover, epiphytic bryophytes and lichens have important ecosystem functions as they increase the structural complexity, influence nutrient cycles and moisture retention, and provide habitats, food and nest material for animals (RHOADES 1995).

Several studies have been conducted to analyse the habitat requirements of epiphytic bryophytes and lichens in temperate and boreal forest ecosystems (synopsis in AUDE & POULSEN 2000). Because bryophytes and lichens are poikilohydrous organisms, they are particularly sensitive to changes in the microclimatic conditions of their habitats (BARKMAN 1958; SÖDERSTRÖM 1988; CHEN et al. 1995). Some species occur exclusively in the moist, shaded forest interior and are less adapted to desiccation. Many populations of these species thus become extinct when atmospheric humidity decreases due to changes in the forest canopy structure (HALLINGBÄCK & HODGETTS 2000). Some epiphytic bryophytes and lichens, particularly the rare ones, are stenotopic and require a long habitat continuity, for example substrates such as old or large trees (GUSTAFSSON et al. 1992). These species are often characterized by low growth rates and low dispersal capacities (STEWARD 1995; SCHEIDEGGER et al. 2000). Moreover, bryophytes and lichens are particularly sensitive to atmospheric pollution (MULGREW & WILLIAMS 2000). Forest management and air pollution are considered to be the major threats for bryophytes and lichens in forests Europe-wide. In managed forests in particular, the population sizes of many bryophytes and lichens have decreased or populations have even become extinct because of the effects of silvicultural measures (HALLINGBÄCK & HODGETTS 2000; SCHEIDEGGER et al. 2000).

In recent years, several studies have analysed the effects of forest management on the species diversity and species composition of epiphytic bryophytes and lichens, mainly in coniferous forests in North America and Europe. Only a few studies have focused on beech (*Fagus sylvatica*) forest ecosystems, and many of them have only considered the bryophyte flora. In addition, there is a lack of studies that compare managed and unmanaged beech forest ecosystems.

The objective of this study is to analyse the effects of management on the species diversity and the species composition of epiphytic bryophytes and lichens in beech forests in the lowlands of northeastern Germany. The following questions have been addressed in our investigations:

(i) Which environmental variables determine the species diversity and the species composition of epiphytic bryophytes and lichens in unmanaged and managed beech forests?
(ii) Which species may serve as indicator species for unmanaged and managed beech forests?
(iii) What are the habitat requirements of these species?

Methods

Study area

Field studies were carried out in two forests (Serrahn, Wilhelminenhof) situated 10 km east of Neustrelitz, in the federal state of Mecklenburg-Vorpommern (53°20′–53°25′ N, 13°8′–13°13′ E). The climate of the study area is suboceanic with a mean annual precipitation of 584 mm and a mean annual temperature of 7.9 °C. Prevailing soil types in both forests are dystric cambisols, podzoluvisols and

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luvisols. The natural forest vegetation can be assigned to acidophytic beech forests (Luzulo-Fagetum) on dystric cambisols and podzoluvisols, and to mesophytic beech forests (Galio-Fagetum) on luvisols (forest types according ELLENBERG 1996). In the unmanaged beech forest Serrahn, a study site of 110 ha was investigated in which no silvicultural measures had been undertaken at least since 1961 (V. OHEIMB et al. 2004b). For comparison, we selected a nearby managed beech forest (Wilhelminenhof, 110 ha in size). In this forest, the shelterwood system is applied. Both forests are shown as forest areas on maps from the 17th century onwards, indicating that these areas have been forested at least since that time.

Sampling design

Our sampling design aimed to represent all structural types that had developed in the two forests. Based on the density and height structure of trees in the uppermost canopy layer, the cover of the canopy layer and the abundance of regeneration, the following developmental phases were distinguished in the unmanaged Serrahn forest: gap, innovation phase, aggregation phase, early biostatic phase, late biostatic phase and degradation phase (cf. OLDEMAN 1990; EMBORG et al. 2000; V. OHEIMB et al. 2004b). The spatial distribution of these developmental phases was registered in a texture map using colour infrared aerial photographs (program Microstation, AFL 1998). With this map, 45 circular sample plots of 0.1 ha were selected to represent the full range of developmental phases within the Serrahn beech forest. Each phase was represented by 10 sample plots, with the exception of the aggregation phase (5 plots) and the early biostatic phase which was not sampled because of its small spatial extent in Serrahn.

In the managed beech forest, 45 circular sample plots were similarly selected. Young stands were considered as the innovation and aggregation phases. Mature stands were assigned to one of the remaining developmental phases depending on the degree to which preparatory cuttings (thinning) and regeneration cuttings had been applied and regeneration had been established. The late biostatic phase was lacking here. Similar to the unmanaged forest, each phase was represented by ten sample plots with the exception of the aggregation phase (5 plots).

In each sample plot, two beech trees of the upper canopy were randomly chosen, and in the sample plots representing the aggregation phase four beech trees were examined. A total of 20 trees per developmental phase was thus analysed in both forest types. The total number of trees investigated amounts to 200 (i.e. 100 in the unmanaged, and 100 in the managed forests).

Data collection

On the selected trees, the presence of all epiphytic bryophytes and lichens was recorded from the trunk base to a height of 2 m during winter and spring 2003. The nomenclature follows KOPERSKI et al. (2000) for bryophytes and SCHOLZ (2000) for lichens. Specimens of the genus *Orthotrichum* are treated as *Orthotrichum* sp. because of the lack of fertile plants. *Hypnum cupressiforme* agg. comprises *Hypnum cupressiforme* and *Hypnum andoi*.

In addition, we recorded

- diameter at breast height (dbh, measured at 1.3 m height), trees designated as big or large have a dbh above 70 cm;
- bark texture at 0–2 m above ground level in a 3-stage ordinal scale: 1: smooth, 2: lightly fissured, 3: strongly fissured;
- number of growth anomalies (scars, tumours, wounds, cavities, epicormic branches) at 0–2 m above ground level.

In each sample plot the following environmental variables were recorded:

- basal area and number of all living trees with a dbh $\geq$ 7 cm (tree density);
- cover of the tree and shrub layer, estimated in percent.

Data analysis

In this study, the term “species diversity” is both used for the total number of species on 100 trees and for the species number per tree. For the comparison of the mean species numbers per tree between the two forest types, we eliminated the species-area effect caused by the different mean dbh of these types by calculating the species density per 1 m^2 for each tree. The relationship between species number (S) and surface area (A) can generally be described by a power function ($S = c \cdot A^z \cdot \log S = \log c + z \cdot \log A$) or an exponential function ($S = k \cdot \log A$; cf. review in DOLNIK 2003). Applying these functions to our data, showed that the relationship between the number of epiphyte taxa and the tree mantle area can be more appropriately described with a power function ($R^2 = 0.575$) than with an exponential function ($R^2 = 0.434$). We thus used the slope of the regression function in the log-log space ($z = 0.459$) to interpolate species numbers to 1 m^2.

Differences between the species densities in the unmanaged and managed forests were tested for statistical significance with the Mann-Whitney U-Test. Spearman rank correlation was applied to detect highly correlated and thus redundant environmental variables. The threshold value for deciding on redundancy was set to a correlation coefficient of 0.8. As none of the correlation coefficients exceeded $r = 0.8$, all of them were used for the further analyses.

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The impact of environmental variables on the species number per tree was analysed with a stepwise multiple regression, considering the species number per tree as dependent variable. This analysis was carried out separately for the trees of the unmanaged and managed forests. All metric data were log transformed before analysis to minimise skewness and to ensure that variables are approximately normally distributed (Zar 1999).

The impact of environmental variables on the species composition was analysed by a Detrended Correspondence Analysis (DCA; using CANOCO version 4.0, Braak & Šmilauer 1998). Only species occurring on at least four trees were included in the analysis following the suggestions of Braak & Prentice (1988). Correlations between the sample scores and the environmental variables are shown with a biplot diagram (cf. Braak & Šmilauer 1998). To detect indicator species, differences in presence degrees between the two forest types were tested with two-tailed χ^2-test. Fisher's exact test was used when one of the expected presence degrees in the contingency table was less than five (Zar 1999). Indicator species are defined as species with statistically significantly higher frequencies in one of the forests. In addition, all species occurring on four trees and restricted to one of the forests were also considered as an indicator species (although the significance level of Fisher's exact test then amounts to 0.06).

To identify the habitat preferences of indicator species in the two forest types, presence-absence values of these species were related to environmental variables by performing a stepwise logistic regression. Selection of predictors was stopped when none of those remaining resulted in a model improvement at 0.05 significance level.

Ecological preferences of species were assessed using indicator values for light, moisture and substrate reaction (Ellenberg et al. 2001). For the toxitolerance of bryophytes we refer to Frahm (1998) and Franzen (2001), and for lichens to Ellenberg et al. (2001). To compare the ecological preferences of the indicator species of the two forest types we calculated the mean indicator values as recommended by Dzwonko (2001). For checking the differences between the mean indicator values the Mann-Whitney U-Test was used. The classification of life strategy types for bryophytes according to the approach of During (1992) follows Dierssen (2001). With the exception of the DCA, all statistical analyses were executed in SPSS version 11.5 (Anonymous 2001).

Results

Environmental variables

Table 1 gives an overview of the mean values, standard deviation and range of the environmental variables. The correlation between these variables are shown in Table 2 (Spearman rank correlations).

Species diversity

A total of 58 taxa was recorded on the 200 trees, 32 bryophytes and 26 lichens. The total diversity was higher in the unmanaged forest than in the managed forest (Table 3), but 60% of the species recorded in the unmanaged forest were found on less than four trunks. The mean number of all species and the mean number of bryophytes did not differ significantly between the unmanaged and managed forests. The mean number of lichens was significantly higher in the unmanaged forest (Table 3).

Table 1

Arithmetic means and standard deviations (SD) for metric environmental variables, and number per class and range for ordinally scaled variables; unmanaged forest: Serrahn, managed forest: Wilhelminenhof; *n* of trees investigated per forest = 100, *n* of sample plots per forest = 45

Variable (abbreviation), unit	Scale	Serrahn		Wilhelminenhof	
		Mean values ± SD	Range	Mean values ± SD	Range
Diameter at breast height, cm	tree	51 ± 28	2–107	46 ± 22	1–94
Bark texture	tree	1: 36; 2: 28; 3: 36	1–3	1: 48; 2: 39; 3: 13	1–3
Number of growth anomalies	tree	0.9 ± 1.0	0–3	0.5 ± 0.8	0–3
Basal area, m^2/ha	plot	25 ± 9	7–49	25 ± 8	2–37
Tree density, number of trees/ha	plot	270 ± 260	40–1030	390 ± 680	20–2510
Cover of tree layer, %	plot	64 ± 28	5–95	64 ± 27	5–95
Cover of shrub layer, %	plot	8 ± 14	0–70	6 ± 17	0–70

Table 2
Spearman rank correlation matrix of the environmental variables
Abbreviations: dbh–diameter at breast height, bark–bark texture, growth–number of growth anomalies, bas area–basal area, tdens–tree density, tlay–cover of tree layer, slay–cover of shrub layer
Statistically significant correlations in boldface characters ($p < 0.05$)

	dbh	bark	growth	bas area	tdens	tlay
bark	**0.51**					
growth	**0.23**	**0.23**				
bas area	0.08	0.00	0.07			
tdens	**−0.32**	**−0.17**	−0.14	**0.28**		
tlay	−0.12	−0.01	0.00	**0.43**	**0.71**	
slay	−0.01	0.03	−0.12	**−0.32**	0.13	−0.14

For both forests, diameter at breast height (dbh) was the most important variable explaining the number of species per tree (Table 4), species number per tree increased with increasing dbh. In addition, for the managed forest tree density was significantly positively related to the species number per tree.

Species composition

The first two DCA axes explained 29% of the total variance of species data (total inertia = 2.322, length of gradients 3.54 and 4.15 SD units, respectively). The first axis (eigenvalue 0.49) mainly represented a light gradient and a gradient in the diameter of the trees (Fig. 1). On this axis, light-demanding species (*Ptilidium pulcherrimum, Hypogymnia physodes, Parmeliopsis ambigua, Hypocenomyce scalaris*) were placed at the low score end. In addition, these species occurred mainly on trees with high diameters (mean dbh 55 to 63 cm). By contrast, shade tolerant species growing on trees with low diameters such as *Porina aenea* (mean dbh 25 cm) were characterized by high scores on the first axis. The second axis (eigenvalue 0.19) was negatively correlated with the number of growth anomalies and with the bark texture. Along this axis, *Brachythecium rutabulum* and *Metzgeria furcata* showed the lowest species scores, and *Plagiothecium laetum* var. *curvifolium* and *Lophocolea heterophylla* were placed at the high score end (Fig. 1).

Indicator species for the unmanaged and managed forests

Five species had significantly higher presence degrees in the unmanaged forest than in the managed forest (*Brachythecium rutabulum, Chaenotheca furfuracea, Dimerella pineti, Graphis scripta, Pyrenula nitida*). Four species (*Aulacomnium androgynum, Lecanora expallens, Parmeliopsis ambigua, Ptilidium pulcherrimum*) showed significantly higher presence degrees in the managed forest (Table 5).

Table 3
Total surface areas, total number of taxa per 100 trunks and mean density of taxa per 1 m^2; ± standard deviation) for bryophytes and lichens in the unmanaged and managed forests Statistically significant differences in boldface characters ($p < 0.05$)

	Unmanaged forest	Managed forest
Total surface area (m^2)	345	296
Total number of species	49	35
Total number of bryophytes	27	18
Total number of lichens	22	17
Mean density of taxa	2.9 ± 1.1	2.7 ± 1.0
Mean density of bryophytes	1.7 ± 1.2	1.5 ± 0.9
Mean density of lichens	**1.1 ± 1.0**	**0.8 ± 0.9**

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Table 4
Multiple regression models for the unmanaged and managed forests, with species number per tree as dependent variable and the environmental parameters of Table 1 as predictor variables

	Variables	*r*	adjusted r^2	*F*	beta	*p*
Unmanaged forest	diameter at breast height	0.75	0.57	127.51	0.75	< 0.001
Managed forest	diameter at breast height	0.80	0.63	73.32	0.58	< 0.001
	tree density				0.32	< 0.001

The presence of indicator species for the unmanaged forest was related to four variables: cover of shrub layer, dbh, number of growth anomalies and tree density (Table 6). According to the results of the logistic regression, the probability of the occurrence of these species increased with increasing cover of the shrub layer, with an increasing dbh, with an increasing number of growth anomalies and with an increasing tree density.

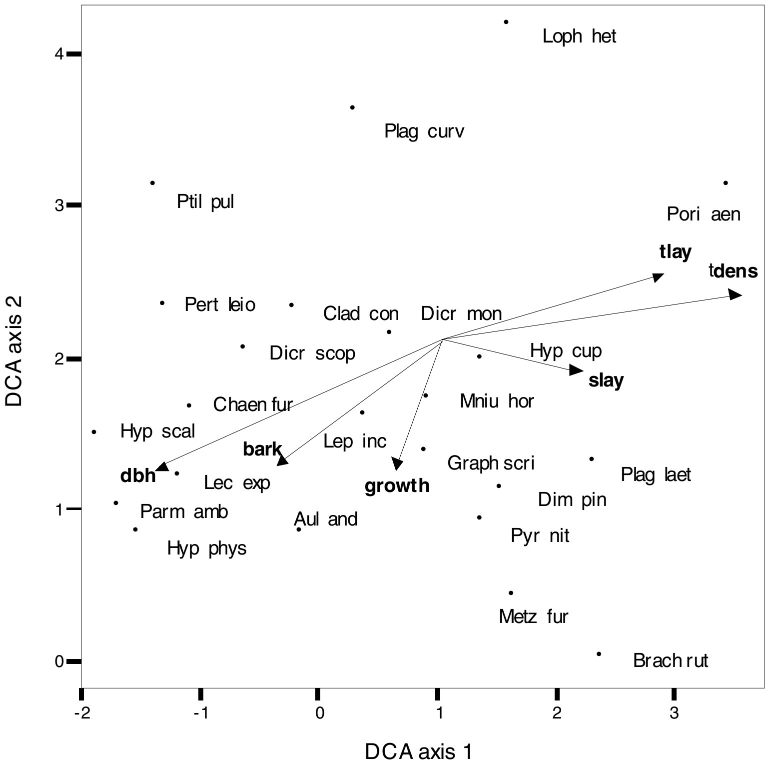

Fig. 1
DCA ordination (biplot) of epiphytic bryophytes lichen s (occurring at least on four trees; $n = 23$). Vectors indicate correlations between tree scores (trees investigated; $n = 200$) and corresponding environmental variables; only correlations significant at the level of $p < 0.05$ are considered

Abbreviations of species names: Aul and: *Aulacomnium androgynum*, Brach rut: *Brachythecium rutabulum*, Chaen fur: *Chaenotheca furfuracea*, Clad con: *Cladonia coniocraea*, Dicr mon: *Dicranum montanum*, Dicr scop: *Dicranum scoparium*, Dim pin: *Dimerella pineti*, Graph scri: *Graphis scripta*, Hyp cup: *Hypnum cupressiforme* agg., Hyp scal: *Hypocenomyce scalaris*, Hyp phys: *Hypogymnia physodes*, Lec exp: *Lecanora expallens*, Lep inc: *Lepraria incana*, Loph het: *Lophocolea heterophylla*, Metz fur: *Metzgeria furcata*, Mniu hor: *Mnium hornum*, Pert leio: *Pertusaria leioplaca*, Parm amb: *Parmeliopsis ambigua*, Plag curv: *Plagiothecium laetum* var. *curvifolium*, Plag laet: *Plagiothecium laetum* var. *laetum*, Pori aen: *Porina aenea*, Ptil pul: *Ptilidium pulcherrimum*, Pyr nit: *Pyrenula nitida*

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Table 5
Presence degrees of epiphytes on *Fagus sylvatica* in the unmanaged (Serrahn = S) and the managed forests (Wilhelminenhof = W; 100 trees per forest). Significantly higher presence degrees in one of the forests in bold type (χ^2-test or Fisher's exact test: $^{\#}$ $p = 0.06$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). Values in parentheses give presence degrees (absolute values) of species on trees with a dbh ≥70 cm (unmanaged forest $n = 26$, managed forest $n = 6$ trees)
Abbreviations: (e): – endangered species according to LUDWIG et al. (1996), WIRTH et al. (1996); (i) – indicator species for ecological continuity or forest continuity according to ROSE (1976) and PRINTZEN et al. (2002); L – light indicator value, M – moisture indicator value; R – reaction indicator value according to ELLENBERG et al. (2001); T – toxitolerance indicator value according to ELLENBERG et al. (2001), for lichens and FRAHM (1998) and FRANZEN (2001) for bryophytes; LS – life strategy types according to DIERSSEN (2001): c – colonists, cp – pionier colonists, s – short-lived shuttle, p – perennials, pc – competitive perennials, ps – stress tolerant perennials, l – long-lived shuttle

Species	S	W	L	M	R	T	LS	Species	S	W	L	M	R	T	LS
Hypnum cupressiforme agg.	87 (26)	82 (6)	–	–	–	–	ps	*Cladonia fimbriata*	0	2	7	×	4	–	
Dicranum montanum	71 (25)	74 (5)	6	5	2	5	pc	*Dicranoweisia cirrata*	0	2	7	5	5	8	cp
Lepraria incana	72 (24)	71 (6)	4	3	3	9		*Dicranum tauricum*	2 (2)	0	4	4	3	8	pc
Lophocolea heterophylla	29 (13)	41 (2)	4	4	3	7	cp	*Isothecium alopecuroides*	2 (1)	0	5	5	6	4	ps
Porina aenea	27 (3)	20	3	4	5	7		*Plagiothecium succulentum*	2	0	5	6	2	–	pc
Dicranum scoparium	30 (12)	20 (1)	5	4	4	8	pc	*Pohlia nutans*	1 (1)	1	5	4	2	–	cp
*Brachythecium rutabulum**	**30** (9)	18	5	4	×	8	cp	*Herzogiella seligeri*	1	1	5	5	4	–	ps
Cladonia coniocraea	30 (12)	19 (1)	5	×	4	–		*Xanthoria candelaria*	0	2	7	3	6	5	
Plagiothecium laetum var. *curv.*	11 (7)	18 (2)	5	4	2	–	pc	*Brachythecium salebrosum*	1	0	6	4	6	–	cp
*Dimerella pineti***	**21** (9)	6 (2)	3	4	4	6		*Bryum subelegans*	1 (1)	0	5	5	6	8	c
*Lecanora expallens***	5 (3)	**17** (1)	5	3	4	9		*Cladonia macilenta*	1	0	7	×	2	–	
Metzgeria furcata (e)	13 (3)	10	5	4	6	3	p	*Dicranum fuscescens*	1	0	7	6	2	–	pc
*Graphis scripta**** (e, i)	**17** (3)	2	3	4	5	5		*Eurhynchium striatum*	1	0	5	5	6	–	p
*Pyrenula nitida**** (e, i)	**14** (2)	1	3	4	5	5		*Frullania dilatata* (e)	1	0	8	4	5	2	l
Hypogymnia physodes	6 (2)	8 (1)	7	3	3	8		*Isothecium myosuroides*	1 (1)	0	4	6	4	4	ps
*Parmeliopsis ambigua**	3 (1)	**10** (1)	6	5	2	7		*Homalothecium sericeum*	1	0	8	2	7	5	p
Hypocenomyce scalaris	5 (2)	3	6	3	2	8		*Lecanora argentata* (e, i)	1 (1)	0	5	4	5	4	
Mnium hornum	4 (1)	3	5	6	3	–	l	*Lecanora chlarothera*	0	1	6	3	6	6	
Ptilidium pulcherrimum $^{\#}$	0	**4**	7	5	2	7	s	*Lepidozia reptans*	0	1	4	5	2	–	cp
Aulacomnium androgynum$^{\#}$	0	**4**	4	5	2	–	c	*Melanelia glabratula*	1	0	–	–	–	–	
Chaenotheca furfuracea$^{\#}$ (e, i)	**4** (2)	0	3	4	3	3		*Opegrapha atra* (e)	1	0	4	4	5	6	
Orthotrichum sp.	2	1	–	–	–	–		*Platygyrium repens* (e)	0	1 (1)	6	6	4	6	ps
Pertusaria leioplaca (e, i)	2 (2)	2 (1)	4	4	5	5		*Pertusaria hymenea* (e, i)	1	0	5	5	5	3	
Plagiothecium laetum var. *laetum*	1 (1)	3	4	4	2	–	ps	*Phlyctis argena*	1	0	5	3	5	6	
Arthonia spadicea (e, i)	2	1	2	4	4	5		*Physcia adcendens*	0	1	7	3	7	8	
Ceratodon purpureus	2	1	8	2	×	9	c	*Plagiothecium nemorale*	1 (1)	0	4	6	5	–	p
Cladonia digitata	3	0	5	×	2	8		*Platismatia glauca* (e)	1	0	7	5	2	5	
Lecanora conizaeoides	1 (1)	2	7	3	2	9		*Polytrichum formosum*	1	0	4	6	2	–	pc
Plagiothecium denticulatum	2 (1)	0	5	4	5	–	pc	*Tetraphis pellucida*	1	0	3	6	1	–	cp

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Table 6
Logistic regression relating the presence degrees of indicator species for the unmanaged forest and the managed forest to environmental variables
Important predictor variables: slay = cover of shrub layer (%), dbh = diameter at breast height (cm), growth = number of growth anomalies, tdens = tree density (number of trees/ha), tlay = cover of tree layer (%)

	Environmental variable	Nagelkerkes r^2	p
Indicator species unmanaged forest	cover of shrub layer	0.24	0.012
	diameter at breast height		0.037
	number of growth anomalies		0.012
	tree density		0.001
Indicator species managed forest	cover of tree layer	0.30	< 0.001
	cover of shrub layer		0.001

Two predictor variables (cover of tree and shrub layer) were important for the explanation of the occurrence of typical species for the managed forest. The probability of the occurrence of these species increased with a decreasing cover of the tree and shrub layer in the sample plots (Table 6).

The mean indicator values for light differed significantly between the indicator species of the unmanaged and managed forests. Indicator species of the unmanaged forest indicated shade conditions, whilst indicator species of the managed forest prefered semi-shade to semi-light conditions. The mean values for moisture, reaction and toxitolerance showed no significant differences, but there was a tendency for the indicator species of the managed forest to tolerate more acid substrates and to be more toxitolerant (Table 7).

Discussion

Species diversity, species composition and determination of environmental variables

The higher total species number of the unmanaged compared to the managed forest (Table 3) is caused by the high number of rare species (occurring on less than four trees; Table 5). Several factors may account for the differences in species diversity patterns between the two forest types:

- differences in the diameter distribution and in the density of large trees;
- the heterogeneity of microsites (habitat availability) and the habitat quality;
- factors influencing the dispersal of diaspores;
- different sized pools of species that are able to colonise the two forest types.

As shown in Table 3, the total tree mantle area is higher in the unmanaged forest than in the managed forest, mostly caused by a higher density of large trees (Table 5). This may be considered as a structural feature of unmanaged stands, which generally show higher mean diameters and higher densities of large trees than managed forests (HALE et al. 1999; SCHUMACHER 2000; TABAKU 2000). In most managed beech stands in Central Europe, the target diameter harvesting leads to the continuous removal of trees with a dbh above the threshold value of 60 cm (DÖBBELER 2004). As species diversity is area-related, the higher tree

Table 7
Comparison of mean indicator values (light, moisture, reaction, toxitolerance) of the indicator species of the unmanaged forest (*Brachythecium rutabulum, Dimerella pineti, Graphis scripta, Pyrenula nitida, Chaenotheca furfuracea*) and the managed forest (*Lecanora expallens, Parmeliopsis ambigua, Ptilidium pulcherrimum, Aulacomnium androgynum*)
Statistically significant differences in boldface characters ($p < 0.05$)

	Light	Moisture	Reaction	Toxitolerance
Indicator species unmanaged forest	**3.4** ($n = 5$)	4.0 ($n = 5$)	4.3 ($n = 4$)	5.4 ($n = 5$)
Indicator species managed forest	**5.5** ($n = 4$)	4.5 ($n = 4$)	2.5 ($n = 4$)	7.3 ($n = 3$)

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mantle area in the unmanaged forest contributes to a higher species diversity. However, the species density was higher in the unmanaged forest for all taxa and for bryophytes, and even significantly higher for lichens (Table 3). The higher total species number in the unmanaged forest thus cannot be a simple area effect. We suppose that the heterogeneity of microsites (i.e. the habitat availability) and the habitat quality affect the species diversity and composition in both forest types.

The dbh was found to be the most important factor affecting the species number per tree and the species composition in both forest types (Fig. 1; Table 4). Moreover the dbh represents information on particular habitat qualities which are related to the dbh. The bark texture becomes increasingly fissured and growth anomalies (e.g. scars, tumours) are more frequent on trees with high dbh. In addition, the dbh is positively related to the age of a tree (V. OHEIMB et al. 2003). Big trees are thus characterized by a larger heterogeneity of microsites and are providing habitats for species with particular ecological requirements. This result is in agreement with the findings of AUDE & POULSEN (2000), SCHUMACHER (2000) and MCGEE & KIMMERER (2002), who also observed an increasing number of species with an increasing phorophyte diameter. As shown in Table 5, the total number of species is related to the high number of large trees with a dbh exceeding 70 cm, particularly in the unmanaged forest. In addition, the occurrence of many of the rare species is restricted to these trees. This suggests that many of the rare species must be considered as stenotopic, as they have particular habitat requirements only to be found on old or large trees. As these microsites are absent in most of the managed forests in Central Europe due to the lack of large trees, many of them are now red-listed. In our study, 75% of the red-listed species are significantly more frequent in the unmanaged forest or are even restricted to it.

With increasing diameter, the physical and chemical bark conditions also change continuously (BARKMAN 1958). Changing habitat conditions during a continuous dilatation growth may lead to a succession of epiphytes and thus to change in the species composition on a single tree (AUDE & POULSEN 2000). For example, the occurrence of subneutrophytic species such as *Pyrenula nitida* (found on trees with a mean dbh of 59 cm) and *Metzgeria furcata* (mean dbh 53 cm) in rough-barked or wounded stem areas of large trees indicates a change of chemical bark properties with increasing diameter. Measurements of the pH value of their localities on *Fagus sylvatica* in Serrahn revealed median values of 6.2 for *Pyrenula nitida* and of 5.5 for *Metzgeria furcata* (FRIEDEL & MÜLLER 2004). An increase in the primarily moderately acid pH-value of smooth *Fagus* bark (pH 4.9 to 5.6, WIRTH 1980) due to the exudation of basic wound sap was also pointed out by MÜLLER (1993). Chemical bark properties as relevant site parameters for epiphytes have also been emphasised by HOBOHM (1998), KOPERSKI (1998) and ERNST & HANSTEIN (2001). In general, the relatively smooth *Fagus* bark becomes less resinous and more porous and absorbent with increasing age and size of the tree (BARKMAN 1958). This facilitates the settlement of bryophyte and lichen species (HOLIEN 1997; SCHUMACHER 2000). DCA and regression analyses thus revealed the dbh, bark texture and number of growth anomalies as important parameters affecting the species diversity and composition in the forests investigated (Fig. 1; Table 4), particularly as regards the indicator species for the unmanaged forest (Table 6).

Furthermore are the cover of the tree layer and the tree density as an expression of the light conditions important parameters affecting the species composition (Fig. 1). All the species found in the sample plots show a wide range of their light indicator values (Table 5), and the two variables mentioned are closely related to the first DCA axis. Moreover, the tree density as a surrogate for the light conditions was positively associated with the species diversity in the managed forest (Table 4). Light conditions may have different effects on the species diversity and composition of the epiphytes. The irradiance levels influence the photosynthetic rates (GAUSLAA & SOLHAUG 2000) and affect the evapotranspiration of the plants as well as the humidity and temperature of their habitats (SCHWERDTNER & CORDES 1992). According to the Ellenberg indicator values for light conditions, 60% of all species in the forests require shade to half-shade condi-

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tions (Table 5). All of these sciophytes were found in the unmanaged forest, but 40% of them were lacking in the managed forest. The decreasing epiphyte number with decreasing tree densities in the managed forest may be caused by the abrupt opening of the canopy after logging. In particular, epiphytes favouring half-shade to shade conditions with a consistent humidity may suffer from this (ESSEEN & RENHORN 1998; VELLAK & PAAL 1999; NEWMASTER & BELL 2002). As pointed out by CHEN et al. (1995), preparation and regeneration cutting result in an abruptly increased incoming radiation, a greater variation in air temperature and lower humidity. In particular, the high variability of light conditions in managed forests in space (cf. Table 1 for the variable "tree density") may damage bryophyte and lichen species adapted to more consistent light und humidity conditions (STEWARD 1995; SCHEIDEGGER et al. 2000).

Several authors have stressed the importance of dispersal capacities for the species diversity and composition of bryophytes and lichens. In our study, the life strategy types for the bryophytes (according to DIERSSEN 2001) revealed a higher proportion of perennials and long-lived shuttle species (73%) in the unmanaged forest than in the managed forest (47%), but a lower proportion of colonists (27% in the unmanaged forest, 53% in the managed forest, Table 5). We interpret this as a consequence of the higher number of old and large trees and a longer habitat continuity in the unmanaged forest (cf. PETERSON & MCCUNE 2001; DETTKI & ESSEEN 2003). As pointed out by STEWARD (1995) and SCHEIDEGGER et al. (2000), stenotopic bryophytes and lichens with low dispersal capacities, which are often rare, require a long habitat continuity, for example substrates such as old or large trees. Time is needed for species to disperse from the nearest source (TIBELL 1992), and the larger the diameter, i.e. the older the tree, the more time species have had for colonising it. The dispersal strategies of the lichens were not considered in this study because they are unknown for most of the species recorded, and the role of dispersal limitations clearly requires additional research. However, if dispersal limits the distribution of species, their restriction to large and old trees may reflect a greater amount of time and surface area available for intercepting propagules (MCGEE & KIMMERER 2002).

The effect of the species pool (PÄRTEL et al. 1996) on species diversity patterns of bryophytes in unmanaged and managed forests is difficult to assess as estimates of the size of the species pool of epiphytic bryophytes typical for (beech) forest ecosystems are not yet available. We consider that the effect of this parameter on the species diversity of bryophytes is comparatively low, as the species diversity of bryophytes per area unit differs only insignificantly between the unmanaged and managed forests (Table 3). This means that the number of woodland bryophytes indicating shady conditions, mesic substrate reaction and intermediate substrate pollution equals the number of more light demanding, acidophytic and toxitolerant species. By contrast, the species diversity of lichens per area unit is significantly higher in the unmanaged forest (Table 3). We consider that this is partly due to a larger species pool of stenotopic lichens finding appropriate conditions in unmanaged forests (Table 5). In NE Germany (Mecklenburg-Vorpommern), 60% of the epiphytic lichens on beech (*Fagus sylvatica*) are red-listed (LITTERSKI 1999). In our study, 78% of the lichens with a significantly higher or restricted abundance in the unmanaged forest are red-listed. These species can be characterised as stenotopic lichens (i.e. shade tolerant and toxiphobous) and a few of them have been characterised as indicators for ecological continuity (see below). As pointed out by BARKMAN (1958), there are more hygrophytic and more toxiphobous species among the woodland lichens as there are among the woodland bryophytes. HOMM & DE BRUYN (2000) also characterised the epiphytic woodland lichen flora as stenoecious in terms of their demands for a humid microclimate and habitat continuity.

Habitat requirements of indicator species of the unmanaged and managed forests

The results of the logistic regressions (Table 6) and the comparison shown in Table 7 supports the hypothesis that indicator species for unmanaged forests are shade-tolerant and/or stenotopic, requiring a humid microclimate and microsites mainly found on old, large trees (HOLIEN 1997; KUUSINEN & SIITONEN 1998;

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AUDE & POULSEN 2000; SCHUMACHER 2000). The crustose lichen *Chaenotheca furfuracea* in particular is restricted to trees with a high dbh. This toxiphobous species was observed in the protected deep bark fissures and root cavities of very large trees (mean dbh 73 cm) and was also classified by HAUCK (1998) and HOLIEN (1997) as a shade-tolerant specialist in cavities. The lichens *Pyrenula nitida* and *Graphis scripta* are characterised as moderately acidophytic to subneutrophytic (ELLENBERG et al. 2001). We mainly found these species on hygric and basified stem areas due to the exit of basic wound sap on trees with growth anomalies such as wounds or scars (cf. V. OHEIMB et al. 2004b). The lichens *Pyrenula nitida, Chaenotheca furfuracea* and *Graphis scripta* are also categorised as indicator species for ecological continuity and forest continuity (ROSE 1976; PRINTZEN et al. 2002). As a consequence of their habitat requirements these three species are generally rare (PYKÄLÄ 2004) and are red-listed. Among the indicator species for the unmanaged forest, *Brachythecium rutabulum*, an ubiquitous and highly toxitolerant bryophyte (NEBEL & PHILIPPI 2001), was observed mainly on root collars. According to SCHUMACHER (2000), this species is a facultative epiphyte, but it is one of the most abundant species on deadwood in beech forests in Central Europe. We therefore consider that the dispersal of this species is promoted by the high quantity and density of deadwood in the unmanaged forest.

By contrast, none of the indicator species for the managed forest (*Lecanora expallens, Parmeliopsis ambigua, Ptilidium pulcherrimum, Aulacomnium androgynum*) is red-listed or can be assessed as a specialist. According to Tables 6 and 7, these species grow at sites with half-shade to half-light conditions and open stand structures. As a consequence, their sites receive higher nutrient and pollutant depositions than the forest interior (WEATHERS et al. 1995). The tendency for a higher toxitolerance in these species is confirmed by Table 7.

Conclusions

In summary, the heterogeneity of microsites (correlated with the dbh, bark texture and growth anomalies of trees) was the most important factor influencing the species diversity and composition of epiphytic bryophytes and lichens in unmanaged and managed forests. In addition, cover of tree and shrub layer as well as the tree density as an expression of the light conditions were of great importance for the species composition, but had a minor impact on the species diversity. Indicator species for unmanaged forests were shade-tolerant and stenotopic, requiring particular microsites which are primarily to be found on trees with a high dbh.

Forest management should therefore ensure the continuous presence of large and old, rough-barked trees with particular growth anomalies to sustain or enhance the diversity of epiphytes. This may be obtained by the single tree selection felling method. As shown by ATLEGRIM & SJÖBERG (2004), this felling method mimics the natural disturbances of small scale gap dynamics. Strong changes in the microclimate due to increased radiation, wind and desiccation could thus be minimised.

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