

This is an author produced version (Accepted Author Manuscript according to Elsevier's article posting policy) of a paper published in *Ecological Indicators*. This paper has been peer-reviewed and is proof corrected, but does not include the journal pagination.

Citation for the published paper:

Mölder, A., Schmidt, M., Schönfelder, E., Engel, F., Schulz, F., 2015. Bryophytes as indicators of ancient woodlands in Schleswig-Holstein (Northern Germany). *Ecological Indicators* 54, 12–30.

<http://dx.doi.org/10.1016/j.ecolind.2015.01.044>

Access to the published version may require journal subscription.

Available at <http://dx.doi.org/10.1016/j.ecolind.2015.01.044>

Should be cited as

Mölder, A., Schmidt, M., Schönfelder, E., Engel, F., Schulz, F., 2015. Bryophytes as indicators of ancient woodlands in Schleswig-Holstein (Northern Germany). *Ecological Indicators* 54, 12–30.

Andreas Mölder^{1*}, Marcus Schmidt¹, Falko Engel¹, Egbert Schönfelder¹, Florian Schulz²

Bryophytes as indicators of ancient woodlands in Schleswig-Holstein (Northern Germany)

¹Northwest German Forest Research Station

Department A (Forest Growth)

Section Forest Conservation and Natural Forest Research

Grätzelstraße 2

D-37079 Göttingen

Germany

²Schulstraße 43

D-21465 Reinbek

Germany

*corresponding author

Phone: +49 551 69 401 313

Fax: +49 551 69 401 160

E-mail: moelder@gmx.de

Abstract

Ancient woodlands, with their long ecological continuity, frequently harbor a high number of typical, rare and threatened species, and are therefore of particular importance for nature conservation. To pinpoint these habitats, a common application is the use of plants as “ancient woodland indicators”. The occurrence of these particular species allows for evaluating the continuity of woodland cover in time. While lists of ancient woodland vascular plants have been derived for many regions, the identification and use of bryophytes as ancient woodland indicators has been widely neglected. This is a bit surprising because certain woodland bryophytes are very sensitive to varying environmental conditions or changes in land management. It therefore appeared promising to compile an ecologically grounded list of ancient woodland indicator bryophytes for practical use.

In this study, we present a set of ancient woodland indicator bryophytes based on the analysis of datasets from the North German federal state of Schleswig-Holstein. To compile this list, we systematically evaluated the bryophyte distribution data from floristic surveys in relation to ancient woodland cover data from state-wide inventories. In this way, we were able to determine ancient woodland bryophytes using consistent and repeatable statistical methods.

The presented list of 31 ancient woodland indicator bryophytes is ecologically sound and corresponds well with data from the sparse literature. We could distinguish two groups of ancient woodland indicator bryophytes. The first group is linked to base-rich, semi-natural deciduous woodlands with high soil and air humidity. The second group comprises acidophilic bryophytes that occur not only in acidic beech and oak woods, but also in acidic mixed or coniferous forests on ancient woodland sites. Apart from the ancient woodland indicator bryophytes, we could identify one group of recent woodland bryophytes and four groups of bryophytes that are more or less indifferent with respect to woodland continuity.

Finally, we provide recommendations for the application of ancient woodland indicator bryophytes in nature conservation practice. Management suggestions for the conservation of the typical bryophyte diversity of ancient semi-natural woodlands are also given.

Keywords:

forest management, liverworts, mosses, nature conservation, recent woodland, woodland continuity

Highlights:

- o Bryophytes as ancient woodland indicators have been widely neglected until now.
- o We closed this gap by evaluating bryophyte distribution and ancient woodland data.
- o We compiled an ecologically grounded list of ancient woodland indicator bryophytes.
- o Area of applicability: Schleswig-Holstein and the adjoining Pleistocene lowlands.
- o We provide implications for nature conservation and forestry practice.

1. Introduction

The use of plants as ecological indicators is an important topic of applied vegetation research. Since the occurrence of many plant species is bound to certain site conditions or shows a linkage to the intensity of land use, indicator species lists have been developed for many purposes (Ferris and Humphrey, 1999; Ellenberg et al., 2001; Diekmann, 2003; Nordén et al., 2007; Culmsee et al., 2014). In European forest nature conservation, a common application is the use of particular plants as “ancient woodland indicators”. The occurrence of these species allows for evaluating the continuity of woodland cover in time (Peterken, 1974; Rose, 1999; Hermy and Verheyen, 2007; Schmidt et al., 2014). Since woodlands with long ecological continuity frequently harbor a high number of typical, rare and threatened species, they are of particular importance for nature conservation (Hermy et al., 1999; Grove, 2002; Rolstad et al., 2002; Buse, 2012; Bhagwat et al., 2014).

The term “ancient woodland” indicates land that has been continuously wooded for several centuries. However, the length of this time span is not consistently defined among different regions. In the British definition, ‘ancient woodland’ describes land that has been continuously wooded since at least 1600 AD (Spencer and Kirby, 1992; Goldberg et al., 2007; Stone and Williamson, 2013). In Central Europe the term “ancient woodland” refers to land that has been continuously wooded since at least 1800 AD, since it is only from this point on that area-wide coverage data on historically old woodland sites are available. In contrast, the term “recent woodland” is used for woodland established after 1800 AD (Wulf, 2003; Glaser and Hauke, 2004; Buse, 2012; Matuszkiewicz et al., 2013). The Central European definition is applied in this study.

While lists of ancient woodland vascular plants have been derived for many regions or even on the supra-regionally scale (Hermy et al., 1999; Rose, 1999; Schmidt et al., 2014), the identification and use of bryophytes as ancient woodland indicators has been the subject of only a few studies (Rose, 1992; Gustafsson et al., 1992; Bates et al., 1993; Homm, 1999; Nitare, 2000; Woodland Trust, 2007; Fichtner and Lüderitz, 2013). This is a bit surprising because certain woodland bryophytes are very sensitive to varying environmental conditions or changes in land management (Ratcliffe, 1968; Laaka, 1992; Nordén and Appelqvist, 2001; Fenton and Frego, 2005; Schulz and Dengler, 2006; Baldwin and Bradfield, 2007; Kriebitzsch et al., 2013). Therefore, it appears promising to compile ecologically grounded lists of ancient woodland indicator bryophytes for practical use. In this study, we develop such an indicator species list for the North German federal state of Schleswig-Holstein (situated in the southern part of the Jutland Peninsula) by generally applying the innovative methodical approach

recently described by Schmidt et al. (2014). Hence, we systematically evaluate the bryophyte distribution data from floristic surveys in relation to ancient woodland cover data from state-wide inventories. In this way, we are able to determine ancient woodland bryophytes using consistent and repeatable statistical methods (Schmidt et al., 2014). This methodical approach also enables us to identify recent woodland bryophytes. These species can be used, for example, for a “negative control” of ancient woodland sites.

In the Pleistocene lowlands of Schleswig-Holstein, ancient woodlands are scattered and embedded within an agricultural landscape (Härdtle, 1995; Hase, 1997; Mölder et al., 2014). We would therefore expect a strong association of certain woodland bryophyte species with these ancient woodlands. If, on the other hand, the ancient woodlands showed a smaller degree of ecological isolation, we would suppose a lower linkage between woodland continuity and the occurrence patterns of woodland plant species (Ferris and Humphrey, 1999; Schmidt et al., 2009). In addition, the study area is covered by a program mapping the distribution of bryophytes with a resolution of ca. 30 km² (Schulz and Dengler, 2006) and so provides a promisingly large data set.

In developing the list of ancient woodland indicator bryophytes for Schleswig-Holstein, we address the following questions:

- (1) Which forest bryophyte species can be classified as ancient or recent woodland bryophytes for the area of Schleswig-Holstein?
- (2) Are there groups of ancient or recent woodland bryophytes that are related to certain environmental conditions of different woodland types?
- (3) Can the identified ancient woodland bryophytes be used as suitable indicators for application in forestry and nature conservation practice?

2. Material and methods

2.1. Study area

The study was conducted in the north German federal state of Schleswig-Holstein and the area of investigation covered 15,799 km². Based on the German network of topographical maps (scale 1:25,000), the study area was divided into a grid of 620 quadrants, of which each grid cell had a resolution of approximately 5.5 × 5.5 km or 30 km² (Fig. 1).

In the Pleistocene lowlands of Schleswig-Holstein, natural woodlands would be dominated by deciduous tree species, especially beech (*Fagus sylvatica*). However, as elsewhere in Central Europe, there are no remaining woodlands that are completely unaffected by long-term human activity (Day, 1993; Härdtle, 1995; Szabó, 2009; Arnold, 2011; Wieckowska et al., 2012). By 1780, after centuries of unregulated logging and clearing for agriculture, only about 75,000 ha (ca. 4.7 % of the present-day area of Schleswig-Holstein) was covered with woodland (Niemann, 1809; Hase, 1983). At the same time, initial attempts were made to establish conifer plantations on infertile heathlands. A century later, for the first time, coniferous and mixed forests (consisting of broadleaved and coniferous trees) reached significant proportions (Hase, 1997). Since the mid-19th century, even deciduous stands on ancient woodland sites have been converted to conifer plantations or mixed forests (see Table 1; “coniferous ancient woodland” or “mixed ancient woodland”). This is especially true for nutrient-poor sandy sites in the less fertile central Geest region. The eastern Schleswig-Holstein hill country is a young moraine landscape characterized by base-rich soils and with a long continuity of beech-dominated woodlands (Niemann, 1815; Hase, 1997; Schulz and Dengler, 2006; Wieckowska et al., 2012). Currently, 166,100 ha (10.5 %) of Schleswig-Holstein are covered by woodlands and about 45 % of these woodlands are ancient (Table 1). The proportion of deciduous ancient woodland amounts to 31 % (Glaser and Hauke, 2004; DESTATIS, 2013).

2.2 Data sets

The floristic data were obtained from the joint database of the Schleswig-Holstein State Agency for Agriculture, Environment and Rural Areas (LLUR) and the AG Geobotanik (AG Geobotanik and LLUR, 2013) and were recorded between 1974 and 2003. From this data set, we considered the 328 bryophyte species that occur in forest habitats according to the German Forest Bryophyte Species List (Schmidt et al., 2011). 65 species belong to category 1.1 (largely restricted to closed forests), 11 species to category 1.2 (preferring forest edges and clearings), 144 species to category 2.1 (occurring in forests, as well as in open habitats), and 108 species to category 2.2 (may occur in forests, but prefers open land). Additionally, we

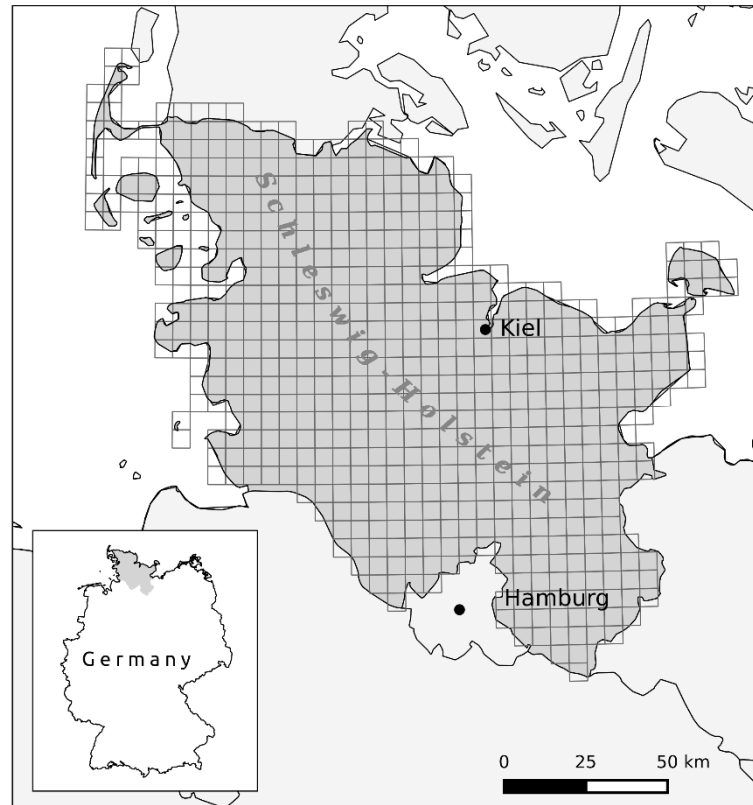


Fig. 1 The study area of Schleswig-Holstein. The displayed 620 grid cells are the basic units for the bryophyte survey program (AG Geobotanik and LLUR, 2013 and Schulz and Dengler, 2006).

Table 1 Woodland area and proportions of recent and ancient woodland in the study area of Schleswig-Holstein (according to DESTATIS, 2013 and Glaser and Hauke, 2004).

Woodland type	Variables	Area (ha)	Proportion (%)
Total woodland area		166.100	100
Recent woodland (younger than ca. 200 years)		91.750	55.2
Deciduous recent woodland		22.755	13.7
Mixed recent woodland		13.289	8.0
Coniferous recent woodland		55.705	33.5
Ancient woodland (older than ca. 200 years)	aw	74.350	44.8
Deciduous ancient woodland	daw	50.816	30.6
Mixed ancient woodland	maw	8.544	5.1
Coniferous ancient woodland	caw	14.990	9.0

determined the linkage of each bryophyte species to the four substrate classes “bark”, “deadwood”, “rocks”, and “soil” (preferred substrates, multiple assignments were possible) according to the German Forest Bryophyte Species List (Schmidt et al. 2011) with some specifications for Schleswig-Holstein following the Distribution Atlas of Bryophytes in Schleswig-Holstein and Hamburg (Schulz and Dengler, 2006). The Red List of Bryophytes of Schleswig-Holstein (Schulz et al., 2002) was used to assess if a bryophyte species is endangered (three main endangerment categories; Fig. 7) or not. Finally, we ascertained the occurrence (presence or absence) of every bryophyte species in each topographic map quadrant. The nomenclature followed Koperski et al. (2000).

We determined the ancient woodland area (area_aw) and proportion (perc_aw) in each quadrant, distinguishing respectively between ancient woodland sites currently dominated by deciduous tree species (perc_daw), coniferous tree species (perc_caw) and a mixture of both types (perc_maw) (Table 1). Data on ancient woodland was obtained from Glaser and Hauke (2004) who utilized historical land survey maps (compiled mostly between 1750 and 1800) and younger topographical maps in order to determine whether current woodland has been continuously wooded since 1800 or not. Woodland with forest continuity since at least 1800 was regarded as ancient, and information on current tree species composition has been derived from land cover data (Glaser and Hauke, 2004; Wulf, 2003).

All spatial data were processed in QGIS (v. 2.2; QGIS Development Team, 2014). We removed 170 quadrants (grid cells) without forest cover and/or bryophyte species occurrence from the data set, thus the combined data on bryophyte species and woodland distributions for 450 quadrants were used in the final analysis.

2.3 Statistical analysis

The following analyses were conducted according to the method described by Schmidt et al. (2014). Based on a sequential matrix (M1, in which each row describes the occurrence of a species in an arbitrary quadrant), we computed an incidence matrix (M2) as follows:

$$M2 = [m_{i,j}] \quad (1),$$

where i is equal to quadrants 1–450, and j is equal to species 1–328, with $m_{i,j}$ either having the value 0 or 1 (binary values).

Another matrix M3, contained data on the five ancient woodland variables for each quadrant (perc_aw, perc_daw, perc_maw, perc_caw, area_aw; Table 1), either expressed in hectares (area_) or as a percentage (perc_). Both matrices M2 and M3 were joined, on the basis of the

unique number of the quadrants, to generate matrix M4. Based on matrix M4, for each combination [species * ancient woodland variable] a generalized linear model (GLM) for binary data (Fahrmeir et al., 2009) was computed. If a species was present in less than 2 % of all quadrants, it was excluded from further analyses due to possible convergence difficulties. Finally, 224 of the 328 species remained in the analysis. The most frequent species *Brachythecium rutabulum* occurred in 99.1 % of all investigated quadrants. Therefore, no upper threshold was necessary. The resulting test statistics for the regression parameter were used for creating matrix M5 (displayed in a variance table, Appendix Table A.1), in which $z_{i,j}$ corresponded to the test statistics $z_{i,j}$ of each GLM:

$$M5 = [z_{i,j}] \quad (2),$$

where i is equal to species 1–224, and j is equal to ancient woodland variables 1–5.

Since all the GLMs featured the same sample size (number of quadrants) and the same structure, we were able to interpret the z-values without further weighting: with regard to an ancient woodland variable, high z-values (>3) hinted at a very close connection, while very low and negative z-values (<0) suggested a connection to recent woodland.

This variance table (Appendix Table A.1) was furthermore used for conducting a principal component analysis (PCA; cf. Venables and Ripley, 2002). In the PCA, we considered five ancient woodland variables (perc_aw, perc_daw, perc_maw, perc_caw, area_aw; Table 1). The variable “area of ancient woodland” (area_aw) in addition to the variable “proportion of ancient woodlands” (perc_aw) provided additional information on the significance of forest area for the distribution patterns of bryophyte species. A biplot was created, which allowed for the analysis not only of the correlation between the variables, but also of the relationship between the ancient woodland variables and the species.

By the use of k -means clustering (cf. Venables and Ripley, 2002), we grouped all species into seven clusters, which were interpretable in a meaningful way. The k -means clustering was also based on the variance table (Appendix Table A.1), the species were classified according to the five ancient woodland variables. The number of seven clusters was confirmed by applying the R software with the “clValid” package (Brock et al., 2008). A combined presentation (biplot) of the clusters and the (species) coordinates of the first and second PCA axis allowed for the interpretation of relationships between cluster composition, species occurrence and ancient woodland variables. With the purpose of interpreting the seven clusters ecologically in our analysis, we also included Ellenberg indicator values (EIV) for light, reaction and moisture (Ellenberg et al., 2001). EIV and z-values were tested for

differences between the seven species clusters (Kruskal Wallis H-test, $p \leq 0.05$, with subsequent Bonferroni-corrected Wilcoxon rank-sum test). For the few species that were lacking particular EIV, we calculated auxiliary indicator values by averaging over all quadrants. In order to then fit the EIV onto the PCA plot, we used the function “envfit” provided by the “vegan” package in R (Oksanen et al., 2012).

All statistical analyses were performed by using the R software version 3.0.1 (R Development Core Team, 2013) with the “vegan” package (Oksanen et al., 2012) and the “clValid” package (Brock et al., 2008). Significance of statistical tests was noted as follows: *** = $p \leq 0.001$; ** = $p \leq 0.01$; * = $p \leq 0.05$; n.s. = $p > 0.05$.

3. Results

The generalized linear models resulted in z-values of 224 species in dependence of five ancient woodland variables (Appendix Table A.1). Z-values ranged from 8.1 to -6.3. The proportion of ancient woodland (perc_aw) was strongly determined by the proportion of deciduous woodland on ancient woodland sites (perc_daw), as shown by the very close correlation of the z-values of both variables (Pearson's $r = 0.98$, $p\text{-value} \leq 0.001$). This relationship was also obvious from the results of the PCA (Fig. 2). Similarly, the proportion of coniferous forests on ancient woodland sites (perc_caw) and the proportion of mixed forests on ancient woodland sites (perc_maw) were quite congruent in PCA results and correlation of the z-values ($r = 0.71$, $p\text{-value} \leq 0.001$).

As a result of the *k*-means cluster analysis, the list of 224 species was divided into seven groups, which were each named after a characteristic bryophyte species (Table 2; see Appendix Table A.1 for the assignment of each species). The seven groups were ordered according to their preference for ancient or recent woodlands and to Ellenberg indicator values (EIV). With respect to woodland continuity, two groups of ancient woodland bryophytes (A, *Eurhynchium striatum* group; B, *Leucobryum glaucum* group) were distinguished from one group of recent woodland bryophytes (G, *Pleurozium schreberi* group), and four further groups of more or less indifferent species (C, *Brachythecium populeum* group; D, *Atrichum undulatum* group; E, *Dicranella heteromalla* group, F, *Dicranum scoparium* group. Fig. 4 shows the position of the groups in the PCA. These groups differed in their z-values (Fig. 3) and in their Ellenberg light values (Fig. 4, Table 2). The groups showed a graduation from the *Eurhynchium striatum* and *Leucobryum glaucum* groups indicating darkest conditions to the *Pleurozium schreberi* group indicating least shaded forest floor conditions. Furthermore, the groups displayed widely varying reaction values (Fig. 4,

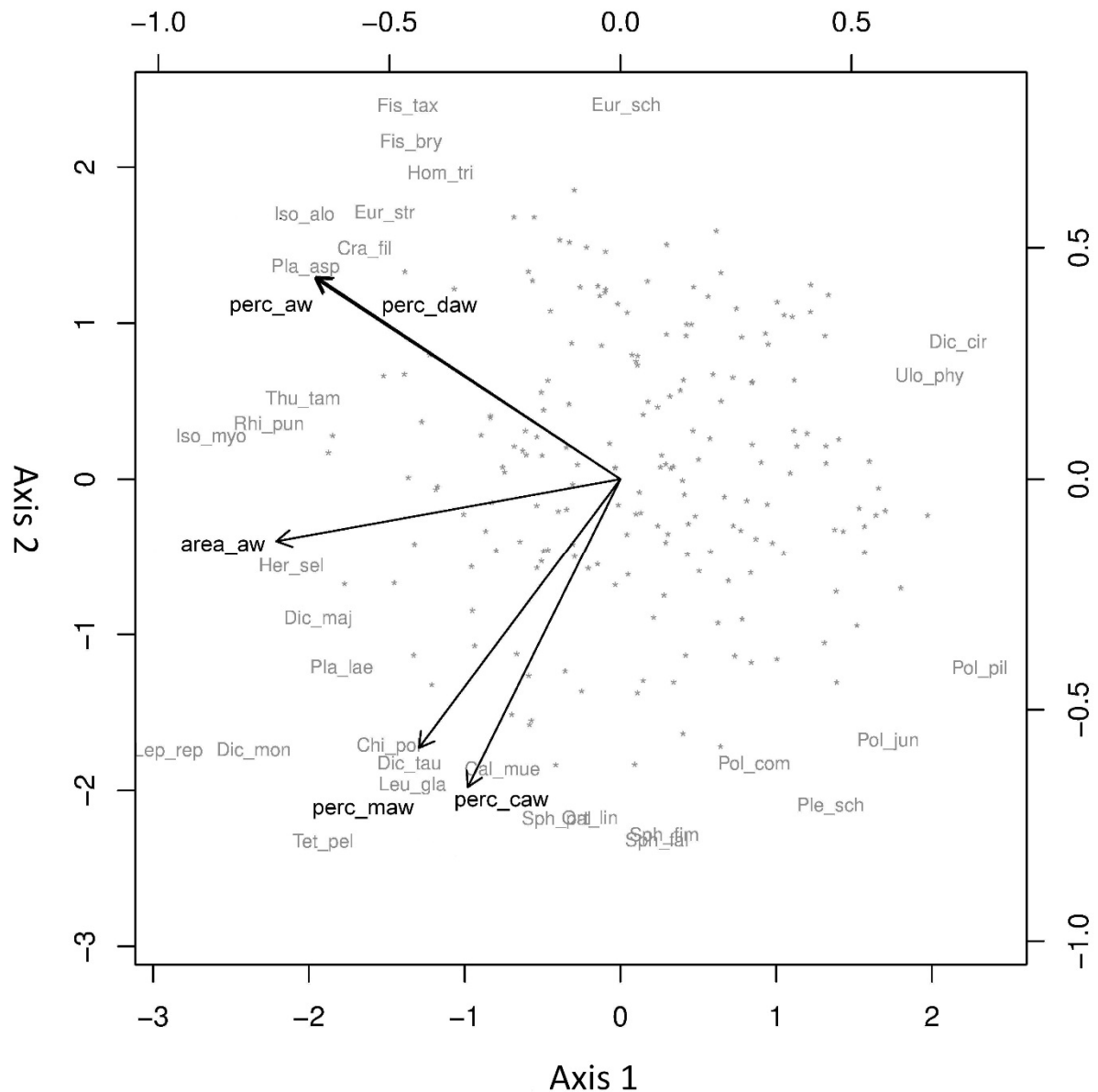


Fig. 2 PCA / biplot of the data listed in the variance table (Appendix Table A.1). Matrix: 224 forest bryophyte species (axis 1: eigenvalue = 1.64, axis 2: eigenvalue = 1.36, combined R^2 of axes 1 and 2 = 0.91). Abbreviations of the species names: see Appendix Table A.1. perc_aw = proportion of ancient woodlands in the total forest area per quadrant (%), perc_daw = proportion of deciduous forests on ancient woodland sites in the total forest area per quadrant (%), perc_caw = proportion of coniferous forests on ancient woodland sites in the total forest area per quadrant (%), perc_maw = proportion of mixed forests on ancient woodland sites in the total forest area per quadrant (%), area_aw = area of ancient woodlands in the total forest area per quadrant (ha).

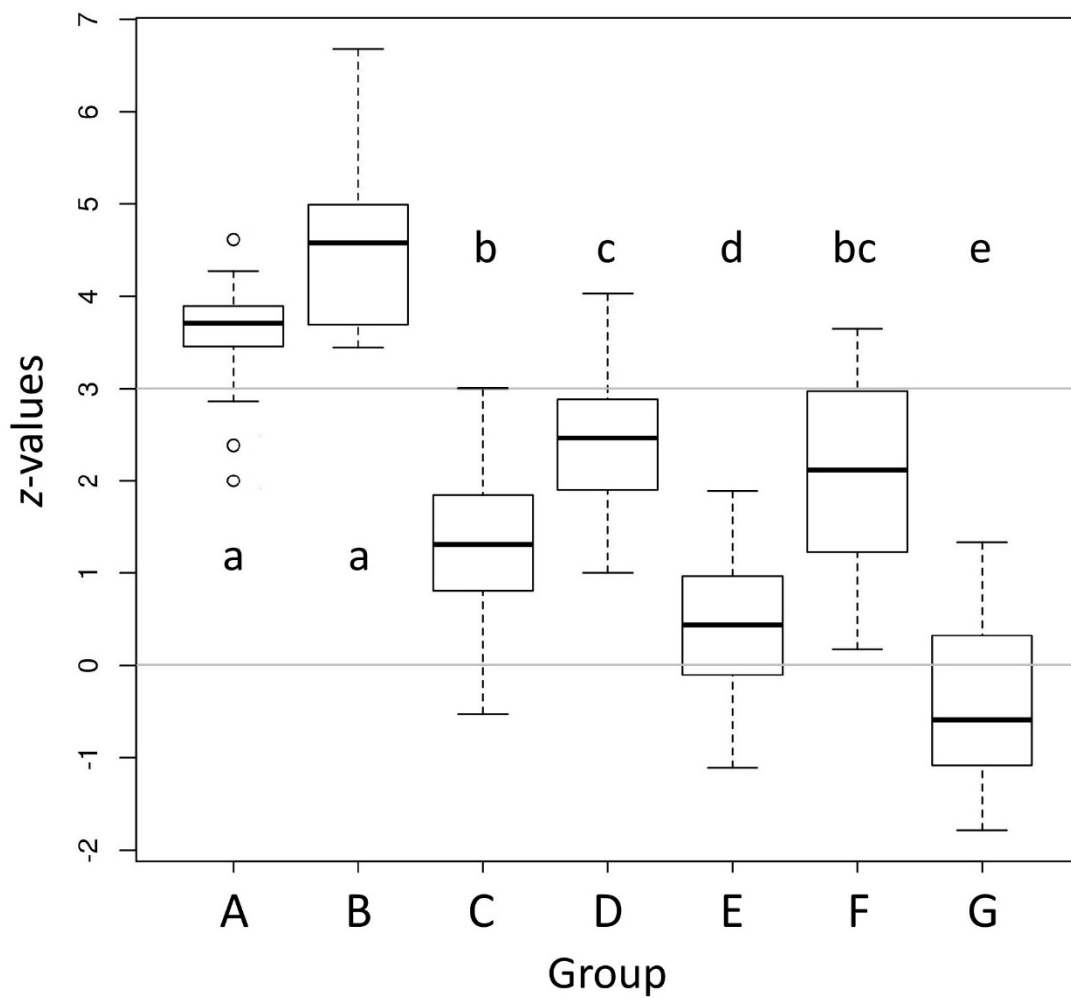


Fig. 3 Variation in z-values of the variable “area of ancient woodland” (area_aw) given for different species groups: A – *Eurhynchium striatum* group, B – *Leucobryum glaucum* group, C – *Brachythecium populeum* group, D – *Atrichum undulatum* group, E – *Dicranella heteromalla* group, F – *Dicranum scoparium* group, G – *Pleurozium schreberi* group. Significant differences are indicated by different lower case letters.

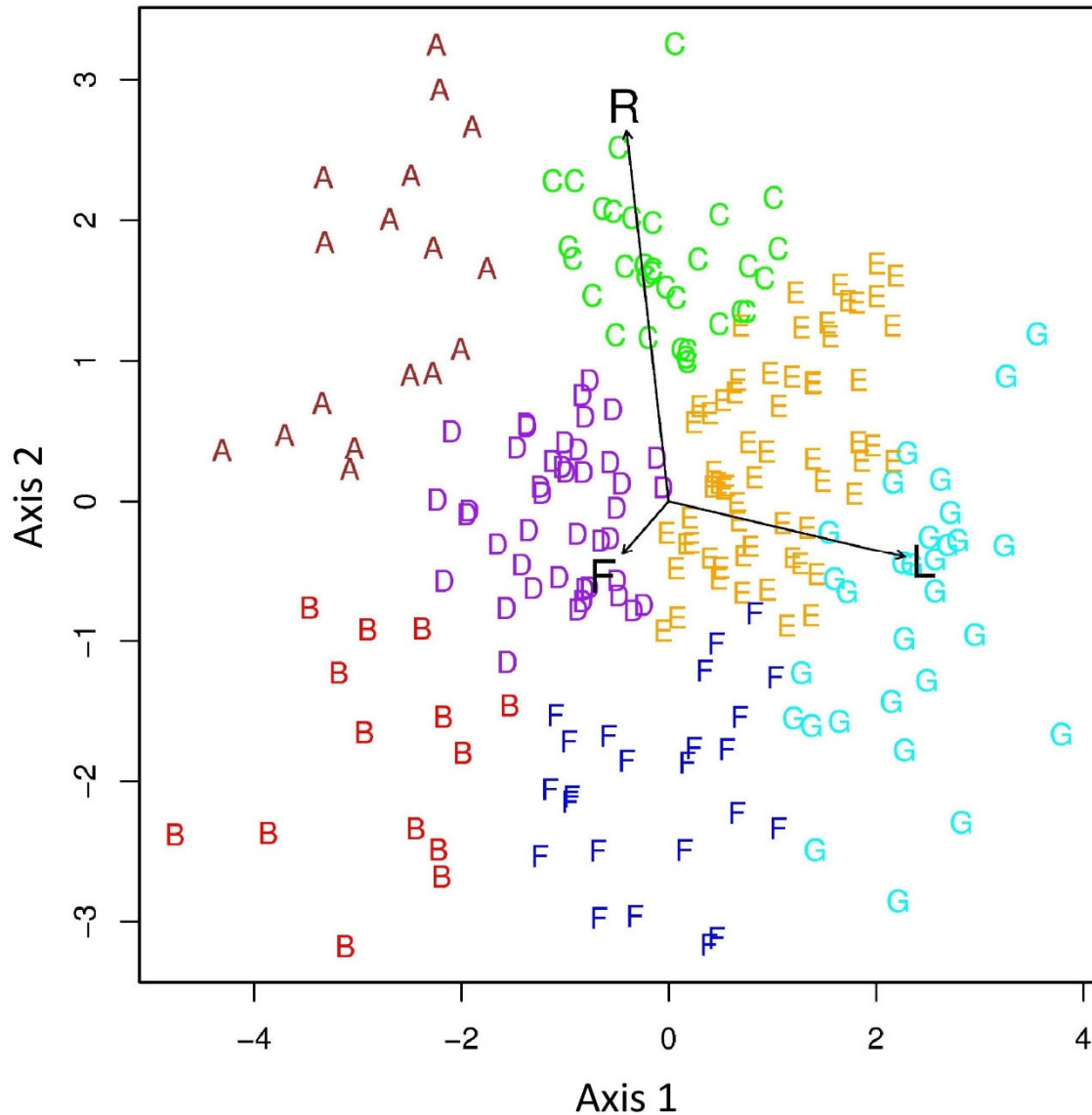


Fig. 4 PCA of the 224 forest species listed in the variance table (Appendix Table A.1). The position of the species corresponds to Fig. 3, the letters indicate the 7 groups identified by *k*-means clustering: A = *Eurhynchium striatum* group (17 species), B = *Leucobryum glaucum* group (14 species), C = *Brachythecium populeum* group (33 species), D = *Atrichum undulatum* group (44 species), E = *Dicranella heteromalla* group (62 species), F = *Dicranum scoparium* group (24 species), G = *Pleurozium schreberi* group (30 species). R = Ellenberg reaction value, L = Ellenberg light value, F = Ellenberg moisture value.

Table 2 Species numbers, mean z values of the variable “area of ancient woodland” (area_aw), and Ellenberg indicator values (EIV) of the seven species groups. p values of significant differences between the EIV of two groups are given in bold. SD = standard deviation. *** = $p \leq 0.001$; ** = $p \leq 0.01$; * = $p \leq 0.05$; n.s. = $p > 0.05$.

[illegible]

Table 2), with the *Eurhynchium striatum* and *Brachythecium populeum* groups indicating most base-rich substrate conditions. Acidic substrate conditions were linked to the *Leucobryum glaucum* and *Dicranum scoparium* groups. Across all groups, Ellenberg soil moisture values showed no significant differences.

Considering z-values (Fig. 2), the *Eurhynchium striatum* and *Leucobryum glaucum* groups (Fig. 3 and 4, A & B, Appendix Table A.1) were most closely associated with ancient woodland. Both groups were mainly characterized by shade-tolerant bryophyte species. While most species of the *Eurhynchium striatum* group are indicators of weakly basic to moderately acidic substrates in deciduous ancient woodlands (perc_daw), those species assigned to the *Leucobryum glaucum* group are particularly linked to acidic substrate conditions in coniferous and mixed ancient woodlands (perc_caw and perc_maw; Fig. 2, Table 2).

Species of the *Atrichum undulatum*, *Brachythecium populeum*, and *Dicranum scoparium* groups were largely indifferent with respect to woodland continuity. Nevertheless, several species of the *Atrichum undulatum* group (Fig. 4, D) were characterized by comparatively high z-values in relation to the area and proportion of ancient woodland (area_aw and perc_aw) and the proportion of deciduous woodland on ancient woodland sites (perc_daw). This showed that it was difficult to draw absolute limits in the group definition. The species of the *Atrichum undulatum* group preferred semi-shade conditions and grew particularly on moderately acidic substrates (Table 2). The species of the *Brachythecium populeum* group, as well as those of the *Dicranum scoparium* group, tended to show a higher affinity to recent woodlands. The former group (Fig. 4, C) included medium shade tolerant bryophytes, and indicators for weakly basic to moderately acidic substrates (Table 2). Species of the latter group (Fig. 4, F) preferred semi-shade conditions and acidic substrates (Table 2). Most species of the *Dicranella heteromalla* group (Fig. 4, E) are indicators of semi-light conditions and thrive particularly on moderate acidic substrates. Considering the z-values, the *Dicranella heteromalla* group was classified as indifferent, even though it showed a higher affinity to recent woodlands.

Finally, the *Pleurozium schreberi* group included recent woodland species (G, Fig. 4), which mostly grew in locations receiving a high amount of light. The respective bryophytes were indicators of acidic to moderately acidic substrates (Table 2). The *Pleurozium schreberi* group was characterized by very low or negative z-values in relation to the area and proportion of ancient woodland (area_aw and perc_aw) and deciduous woodland on ancient woodland sites (perc_daw; Fig. 2).

We found obvious differences in the linkage to forest habitats between the seven bryophyte species groups (Fig. 5; see Appendix Table A.1 for the assignment of each species). The proportion of species that were largely restricted to closed forests (category 1.1) was highest in the clusters of ancient woodland species (*Eurhynchium striatum* group and *Leucobryum glaucum* groups). In contrast, indifferent species (*Brachythecium populeum*, *Atrichum undulatum*, *Dicranella heteromalla*, and *Dicranum scoparium* groups) and recent woodland species (*Pleurozium schreberi* group) grew predominantly in forests, as well as in open areas (category 2.1) or even preferred open land as their main habitat (category 2.2). No species closely linked to closed forests (category 1.1) occurred in the *Pleurozium schreberi* group of recent woodland species, while species that may occur in forests, but prefer open land (category 2.2) were absent from both clusters of ancient woodland species.

We found some differences between the seven species groups when considering the linkage to the preferred substrates (Fig. 6; see Appendix Table A.1 for the assignment of each species). The highest proportions of the substrate category “rocks” occurred in the *Eurhynchium striatum* ancient woodland species cluster. In the *Leucobryum glaucum* group of ancient woodland species, the substrate category “deadwood” was predominant, while this category was almost negligible in the *Eurhynchium striatum* group. Instead, the *Eurhynchium striatum* group was characterized by higher proportions of the substrate category “bark”. The highest proportions of the substrate category “soil” were to be found in the *Pleurozium schreberi* group of recent woodland species.

When considering the proportion of endangered bryophyte species in the seven clusters (Fig. 7; see Appendix Table A.1 for the assignment of each species), it becomes obvious that no species of the *Eurhynchium striatum* ancient woodland species cluster belonged to the three main endangerment categories of the Red List (1: “threatened with extinction”, 2: “highly endangered”, 3: “endangered”). All other clusters contained at least some species assigned to the endangerment category 3. The highest proportion of endangered bryophytes occurred in the indifferent *Dicranella heteromalla* group. However, due to the necessary exclusion of species that were present in less than 2 % of all quadrants (chapter 2.3), several rare species of the Red List categories 1 and 2 were not considered in the analysis. These species are listed in Appendix Table A.2.

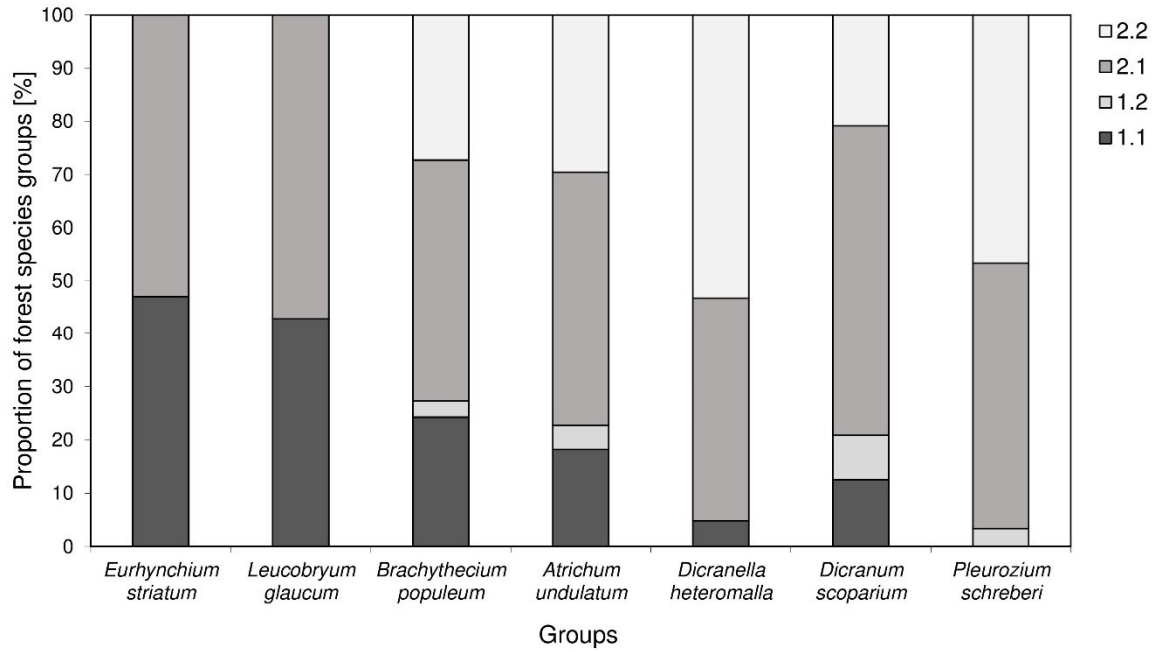


Fig. 5 Linkage to forest habitats (according to Schmidt et al., 2011) within the seven bryophytes species groups identified by *k*-means clustering. The bars show the proportion of species belonging to four different habitat types in each group. 1.1 – largely restricted to closed forests, 1.2 – preferring forest edges and clearings, 2.1 – occurring in forests, as well as in open areas, 2.2 – may occur in forests, but prefers open land.

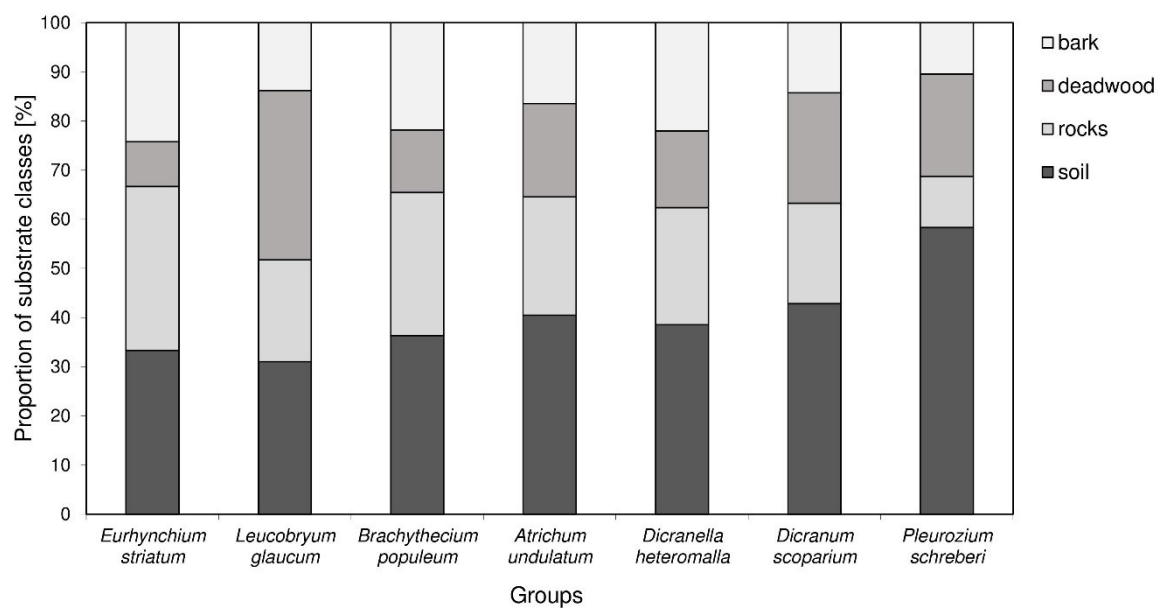


Fig. 6 Assignment to substrate categories (according to Schulz and Dengler, 2006; Schmidt et al., 2011) within the seven bryophytes species groups identified by *k*-means clustering. Multiple assignments were possible.

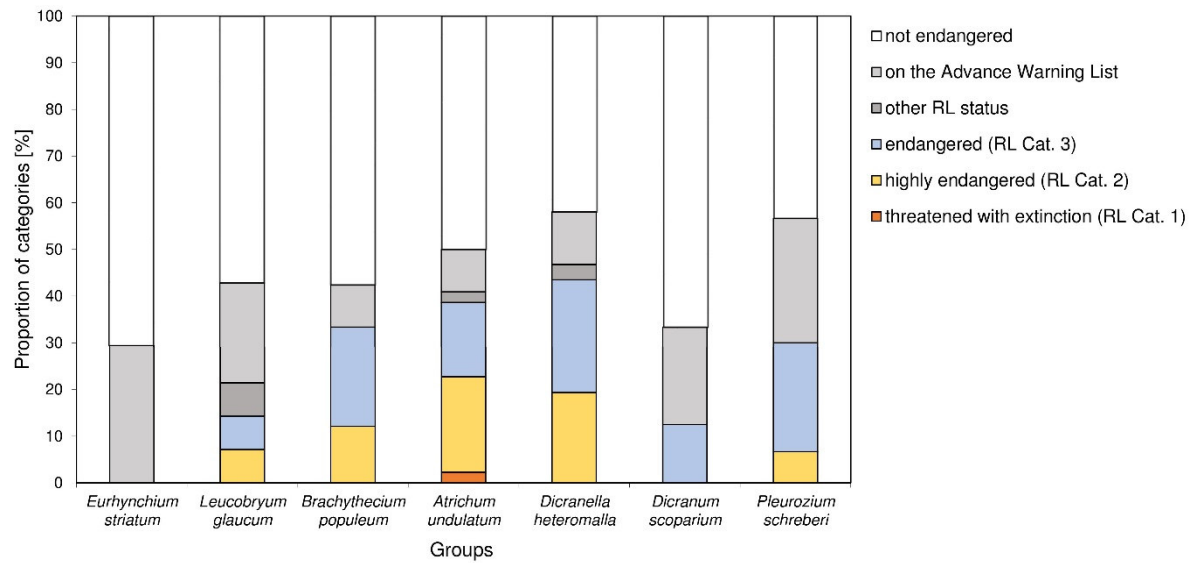


Fig. 7 Assignment to endangerness categories (according to Schulz et al., 2002) within the seven bryophytes species groups identified by *k*-means clustering. RL = Red List of Bryophytes of Schleswig-Holstein. Other RL status = categories “extremely rare”, “presumably endangered”, “data are inadequate for assessment”.

4. Discussion

4.1 Bryophyte species groups and their ecological characteristics

4.1.1 Ancient woodland bryophyte species groups

Of the seven woodland bryophyte species groups identified for our study area, we found two main groups of ancient woodland bryophytes; the *Eurhynchium striatum* and the *Leucobryum glaucum* group. Both groups are characterized by a high proportion of bryophytes that are restricted to closed and mature forests, while bryophytes that prefer open land as their main habitat are totally missing. The comparatively low proportion of threatened species can be partly related to the relatively wide-ranging distribution of the respective forest communities (Härdtle, 1995; Härdtle et al., 2003; Ellenberg and Leuschner, 2010). However, several very rare bryophytes of the Red List categories 1 and 2 do thrive in the respective ancient woodland habitats, but could not be considered in the analysis due to their rareness (Appendix Table A.2.). Three example species are *Frullania fragilifolia*, *Neckera pumila* (RL cat. 1), and *Dicranum flagellare* (RL cat. 2), which are considered to be closely linked to ancient woodlands (Rose, 1992; Schulz et al., 2002; Schulz and Dengler, 2006). Consequently, the comparatively low proportion of threatened species in the *Eurhynchium striatum* and the *Leucobryum glaucum* group does not diminish the value of ancient woodland habitats for bryophyte species conservation. Even regional extinctions of bryophytes species are reported for ancient woodlands in Schleswig-Holstein (Schulz and Dengler, 2006).

The *Eurhynchium striatum* group comprises 17 bryophyte species, of which 11 species or 65 % are listed as ancient woodland bryophytes in the literature (Rose, 1992; Gustafsson et al., 1992; Homm, 1999; Nitare, 2000; Fichtner and Lüderitz, 2013). Given the low number of publications dealing with ancient woodland bryophytes, this is a remarkable consistency. Of particular importance are *Homalia trichomanoides* and *Neckera complanata*, both species are mentioned by 4 or 5 studies, respectively. Gustafsson et al. (1992) found *Homalia trichomanoides* to be positively correlated with the habitat factors “deciduous forest surrounded by other deciduous broadleaved stands”, “growing stock”, “deciduous trees older than 150 years”, and “slopes”. The factor “slopes” was also positively correlated with *Neckera complanata*. The importance of the factor “slopes” has to be seen in relation to the main habitat not only of *Homalia trichomanoides* and *Neckera complanata*, but also of the other 15 species in the *Eurhynchium striatum* group. Following Schulz and Dengler (2006), all these species occur in semi-natural deciduous woodlands with high soil and air humidity, which are frequently characterized by gullies, springs and rivulets. The high proportions of the substrate categories “rocks” and “bark” reflect the habitat conditions, since erratic rocks

are numerous along streams, and corticolous bryophytes depend on high air humidity (Schulz and Dengler, 2006; Király et al., 2013). In Schleswig-Holstein, these habitats are well-supplied with bases (Härdtle et al., 2003), so that the EIV for soil reaction are highest in the *Eurhynchium striatum* group. However, since all seven woodland bryophyte species groups frequently contain bryophytes with a preference for moist conditions, we could not ascertain higher EIV for moisture in the *Eurhynchium striatum* group. The dense canopy of the broadleaved trees results in very low EIV for light, which is typical of semi-natural deciduous woodlands in Central Europe (Ellenberg and Leuschner, 2010). Since the conversion of moist woodlands in heterogeneous terrain to arable land was unusual, a particularly high amount of ancient woodland is to be found in these habitats. Fig. 8 displays the numbers of ancient woodland bryophytes from the *Eurhynchium striatum* group (forest species category 1.1) present in the grid quadrants for Schleswig-Holstein. The highest numbers of species were found in the eastern hill country, which is a young moraine landscape with heterogeneous terrain. The small and fragmented ancient woodlands, which are predominant in this region, are characterized by nutrient-rich soils with a good water supply (Niemann, 1809; Hase, 1997). Schmidt et al. (2014) found similar distribution patterns when investigating the occurrence of ancient woodland vascular plant species in Schleswig-Holstein.

The *Leucobryum glaucum* group contains 14 bryophyte species, of which 6 species, or 43 %, are listed as ancient woodland bryophytes in the literature (Gustafsson et al. 1992; Rose 1992; Nitare 2000; Fichtner and Lüderitz 2013). This lower consistency can be explained by the fact that the species of the *Leucobryum glaucum* group are much more acidophilic than those of the *Eurhynchium striatum* group. This is made clear by the very low EIV for soil reaction. Most of these acidophilic bryophytes occur not only in acidic beech and oak woods, but also in acidic mixed or coniferous forests on ancient woodland sites, which have been less regarded in studies on ancient woodland species (Schulz and Dengler, 2006; Matuszkiewicz et al., 2013; Schmidt et al., 2014). *Rhytidiadelphus loreus*, which is listed by all above-mentioned studies on ancient woodland bryophytes, can be taken as a good example species that thrives in this wide range of ancient woodland habitats (Gustafsson et al., 1992; Homm and de Bruyn, 2000; Humphrey et al., 2002; Schulz and Dengler, 2006). The EIV for light are very low in the *Leucobryum glaucum* group which can be attributed both to the broadleaved trees and to conifers with dense crowns such as *Picea abies* (Pretzsch and Schütze, 2005). Erratic rocks are rare in the respective forest habitats (Schulz and Dengler, 2006) and the bark of immature *Pinus sylvestris* and *Picea abies* trees is no suitable substrate for corticolous bryophytes (Kuusinen 1996; Király and Ódor, 2010), so that the substrate category

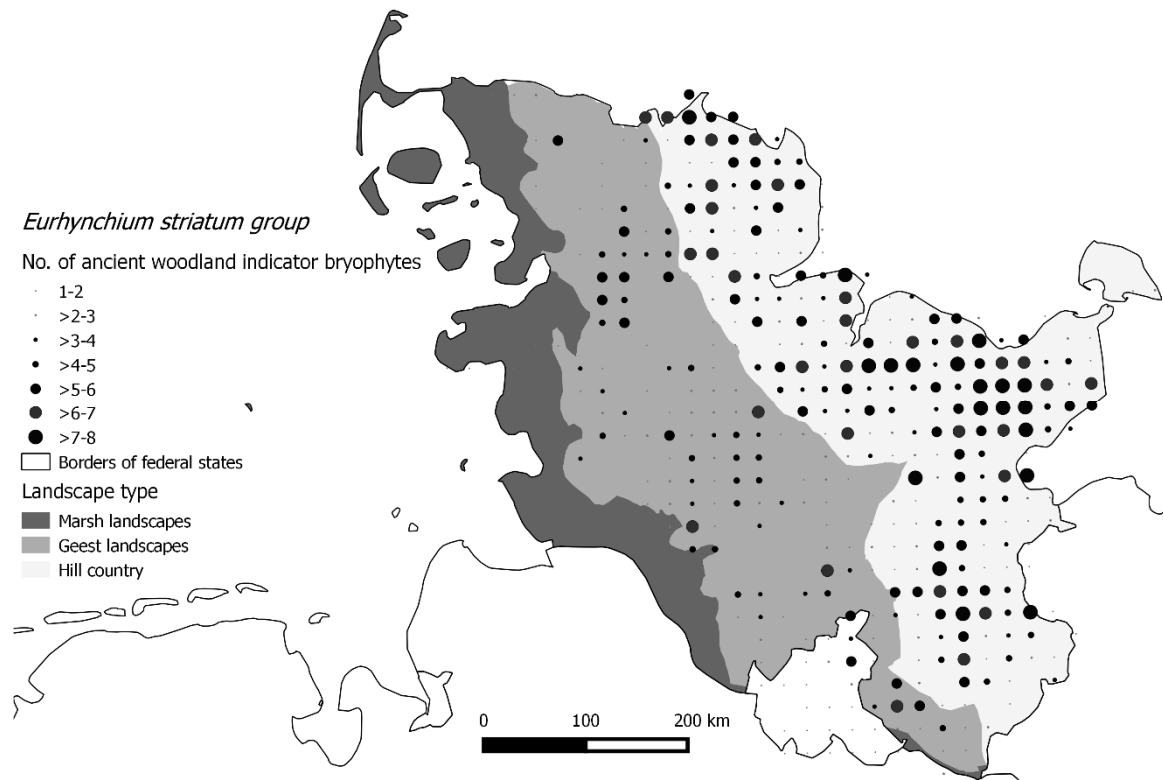


Fig. 8 *Eurhynchium striatum* group: number of ancient woodland indicator bryophytes per topographic map quadrant in Schleswig-Holstein and Hamburg, considering only forest species of category 1.1 (largely restricted to closed forests). Landscapes types according to BfN (2012) with slight modifications.

“deadwood” predominates in the *Leucobryum glaucum* group. Fig. 9 illustrates that the species of the *Leucobryum glaucum* group (forest species category 1.1) frequently occur in the less fertile, sandy central Geest region, where deciduous stands have been commonly converted to conifer plantations or mixed forests (Hase, 1997; Schulz and Dengler, 2006). However, even in the generally base-rich woodland sites of the eastern hill country, species of the *Leucobryum glaucum* group can occur where nitrification and acidification processes or coniferization were significant (Schulz and Dengler, 2006).

4.1.2 Recent woodland bryophytes

We distinguished the *Pleurozium schreberi* group as a cluster of 30 very light-demanding bryophyte species with a strong linkage to recent woodlands and therefore to areas which have been subject to human disturbance. The bryophytes in the *Pleurozium schreberi* group generally show a preference for open land, which is also reflected in the high portion of the substrate category “soil“. Species that are restricted to closed forests are completely absent from this group. The quite low mean EIV for soil reaction can be attributed to the fact that afforestation and recent natural forest development in Schleswig-Holstein mainly occurred on sites with acidic soils, particularly former heathland (Pflug, 1892; Hase, 1997). Therefore, many the bryophytes in the *Pleurozium schreberi* group have their main habitat in dry or moist heathland (e.g., *Gymnocolea inflata*, *Hypnum cupressiforme* var. *lacunosum*, *Polytrichum piliferum*, and *Ptilidium ciliare*). Additionally, among the bryophytes in the *Pleurozium schreberi* group several species occur whose main habitats are peat bogs and fens, e.g., *Polytrichum longisetum*, *Odontoschisma sphagni*, and *Sphagnum denticulatum* (Schulz and Dengler, 2006). After peat digging and moorland drainage birch-dominated recent woodland or even pine woods frequently developed, where these species found refuge habitats (Wagner, 1994; Eigner, 2003). In Schleswig-Holstein, 9 % of the peat soil sites are nowadays covered by secondary woodland (Schulz and Dengler, 2006). More than half of the species in the *Pleurozium schreberi* group are ranked among the Red List categories “highly endangered” and “endangered” or belong to the Advance Warning List (Schulz et al., 2002). This is particularly true for bryophytes which primarily occur in heathlands, peat bogs, and fens. Thus, the role of some recent woodlands as refuge habitats for open-land species is highlighted (Peterken, 1993).

4.1.3 Indifferent bryophyte species groups

Most of the forest bryophytes included in our analysis belong to one of the four groups (containing a total of 163 species) that are more or less indifferent to woodland continuity (i.e.

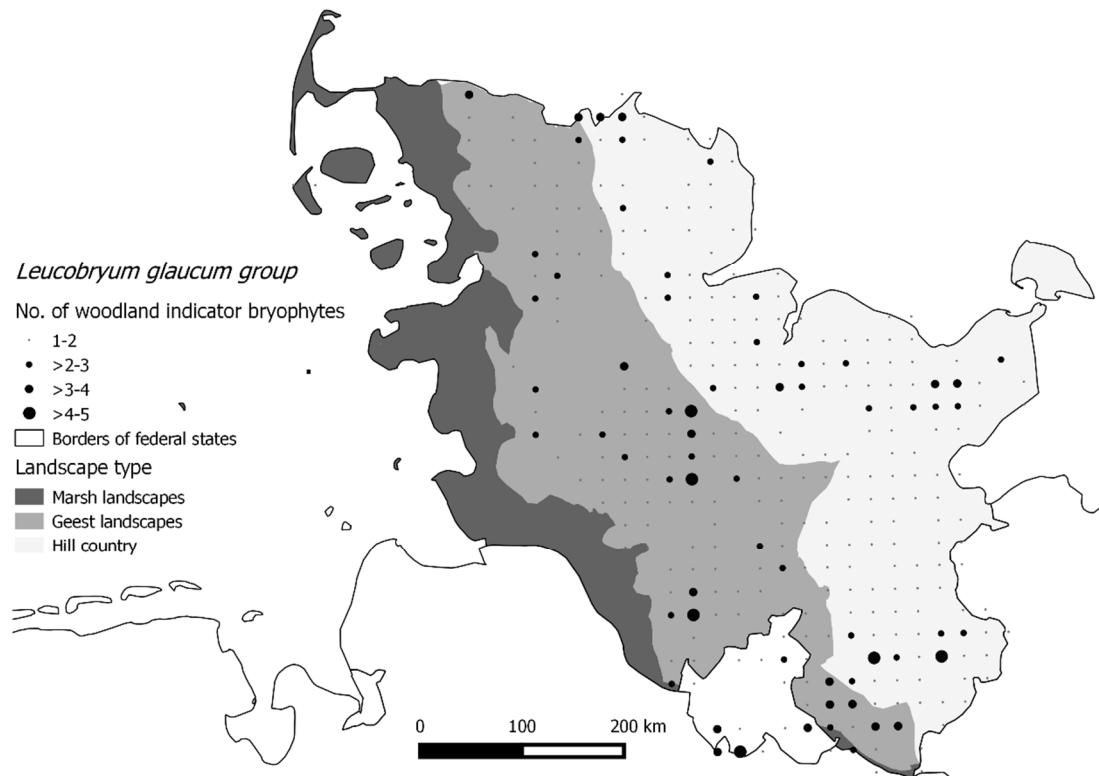


Fig. 9 *Leucobryum glaucum* group: number of ancient woodland indicator bryophytes per topographic map quadrant in Schleswig-Holstein and Hamburg considering only forest species of category 1.1 (largely restricted to closed forests). Landscapes types according to BfN (2012) with slight modifications.

the *Brachythecium populeum*, *Atrichum undulatum*, *Dicranella heteromalla*, and *Dicranum scoparium* groups). These groups contain very common and ubiquitous bryophyte species without any linkage to ancient woodlands, among others the five most common soil-dwelling mosses in Schleswig-Holstein, *Brachythecium rutabulum*, *Hypnum cupressiforme*, *Mnium hornum*, *Polytrichum formosum*, and *Atrichum undulatum* (Schulz and Dengler, 2006). Furthermore, there are many rare species included, whose possible (local or regional) linkage to ancient or recent woodlands could not be statistically verified. This is especially true for the *Atrichum undulatum* and *Dicranella heteromalla* groups, out of which ca. 40 % of the species belong to the Red List categories “highly endangered”, “endangered”, or even “threatened with extinction”. All four groups show a wide range of EIV for soil reaction and light with the *Dicranella heteromalla* group taking a middle position between the light values of the ancient and the recent woodland bryophyte species groups. This pattern corresponds to those described by Schmidt et al. (2014), who found three groups of vascular plants indifferent to woodland continuity in a total set of seven woodland vascular plant species groups.

4.2 Implications for nature conservation and forestry practice

As we discussed above, the list of 31 ancient woodland bryophytes presented here is ecologically sound and corresponds well with literature data. It therefore seems to us to be quite appropriate to characterize all these 31 bryophyte species as “ancient woodland indicator bryophytes” (Table 3). We kindly invite other researchers to apply and critique the usefulness of this list. However, it has to be considered that, in the century-old cultural landscape, there are no bryophyte species that grow exclusively on ancient woodland sites (Rose, 1992). In order to identify an ancient woodland site with high accuracy, one has to detect multiple ancient woodland indicator plants (Rose, 1999; Kühn, 2000; Schmidt et al., 2009), and we highly recommend using the here presented ancient woodland bryophytes list in combination with the list of ancient woodland vascular indicator plants published by Schmidt et al. (2014). Within the ancient woodland bryophytes, those species designated as “signal species” (Table 3) play a particularly important role in ancient woodland inventories, since they are easy to find and to identify. The presence of signal species in a woodland site indicates that other demanding species, which are harder to find or identify, may also be present (Nitare, 2000; Fichtner and Lüderitz, 2013). When mapping ancient woodland indicator plants, and particularly ancient woodland indicator bryophytes, it must be ensured that only occurrences on autochthonous substrates are recorded and that other occurrences, e.g., in the vicinity of limestone-gravel roads, are ignored (Schulz and Dengler, 2006; Avon et al., 2010). The determination of the necessary number of ancient woodland indicator plants

Table 3 List of ancient woodland indicator bryophytes for Schleswig-Holstein. FSG = Forest species group according to the German Forest Bryophyte Species List (Schmidt et al., 2011), 1.1 = largely restricted to closed forests, 2.1 = occurring in forests, as well as in open habitats. Assignment to substrate categories follows Schulz and Dengler (2006) and Schmidt et al. (2011). Endangerment categories according to Schulz et al. (2002). Signal species status according to Nitare (2000).

Bryophyte species	FSG	Woodland species group	Substrates				Endangerment category	Signal species
			Soil	Rocks	Deadwood	Bark		
<i>Amblystegium tenax</i>	2.1	Eurhynchium striatum		x		x	not endangered	
<i>Brachythecium plumosum</i>	2.1	Eurhynchium striatum	x	x			Advance Warning List	
<i>Conocephalum conicum</i>	2.1	Eurhynchium striatum	x	x			Advance Warning List	x
<i>Cratoneuron filicinum</i>	2.1	Eurhynchium striatum	x				not endangered	
<i>Eurhynchium striatum</i>	1.1	Eurhynchium striatum	x		x		not endangered	x
<i>Fissidens bryoides</i>	2.1	Eurhynchium striatum	x				not endangered	
<i>Fissidens taxifolius</i>	2.1	Eurhynchium striatum	x				not endangered	
<i>Homalia trichomanoides</i>	1.1	Eurhynchium striatum		x		x	Advance Warning List	x
<i>Isothecium alopecuroides</i>	1.1	Eurhynchium striatum		x		x	not endangered	
<i>Isothecium myosuroides</i>	1.1	Eurhynchium striatum		x		x	not endangered	
<i>Metzgeria furcata</i>	2.1	Eurhynchium striatum		x		x	Advance Warning List	
<i>Neckera complanata</i>	1.1	Eurhynchium striatum		x		x	Advance Warning List	x
<i>Plagiochila asplenioides</i>	1.1	Eurhynchium striatum	x	x			not endangered	
<i>Plagiochila porelloides</i>	1.1	Eurhynchium striatum	x	x		x	not endangered	
<i>Plagiomnium undulatum</i>	2.1	Eurhynchium striatum	x				not endangered	
<i>Rhizomnium punctatum</i>	1.1	Eurhynchium striatum	x	x	x		not endangered	
<i>Thuidium tamariscinum</i>	2.1	Eurhynchium striatum	x		x	x	not endangered	
<i>Chiloscyphus polyanthos</i>	2.1	Leucobryum glaucum		x			extremely rare	
<i>Dicranum majus</i>	1.1	Leucobryum glaucum	x				Advance Warning List	
<i>Dicranum montanum</i>	2.1	Leucobryum glaucum				x	not endangered	
<i>Dicranum tauricum</i>	1.1	Leucobryum glaucum			x	x	not endangered	
<i>Diplophyllum albicans</i>	2.1	Leucobryum glaucum	x				not endangered	
<i>Herzogiella seligeri</i>	1.1	Leucobryum glaucum			x		not endangered	x
<i>Lepidozia reptans</i>	1.1	Leucobryum glaucum	x	x	x	x	not endangered	
<i>Leucobryum glaucum</i>	2.1	Leucobryum glaucum	x		x		Advance Warning List	x
<i>Pellia epiphylla</i>	2.1	Leucobryum glaucum	x	x	x		not endangered	
<i>Plagiothecium denticulatum</i> var. <i>undulatum</i>	2.1	Leucobryum glaucum	x		x		not endangered	
<i>Plagiothecium laetum</i>	2.1	Leucobryum glaucum	x	x	x	x	Advance Warning List	
<i>Rhytidiadelphus loreus</i>	1.1	Leucobryum glaucum	x	x	x		endangered (Cat. 3)	x
<i>Scapania nemorea</i>	1.1	Leucobryum glaucum	x	x	x		highly endangered (Cat. 2)	
<i>Tetraphis pellucida</i>	2.1	Leucobryum glaucum			x		not endangered	

for reliably identifying ancient woodlands will be the object of future research. For vascular plants, the respective values in the literature range from 2 (Kühn, 2000) to 27 in a study by Honnay et al. (1998), in which the authors also argue that the indicative value of ancient woodland plant species is scale dependent.

Ancient woodland indicator plant lists are regarded as a useful tool for nature conservation practice, where important applications are (Schmidt et al. 2014) 1) the identification of ancient woodlands in areas where historical maps are lacking, 2) the identification of biodiversity hotspots of ancient woodland indicator plants, and 3) the localization of ancient semi-natural woodlands. We think that the applicability of the presented ancient woodland indicator bryophytes list is not limited to Schleswig-Holstein. In our opinion, it can also be used in adjoining Pleistocene lowland areas, not only in the German federal states of Hamburg, Niedersachsen and Mecklenburg-Vorpommern, but also in Denmark.

In order to conserve the typical bryophyte diversity of ancient semi-natural woodlands, effective conservation management should strongly support the preservation of ancient deciduous woodlands and inhibit their conversion to coniferous or mixed stands (Gustafsson et al., 1992; Kriebitzsch et al., 2013; Verstraeten et al., 2013). The forest management of deciduous ancient woodland sites with a high typical woodland bryophyte diversity has to be carefully conducted to avoid soil damage and desiccation (Gustafsson et al., 1992; Rose, 1992; Worrell and Hampson, 1997). Particularly, as Kriebitzsch et al. (2013) and Ódor et al. (2013) emphasize, shade and humidity should be maintained by selective logging and retention. As continuity of microclimate is important for bryophytes, it is also crucial to retain large groups of trees without harvesting (Baldwin and Bradfield, 2007; Perhans et al., 2009; Fedrowitz et al., 2014; Kriebitzsch et al., 2013). Additionally, management should preserve and create niches for epiphytic and epixylic bryophytes that require old trees, deadwood, and certain key tree species (Laaka, 1992; Ódor et al., 2006; Schulz and Dengler, 2006; Király and Ódor, 2010; Kriebitzsch et al., 2013). These bryophytes depend on the continuity of their substrates, have low dispersal ability and limited potential for recolonization (Laaka, 1992; Friedel et al., 2006; Muir et al., 2006). Buffer zones with low management intensity along gullies, spring areas and rivulets are highly recommended (Gustafsson et al., 1992; Stewart and Mallik, 2006). These actions must be taken for tree stands within protected areas (Thomas et al., 1997; Schmiedel et al., 2013) but should also be promoted beyond, since existing protected area networks usually cover only part of the ecologically valuable ancient woodlands in which forest floor diversity is particularly difficult to restore (Thomas et al., 1997; Thompson et al., 2003).

Acknowledgments

This study was made possible by innumerable volunteers and professionals who reported bryophyte species occurrences in the federal state of Schleswig-Holstein. We thank Silke Lütt (Schleswig-Holstein State Agency for Agriculture, Environment and Rural Areas, LLUR) for providing floristic data. We gratefully acknowledge the funding of the project “Identification and protection of forest stands of special importance for biodiversity conservation” (grant number DBU 29677) by the German Federal Foundation for the Environment (DBU). We thank Robert Larkin for language polishing. We are also indebted to two anonymous reviewers for suggestions that have greatly improved the paper.

References

- AG Geobotanik, LLUR, 2013. Gemeinsame Datenbank der AG Geobotanik in Schleswig-Holstein und Hamburg e. V. und des Landesamtes für Landwirtschaft, Umwelt und ländliche Räume des Landes Schleswig-Holstein [Conjoint Database of the Geobotanical Working Group of Schleswig-Holstein and Hamburg and the Schleswig-Holstein State Agency for Agriculture, Environment and Rural Areas (LLUR)]. Kiel and Flintbek.
- Arnold, V., 2011. Celtic Fields und andere urgeschichtliche Ackersysteme in historisch alten Waldstandorten Schleswig-Holsteins aus Laserscan-Daten [“Celtic Fields“ and other prehistoric field systems in historical forests of Schleswig-Holstein from laser-scan dates]. A. Korr.bl. 41, 439–455.
- Avon, C., Bergès, L., Dumas, Y., Dupouey, J.-L., 2010. Does the effect of forest roads extend a few meters or more into the adjacent forest? A study on understory plant diversity in managed oak stands. *For. Ecol. Manag.* 259, 1546–1555. doi:10.1016/j.foreco.2010.01.031
- Baldwin, L.K., Bradfield, G.E., 2007. Bryophyte responses to fragmentation in temperate coastal rainforests: A functional group approach. *Biol. Conserv.* 136, 408–422. doi:10.1016/j.biocon.2006.12.006
- Bates, J.W., Perry, A.R., Proctor, M.C.F., 1993. The natural history of Slapton Ley National Nature Reserve. XX: The changing bryophyte Flora. *Field Studies* 8, 279–333.
- BfN, 2012. Daten zur Natur 2012 [Nature Data 2012]. Landwirtschaftsverlag, Münster.
- Bhagwat, S.A., Nogué, S., Willis, K.J., 2014. Cultural drivers of reforestation in tropical forest groves of the Western Ghats of India. *For. Ecol. Manag.* doi:10.1016/j.foreco.2013.11.017
- Brock, G., Pihur, V., Datta, S., Datta, S., 2008. cIValid: an R package for cluster validation. *J. Stat. Softw.* 25, 1–22.

- Buse, J., 2012. "Ghosts of the past": flightless saproxylic weevils (Coleoptera: Curculionidae) are relict species in ancient woodlands. *J. Insect. Conserv.* 16, 93–102. doi:10.1007/s10841-011-9396-5
- Culmsee, H., Schmidt, M., Schmiedel, I., Schacherer, A., Meyer, P., Leuschner, C., 2014. Predicting the distribution of forest habitat types using indicator species to facilitate systematic conservation planning. *Ecol. Indic.* 37, Part A, 131–144. doi:10.1016/j.ecolind.2013.10.010
- Day, S.P., 1993. Woodland origin and "ancient woodland indicators": a case-study from Sidlings Copse, Oxfordshire, UK. *Holocene* 3, 45–53. doi:10.1177/095968369300300105
- DESTATIS, 2013. Land- und Forstwirtschaft, Fischerei: Bodenfläche nach Art der tatsächlichen Nutzung 2012 [Agriculture and Forestry, Fishery: Area of Actual Use in 2012]. Statistisches Bundesamt, Wiesbaden.
- Diekmann, M., 2003. Species indicator values as an important tool in applied plant ecology - a review. *Basic Appl. Ecol.* 4, 493–506. doi:10.1078/1439-1791-00185
- Eigner, J., 2003. Möglichkeiten und Grenzen der Renaturierung von Hochmooren [Possibilities and limits of peat bog restoration]. *Laufener Seminarbeitr.* 1/03, 23–36.
- Ellenberg, H., Leuschner, C., 2010. Vegetation Mitteleuropas mit den Alpen in ökologischer, dynamischer und historischer Sicht [Vegetation of Central Europe and the Alps: An Ecological, Dynamical and Historical Perspective], 6th ed. Ulmer, Stuttgart.
- Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W., 2001. Zeigerwerte von Pflanzen in Mitteleuropa [Indicator values of plants in Central Europe]. *Scr. Geobot.* 18, 1–264.
- Fahrmeir, L., Kneib, T., Lang, S., 2009. Regression: Modelle, Methoden und Anwendungen [Regression: Models, Methods and Applications], 2nd ed. Springer, Berlin and Heidelberg.
- Fedrowitz, K., Koricheva, J., Baker, S.C., Lindenmayer, D.B., Palik, B., Rosenthal, R., Beese, W., Franklin, J.F., Kouki, J., Macdonald, E., Messier, C., Sverdrup-Thygeson, A., Gustafsson, L., 2014. Can retention forestry help conserve biodiversity? A meta-analysis. *J. Appl. Ecol.* 51, 1669–1679. doi:10.1111/1365-2664.12289
- Fenton, N.J., Frego, K.A., 2005. Bryophyte (moss and liverwort) conservation under remnant canopy in managed forests. *Biol. Conserv.* 122, 417–430. doi:10.1016/j.biocon.2004.09.003
- Ferris, R., Humphrey, J.W., 1999. A review of potential biodiversity indicators for application in British forests. *Forestry* 72, 313–328. doi:10.1093/forestry/72.4.313

- Fichtner, A., Lüderitz, M., 2013. Signalarten - ein praxisnaher Beitrag zur Erfassung der Naturnähe und Biodiversität von Wäldern [Signal species – A practical tool for the assessment of naturalness and biodiversity in forest ecosystems]. *Nat. Landsch.* 88, 392–399.
- Friedel, A., Oheimb, G. v., Dengler, J., Härdtle, W., 2006. Species diversity and species composition of epiphytic bryophytes and lichens – a comparison of managed and unmanaged beech forests in NE Germany. *Feddes Repert.* 117, 172–185. doi:10.1002/fedr.200511084
- Glaser, F.F., Hauke, U., 2004. Historisch alte Waldstandorte und Hutewälder in Deutschland [Ancient woodlands and pasture woodlands in Germany]. *Angew. Landsch.ökol.* 61, 1–193.
- Goldberg, E., Kirby, K., Hall, J., Latham, J., 2007. The ancient woodland concept as a practical conservation tool in Great Britain. *J. Nat. Conserv.* 15, 109–119. doi:10.1016/j.jnc.2007.04.001
- Grove, S.J., 2002. Saproxylic insect ecology and the sustainable management of forests. *Annu. Rev. Ecol. Syst.* 33, 1–23. doi:10.1146/annurev.ecolsys.33.010802.150507
- Gustafsson, L., Fiskesjö, A., Hallingbäck, T., Ingelög, T., Pettersson, B., 1992. Semi-natural deciduous broadleaved woods in southern Sweden - habitat factors of importance to some bryophyte species. *Biol. Conserv.* 59, 175–181. doi:10.1016/0006-3207(92)90579-C
- Härdtle, W., 1995. Vegetation und Standort der Laubwaldgesellschaften (Querco-Fagetea) im nördlichen Schleswig-Holstein [Vegetation and Sites of Deciduous Forest Communities (Querco-Fagetea) in Northern Schleswig-Holstein]. *Arbeitsgemeinschaft Geobotanik in Schleswig-Holstein und Hamburg*, Kiel.
- Härdtle, W., von Oheimb, G., Westphal, C., 2003. The effects of light and soil conditions on the species richness of the ground vegetation of deciduous forests in Northern Germany (Schleswig-Holstein). *For. Ecol. Manag.* 182, 327–338. doi:10.1016/S0378-1127(03)00091-4
- Hase, W., 1983. Abriß der Wald- und Forstgeschichte Schleswig-Holsteins im letzten Jahrtausend [Abstract of the woodland and forestry history of Schleswig-Holstein in the last millennium]. *Schr. Naturwiss. Ver. Schlesw.-Holst.* 53, 83–124.
- Hase, W., 1997. Wald- und Forstchronologie Schleswig-Holsteins seit der Nacheiszeit [Woodland and Forestry Chronology of Schleswig-Holstein Since the Postglacial]. *Struve's Buchdruckerei und Verlag*, Eutin.
- Hermý, M., Honnay, O., Firbank, L., Grashof-Bokdam, C., Lawesson, J.E., 1999. An ecological comparison between ancient and other forest plant species of Europe, and the implications for forest conservation. *Biol. Conserv.* 91, 9–22. doi:10.1016/S0006-3207(99)00045-2

- Hermy, M., Verheyen, K., 2007. Legacies of the past in the present-day forest biodiversity: a review of past land-use effects on forest plant species composition and diversity, in: Nakashizuka, T. (Ed.), *Sustainability and Diversity of Forest Ecosystems*. Springer Japan, pp. 361–371.
- Homm, T., 1999. Moose und Flechten des Hasbruchs [Bryophytes and lichens of the Hasbruch area]. *Schriftenr. Waldentwicklung Niedersachs.* 8, 52–63.
- Homm, T., de Bruyn, U., 2000. Moose und Flechten im Naturschutzgebiet “Hasbruch”, einer Naturwaldparzelle in einer ehemaligen Hudelandschaft Nordwestdeutschlands [Bryophytes and lichens in the “Hasbruch”, a natural forest reserve in a former woodland pasture of Northwest Germany]. *Herzogia* 14, 171–194.
- Honnay, O., Degroote, B., Hermy, M., 1998. Ancient forest plant species in western Belgium: a species list and possible ecological mechanisms. *Belg. Journ. Bot.* 130, 139–154.
- 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, 165–180. doi:10.1016/S0006-3207(02)00057-5
- 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. *Biol. Conserv.* 143, 2063–2069. doi:10.1016/j.biocon.2010.05.014
- Király, I., Nascimbene, J., Tinya, F., Ódor, P., 2013. Factors influencing epiphytic bryophyte and lichen species richness at different spatial scales in managed temperate forests. *Biodivers. Conserv.* 22, 209–223. doi:10.1007/s10531-012-0415-y
- Koperski, M., Sauer, M., Braun, W., Gradstein, S.R., 2000. Referenzliste der Moose Deutschlands [German Reference List of Mosses]. *Schriftenr. Vegetationskd.* 34, 1–519.
- Kriebitzsch, W.-U., Bültmann, H., Oheimb, G. v., Schmidt, M., Thiel, H., Ewald, J., 2013. Forest-specific diversity of vascular plants, bryophytes, and lichens, in: Kraus, D., Krumm, F. (Eds.), *Integrative Approaches as an Opportunity for the Conservation of Forest Biodiversity*. European Forest Institute, Joensuu, pp. 158–169.
- Kühn, I., 2000. Ökologisch-numerische Untersuchungen an Wäldern in der Westfälischen Bucht - Ein Beitrag zur Biodiversitäts- und Altwald-Forschung [Ecological-numerical investigations in woodlands of the Westphalian Bight – A contribution to biodiversity and ancient woodland research]. *Arch. Naturwiss. Diss.* 12, 1–192.
- Kuusinen, M., 1996. Epiphyte flora and diversity on basal trunks of six old-growth forest tree species in southern and middle boreal Finland. *Lichenologist* 28, 443–463. doi:10.1006/lich.1996.0043

- Laaka, S., 1992. The threatened epixylic bryophytes in old primeval forests in Finland. *Biol. Conserv.* 59, 151–154. doi:10.1016/0006-3207(92)90575-8
- Matuszkiewicz, J.M., Kowalska, A., Kozłowska, A., Roo-Zielińska, E., Solon, J., 2013. Differences in plant-species composition, richness and community structure in ancient and post-agricultural pine forests in central Poland. *For. Ecol. Manag.* 310, 567–576. doi:10.1016/j.foreco.2013.08.060
- Mölder, A., Gürlich, S., Engel, F., 2014. Die Verbreitung von gefährdeten Holz bewohnenden Käfern in Schleswig-Holstein unter dem Einfluss von Forstgeschichte und Besitzstruktur [The distribution of endangered saproxylic beetles in Schleswig-Holstein (Northern Germany) as influenced by forest history and land tenure]. *Forstarchiv* 85, 84–101. doi:10.4432/0300-4112-85-84
- Muir, P.S., Rambo, T.R., Kimmerer, R.W., Keon, D.B., 2006. Influence of overstory removal on growth of epiphytic mosses and lichens in western Oregon. *Ecol. Appl.* 16, 1207–1221. doi:10.1890/1051-0761(2006)016[1207:IOOROG]2.0.CO;2
- Niemann, A.C.H., 1809. *Forststatistik der dänischen Staten* [Forestry Statistics of the Danish States]. Johann Friedrich Hammerich, Altona.
- Niemann, A.C.H., 1815. *Holsteins Eichen und Buchen* [Holstein's oaks and beeches]. *Kieler Blätter* 1, 377–403.
- Nitare, J., 2000. *Signalarter - indikatorer på skyddsvärd skog. Flora över kryptogamer* [Signal species: Indicator Species for Assessing the Nature Conservation Value of Woodland Sites – A Flora of Selected Cryptogams]. Skogsstyrelsen, Jönköping.
- Nordén, B., Appelqvist, T., 2001. Conceptual problems of Ecological Continuity and its bioindicators. *Biodivers. Conserv.* 10, 779–791. doi:10.1023/A:1016675103935
- Nordén, B., Paltto, H., Götmark, F., Wallin, K., 2007. Indicators of biodiversity, what do they indicate? – Lessons for conservation of cryptogams in oak-rich forest. *Biol. Conserv.* 135, 369–379. doi:10.1016/j.biocon.2006.10.007
- Ódor, P., Heilmann-Clausen, J., Christensen, M., Aude, E., van Dort, K.W., Piltaver, A., Siller, I., Veerkamp, M.T., Walley, R., Standovár, T., van Hees, A.F.M., Kosec, J., Matošec, N., Kraigher, H., Grebenc, T., 2006. Diversity of dead wood inhabiting fungi and bryophytes in semi-natural beech forests in Europe. *Biol. Conserv.* 131, 58–71. doi:10.1016/j.biocon.2006.02.004

- Ódor, P., Király, I., Tinya, F., Bortignon, F., Nascimbene, J., 2013. Patterns and drivers of species composition of epiphytic bryophytes and lichens in managed temperate forests. *For. Ecol. Manag.* 306, 256–265. doi:10.1016/j.foreco.2013.07.001
- Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., 2012. *vegan: Community Ecology Package*.
- Perhans, K., Appelgren, L., Jonsson, F., Nordin, U., Söderström, B., Gustafsson, L., 2009. Retention patches as potential refugia for bryophytes and lichens in managed forest landscapes. *Biol. Conserv.* 142, 1125–1133. doi:10.1016/j.biocon.2008.12.033
- Peterken, G.F., 1974. A method for assessing woodland flora for conservation using indicator species. *Biol. Conserv.* 6, 239–245. doi:10.1016/0006-3207(74)90001-9
- Peterken, G.F., 1993. *Woodland Conservation and Management*, 2nd ed. Chapman & Hall, London.
- Pflug, A., 1892. Die wirtschaftliche Erschließung öder und geringwertiger Liegenschaften durch künstliche Aufforstungen [The economic development of barren and inferior land by artificial afforestation]. *Z. ges. Staatswiss* 48, 79–122.
- Pretzsch, H., Schütze, G., 2005. Crown allometry and growing space efficiency of Norway spruce (*Picea abies* [L.] Karst.) and European beech (*Fagus sylvatica* L.) in pure and mixed stands. *Plant. Biol.* 7, 628–639. doi:10.1055/s-2005-865965
- QGIS Development Team, 2014. QGIS Geographic Information System. Open Source Geospatial Foundation Project, <http://qgis.osgeo.org>.
- Ratcliffe, D.A., 1968. An ecological account of Atlantic bryophytes in the British Isles. *New. Phytol.* 67, 365–439. doi:10.1111/j.1469-8137.1968.tb06392.x
- R Development Core Team, 2013. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, www.R-project.org.
- Rolstad, J., Gjerde, I., Gundersen, V.S., Sætersdal, M., 2002. Use of indicator species to assess forest continuity: a critique. *Conserv. Biol.* 16, 253–257. doi:10.1046/j.1523-1739.2002.00552.x
- Rose, F., 1992. Temperate forest management: its effects on bryophyte and lichen floras and habitats, in: Bates, J.W., Farmer, A.M. (Eds.), *Bryophytes and Lichens in a Changing Environment*. Clarendon Press, Oxford, pp. 211–233.
- Rose, F., 1999. Indicators of ancient woodland - The use of vascular plants in evaluating ancient woods for nature conservation. *Br. Wildl.* 10, 241–251.

- Schmidt, M., Kriebitzsch, W.-U., Ewald, J. (Eds.), 2011. Waldartenlisten der Farn- und Blütenpflanzen, Moose und Flechten Deutschlands [German forest species lists of ferns, phanerogams, bryophytes, and lichens]. BfN-Skripten 299, 1–111.
- Schmidt, M., Meyer, P., Paar, U., Evers, J., 2009. Bedeutung der Habitatkontinuität für die Artenzusammensetzung und -vielfalt der Waldvegetation [The importance of habitat continuity for species composition and phytodiversity of forest vegetation]. Forstarchiv 80, 195–202. doi: 10.237603004112-80-195
- Schmidt, M., Mölder, A., Schönfelder, E., Engel, F., Schmiedel, I., Culmsee, H., 2014. Determining ancient woodland indicator plants for practical use: A new approach developed in northwest Germany. For. Ecol. Manag. 330, 228–239. doi:10.1016/j.foreco.2014.06.043
- Schmiedel, I., Schmidt, M., Schacherer, A., Culmsee, H., 2013. Die Effektivität von Schutzgebieten für die Erhaltung seltener und gefährdeter Gefäßpflanzenarten - Eine Untersuchung im niedersächsischen Tiefland [Effectiveness of protection areas for the conservation of rare and endangered vascular plant species – investigations in the lowlands of Lower Saxony, Germany]. Nat.schutz Landsch.plan. 45, 45–52.
- Schulz, F., Dengler, J. (Eds.), 2006. Verbreitungsatlas der Moose in Schleswig-Holstein und Hamburg [Distribution Atlas of Bryophytes in Schleswig-Holstein and Hamburg]. Landesamt für Natur und Umwelt des Landes Schleswig-Holstein, Flintbek.
- Schulz, F., Dierßen, K., Lütt, S., Martin, C., Schröder, W., Siemsen, M., Wolfram, C., 2002. Die Moose Schleswig-Holsteins - Rote Liste [The Bryophytes of Schleswig-Holstein – Red List]. Landesamt für Natur und Umwelt des Landes Schleswig-Holstein, Flintbek.
- Spencer, J.W., Kirby, K.J., 1992. An inventory of ancient woodland for England and Wales. Biol. Conserv. 62, 77–93. doi:10.1016/0006-3207(92)90929-H
- Stewart, K.J., Mallik, A.U., 2006. Bryophyte responses to microclimatic edge effects across riparian buffers. Ecol. Appl. 16, 1474–1486. doi:10.1890/1051-0761(2006)016[1474:BRTMEE]2.0.CO;2
- Stone, A., Williamson, T., 2013. “Pseudo-Ancient Woodland” and the Ancient Woodland Inventory. Landscapes 14, 141–154. doi:10.1179/1466203513Z.00000000016
- Szabó, P., 2009. Open woodland in Europe in the Mesolithic and in the Middle Ages: Can there be a connection? For. Ecol. Manag. 257, 2327–2330. doi:10.1016/j.foreco.2009.03.035
- Thomas, R.C., Kirby, K.J., Reid, C.M., 1997. The conservation of a fragmented ecosystem within a cultural landscape - the case of ancient woodland in England. Biol. Conserv. 82, 243–252. doi:10.1016/S0006-3207(97)00039-6

- Thompson, R.N., Humphrey, J.W., Harmer, R., Ferris, R., 2003. Restoration of Native Woodland on Ancient Woodland Sites - Forestry Commission Practice Guide. Forestry Commission, Edinburgh.
- Venables, W.N., Ripley, B.D., 2002. Modern Applied Statistics with S, 4th ed. Springer, New York.
- Verstraeten, G., Baeten, L., De Frenne, P., Vanhellemont, M., Thomaes, A., Boonen, W., Muys, B., Verheyen, K., 2013. Understorey vegetation shifts following the conversion of temperate deciduous forest to spruce plantation. *For. Ecol. Manag.* 289, 363–370.
doi:10.1016/j.foreco.2012.10.049
- Wagner, C., 1994. Zur Ökologie der Moorbirke *Betula pubescens* Ehrh. in Hochmooren Schleswig-Holsteins unter besonderer Berücksichtigung von Regenerationsprozessen in Torfstichen [On the ecology of downy birch *Betula pubescens* Ehrh. in peat bogs of Schleswig-Holstein, with special consideration of regeneration processes in peat-cutting areas]. *Mitt. Arb.gem. Geobot. Schlesw.-Holst. Hambg.* 47, 1–182.
- Wieckowska, M., Dörfler, W., Kirleis, W., 2012. Vegetation and settlement history of the past 9000 years as recorded by lake deposits from Großer Eutiner See (Northern Germany). *Rev. Palaeobot. Palynol.* 174, 79–90. doi:10.1016/j.revpalbo.2012.01.003
- Woodland Trust, 2007. Back on the Map. An Inventory of Ancient and Long-Established Woodland in Northern Ireland. The Woodland Trust, Bangor.
- Worrell, R., Hampson, A., 1997. The influence of some forest operations on the sustainable management of forest soils – a review. *Forestry* 70, 61–85. doi:10.1093/forestry/70.1.61
- Wulf, M., 2003. Preference of plant species for woodlands with differing habitat continuities. *Flora* 198, 444–460. doi:10.1078/0367-2530-00118

Appendix Table A.1: Variance table. AWI = Ancient woodland indicator bryophyte; FSG = Forest species group according to the German Forest Bryophyte Species List (Schmidt et al., 2011), 1.1 = largely restricted to closed forests, 1.2 = preferring forest edges and clearings, 2.1 = occurring in forests, as well as in open habitats, 2.2 = may occur in forests, but prefers open land; Assignment to substrate categories follows Schulz and Dengler (2006) and Schmidt et al. (2011); Percent = frequency in all grid cells (%); area_aw = area of ancient woodlands in the total forest area per grid cell (ha), perc_aw = proportion of ancient woodlands in the total forest area per grid cell (%), perc_daw = proportion of deciduous forests on ancient woodland sites in the total forest area per grid cell (%), perc_caw = proportion of coniferous forests on ancient woodland sites in the total forest area per grid cell (%), perc_maw = proportion of mixed forests on ancient woodland sites in the total forest area per grid cell (%).

Species Name	Abbreviation	AWI	Woodland species group	FSG	Substrates				Percent	z-values				
					Soil	Rocks	Deadwood	Bark		area_aw	perc_aw	perc_daw	perc_caw	perc_maw
<i>Amblystegium humile</i>	Amb_hum		<i>Dicranella heteromalla</i>	2.2	x		x		2,7	0,09	-0,89	-0,57	-0,89	0,62
<i>Amblystegium serpens</i>	Amb_ser		<i>Atrichum undulatum</i>	2.1		x	x	x	90,2	2,31	3,15	1,01	2,43	1,52
<i>Amblystegium serpens</i> var. <i>juratzkanum</i>	Amb_sej		<i>Dicranella heteromalla</i>	1.1			x	x	3,6	0,96	0,81	1,05	0,15	-0,20
<i>Amblystegium tenax</i>	Amb_ten	AWI	<i>Eurhynchium striatum</i>	2.1		x		x	26,0	3,78	4,20	-0,49	4,25	1,43
<i>Aneura pinguis</i>	Ane_pin		<i>Dicranella heteromalla</i>	2.2	x	x	x		25,1	1,55	1,00	0,27	0,38	1,58
<i>Anomodon viticulosus</i>	Ano_vit		<i>Brachythecium populeum</i>	2.1		x		x	5,1	1,84	3,02	-0,84	2,53	-0,48
<i>Atrichum undulatum</i>	Atr_und		<i>Atrichum undulatum</i>	2.1	x				92,7	1,00	2,05	0,50	2,02	2,04
<i>Aulacomnium androgynum</i>	Aul_and		<i>Dicranum scoparium</i>	1.2	x	x	x	x	84,2	1,90	-2,19	2,62	-1,57	2,68
<i>Aulacomnium palustre</i>	Aul_pal		<i>Pleurozium schreberi</i>	2.1	x				41,8	-0,26	-4,58	0,52	-3,43	1,96
<i>Barbula unguiculata</i>	Bar_ung		<i>Brachythecium populeum</i>	2.2	x	x			76,9	1,27	1,63	0,25	1,93	-0,59
<i>Bartramia pomiformis</i>	Bar_pom		<i>Pleurozium schreberi</i>	1.2	x				14,4	0,44	-2,27	-0,52	-1,80	1,39
<i>Blasia pusilla</i>	Bla_pus		<i>Dicranella heteromalla</i>	2.2	x				4,2	0,04	0,39	2,01	-0,32	0,53
<i>Brachythecium albicans</i>	Bra_alb		<i>Pleurozium schreberi</i>	2.2	x	x			82,4	-0,64	-3,07	1,12	-2,59	0,25
<i>Brachythecium plumosum</i>	Bra_plu	AWI	<i>Eurhynchium striatum</i>	2.1	x	x			16,0	3,90	5,06	0,48	4,87	1,37
<i>Brachythecium populeum</i>	Bra_pop		<i>Brachythecium populeum</i>	2.1		x	x	x	38,2	2,39	4,20	-1,18	4,27	-0,58
<i>Brachythecium rivulare</i>	Bra_riv		<i>Atrichum undulatum</i>	2.1	x				26,7	3,86	3,99	0,74	3,81	1,28
<i>Brachythecium rutabulum</i>	Bra_rut		<i>Dicranella heteromalla</i>	2.1	x	x	x	x	99,1	1,07	1,04	0,10	1,16	0,02
<i>Brachythecium salebrosum</i>	Bra_sal		<i>Atrichum undulatum</i>	2.1	x	x	x	x	31,8	2,98	1,43	0,97	0,47	0,82
<i>Brachythecium velutinum</i>	Bra_vel		<i>Brachythecium populeum</i>	2.1	x	x	x	x	65,6	0,94	1,94	-0,76	1,82	0,47
<i>Bryoerythrophyllum recurvirostrum</i>	Bry_rec		<i>Atrichum undulatum</i>	2.1	x	x			32,7	2,97	2,68	0,93	2,30	0,68
<i>Bryum caespitium</i>	Bry_cae		<i>Dicranella heteromalla</i>	2.2	x	x			33,8	-0,28	0,55	0,54	0,61	1,33
<i>Bryum capillare</i>	Bry_cap		<i>Atrichum undulatum</i>	2.1		x	x	x	67,3	2,46	2,51	-0,62	2,39	2,12
<i>Bryum pallens</i>	Bry_pal		<i>Dicranella heteromalla</i>	2.2	x	x			5,1	0,73	1,19	-0,74	0,61	0,48
<i>Bryum pseudotriquetrum</i>	Bry_pse		<i>Dicranella heteromalla</i>	2.2	x				15,3	0,62	-1,06	-1,20	-1,15	-0,78
<i>Bryum rubens</i>	Bry_rub		<i>Brachythecium populeum</i>	2.2	x				38,4	0,40	1,53	-1,68	1,96	-1,28
<i>Calliergon cordifolium</i>	Cal_cor		<i>Dicranella heteromalla</i>	2.1	x				47,3	0,40	-1,20	0,48	-1,11	0,69
<i>Calliergon stramineum</i>	Cal_str		<i>Dicranum scoparium</i>	2.2	x				15,8	1,64	-1,29	2,68	-0,93	1,68
<i>Calliergonella cuspidata</i>	Cal_cus		<i>Atrichum undulatum</i>	2.2	x				81,1	2,02	4,00	-0,46	2,98	2,94
<i>Calypogeia fissa</i>	Cal_fis		<i>Brachythecium populeum</i>	1.1	x	x			24,9	2,48	1,55	-0,88	1,72	-0,86
<i>Calypogeia muelleriana</i>	Cal_mue		<i>Dicranum scoparium</i>	1.1	x	x	x		46,2	3,25	-0,13	3,59	0,00	2,87
<i>Calypogeia neesiana</i>	Cal_nee		<i>Atrichum undulatum</i>	2.1	x		x		7,1	1,32	0,58	2,59	1,62	0,81
<i>Calypogeia sphagnicola</i>	Cal_sph		<i>Dicranella heteromalla</i>	2.2	x				2,4	-0,81	-0,98	-0,33	-1,03	0,67
<i>Campylium stellatum</i>	Cam_ste		<i>Dicranella heteromalla</i>	2.2	x				2,9	0,26	0,48	0,60	0,54	-0,98
<i>Campylopus flexuosus</i>	Cam_fle		<i>Pleurozium schreberi</i>	2.1	x		x	x	36,9	1,33	-3,63	1,11	-3,23	0,91

Species Name	Abbreviation	AWI	Woodland species group	FSG	Substrates				Percent	z-values				
					Soil	Rocks	Deadwood	Bark		area_aw	perc_aw	perc_daw	perc_caw	perc_maw
<i>Campylopus introflexus</i>	Cam_int		<i>Pleurozium schreberi</i>	2.2	x		x		47,8	0,26	-3,95	0,41	-3,43	1,33
<i>Campylopus pyriformis</i>	Cam_pyr		<i>Dicranum scoparium</i>	2.2	x		x		52,0	0,90	-2,99	2,73	-2,48	1,69
<i>Cephalozia bicuspidata</i>	Cep_bic		<i>Dicranum scoparium</i>	2.1	x	x	x		27,3	3,11	0,72	2,33	0,55	2,27
<i>Cephalozia connivens</i>	Cep_con		<i>Pleurozium schreberi</i>	2.1	x		x		21,8	-0,73	-1,81	0,97	-1,17	0,63
<i>Cephalozia macrostachya</i>	Cep_mac		<i>Dicranella heteromalla</i>	2.2	x				4,2	0,46	0,68	0,71	0,99	1,60
<i>Cephaloziella divaricata</i>	Cep_div		<i>Pleurozium schreberi</i>	2.2	x	x	x		23,3	-0,54	-4,30	0,92	-2,95	0,59
<i>Ceratodon purpureus</i>	Cer_pur		<i>Dicranella heteromalla</i>	2.2	x	x	x	x	95,1	1,19	0,05	0,78	-0,59	1,17
<i>Chiloscyphus pallescens</i>	Chi_pal		<i>Atrichum undulatum</i>	2.1	x		x		26,7	2,92	2,72	0,50	2,20	1,61
<i>Chiloscyphus polyanthos</i>	Chi_pol	AWI	<i>Leucobryum glaucum</i>	2.1		x			8,4	3,45	2,32	3,96	2,05	3,67
<i>Cinclidotus fontinaloides</i>	Cin_fon		<i>Dicranella heteromalla</i>	2.2		x		x	2,2	0,77	0,44	-0,98	0,33	-0,02
<i>Cirriphyllum piliferum</i>	Cir_pil		<i>Brachythecium populeum</i>	2.1	x				38,9	2,67	4,80	-0,55	4,33	-1,09
<i>Climacium dendroides</i>	Cli_den		<i>Dicranella heteromalla</i>	2.1	x				27,8	1,11	0,37	0,74	0,22	2,62
<i>Conocephalum conicum</i>	Con_con	AWI	<i>Eurhynchium striatum</i>	2.1	x	x			23,1	4,28	5,42	0,80	4,97	2,44
<i>Cratoneuron filicinum</i>	Cra_fil	AWI	<i>Eurhynchium striatum</i>	2.1	x				36,4	3,83	6,60	0,42	6,45	-0,14
<i>Dichodontium pellucidum</i> var. <i>pellucidum</i>	Dic_pel		<i>Atrichum undulatum</i>	2.1		x			2,4	3,56	2,07	1,24	1,82	1,69
<i>Dicranella cerviculata</i>	Dic_cer		<i>Pleurozium schreberi</i>	2.2	x		x		15,6	0,32	-2,38	1,17	-1,81	2,03
<i>Dicranella heteromalla</i>	Dic_het		<i>Dicranella heteromalla</i>	2.1	x	x	x	x	95,1	1,39	0,38	0,99	0,50	1,29
<i>Dicranella schreberiana</i>	Dic_sch		<i>Brachythecium populeum</i>	2.2	x				12,2	2,37	3,85	-0,57	3,10	-1,30
<i>Dicranella staphylina</i>	Dic_sta		<i>Brachythecium populeum</i>	2.2	x				26,7	0,49	1,73	-0,91	2,66	0,96
<i>Dicranoweisia cirrata</i>	Dic_cir		<i>Pleurozium schreberi</i>	2.1		x	x	x	92,9	-1,78	-2,73	-2,34	-2,58	-1,10
<i>Dicranum bonjeanii</i>	Dic_bon		<i>Dicranella heteromalla</i>	2.2	x		x		8,0	0,55	-0,97	0,07	-0,94	1,76
<i>Dicranum majus</i>	Dic_maj	AWI	<i>Leucobryum glaucum</i>	1.1	x				8,4	4,56	4,10	2,71	3,67	3,34
<i>Dicranum montanum</i>	Dic_mon	AWI	<i>Leucobryum glaucum</i>	2.1				x	41,8	6,08	3,27	3,90	3,15	4,11
<i>Dicranum polysetum</i>	Dic_pol		<i>Dicranum scoparium</i>	2.1	x	x			19,8	1,38	-2,09	1,05	-1,43	2,20
<i>Dicranum scoparium</i>	Dic_sco		<i>Dicranum scoparium</i>	2.1	x	x	x	x	90,2	2,93	-1,03	1,90	-0,74	2,43
<i>Dicranum tauricum</i>	Dic_tau	AWI	<i>Leucobryum glaucum</i>	1.1			x	x	7,3	3,62	2,38	3,46	0,63	4,02
<i>Didymodon fallax</i>	Did_fal		<i>Dicranella heteromalla</i>	2.2	x				28,4	1,79	0,82	-0,13	0,94	0,12
<i>Didymodon rigidulus</i>	Did_rig		<i>Dicranella heteromalla</i>	2.2	x	x			5,8	0,41	-0,17	-0,79	0,28	1,02
<i>Didymodon sinuosus</i>	Did_sin		<i>Brachythecium populeum</i>	2.1		x			6,7	1,26	2,33	-1,60	2,50	0,61
<i>Didymodon tophaceus</i>	Did_top		<i>Dicranella heteromalla</i>	2.2	x	x			6,0	-0,26	1,39	-0,59	0,98	-1,08
<i>Didymodon vinealis</i> var. <i>flaccidus</i>	Did_vin		<i>Atrichum undulatum</i>	2.2		x			5,1	1,43	2,10	0,55	1,74	1,36
<i>Diplophyllum albicans</i>	Dip_alb	AWI	<i>Leucobryum glaucum</i>	2.1	x				23,6	4,95	3,33	2,34	3,57	2,56
<i>Ditrichum cylindricum</i>	Dit_cyl		<i>Dicranella heteromalla</i>	2.2	x				29,6	-0,15	0,00	-0,51	0,30	-0,37
<i>Drepanocladus aduncus</i>	Dre_adu		<i>Pleurozium schreberi</i>	2.2	x				24,2	-0,32	-1,99	-0,63	-1,78	0,00
<i>Encalypta streptocarpa</i>	Enc_str		<i>Dicranella heteromalla</i>	2.1	x	x			2,7	1,47	-0,16	1,13	-0,48	0,50
<i>Eurhynchium hians</i>	Eur_hia		<i>Brachythecium populeum</i>	2.1	x				52,9	1,19	4,49	-0,80	4,26	0,74
<i>Eurhynchium praelongum</i>	Eur_pra		<i>Dicranella heteromalla</i>	2.1	x	x	x	x	96,2	1,47	1,01	-0,75	0,96	0,67
<i>Eurhynchium schleicheri</i>	Eur_sch		<i>Brachythecium populeum</i>	1.1	x				13,6	0,93	4,22	-2,45	4,14	-1,42
<i>Eurhynchium speciosum</i>	Eur_spe		<i>Dicranella heteromalla</i>	2.1	x	x	x	x	2,2	0,73	-0,07	-0,58	0,77	1,63

Species Name	Abbreviation	AWI	Woodland species group	FSG	Substrates				Percent	z-values				
					Soil	Rocks	Deadwood	Bark		area_aw	perc_aw	perc_daw	perc_caw	perc_maw
<i>Eurhynchium striatum</i>	Eur_str	AWI	<i>Eurhynchium striatum</i>	1.1	x		x		59,3	2,00	7,18	-0,76	7,38	1,33
<i>Fissidens adianthoides</i>	Fis_adi		<i>Atrichum undulatum</i>	2.2	x				9,8	2,01	2,02	1,01	2,06	0,45
<i>Fissidens bryoides</i>	Fis_bry	AWI	<i>Eurhynchium striatum</i>	2.1	x				42,2	2,39	7,38	-1,29	6,97	0,19
<i>Fissidens exilis</i>	Fis_exi		<i>Brachythecium populeum</i>	2.1	x				2,4	-0,01	1,70	-0,12	1,89	-0,82
<i>Fissidens gracilifolius</i>	Fis_gra		<i>Dicranella heteromalla</i>	1.1		x			2,9	1,09	0,61	0,12	0,23	0,72
<i>Fissidens taxifolius</i>	Fis_tax	AWI	<i>Eurhynchium striatum</i>	2.1	x				53,6	2,99	7,29	-1,10	7,28	-0,87
<i>Fontinalis antipyretica</i>	Fon_ant		<i>Atrichum undulatum</i>	2.1		x	x		11,6	2,92	2,82	0,93	1,54	3,11
<i>Fossombronina wondraczekii</i>	Fos_won		<i>Dicranella heteromalla</i>	2.1	x				3,8	0,59	0,45	0,25	0,57	0,00
<i>Frullania dilatata</i>	Fru_dil		<i>Dicranella heteromalla</i>	2.1				x	17,6	-1,11	0,51	-1,60	0,24	-0,25
<i>Frullania tamarisci</i>	Fru_tam		<i>Atrichum undulatum</i>	2.1		x		x	2,7	1,63	2,79	0,86	2,40	1,30
<i>Funaria hygrometrica</i>	Fun_hyg		<i>Atrichum undulatum</i>	2.2	x		x		71,3	2,48	2,53	1,51	1,86	2,22
<i>Grimmia hartmanii</i>	Gri_har		<i>Brachythecium populeum</i>	1.2		x			7,3	1,44	3,47	-1,76	3,35	0,27
<i>Grimmia trichophylla</i>	Gri_tri		<i>Brachythecium populeum</i>	2.2		x			5,8	0,06	2,23	-0,73	1,84	0,25
<i>Gymnocolea inflata</i>	Gym_inf		<i>Pleurozium schreberi</i>	2.2	x				6,2	-1,74	-3,15	-0,04	-3,59	-0,38
<i>Herzogiella seligeri</i>	Her_sel	AWI	<i>Leucobryum glaucum</i>	1.1			x		55,3	5,06	4,55	2,91	4,71	2,42
<i>Homalia trichomanoides</i>	Hom_tri	AWI	<i>Eurhynchium striatum</i>	1.1		x		x	24,4	3,83	5,74	-0,80	5,58	-1,15
<i>Homalothecium lutescens</i>	Hom_lut		<i>Dicranella heteromalla</i>	2.1	x				3,8	0,03	-0,11	0,16	0,43	-1,12
<i>Homalothecium sericeum</i>	Hom_ser		<i>Brachythecium populeum</i>	2.1		x		x	42,9	2,55	1,66	-0,72	1,91	-0,20
<i>Hygrohypnum luridum</i>	Hyg_lur		<i>Dicranella heteromalla</i>	2.1		x			4,2	1,18	1,18	-1,34	0,77	-0,10
<i>Hylocomium splendens</i>	Hyl_spl		<i>Pleurozium schreberi</i>	2.1	x				20,7	-0,65	-2,99	-1,38	-3,44	1,01
<i>Hypnum andoi</i>	Hyp_and		<i>Brachythecium populeum</i>	2.1		x	x	x	10,4	1,40	3,18	-0,43	2,73	-0,49
<i>Hypnum cupressiforme</i>	Hyp_cup		<i>Dicranella heteromalla</i>	2.1	x	x	x	x	96,7	1,64	-0,74	0,35	0,15	1,19
<i>Hypnum cupressiforme</i> var. <i>lacunosum</i>	Hyp_cul		<i>Pleurozium schreberi</i>	2.2	x				11,3	-1,40	-1,35	-0,04	-2,59	0,96
<i>Hypnum cupressiforme</i> var. <i>resupinatum</i>	Hyp_cur		<i>Dicranella heteromalla</i>	2.1		x		x	3,1	-1,11	-0,61	-0,13	-0,88	-0,17
<i>Hypnum jutlandicum</i>	Hyp_jut		<i>Dicranum scoparium</i>	2.1	x				41,3	1,07	-1,64	2,15	-1,27	1,86
<i>Isothecium alopecuroides</i>	Iso_alo	AWI	<i>Eurhynchium striatum</i>	1.1		x		x	47,1	4,10	7,57	0,30	7,99	0,17
<i>Isothecium myosuroides</i>	Iso_myo	AWI	<i>Eurhynchium striatum</i>	1.1		x		x	57,8	4,05	8,13	2,11	7,33	3,06
<i>Jungermannia gracillima</i>	Jun_gra		<i>Atrichum undulatum</i>	2.1	x				3,3	1,79	0,60	1,76	0,62	1,15
<i>Lejeunea cavifolia</i>	Lej_cav		<i>Atrichum undulatum</i>	1.1		x		x	5,6	2,62	2,58	0,47	2,62	-0,12
<i>Lepidozia reptans</i>	Lep_rep	AWI	<i>Leucobryum glaucum</i>	1.1	x	x	x	x	38,9	6,68	4,65	4,38	4,40	4,51
<i>Leptobryum pyriforme</i>	Lep_pyr		<i>Dicranella heteromalla</i>	2.2	x				14,0	0,00	-1,43	0,43	-0,96	-1,07
<i>Leptodictyum riparium</i>	Lep_rip		<i>Atrichum undulatum</i>	2.1	x	x	x	x	62,9	2,02	3,47	0,76	2,25	2,57
<i>Leskea polycarpa</i>	Les_pol		<i>Dicranella heteromalla</i>	2.1		x	x	x	13,6	0,60	-0,08	-0,28	-0,19	-1,83
<i>Leucobryum glaucum</i>	Leu_gla	AWI	<i>Leucobryum glaucum</i>	2.1	x		x		40,4	3,69	1,03	3,97	1,45	3,75
<i>Leucodon sciuroides</i>	Leu_sci		<i>Brachythecium populeum</i>	2.1		x		x	6,2	0,26	1,55	0,10	2,00	-1,13
<i>Lophocolea bidentata</i>	Lop_bid		<i>Atrichum undulatum</i>	2.1	x				80,2	2,41	1,28	1,10	1,21	2,33
<i>Lophocolea heterophylla</i>	Lop_het		<i>Dicranum scoparium</i>	1.1		x	x	x	97,1	1,50	-1,51	0,69	-1,16	1,02
<i>Lophozia bicrenata</i>	Lop_bic		<i>Dicranella heteromalla</i>	2.2	x	x			6,7	1,64	-0,97	1,01	-0,48	0,07
<i>Lophozia excisa</i>	Lop_exc		<i>Pleurozium schreberi</i>	2.2	x				2,4	-0,82	-2,18	-0,14	-2,43	-0,82

Species Name	Abbreviation	AWI	Woodland species group	FSG	Substrates				Percent	z-values				
					Soil	Rocks	Deadwood	Bark		area_aw	perc_aw	perc_daw	perc_caw	perc_maw
<i>Lophozia ventricosa</i>	Lop_ven		<i>Pleurozium schreberi</i>	2.1	x	x	x		9,1	-1,32	-2,19	-0,09	-2,24	0,86
<i>Lunularia cruciata</i>	Lun_cru		<i>Atrichum undulatum</i>	2.2	x				4,4	2,03	2,88	0,50	2,56	1,61
<i>Marchantia polymorpha</i>	Mar_pol		<i>Dicranella heteromalla</i>	2.2	x	x			43,1	0,62	0,74	0,41	0,02	2,90
<i>Metzgeria furcata</i>	Met_fur	AWI	<i>Eurhynchium striatum</i>	2.1		x		x	38,4	2,86	5,97	1,70	4,76	0,49
<i>Mnium hornum</i>	Mni_hor		<i>Atrichum undulatum</i>	1.1	x		x	x	93,6	2,65	1,53	1,58	1,96	1,57
<i>Mnium stellare</i>	Mni_ste		<i>Brachythecium populeum</i>	1.1	x				7,6	1,38	3,47	-0,66	3,00	-0,99
<i>Mylia anomala</i>	Myl_ano		<i>Dicranella heteromalla</i>	2.2	x		x		6,4	0,48	0,31	0,18	1,46	0,95
<i>Nardia scalaris</i>	Nar_sca		<i>Dicranella heteromalla</i>	2.1	x				4,2	0,24	-0,32	-0,51	-0,92	0,33
<i>Neckera complanata</i>	Nec_com	AWI	<i>Eurhynchium striatum</i>	1.1		x		x	25,6	3,46	5,86	0,34	5,66	-0,07
<i>Odontoschisma sphagni</i>	Odo_sph		<i>Pleurozium schreberi</i>	2.2	x				14,0	-1,22	-2,90	-0,13	-1,84	0,26
<i>Orthodontium lineare</i>	Ort_lin		<i>Dicranum scoparium</i>	2.1			x	x	58,0	3,56	-2,82	2,46	-2,12	3,27
<i>Orthotrichum affine</i>	Ort_aff		<i>Dicranella heteromalla</i>	2.1		x	x	x	64,2	-1,11	0,53	-2,46	-0,11	-0,14
<i>Orthotrichum anomalum</i>	Ort_ano		<i>Dicranella heteromalla</i>	2.2		x		x	66,9	0,40	1,38	-0,35	1,15	0,53
<i>Orthotrichum diaphanum</i>	Ort_dia		<i>Dicranella heteromalla</i>	2.2		x		x	77,6	-0,11	-0,20	-2,04	-1,13	-1,27
<i>Orthotrichum lyellii</i>	Ort_lye		<i>Dicranella heteromalla</i>	2.1				x	16,7	-0,92	-0,09	-1,33	0,14	-0,97
<i>Orthotrichum pulchellum</i>	Ort_pul		<i>Dicranella heteromalla</i>	2.2				x	11,3	-0,40	-0,55	-1,36	-0,92	-1,10
<i>Orthotrichum stramineum</i>	Ort_str		<i>Atrichum undulatum</i>	1.1				x	4,4	3,63	2,61	1,32	2,35	1,62
<i>Pallavicinia lyellii</i>	Pal_lye		<i>Dicranella heteromalla</i>	2.1	x				3,6	-0,40	0,86	0,85	0,67	0,37
<i>Pellia endiviifolia</i>	Pel_end		<i>Brachythecium populeum</i>	2.1	x				28,4	1,54	4,50	-0,10	3,87	-1,16
<i>Pellia epiphylla</i>	Pel_epi	AWI	<i>Leucobryum glaucum</i>	2.1	x	x	x		51,3	3,52	1,71	2,92	1,83	3,11
<i>Philonotis fontana</i>	Phi_fon		<i>Dicranum scoparium</i>	2.2	x				4,9	1,08	-0,46	0,97	-0,82	1,88
<i>Physcomitrium pyriforme</i>	Phy_pyr		<i>Atrichum undulatum</i>	2.2	x		x		30,7	2,53	3,19	0,42	3,47	1,36
<i>Plagiochila asplenioides</i>	Pla_asp	AWI	<i>Eurhynchium striatum</i>	1.1	x	x			32,4	3,51	7,63	0,15	7,49	1,45
<i>Plagiochila porelloides</i>	Pla_por	AWI	<i>Eurhynchium striatum</i>	1.1	x	x		x	13,6	3,59	4,65	-0,67	4,30	0,40
<i>Plagiomnium affine</i>	Pla_aff		<i>Atrichum undulatum</i>	2.1	x	x	x	x	70,9	3,33	3,56	1,55	3,03	2,74
<i>Plagiomnium cuspidatum</i>	Pla_cus		<i>Atrichum undulatum</i>	2.1	x	x	x	x	11,1	2,68	2,47	0,80	2,12	0,51
<i>Plagiomnium elatum</i>	Pla_ela		<i>Atrichum undulatum</i>	2.2	x				7,6	1,50	2,68	1,32	1,19	1,52
<i>Plagiomnium ellipticum</i>	Pla_ell		<i>Dicranella heteromalla</i>	2.2	x				12,2	1,34	0,62	-0,21	0,28	1,69
<i>Plagiomnium rostratum</i>	Pla_ros		<i>Brachythecium populeum</i>	2.1	x				6,4	2,19	2,16	-1,03	2,57	-0,50
<i>Plagiomnium undulatum</i>	Plm_und	AWI	<i>Eurhynchium striatum</i>	2.1	x				79,6	3,71	5,65	1,13	5,27	2,78
<i>Plagiothecium cavifolium</i>	Pla_cav		<i>Brachythecium populeum</i>	1.1	x				8,0	1,42	2,33	-1,06	1,89	-0,78
<i>Plagiothecium denticulatum</i>	Pla_den		<i>Dicranum scoparium</i>	2.1	x	x	x	x	44,7	2,38	0,86	3,33	0,55	2,71
<i>Plagiothecium denticulatum</i> var. <i>undulatum</i>	Pla_deu	AWI	<i>Leucobryum glaucum</i>	2.1	x		x		13,8	3,81	1,33	3,07	1,13	1,60
<i>Plagiothecium laetum</i>	Pla_lae	AWI	<i>Leucobryum glaucum</i>	2.1	x	x	x	x	10,9	4,70	2,90	3,02	3,02	3,33
<i>Plagiothecium laetum</i> var. <i>curvifolium</i>	Pla_lac		<i>Dicranum scoparium</i>	2.1	x	x	x	x	80,2	3,03	-1,38	2,72	-0,68	3,02
<i>Plagiothecium latebricola</i>	Pla_lat		<i>Dicranella heteromalla</i>	1.1			x	x	12,2	1,61	-0,04	-0,08	0,39	1,76
<i>Plagiothecium nemorale</i>	Pla_nem		<i>Atrichum undulatum</i>	1.1	x	x	x	x	7,6	2,46	2,51	0,43	2,45	0,53
<i>Plagiothecium succulentum</i>	Pla_suc		<i>Atrichum undulatum</i>	2.1	x	x	x	x	53,6	1,36	2,61	0,15	2,60	1,02
<i>Plagiothecium undulatum</i>	Pla_und		<i>Dicranum scoparium</i>	1.1	x	x	x		44,4	2,44	0,01	3,20	0,43	2,60

Species Name	Abbreviation	AWI	Woodland species group	FSG	Substrates				Percent	z -values				
					Soil	Rocks	Deadwood	Bark		area_aw	perc_aw	perc_daw	perc_caw	perc_maw
<i>Platygyrium repens</i>	Pla_rep		<i>Brachythecium populeum</i>	1.1			x	x	13,1	3,00	3,60	-0,69	3,56	-0,55
<i>Platyhypnidium riparioides</i>	Pla_rip		<i>Dicranella heteromalla</i>	2.1		x		x	10,9	0,50	0,26	-1,37	0,32	-0,43
<i>Pleuridium acuminatum</i>	Ple_acu		<i>Atrichum undulatum</i>	1.1	x				3,1	1,45	1,67	-0,04	0,55	1,43
<i>Pleuridium subulatum</i>	Ple_sub		<i>Brachythecium populeum</i>	2.2	x				11,8	0,78	2,43	-1,26	2,36	-1,01
<i>Pleurozium schreberi</i>	Ple_sch		<i>Pleurozium schreberi</i>	2.1	x				70,7	1,09	-5,86	1,56	-5,32	2,03
<i>Pogonatum aloides</i>	Pog_alo		<i>Atrichum undulatum</i>	1.2	x				7,6	2,77	2,02	0,34	1,06	1,94
<i>Pogonatum nanum</i>	Pog_nan		<i>Pleurozium schreberi</i>	2.1	x				15,1	0,77	-3,06	-0,04	-0,38	0,21
<i>Pogonatum urnigerum</i>	Pog_urn		<i>Dicranum scoparium</i>	2.1	x				7,3	0,17	-1,99	0,80	-0,93	2,24
<i>Pohlia lutescens</i>	Poh_lut		<i>Atrichum undulatum</i>	1.2	x				3,3	2,50	2,63	0,85	2,23	0,99
<i>Pohlia melanodon</i>	Poh_mel		<i>Atrichum undulatum</i>	2.2	x				13,3	2,18	3,88	1,05	3,43	0,93
<i>Pohlia nutans</i>	Poh_nut		<i>Dicranum scoparium</i>	2.1	x				85,6	2,65	-0,23	2,02	-0,21	2,41
<i>Pohlia wahlenbergii</i>	Poh_wah		<i>Atrichum undulatum</i>	2.2	x				39,8	3,29	3,54	1,08	3,19	2,03
<i>Polytrichum commune</i>	Pol_com		<i>Pleurozium schreberi</i>	2.1	x				41,6	1,15	-4,12	2,83	-3,17	1,20
<i>Polytrichum formosum</i>	Pol_for		<i>Atrichum undulatum</i>	2.1	x		x		92,0	2,19	1,17	1,36	1,70	1,87
<i>Polytrichum juniperinum</i>	Pol_jun		<i>Pleurozium schreberi</i>	2.2	x		x		54,2	0,26	-5,70	1,23	-5,60	1,07
<i>Polytrichum longisetum</i>	Pol_lon		<i>Pleurozium schreberi</i>	2.2	x		x		25,1	-1,08	-3,14	-0,80	-2,48	1,03
<i>Polytrichum piliferum</i>	Pol_pil		<i>Pleurozium schreberi</i>	2.2	x				44,9	-0,96	-5,80	0,97	-6,26	-0,31
<i>Polytrichum strictum</i>	Pol_str		<i>Dicranella heteromalla</i>	2.1	x				14,2	0,37	-1,47	1,44	-1,03	0,70
<i>Porella cordaeana</i>	Por_cor		<i>Brachythecium populeum</i>	1.1		x	x	x	4,4	1,71	2,82	-0,91	2,73	0,90
<i>Porella platyphylla</i>	Por_pla		<i>Atrichum undulatum</i>	1.1	x	x		x	6,2	2,85	2,32	-0,05	2,48	0,53
<i>Pseudephemerum nitidum</i>	Pse_nit		<i>Brachythecium populeum</i>	2.2	x				6,9	1,40	3,27	-1,19	3,26	0,42
<i>Pseudotaxiphyllum elegans</i>	Pse_ele		<i>Atrichum undulatum</i>	1.1	x				64,7	4,03	3,68	0,99	3,46	1,95
<i>Ptilidium ciliare</i>	Pti_cil		<i>Pleurozium schreberi</i>	2.1	x	x	x	x	12,2	-0,52	-4,16	0,05	-4,25	0,26
<i>Ptilidium pulcherrimum</i>	Pti_pul		<i>Dicranum scoparium</i>	1.2		x	x	x	29,3	3,65	0,34	1,67	-0,67	2,74
<i>Pylaisia polyantha</i>	Pyl_pol		<i>Dicranella heteromalla</i>	2.1				x	4,7	-0,32	-0,12	-0,73	0,60	-1,50
<i>Racomitrium aciculare</i>	Rac_aci		<i>Atrichum undulatum</i>	2.1		x			2,7	1,53	1,37	0,61	0,93	0,75
<i>Racomitrium canescens</i>	Rac_can		<i>Pleurozium schreberi</i>	2.2	x				7,3	-1,31	-2,50	-0,39	-3,20	1,16
<i>Racomitrium fasciculare</i>	Rac_fas		<i>Atrichum undulatum</i>	2.2		x			2,4	1,30	1,35	0,43	0,96	2,97
<i>Racomitrium heterostichum</i>	Rac_het		<i>Atrichum undulatum</i>	2.2		x			12,0	3,98	2,91	0,32	2,84	2,42
<i>Radula complanata</i>	Rad_com		<i>Brachythecium populeum</i>	2.1				x	14,0	2,53	3,41	-0,35	2,85	-0,33
<i>Rhizomnium punctatum</i>	Rhi_pun	AWI	<i>Eurhynchium striatum</i>	1.1	x	x	x		51,3	4,62	6,24	1,49	6,51	2,32
<i>Rhynchostegium confertum</i>	Rhy_con		<i>Dicranella heteromalla</i>	2.1		x	x	x	15,1	0,93	0,36	0,65	-0,10	0,29
<i>Rhynchostegium murale</i>	Rhy_mur		<i>Atrichum undulatum</i>	2.1		x			24,4	1,27	1,81	0,58	1,44	0,65
<i>Rhytidiadelphus loreus</i>	Rhy_lor	AWI	<i>Leucobryum glaucum</i>	1.1	x	x	x		9,6	4,59	2,75	2,79	2,88	1,61
<i>Rhytidiadelphus squarrosus</i>	Rhy_squ		<i>Dicranella heteromalla</i>	2.2	x		x		92,2	0,58	-1,30	-0,16	-1,08	0,68
<i>Rhytidiadelphus triquetrus</i>	Rhy_tri		<i>Brachythecium populeum</i>	2.1	x				10,2	-0,53	2,48	-0,70	2,12	-0,51
<i>Riccardia chamedryfolia</i>	Ric_cha		<i>Dicranella heteromalla</i>	2.1	x				10,9	0,89	-0,22	-0,41	-0,93	1,71
<i>Riccia fluitans</i>	Ric_flu		<i>Atrichum undulatum</i>	2.2	x				22,4	2,13	1,90	1,42	0,98	2,03
<i>Riccia sorocarpa</i>	Ric_sor		<i>Brachythecium populeum</i>	2.2	x				24,7	1,25	1,42	-0,68	1,98	0,30

Species Name	Abbreviation	AWI	Woodland species group	FSG	Substrates				Percent	z -values				
					Soil	Rocks	Deadwood	Bark		area_aw	perc_aw	perc_daw	perc_caw	perc_maw
<i>Sanionia uncinata</i>	San_unc		<i>Pleurozium schreberi</i>	2.1	x			x	24,4	-0,67	-2,84	-0,09	-2,76	-0,69
<i>Scapania nemorea</i>	Sca_nem	AWI	<i>Leucobryum glaucum</i>	1.1	x	x	x		4,4	3,85	1,91	2,56	2,36	3,09
<i>Scleropodium purum</i>	Scl_pur		<i>Pleurozium schreberi</i>	2.1	x				84,2	0,84	-2,35	1,03	-1,99	1,19
<i>Sphagnum capillifolium</i>	Sph_cap		<i>Dicranum scoparium</i>	2.1	x				16,4	2,51	0,38	2,81	-0,12	3,03
<i>Sphagnum cuspidatum</i>	Sph_cus		<i>Pleurozium schreberi</i>	2.2	x				20,4	0,37	-2,29	1,71	-2,47	1,32
<i>Sphagnum denticulatum</i>	Sph_den		<i>Pleurozium schreberi</i>	2.1	x				12,9	-0,52	-3,21	0,85	-2,93	-1,47
<i>Sphagnum denticulatum</i> var. <i>inundatum</i>	Sph_dei		<i>Pleurozium schreberi</i>	2.1	x				4,4	-0,80	-1,75	-0,21	-1,40	-0,65
<i>Sphagnum fallax</i>	Sph_fal		<i>Dicranum scoparium</i>	2.1	x				45,6	2,28	-3,53	3,45	-2,65	2,45
<i>Sphagnum fimbriatum</i>	Sph_fim		<i>Dicranum scoparium</i>	2.1	x				54,2	1,96	-3,43	3,13	-2,67	2,78
<i>Sphagnum flexuosum</i>	Sph_fle		<i>Atrichum undulatum</i>	2.2	x				3,8	2,59	0,74	1,99	1,76	0,92
<i>Sphagnum magellanicum</i>	Sph_mag		<i>Dicranum scoparium</i>	2.2	x				18,4	0,82	-0,48	1,88	-0,30	1,61
<i>Sphagnum palustre</i>	Sph_pal		<i>Dicranum scoparium</i>	2.1	x				53,1	3,10	-1,63	3,70	-1,23	2,82
<i>Sphagnum papillosum</i>	Sph_pap		<i>Dicranella heteromalla</i>	2.2	x				9,6	-1,06	-1,99	0,27	-0,43	-0,67
<i>Sphagnum riparium</i>	Sph_rip		<i>Dicranella heteromalla</i>	2.1	x				2,4	0,07	-0,76	1,29	0,24	-0,17
<i>Sphagnum rubellum</i>	Sph_rub		<i>Dicranella heteromalla</i>	2.2	x				12,7	-0,50	-1,78	0,88	-0,66	1,34
<i>Sphagnum russowii</i>	Sph_rus		<i>Atrichum undulatum</i>	2.1	x				4,2	2,54	0,97	0,82	0,45	1,66
<i>Sphagnum squarrosum</i>	Sph_squ		<i>Dicranum scoparium</i>	2.1	x				38,0	1,53	-1,43	2,58	-0,70	1,57
<i>Sphagnum subnitens</i>	Sph_sun		<i>Dicranella heteromalla</i>	2.2	x				4,7	-0,22	-1,14	0,13	-0,73	-0,83
<i>Sphagnum subsecundum</i>	Sph_sub		<i>Dicranella heteromalla</i>	2.2	x				2,9	-0,07	-0,60	1,96	-0,40	-0,44
<i>Sphagnum teres</i>	Sph_ter		<i>Dicranella heteromalla</i>	2.2	x				4,2	0,15	-1,47	0,16	-1,39	1,08
<i>Taxiphyllum wissgrillii</i>	Tax_wis		<i>Brachythecium populeum</i>	1.1		x		x	7,3	1,14	2,85	-1,69	2,82	0,73
<i>Tetraphis pellucida</i>	Tet_pel	AWI	<i>Leucobryum glaucum</i>	2.1			x		51,6	4,99	1,80	4,02	1,51	5,01
<i>Thamnobryum alopecurum</i>	Tha_alo		<i>Brachythecium populeum</i>	1.1	x	x	x	x	18,0	1,31	4,45	-2,22	3,90	0,13
<i>Thuidium tamariscinum</i>	Thu_tam	AWI	<i>Eurhynchium striatum</i>	2.1	x		x	x	56,7	3,53	6,66	1,08	6,38	2,51
<i>Tortula latifolia</i>	Tor_lat		<i>Brachythecium populeum</i>	2.2		x	x	x	25,3	0,51	1,23	-0,58	1,56	-1,34
<i>Tortula muralis</i>	Tor_mur		<i>Dicranella heteromalla</i>	2.2		x	x	x	90,7	0,31	-0,01	-1,65	-0,10	-0,44
<i>Tortula papillosa</i>	Tor_pap		<i>Dicranella heteromalla</i>	2.2				x	7,8	-0,53	0,29	-1,71	0,63	-0,50
<i>Tortula subulata</i>	Tor_sub		<i>Brachythecium populeum</i>	2.1	x	x			16,7	0,81	1,44	-0,89	0,97	-1,75
<i>Trichocolea tomentella</i>	Tri_tom		<i>Atrichum undulatum</i>	1.1	x				2,9	2,59	1,92	2,01	2,21	2,89
<i>Ulotrichum bruchii</i>	Ulo_bru		<i>Dicranella heteromalla</i>	2.1				x	10,7	0,61	1,58	-0,55	0,50	0,17
<i>Ulotrichum phyllantha</i>	Ulo_phy		<i>Pleurozium schreberi</i>	2.1				x	7,3	-1,33	-2,18	-1,18	-2,83	-1,60
<i>Warnstorfia fluitans</i>	War_flu		<i>Dicranum scoparium</i>	2.2	x				20,0	1,05	-1,71	3,59	-2,01	1,09
<i>Weissia controversa</i>	Wei_con		<i>Dicranella heteromalla</i>	2.2	x				3,6	1,88	0,10	1,17	0,34	-0,69
<i>Zygodon viridissimus</i>	Zyg_vir		<i>Dicranella heteromalla</i>	2.1		x		x	16,4	0,41	0,33	-0,17	0,30	-0,84

Appendix Table A.2: Red List species (categories 1, 2 and 3) in the basic data set. Red List category 1 = threatened with extinction, Red List category 2 = highly endangered, Red List category 3 = endangered (Schulz et al., 2002). FSG = Forest species group according to the German Forest Bryophyte Species List (Schmidt et al., 2011), 1.1 = largely restricted to closed forests, 1.2 = preferring forest edges and clearings, 2.1 = occurring in forests, as well as in open habitats, 2.2 = may occur in forests, but prefers open land.

Species name	FSG	Red List category	Woodland species group
<i>Barbilophozia attenuata</i>	1.1	1	-
<i>Bartramia ithyphylla</i>	1.1	1	-
<i>Blepharostoma trichophyllum</i>	1.1	1	-
<i>Jungermannia leiantha</i>	1.1	1	-
<i>Metzgeria fruticulosa</i>	1.1	1	-
<i>Mnium marginatum</i>	1.1	1	-
<i>Neckera pumila</i>	1.1	1	-
<i>Paraleucobryum longifolium</i>	1.1	1	-
<i>Pleurodium acuminatum</i>	1.1	1	<i>Atrichum undulatum</i>
<i>Pohlia cruda</i>	1.1	1	-
<i>Sphagnum girgensohnii</i>	1.1	1	-
<i>Buxbaumia aphylla</i>	1.2	1	-
<i>Diphyscium foliosum</i>	1.2	1	-
<i>Orthotrichum rupestre</i>	1.2	1	-
<i>Antitrichia curtipendula</i>	2.1	1	-
<i>Brachythecium glareosum</i>	2.1	1	-
<i>Campylium calcareum</i>	2.1	1	-
<i>Ctenidium molluscum</i>	2.1	1	-
<i>Dicranella rufescens</i>	2.1	1	-
<i>Dicranum spurium</i>	2.1	1	-
<i>Ditrichum heteromallum</i>	2.1	1	-
<i>Eurhynchium crassinervium</i>	2.1	1	-
<i>Fissidens dubius</i>	2.1	1	-
<i>Frullania fragilifolia</i>	2.1	1	-
<i>Jungermannia atrovirens</i>	2.1	1	-
<i>Kurzia sylvatica</i>	2.1	1	-
<i>Lophozia incisa</i>	2.1	1	-
<i>Nardia geoscyphus</i>	2.1	1	-
<i>Odontoschisma denudatum</i>	2.1	1	-
<i>Orthotrichum speciosum</i>	2.1	1	-
<i>Orthotrichum striatum</i>	2.1	1	-
<i>Pseudobryum cinclidioides</i>	2.1	1	-
<i>Riccardia latifrons</i>	2.1	1	-
<i>Scapania undulata</i>	2.1	1	-
<i>Sphagnum angustifolium</i>	2.1	1	-
<i>Sphagnum contortum</i>	2.1	1	-
<i>Sphagnum obtusum</i>	2.1	1	-
<i>Sphagnum warnstorffii</i>	2.1	1	-
<i>Thuidium delicatulum</i>	2.1	1	-
<i>Tritomaria exsectiformis</i>	2.1	1	-
<i>Warnstorffia pseudostraminea</i>	2.1	1	-
<i>Andreaea rupestris</i>	2.2	1	-
<i>Diplophyllum obtusifolium</i>	2.2	1	-

Species name	FSG	Red List category	Woodland species group
<i>Ditrichum lineare</i>	2.2	1	-
<i>Ditrichum pusillum</i>	2.2	1	-
<i>Drepanocladus revolvens</i>	2.2	1	-
<i>Helodium blandowii</i>	2.2	1	-
<i>Hypnum imponens</i>	2.2	1	-
<i>Hypnum lindbergii</i>	2.2	1	-
<i>Orthotrichum obtusifolium</i>	2.2	1	-
<i>Orthotrichum pumilum</i>	2.2	1	-
<i>Philonotis caespitosa</i>	2.2	1	-
<i>Preissia quadrata</i>	2.2	1	-
<i>Rhizomnium pseudopunctatum</i>	2.2	1	-
<i>Riccardia multifida</i>	2.2	1	-
<i>Scapania compacta</i>	2.2	1	-
<i>Scapania curta</i>	2.2	1	-
<i>Sphagnum fuscum</i>	2.2	1	-
<i>Sphagnum majus</i>	2.2	1	-
<i>Dicranum flagellare</i>	1.1	2	-
<i>Dicranum fuscescens</i>	1.1	2	-
<i>Eurhynchium angustirete</i>	1.1	2	-
<i>Lejeunea cavifolia</i>	1.1	2	<i>Atrichum undulatum</i>
<i>Ptilium crista-castrensis</i>	1.1	2	-
<i>Scapania nemorea</i>	1.1	2	<i>Leucobryum glaucum</i>
<i>Tortella tortuosa</i>	1.1	2	-
<i>Trichocolea tomentella</i>	1.1	2	<i>Atrichum undulatum</i>
<i>Barbilophozia barbata</i>	1.2	2	-
<i>Grimmia hartmanii</i>	1.2	2	<i>Brachythecium populeum</i>
<i>Pohlia lutescens</i>	1.2	2	<i>Atrichum undulatum</i>
<i>Dichodontium pellucidum</i> var. <i>pellucidum</i>	2.1	2	<i>Atrichum undulatum</i>
<i>Fissidens exilis</i>	2.1	2	<i>Brachythecium populeum</i>
<i>Frullania tamarisci</i>	2.1	2	<i>Atrichum undulatum</i>
<i>Leucodon sciuroides</i>	2.1	2	<i>Brachythecium populeum</i>
<i>Nardia scalaris</i>	2.1	2	<i>Dicranella heteromalla</i>
<i>Pallavicinia lyellii</i>	2.1	2	<i>Dicranella heteromalla</i>
<i>Palustriella commutata</i>	2.1	2	-
<i>Pylaisia polyantha</i>	2.1	2	<i>Dicranella heteromalla</i>
<i>Racomitrium aciculare</i>	2.1	2	<i>Atrichum undulatum</i>
<i>Rhodobryum roseum</i>	2.1	2	-
<i>Sphagnum denticulatum</i> var. <i>inundatum</i>	2.1	2	<i>Pleurozium schreberi</i>
<i>Sphagnum riparium</i>	2.1	2	<i>Dicranella heteromalla</i>
<i>Sphagnum russowii</i>	2.1	2	<i>Atrichum undulatum</i>
<i>Zygodon conoideus</i>	2.1	2	-
<i>Blasia pusilla</i>	2.2	2	<i>Dicranella heteromalla</i>
<i>Bryum pallens</i>	2.2	2	<i>Dicranella heteromalla</i>
<i>Calypogeia sphagnicola</i>	2.2	2	<i>Dicranella heteromalla</i>
<i>Campylium chrysophyllum</i>	2.2	2	-
<i>Campylium stellatum</i>	2.2	2	<i>Dicranella heteromalla</i>
<i>Fissidens adianthoides</i>	2.2	2	<i>Atrichum undulatum</i>
<i>Grimmia trichophylla</i>	2.2	2	<i>Brachythecium populeum</i>
<i>Lophozia excisa</i>	2.2	2	<i>Pleurozium schreberi</i>

Species name	FSG	Red List category	Woodland species group
<i>Mylia anomala</i>	2.2	2	<i>Dicranella heteromalla</i>
<i>Racomitrium fasciculare</i>	2.2	2	<i>Atrichum undulatum</i>
<i>Ricciocarpos natans</i>	2.2	2	-
<i>Sphagnum compactum</i>	2.2	2	-
<i>Sphagnum subsecundum</i>	2.2	2	<i>Dicranella heteromalla</i>
<i>Sphagnum teres</i>	2.2	2	<i>Dicranella heteromalla</i>
<i>Thuidium philibertii</i>	2.2	2	-
<i>Tortula papillosa</i>	2.2	2	<i>Dicranella heteromalla</i>
<i>Mnium stellare</i>	1.1	3	<i>Brachythecium populeum</i>
<i>Orthotrichum stramineum</i>	1.1	3	<i>Atrichum undulatum</i>
<i>Porella cordaeana</i>	1.1	3	<i>Brachythecium populeum</i>
<i>Porella platyphylla</i>	1.1	3	<i>Atrichum undulatum</i>
<i>Rhytidiadelphus loreus</i>	1.1	3	<i>Leucobryum glaucum</i>
<i>Taxiphyllum wissgrillii</i>	1.1	3	<i>Brachythecium populeum</i>
<i>Bartramia pomiformis</i>	1.2	3	<i>Pleurozium schreberi</i>
<i>Pogonatum aloides</i>	1.2	3	<i>Atrichum undulatum</i>
<i>Anomodon viticulosus</i>	2.1	3	<i>Brachythecium populeum</i>
<i>Didymodon sinuosus</i>	2.1	3	<i>Brachythecium populeum</i>
<i>Encalypta streptocarpa</i>	2.1	3	<i>Dicranella heteromalla</i>
<i>Fontinalis antipyretica</i>	2.1	3	<i>Atrichum undulatum</i>
<i>Fossombronia wondraczekii</i>	2.1	3	<i>Dicranella heteromalla</i>
<i>Frullania dilatata</i>	2.1	3	<i>Dicranella heteromalla</i>
<i>Homalothecium lutescens</i>	2.1	3	<i>Dicranella heteromalla</i>
<i>Hygrohypnum luridum</i>	2.1	3	<i>Dicranella heteromalla</i>
<i>Hylocomium splendens</i>	2.1	3	<i>Pleurozium schreberi</i>
<i>Jungermannia gracillima</i>	2.1	3	<i>Atrichum undulatum</i>
<i>Pogonatum nanum</i>	2.1	3	<i>Pleurozium schreberi</i>
<i>Pogonatum urnigerum</i>	2.1	3	<i>Dicranum scoparium</i>
<i>Polytrichum strictum</i>	2.1	3	<i>Dicranella heteromalla</i>
<i>Ptilidium ciliare</i>	2.1	3	<i>Pleurozium schreberi</i>
<i>Rhytidiadelphus triquetrus</i>	2.1	3	<i>Brachythecium populeum</i>
<i>Sphagnum capillifolium</i>	2.1	3	<i>Dicranum scoparium</i>
<i>Sphagnum denticulatum</i>	2.1	3	<i>Pleurozium schreberi</i>
<i>Cephalozia macrostachya</i>	2.2	3	<i>Dicranella heteromalla</i>
<i>Cinclidotus fontinaloides</i>	2.2	3	<i>Dicranella heteromalla</i>
<i>Dicranum bonjeanii</i>	2.2	3	<i>Dicranella heteromalla</i>
<i>Didymodon tophaceus</i>	2.2	3	<i>Dicranella heteromalla</i>
<i>Gymnocolea inflata</i>	2.2	3	<i>Pleurozium schreberi</i>
<i>Lophozia bicrenata</i>	2.2	3	<i>Dicranella heteromalla</i>
<i>Odontoschisma sphagni</i>	2.2	3	<i>Pleurozium schreberi</i>
<i>Philonotis fontana</i>	2.2	3	<i>Dicranum scoparium</i>
<i>Polytrichum commune</i> var. <i>perigoniale</i>	2.2	3	-
<i>Pseudephemerum nitidum</i>	2.2	3	<i>Brachythecium populeum</i>
<i>Racomitrium heterostichum</i>	2.2	3	<i>Atrichum undulatum</i>
<i>Sphagnum flexuosum</i>	2.2	3	<i>Atrichum undulatum</i>
<i>Sphagnum papillosum</i>	2.2	3	<i>Dicranella heteromalla</i>
<i>Sphagnum rubellum</i>	2.2	3	<i>Dicranella heteromalla</i>
<i>Sphagnum subnitens</i>	2.2	3	<i>Dicranella heteromalla</i>
<i>Weissia controversa</i>	2.2	3	<i>Dicranella heteromalla</i>