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# Tree age is a key factor for the conservation of epiphytic lichens and bryophytes in beech forests

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## Abstract

**Questions:** What factors limit the distribution of epiphytic lichens and bryophytes at plot and tree level in beech forests? At what ages do epiphytic species, and species of conservation concern in particular, occur along a chronosequence of beech?

**Location:** South-west Sweden.

**Method:** Five hundred and seventy-one age-determined trees from 37 plots distributed among 29 beech-dominated stands were surveyed along with a number of environmental (16) and substrate (seven) variables in a landscape of ca. 550 ha. Non-metric multidimensional scaling (NMS) and indicator species analysis (ISA) were used for data analysis.

**Results:** Plots containing old trees, confined to the base of slopes and with low impacts of recent forestry (thinning), generally had a high richness of species of conservation concern. Richness of common species and red-listed bryophytes were mostly related to the surveyed bark area. At tree level, primary factors explaining both species richness and composition were age, diameter at breast height and moss cover. There was a gradual replacement of tree age ranges for 58 lichens and 37 bryophytes along the chronosequence of beech. Red-listed lichens favoured damaged beech trees ( $\geq$ 180 years), whereas red-listed bryophytes were found on old and young stems in dense stands.

**Conclusions:** Tree age exerts a profound influence on epiphytic lichens and bryophytes growing on beech. Many of the habitat specialists were found mainly on old beech because they inhabit specific substrates that occur on older trees. The association to high tree age commonly excludes red-listed lichens from conventionally managed beech forests with a 100- to 140-year rotation period.

**Keywords:** Biskopstorp; Dendrochronology; *Fagus sylvatica*; Non-Parametric Multivariate Analysis; Red-Listed Species; Substrate Quality.

**Nomenclature:** Santesson et al. (2004); Hallingbäck et al. (2006).

## Introduction

The European beech, *Fagus sylvatica*, is inhabited by a specialised set of lichens (Berg et al. 2002). These species have been severely affected by habitat loss and air pollution, resulting in many species being red-listed (Gärdenfors 2005). To secure these species, beech habitat is of high priority in the current Swedish forest conservation strategy (SEPA & NBF 2005). Successful conservation of red-listed beech epiphytes requires knowledge of the ecological factors limiting the species' distribution. In southern Swedish beech forests, light, temperature, moisture, bark characteristics and historic factors have been suggested to play a role (Almborn 1948). The availability of suitable substrates, stand age and forest history have recently been shown to significantly influence distribution patterns of red-listed and indicator lichens in stands at the landscape scale (Fritz et al. 2008). Such ecological information is essential in order to successfully protect and manage the remaining old-growth beech forests in reserves, as well as to preserve diverse epiphytic communities in managed stands.

A number of studies have emphasized the importance of tree age for epiphytic species, in particular for lichens (e.g. Gustafsson et al. 1992). The association with older trees may depend on various age-dependent factors that are difficult to separate, i.e. increased bark surface area, formation of age-related substrate qualities and a longer periods of time available for colonisation (Ranius et al. 2008). Analysing tree age in combination with diameter and substrate type of individual trees may indicate the relative importance of each factor.

In conservation, it is important to understand the succession of epiphyte species, primarily red-listed species, along the chronosequence of beech. There are some ecological studies on epiphytic bryophytes and/or lichens in beech forests (Rasmussen 1975; Pirintsos et al. 1995; Loppi et al. 1999); however, this is the first extensive study of tree variables and the occurrence of epiphytes on a large number of age-determined beech. The substantial number of cored beech at Biskopstorp (Fahlvik 1999; Niklasson et al. 2005) in southern Sweden offers an excellent opportunity to analyse epiphyte occurrence in relation to tree age. Conducting the study in an area with little macroecological variation makes it easier to establish chronosequences and to detect effects of tree age-related factors on species distribution (Crites & Dale 1998).

This paper aimed to study the relationship between a number of environmental and substrate factors to the species richness and composition of epiphytic lichens and bryophytes. This was studied both at plot and tree level in beech stands. Furthermore, we address questions about epiphytes of conservation concern, i.e. red-listed and indicator species: At what ages do these species occur along a chronosequence of beech? Are damaged trees more important than viable trees of the same age? What are the implications for the conservation and management of rare epiphytes?

## Materials and Methods

### *Study area*

The study area comprises ca. 550 ha of the nature reserve of Biskopstorp (56°48′5N12°53′47E) in the county of Halland, SW Sweden (Fig. 1). Biskopstorp is considered to be one of the most important areas in Sweden for biodiversity associated with beech (Fritz 2006). It is a hilly area with altitudes ranging from about 25 to 170 m.a.s.l. Mean annual precipitation is about 1100-1200 mm, and the mean annual temperature is 7°C (Raab & Vedin 1995). Almost all beech stands belong to the *Fagus sylvatica-Sorbus aucuparia-Deschampsia flexuosa* community (Diekmann et al. 1999).

Beech and oak-dominated forest stands are located in a matrix of Norway spruce plantations, pine mires, mixed and other deciduous forests. The broadleaf stands are the remnants of the deciduous forest landscape, which was transformed to

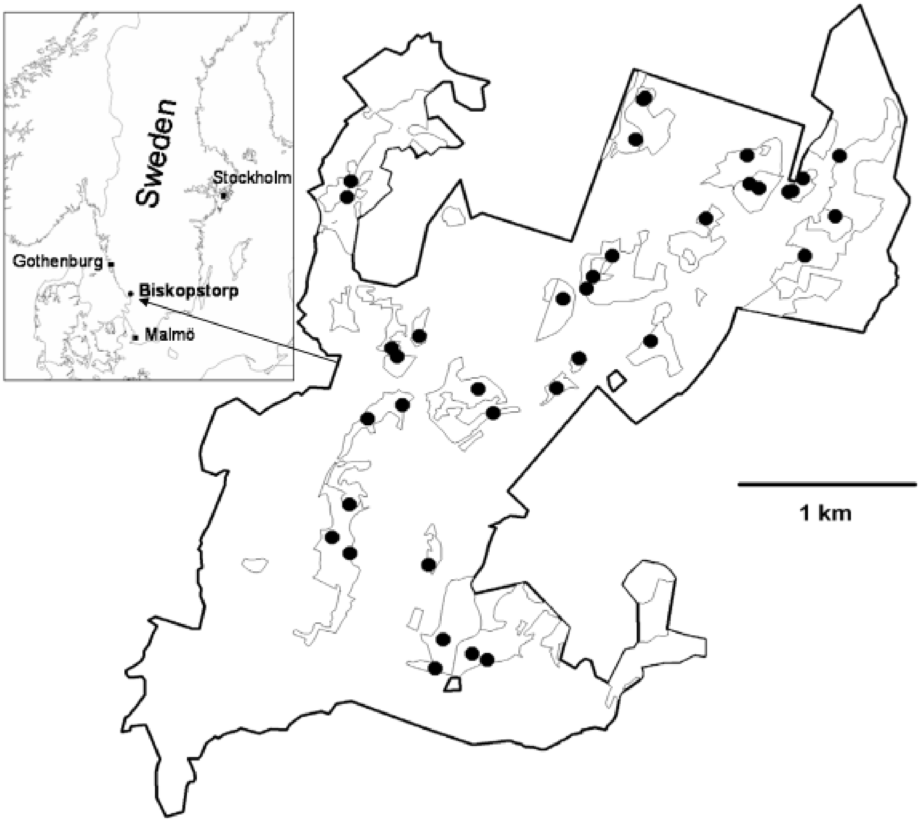

**Fig. 1.** Geographic position of Biskopstorp in Sweden, and distribution of the studied plots (•, $n = 37$) in the beech-dominated stands (delimited by thin lines) of Biskopstorp.

a coniferous landscape during the 20th century (Lindbladh et al. 2008). Up to the 1900s, the Biskopstorp area was extensively grazed by cattle and mainly used for firewood (Simonsson & Larsson 2007). All present beech stands are high forests influenced by forest management, resulting in one or sometimes two or three distinct regenerations at restricted periods ('cohorts'), in contrast to an all-age pattern in natural beech stands with gap phase dynamics (Niklasson et al. 2005). However, the past management has generally been conducted at a lower intensity compared to recent beech silviculture, as reflected in the large number of old beech stands and old trees mixed in amongst other stands at a substantially higher frequency than in normal production forest landscapes.

### *Selection of plots and trees*

A total of 571 cored and age-determined living beech trees within 37 plots trees that were well distributed over the beech forest landscape in Biskopstorp were studied (Fig. 1). Studied stands were beech-dominated without or with a low proportion of other trees, such as Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), birch (*Betula* spp.), oak (*Quercus* spp.) and rowan (*Sorbus aucuparia*).

The sampling design was based on permanently marked tree age plots in the beech stands. In this study we used beech ($n = 144$) from circular sample plots of 7-m radius (Fahlvik 1999), in combination with the beech ($n = 427$) from plots of 20-m radius (Niklasson et al. 2005). The sample plots of 7-m radius ($157\,m^2$) were placed in a typical part of each stand, whereas the majority of the sample plots of 20-m radius ($1257\,m^2$) were randomly distributed and originated from an earlier study (Fritz 2006). In eight of the 29 studied stands more than one plot was surveyed because of obvious heterogeneity in the stand with respect to age of the dominant cohort. The combined set of plots covered all cored age cohorts and 70% of all beech-dominated stands in Biskopstorp (Fig. 1).

Trees were sampled with an increment borer (Pressler type) at the lowest possible height above soil level. All samples were mounted on wooden sticks, dried and polished to give a smooth surface. The age was assessed under the microscope by ring counting. In order to eliminate missing and wedging rings, cross dating was applied for the trees in the 20-m radius plots based on the following pointer years: 1869, 1890, 1911, 1925, 1956, 1960 and 1974 (Niklasson 2002; Niklasson et al. 2005). The estimated germination age of every cored beech tree was calculated by adding years to the coring height on the stems, calibrated from young beech in the area (Fahlvik 1999).

### *Sampling of variables*

At plot level, forest canopy cover, layering (forest stratification), soil humidity and vegetation type were assessed according to the woodland key habitat (WKH) methodology (Norén et al. 2002). From this methodology, we narrowed the variable 'human impact' to *recent forestry impact* (RFI), i.e. estimating the impact only from recent thinning and cutting in three frequency classes as assessed by stumps and forest structure. Some of the variables were later omitted in the analyses due to low variation (soil humidity, vegetation type), or better representation from other variables (canopy cover).

At tree level, tree type was broadly defined in two categories; viable healthy beech and 'damaged' beech, i.e. rot (decay fungi) or other visible bark wounds on the stem, or otherwise suppressed. Bark type refers to three categories of bark texture. The variables tree age and diameter at breast height (DBH) were obtained from previous studies (Fahlvik 1999; Niklasson et al. 2005). In all, we used 16 environmental and spatial variables and seven substrate variables in the final analyses (Table 1).

### *Species survey*

The focus on determining species presence/absence, particularly of species of conservation concern, directed the choice of method. To increase the number of species identified, priority was given to cover a large bark area rather than focusing on quantitative accuracy. For each beech tree, all epiphytic lichens and bryophytes on the stem up to 2 m in height were surveyed using a hand lens (×10). The cover was estimated for each species on the scale: 1 = rare, $< 1\,dm^2$; 2 = sparse to moderate, $1\text{-}3\,dm^2$; 3 = abundant, $> 3\,dm^2$. Time spent on each tree was normally about 10 min, but varied with trunk size, bark structural complexity and species richness. Unidentified species were collected and later determined by chemical spot tests or under a microscope (stereo ×20-60 and light ×100-660).

The epiphytes were divided into groups: red-listed, indicator (species of conservation concern, primarily habitat specialists) and other species (presumably mostly habitat generalists) for each organism (lichen/bryophyte) category. The classification of red-listed species is according to Gärdenfors (2005). Indicator species, which indicate

**Table 1.** Description of response and predictor variables used in the final analyses.

| Predictors | Scale | Description |
|---|---|---|
| PLOT level | (16) | |
| Basal area | Ordinal | Measure of stem basal area in m$^2$/ha using a relascope in plot centre |
| Elevation | Ordinal | In metres (m.a.s.l.) measured in plot centre using a GPS |
| Exposure | Nominal | Dominant cardinal direction: 0 = northern aspect (NW-E), 1 = southern aspect (SE-W) |
| Inclination | Ordinal | Mean slope inclination in degrees (range 0-90) measured at five spots in a plot using a clinometer |
| Latitude | Ordinal | North coordinate from the Swedish national grid: GPS coordinates of centre of each plot. GPS 10–30 m precision |
| Layering | Ordinal | Forest stratification in plot: 1 = one layer, 2 = 2 layers, 3 = multi-layered |
| Light | Ordinal | The canopy scope method (Brown et al. 2000) measured from 0 to 25 points in the plot centre |
| Location | Ordinal | Plot location 1 = 0–20 m to forest edge, 2 = 20–40 m to edge, 3 = inside (>40 m) forest |
| Longitude | Ordinal | East coordinate from the Swedish national grid: GPS coordinates of centre of each plot. GPS 10–30 m precision |
| Recent forestry impact | Ordinal | Classes reflect 'low, moderate, high' impact (former thinning, cutting), see Norén et al. (2002) |
| Rocks and stones | Ordinal | Classes reflect 'zero, low, moderate, high' frequency |
| Stem density | Ordinal | Number of stems > 5 cm in diameter and exceeding breast height within a 10-m radius from plot centre |
| Surveyed bark area | Ordinal | Total bark surface area of all surveyed beech up to 2 m high in the plot |
| Topography | Ordinal | Plot situation: 1 = low part of slope, 2 = middle part, 3 = high part/top |
| Tree age, max | Ordinal | Maximum age of beech in the plot |
| Tree height, max | Ordinal | Measure of the height of the tallest beech tree in plot: a measure of soil fertility |
| TREE level | (7) | |
| Age | Ordinal | Actual calculated age of beech in years |
| Bark diversity | Ordinal | Number of bark texture types (1–3): smooth, rough or creviced |
| DBH | Ordinal | Diameter at breast height measured in cm |
| Inclination | Ordinal | Inclination of stem measured with a clinometer in degrees at a height of 1 m |
| Light | Ordinal | Average value of largest canopy opening measured at breast height on south and north side of stem using the canopy scope method (Brown et al. 2000) |
| Moss cover | Ordinal | Estimated percentage cover of mosses in 10% classes on stem from 0–2 m in height |
| Tree viability | Nominal | 0 = damaged, often with decay and/or suppressed trees; 1 = viable, healthy tree |

**Table 1.** (*continued*).

| Responses | Scale | Description |
|---|---|---|
| Species groups | (6) | At plot and tree level |
| Red-listed lichens | Ordinal | Number of red-listed lichens |
| Indicator lichens | Ordinal | Number of indicator lichens excluding red-listed lichens |
| Other lichens | Ordinal | Number of lichens not red-listed or considered as indicators |
| Red-listed bryophytes | Ordinal | Number of red-listed bryophytes |
| Indicator bryophytes | Ordinal | Number of indicator bryophytes excluding red-listed bryophytes |
| Other bryophytes | Ordinal | Number of other bryophytes not red-listed or considered as indicators |
| | (156) | At plot level |
| Single species | Ordinal | Frequency in each plot calculated as number of stem occurrences by each species divided by total number of surveyed beech trees in plot |
| | (156) | At tree level |
| Single species | Ordinal | Abundance on each stem (<2 m high): 0 = no record, 1 = cover <1 dm$^2$, 2 = 1–3 dm$^2$, 3 = >3 dm$^2$ |

the presence of red-listed species and thus woodland key habitats, follow Norén et al. (2002) and were independently selected prior to this study. To the list of indicator species, we added the lichens *Bacidia trachona*, *B. viridifarinosa* and *Peltigera praetextata*, and the bryophyte *Zygodon rupestris*, which, according to our field experience, may be suitable indicators in the study area. Some red-listed species were also indicator species (Norén et al. 2002), but these groups were separated, with priority given to the red-listed species to avoid overlap.

### *Statistical treatment*

We analysed data using non-metric multidimensional scaling (NMS) in the program PC-Ord version 5.12 (McCune & Mefford 1999). NMS may provide a more accurate representation of the underlying data structure than other ordination techniques for ecological community data (McCune & Grace 2002).

The variables (plot level: 37 plots ×16 variables; tree level: 571 trees ×7 variables) were related to both the number of species in each of the six species groups (species richness) (Table 1), and to the frequency of each single species (species composition) (plot level: 37 plots ×156 species; tree level: 571 trees ×156 species) (Table 1). In the plots, the frequency was calculated by dividing the number of beech on which a species was found by the total number of trees surveyed in each plot. At tree level, abundance classes (1-3) for each recorded epiphyte on each tree were used as a measure of abundance. All species found were included in the analyses.

In the final analysis, untransformed data were used because transformed data did not increase performance. All NMS ordinations were done in autopilot mode comparing one- to six-dimensional solutions. At plot level, the Sørensen distance measure was used with 250 runs (50 at tree level) for the real data and 250 runs (50) of randomised data with 500 (100) iterations each. The run with the lowest final stress was then used. In the final ordinations, stress levels differed significantly ($P < 0.01$) from the randomised Monte Carlo tests. Correlations between the ordination axes and the variables and species groups, respectively, were calculated with Pearson correlation. Cumulative correlations between distances in the original n-dimensional space and distances on the ordination axes were also calculated.

The range along the chronosequence of beech was analysed in two ways for each epiphyte species with at least five records. The first analysis was based on the qualitative occurrences of species on the trees. From the average age of occurrence, the standard deviation for each species was calculated, resulting in the main distribution of the species (average ± 1 SD). Including minimum and maximum age, time lines for presence were constructed. The second analysis was an indicator species analysis (ISA), performed in PC-Ord (McCune & Mefford 1999), in order to test if species were significantly over-represented in a particular age class of beech. Class 1 represented an ordinary rotation period in forestry ($\leq$ 120 years), class 2 was over-mature beech (121-180 years) and class 3 was old beech ($>$180 years). The ISA analysis combines relative frequency and faithfulness of a species to a particular age class and calculates indicator values that are tested by 10 000 Monte Carlo runs.

Tree viability was tested against the number of species in each of the six species groups by a two-sample *t*-test in the program MINITAB (MiniTab Inc. 1972-2003). To obtain comparable groups, the analysis was limited to trees older than 200 years having very similar ages and sizes (viable, $n = 40$; damaged, $n = 77$).

## Results

### Tree ages

The age of the cored beech varied from 37 to 292 years (mean 137 ± SD 67 years). Tree ages from 51 to 170 years were best represented, with at least 24 trees in each 10-year class. Trees aged between 211 and 280 years were also well represented, with generally at least ten trees in each 10-year class. Few trees were cored in the youngest ($<$50 years) and oldest ($>$281 years) age classes. In addition, trees aged between 171 and 210 years were rare.

### Species

A total of 156 species were identified, 104 lichens and 52 bryophytes (App. 1). Most species occurred at low frequencies; 86% of the lichen species were found on $<$10% of the trees, whereas the corresponding frequency for bryophytes was 71%. Thirty species were recorded only once. The maximum number of species in one plot was 73, and on one tree 34. The average number of species per plot was 41 (21 lichens, 20 bryophytes), and per tree 12 (six lichens, six bryophytes). In total, we found 22 nationally red-listed and 25 indicator species, of which 17 and 18, respectively, were lichens. There was a highly significant correlation between species frequencies in the plots and on the trees (lichens: $R^2 = 0.84$; bryophytes: $R^2 = 0.83$, $P < 0.001$, Pearson's squared correlation coefficient).

### Environmental variables at plot level

Maximum tree age in plots was correlated (negatively) only with stem density (App. 2A). The ordination of species richness in species groups resulted in a two-dimensional solution with a final stability of 0.07620 and a stress of 16.4, accounting for 86% of the variance in the distance matrix. The most important gradient, axis 2 ($r^2 = 0.54$), largely reflected maximum tree age ($r = 0.51$) and the area of surveyed bark ($r = 0.40$). Other lichens, red-listed and other bryophytes, were all positively correlated with this gradient. The other gradient, axis 1 ($r^2 = 0.32$), was also mostly related to maximum tree age ($r = 0.71$), but also inclination ($r = 0.34$), steepness of slope and topography ($r = -0.38$), i.e. the position on the slope. In particular, red-listed and indicator species of lichens and indicator species of bryophytes were strongly positively related to this last gradient.

The ordination of species frequencies (composition) also resulted in a two-dimensional solution with a final stability of 0.00000 and a stress of 15.0, accounting for 88% of the variance (Fig. 2). The most important gradient, axis 1 ($r^2 = 0.67$), was largely reflected in maximum tree age ($r = 0.73$) and inclination of slope ($r = 0.33$). A large number of red-listed and indicator species, for example the lichen *Lobaria pulmonaria*, were strongly correlated to the age gradient. Stem density ($r = -0.71$) and recent forestry impact ($r = 0.62$) were the most important variables connected to the second gradient, axis 2 ($r^2 = 0.20$) (Fig. 2).

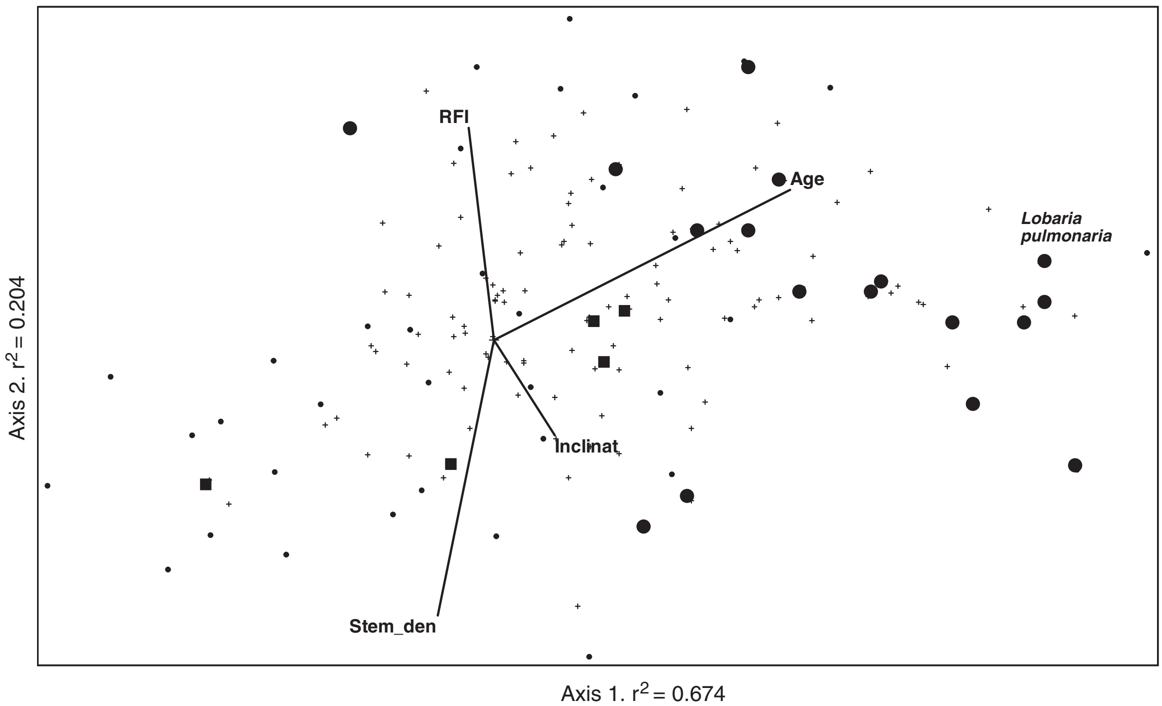

**Fig. 2.** NMS ordination of plots (•) based on species frequencies (+). Correlations with environmental variables are shown with a joint plot. Only variables with $r^2 > 0.2$ are shown. Red-listed lichens (●), e.g. *Lobaria pulmonaria*, and red-listed bryophytes (■) are marked. Age = maximum tree age, Inclinat = inclination, RFI = recent forestry impact, and Stem_den = stem density

### *Substrate variables at tree level*

Many of the variables were inter-correlated, especially to DBH and tree age, which, in turn, were also positively correlated (App. 2B). The ordination of species richness in species groups resulted in a two-dimensional solution with a final stability of 0.00001 and a stress of 11.8, accounting for 92% of the variation in the distance matrix (App. 3). Tree age and DBH were the variables best correlated with axis 2, the most important gradient ($r^2 = 0.72$). Moss cover was most positively correlated with axis 1. All species groups were more or less correlated to axis 2, other bryophytes were the most and red-listed bryophytes were the least correlated. In contrast, other lichens were the only group that correlated strongly (negatively) to axis 1.

Ordination of species abundances (composition) resulted in tree age being the best correlated variable to axis 3, followed by moss cover and DBH (App. 3). This was the most important gradient ($r^2 = 0.31$) in a three-dimensional solution with a final stability of 0.00456 and a stress of 19.4, accounting for 75% of the variation.

### *Species occupancy along the chronosequence of beech*

The occupancy of species along the age range of beech could be described as a gradual replacement sequence (Fig. 3). Some species, such as the crustose lichen *Mycoblastus fucatus*, had a wide age distribution range, but there were also many species showing specific age associations. The lichen *Pseudosagedia aenea* and the bryophyte *Ulota crispa* were examples of species noted mostly on young to mature stems ($\leq 120$ years). The lichen *Bacidina arnoldiana* and the bryophyte *Isothecium myosuroides* were more frequent on over-mature beech (121-180 years). However, most species in this study grew on old beech ($>180$ years), e.g. the lichen *Bacidia rubella* and the bryophyte *Isothecium alopecuroides*. The crustose lichens *Pyrenula nitida* and *Lecanora glabrata* grow on rather smooth bark, but were still not found on stems younger than 128 and 152 years, respectively. A group of rare crustose lichens, e.g. *Bacidina phacodes, Pachyphiale carneola* and *Thelopsis rubella*, all growing on rough bark, were not found on beech below 200 years of age.

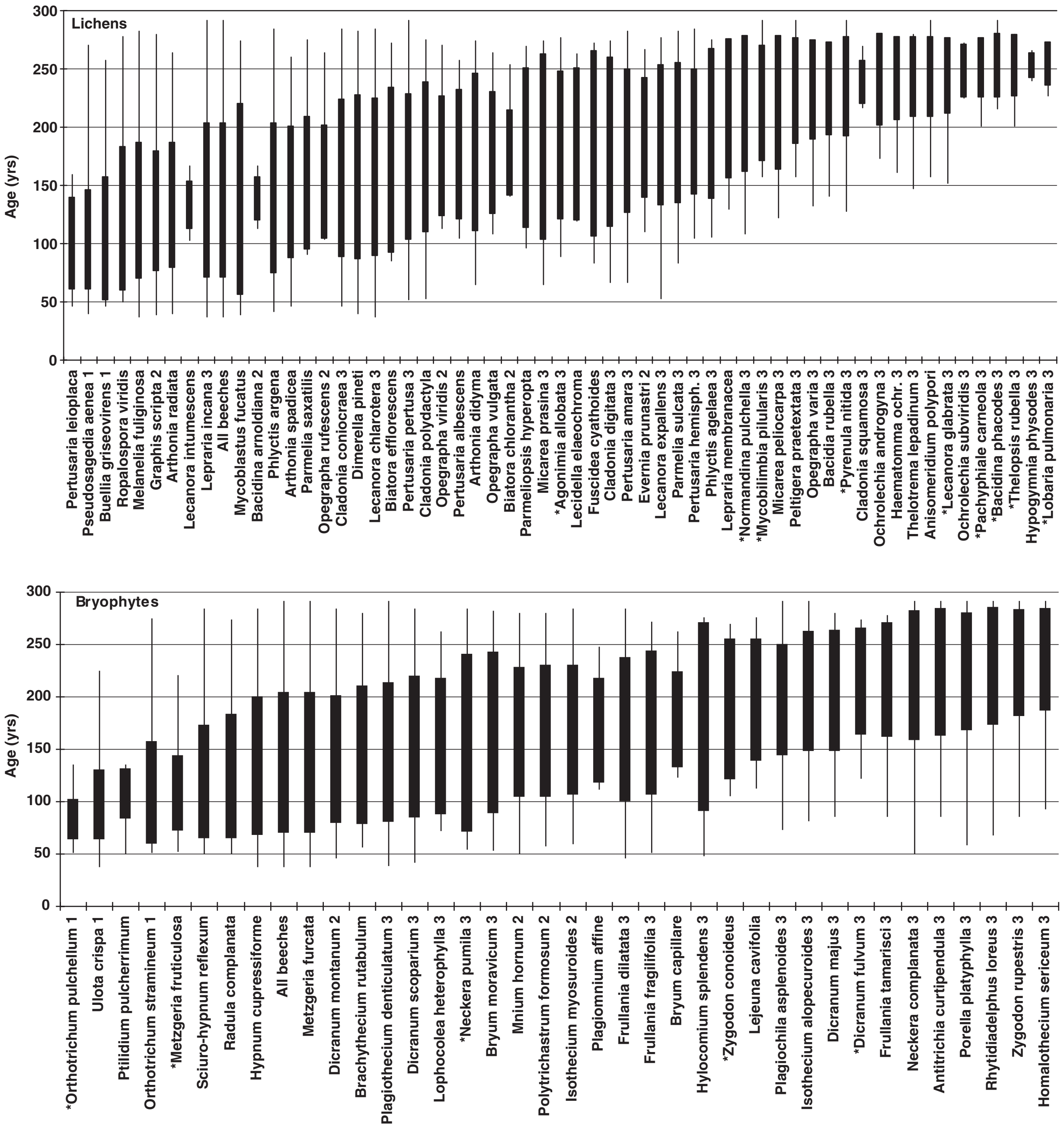

**Fig. 3.** Distribution along the chronosequence of beech for epiphytic lichens and bryophytes. Red-listed species are preceded by a *. Species that were significantly over-represented ($P<0.05$) in one age class have been noted by that class number: 1 = age ≤ 120 years, 2 = 121-180 years and 3 = >180 years. The bar for all cored beech has a mean age 137 ± SD 67 years (min 37, max 292 years). Column = mean age ± 1 SD; lower line = age from − 1 SD to minimum; upper line = age from+1 SD to maximum.

The indicator species analysis resulted in significant ($P<0.05$) over-representation in certain age classes for 66 of the 95 tested species. In particular, the oldest age class (>180 years) showed a high aggregation of species (76% of the species over-represented in one age class), followed by the over-mature age class (17%) and the young to mature age class (8%).

Frequencies of red-listed lichens increased dramatically when tree age exceeded 180 years (Fig. 4). In trees more than 180 years of age, red-listed lichens were found on 77% of all stems. This pattern was less obvious for red-listed bryophytes. In contrast, the moss *Orthotrichum pulchellum* and the liverwort *Metzgeria fruticulosa* had peak distribu-

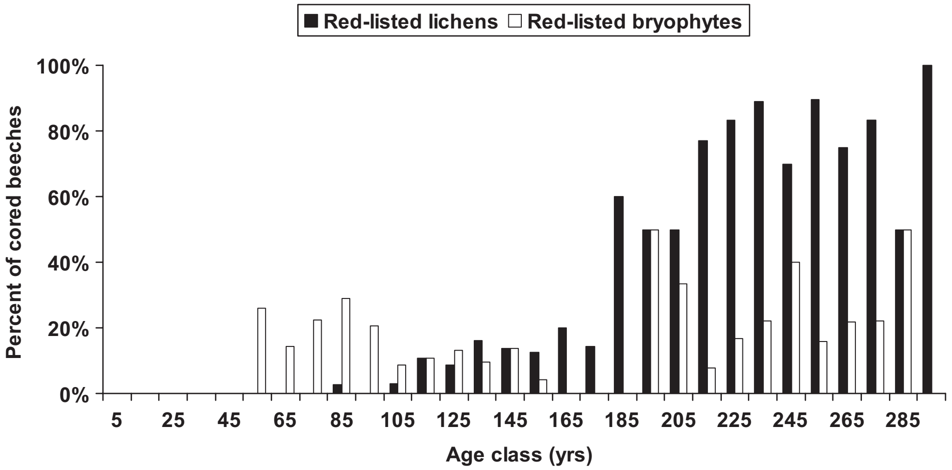

**Fig. 4.** Frequency of red-listed lichens and bryophytes on cored beech ($n = 571$, 37-292 years) at 10-year intervals.

tion on beech aged as young as 50-100 years. The moss *Neckera pumila* occurred both on young and on very old beech. Altogether, this resulted in a bimodal distribution along the chronosequence of beech of the few red-listed bryophytes (Fig. 4).

### *Viability of old trees reflects species group associations*

Significantly more species of red-listed (*t*-test, $P<0.001$) and indicator ($P<0.001$) lichens were found on damaged compared to viable beech, whereas no such relationship was found for other lichens ($P = 0.246$). For bryophytes, there was a highly significant difference for indicators ($P< 0.001$), a slight difference for red-listed species ($P = 0.038$) but no significant difference for other bryophytes ($P = 0.072$).

## Discussion

The age of the oldest tree was the most important variable for species richness and species composition at plot level. The effect of tree age differed, however, among the species groups. The red-listed lichens, indicator lichens and indicator bryophytes were strongly related to increased tree age. The richness of red-listed bryophytes, other bryophytes and other lichens was more related to total area of surveyed bark, indicating that space is the limiting factor.

A low elevational position on steep slopes favoured species richness. Higher up on the slopes, trees are more exposed to extreme conditions in terms of desiccating winds and sun exposure. Furthermore, air pollution is likely to have a greater effect in more exposed plots than in a sheltered location (Gauslaa 1995). In addition, the impact from logging is less on steep slopes compared to flat ground.

Our results clearly show that tree age was also the most important variable determining species richness of individual beech. Many species may require old beech predominantly because the suitable substrate only develops with increased tree age. Similar results have recently been found in a study of crustose lichens of conservation value on age-determined oak (Ranius et al. 2008), whereas the positive relationship between total species richness of crustose lichens and tree age levelled off earlier on ash (*Fraxinus excelsior*) (Johansson et al. 2007). However, there are also studies showing no or a negative relationship between tree age and epiphyte species diversity (e.g. Heylen et al. 2005). Conflicting results may arise from site-specific differences in climate and edaphic conditions, phorophyte characteristics and the tree age ranges studied, but also from human influences, e.g. air pollution, which may terminate ‘climax’ epiphyte communities.

Tree age is a complex factor to interpret, because it co-varies with growth and the subsequent formation of different bark characteristics, such as bark crevices (Johansson et al. 2007). In addition, certain substrates, such as rot holes and sap flows associated with a large proportion of the damaged tree type are more common on older, but not necessarily larger, stems. All these age-dependent tree characteristics might influence epiphyte diversity, species composition and succession (Barkman 1958). Age was consistently more important in the ordinations than DBH for species richness and species composition. Thus, the epiphyte richness in this study may not solely be a function of bark area, although this factor seems to be the most important among factors associated with tree age that were studied. DBH was correlated to many other tree characteristics, especially bark diversity, supporting Friedel et al. (2006) who used DBH as an indicator for substrate diversity. For most species of conservation concern, tree age was indeed more important than tree size.

The changes in species composition along the chronosequence of the phorophyte are in agreement with a study on aspen (*Populus tremula*) in boreal forest (Hedenås & Ericson 2000). For example we recorded most indicator species in the oldest age class. This does not imply, however, that all these species require old trees. Old beech trunks provided the most diverse bark substrates, including smooth bark, that are also suitable for early colonisers such as *Graphis scripta*. This enables more species to coexist on a trunk, increasing the total species richness (cf. Kantvilas & Jarman 2004), but also lowering the faithfulness of species limited exclusively to smooth bark on young trees. Furthermore, the low incidence of cored beech between 170 and 210 years old may have contributed to an overestimation of the importance of age for some of the very late successional species. Many of these species were, however, either not or seldom noted on beech of 51-170 years old, despite numerous surveyed trees.

Results from this study also showed that the presence of old trees is not enough for the occurrence of the assumed habitat specialists. Apparently, not all old trees offer a substrate quality suitable for these species. There were significantly more species, particularly red-listed lichens, indicator lichens and indicator bryophytes, on damaged compared to viable old beech. These results correspond with studies that emphasized the importance of damaged trees for certain epiphytes (Barkman 1958; Bates 1992; Gauslaa 1995; Mikhailova et al. 2005).

### *Management implications*

The removal of old trees and abruptly changing microclimate during the management rotation may adversely affect epiphytes (Bardat & Aubert 2007) and makes a combination of conventional shelterwood beech forestry and conservation of epiphytes difficult to achieve in the same stand. Comparisons between forests managed with shelterwood forestry with unmanaged and less managed beech forests also show a lower total number of species and/or fewer specialist species of epiphytes in the former forests (Aude & Poulsen 2000; Friedel et al. 2006; Nascimbene et al. 2007).

Short rotation forestry reduces the survival of many epiphyte species in the long term. The long period between rotation age (100-140 years) and required age ($\geq 180$ years) for those species emphasizes the need for conservation rather than for silvicultural management. Damaged and suppressed beech trees contain a significant part of the threatened lichens. If suitable old trees were kept as retained trees, more demanding species may remain in the stands (Boudreault et al. 2000). Canopy thinning at the end of the rotation period causes a rapid shift to more exposed conditions (sun and wind), which makes the epiphytes vulnerable to desiccation. Conversely, after regeneration, a dense cohort of beech saplings shades the lower part of the stem of the retained trees. To improve success of conservation of epiphytes in managed shelterwood forests, we suggest a spatial separation of the beech stands in production units from areas set aside for sensitive, substrate- and dispersal-limited lichens. These set asides should ideally contain a mixture of young, mature and old trees, preferably in sheltered humid conditions.

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**App. 1**

**Table A1.** List of lichens (A) and bryophytes (B) found in the study. For each species, scientific name, abbreviation, species group, growth form and frequency in surveyed plots ($n = 37$) and on trees ($n = 571$) are provided. [1] = includes all *Lepraria* except the easily identified *L. membranacea*. [2] = mainly *Orthotrichum stramineum*, but can include some *O. affine* and *O. speciosum*

| Scientific name | Abbreviation | Species group | Growth form | Plots | Trees |
|---|---|---|---|---|---|
| *(A) Lichens (n = 104)* | | | | | |
| *Acrocordia gemmata* | Acr_gemm | Indicator | Crustose | 0.03 | 0.002 |
| *Agonimia allobata* | Ago_allo | Red-listed | Crustose | 0.27 | 0.025 |
| *Anisomeridium biforme* | Ani_bifo | Indicator | Crustose | 0.03 | 0.002 |
| *Anisomeridium polypori* | Ani_poly | Other | Crustose | 0.32 | 0.046 |
| *Arthonia didyma* | Art_didy | Other | Crustose | 0.24 | 0.019 |
| *Arthonia radiata* | Art_radi | Other | Crustose | 0.38 | 0.060 |
| *Arthonia spadicea* | Art_spad | Indicator | Crustose | 0.24 | 0.037 |
| *Arthonia vinosa* | Art_vino | Indicator | Crustose | 0.08 | 0.007 |
| *Arthopyrenia* sp | Art_sp. | Other | Crustose | 0.03 | 0.004 |
| *Bacidia incompta* | Bac_inco | Red-listed | Crustose | 0.05 | 0.004 |
| *Bacidia rosella* | Bac_rose | Red-listed | Crustose | 0.03 | 0.002 |
| *Bacidia rubella* | Bac_rube | Indicator | Crustose | 0.16 | 0.014 |
| *Bacidia trachona* | Bac_trac | Indicator | Crustose | 0.03 | 0.002 |
| *Bacidia viridifarinosa* | Bac_viri | Indicator | Crustose | 0.08 | 0.007 |
| *Bacidina arnoldiana* | Bac_arno | Other | Crustose | 0.08 | 0.014 |
| *Bacidina phacodes* | Bac_phac | Red-listed | Crustose | 0.11 | 0.011 |
| *Biatora chrysantha* | Bia_chry | Other | Crustose | 0.16 | 0.014 |
| *Biatora efflorescens* | Bia_effl | Other | Crustose | 0.16 | 0.012 |
| *Biatoridium monasteriense* | Bia_mona | Red-listed | Crustose | 0.05 | 0.004 |
| *Buellia griseovirens* | Bue_gris | Other | Crustose | 0.32 | 0.065 |
| *Candelaria concolor* | Can_conc | Other | Foliose | 0.08 | 0.005 |
| *Chaenotheca brachypoda* | Cha_brac | Indicator | Crustose | 0.03 | 0.002 |
| *Cladonia coniocraea* | Cla_coni | Other | Fruticose | 0.95 | 0.440 |
| *Cladonia digitata* | Cla_digi | Other | Fruticose | 0.51 | 0.075 |
| *Cladonia fimbriata* | Cla_fimb | Other | Fruticose | 0.03 | 0.002 |
| *Cladonia pleurota* | Cla_pleu | Other | Fruticose | 0.03 | 0.004 |
| *Cladonia polydactyla* | Cla_poly | Other | Fruticose | 0.22 | 0.021 |
| *Cladonia squamosa* | Cla_squa | Other | Fruticose | 0.11 | 0.011 |
| *Cliostomum griffithii* | Cli_grif | Other | Crustose | 0.03 | 0.002 |
| *Dimerella pineti* | Dim_pine | Other | Crustose | 0.65 | 0.107 |
| *Enterographa zonata* | Ent_zona | Other | Crustose | 0.05 | 0.004 |
| *Evernia prunastri* | Eve_prun | Other | Fruticose | 0.32 | 0.044 |
| *Fuscidea cyathoides* var. *corticola* | Fus_cyat | Other | Crustose | 0.16 | 0.014 |
| *Graphis scripta* | Gra_scri | Other | Crustose | 0.89 | 0.538 |
| *Gyalecta flotowii* | Gya_flot | Red-listed | Crustose | 0.03 | 0.002 |
| *Gyalideopsis anastomosans* | Gya_anas | Other | Crustose | 0.05 | 0.004 |
| *Haematomma ochroleucum* | Hae_ochr | Other | Crustose | 0.24 | 0.021 |
| *Hypogymnia physodes* | Hyp_phys | Other | Foliose | 0.16 | 0.012 |
| *Lecania cyrtella* | Lec_cyr1 | Other | Crustose | 0.03 | 0.002 |
| *Lecania cyrtellina* | Lec_cyr2 | Other | Crustose | 0.03 | 0.002 |
| *Lecania hyalina* | Lec_hyal | Other | Crustose | 0.05 | 0.004 |
| *Lecanora allophana* | Lec_allo | Other | Crustose | 0.05 | 0.004 |
| *Lecanora argentata* | Lec_arge | Other | Crustose | 0.03 | 0.004 |
| *Lecanora chlarotera* | Lec_chla | Other | Crustose | 0.68 | 0.208 |
| *Lecanora expallens* | Lec_expa | Other | Crustose | 0.38 | 0.047 |
| *Lecanora glabrata* | Lec_glab | Red-listed | Crustose | 0.38 | 0.063 |
| *Lecanora intumescens* | Lec_intu | Other | Crustose | 0.19 | 0.025 |
| *Lecidella elaeochroma* | Lec_elae | Other | Crustose | 0.14 | 0.009 |
| *Lepraria incana*[1] | Lep_inca | Other | Crustose | 1.00 | 0.925 |
| *Lepraria membranacea* | Lep_memb | Other | Foliose | 0.14 | 0.012 |

**Table A1.** *(Continued)*.

| Scientific name | Abbreviation | Species group | Growth form | Plots | Trees |
|---|---|---|---|---|---|
| *Leptogium lichenoides* | Lep_lich | Indicator | Foliose | 0.08 | 0.007 |
| *Lobaria pulmonaria* | Lob_pulm | Red-listed | Foliose | 0.11 | 0.012 |
| *Lopadium disciforme* | Lop_disc | Indicator | Crustose | 0.03 | 0.005 |
| *Megalaria laureri* | Meg_laur | Red-listed | Crustose | 0.08 | 0.007 |
| *Melanelia fuliginosa* | Mel_fuli | Other | Foliose | 0.81 | 0.250 |
| *Menegazzia terebrata* | Men_tere | Red-listed | Foliose | 0.03 | 0.002 |
| *Micarea peliocarpa* | Mic_peli | Other | Crustose | 0.11 | 0.012 |
| *Micarea prasina* | Mic_pras | Other | Crustose | 0.38 | 0.054 |
| *Mycobilimbia epixanthoides* | Myc_epix | Other | Crustose | 0.05 | 0.004 |
| *Mycobilimbia pilularis* | Myc_pilu | Red-listed | Crustose | 0.14 | 0.012 |
| *Mycoblastus fucatus* | Myc_fuca | Other | Crustose | 0.27 | 0.053 |
| *Nephroma parile* | Nep_pari | Indicator | Foliose | 0.03 | 0.002 |
| *Normandina pulchella* | Nor_pulc | Red-listed | Foliose | 0.46 | 0.063 |
| *Ochrolechia androgyna* | Och_andr | Other | Crustose | 0.11 | 0.009 |
| *Ochrolechia subviridis* | Och_subv | Other | Crustose | 0.11 | 0.009 |
| *Ochrolechia turneri* | Och_turn | Other | Crustose | 0.05 | 0.004 |
| *Opegrapha ochrocheila* | Ope_ochr | Red-listed | Crustose | 0.03 | 0.002 |
| *Opegrapha rufescens* | Ope_rufe | Other | Crustose | 0.19 | 0.018 |
| *Opegrapha sorediifera* | Ope_sore | Indicator | Crustose | 0.03 | 0.002 |
| *Opegrapha varia* | Ope_vari | Other | Crustose | 0.24 | 0.030 |
| *Opegrapha viridis* | Ope_viri | Indicator | Crustose | 0.19 | 0.040 |
| *Opegrapha vulgata* | Ope_vulg | Other | Crustose | 0.16 | 0.019 |
| *Pachyphiale carneola* | Pac_carn | Red-listed | Crustose | 0.11 | 0.016 |
| *Parmelia ernstiae* | Par_erns | Other | Foliose | 0.03 | 0.005 |
| *Parmelia saxatilis* | Par_saxa | Other | Foliose | 0.43 | 0.126 |
| *Parmelia sulcata* | Par_sulc | Other | Foliose | 0.76 | 0.170 |
| *Parmeliopsis ambigua* | Par_ambi | Other | Foliose | 0.05 | 0.005 |
| *Parmeliopsis hyperopta* | Par_hype | Other | Foliose | 0.24 | 0.023 |
| *Peltigera praetextata* | Pel_prae | Indicator | Foliose | 0.14 | 0.016 |
| *Pertusaria albescens* | Per_albe | Other | Crustose | 0.11 | 0.012 |
| *Pertusaria amara* | Per_amar | Other | Crustose | 0.68 | 0.117 |
| *Pertusaria flavida* | Per_flav | Other | Crustose | 0.03 | 0.002 |
| *Pertusaria hemisphaerica* | Per_hemi | Other | Crustose | 0.65 | 0.114 |
| *Pertusaria hymenea* | Per_hyme | Other | Crustose | 0.03 | 0.002 |
| *Pertusaria leioplaca* | Per_leio | Other | Crustose | 0.14 | 0.021 |
| *Pertusaria pertusa* | Per_pert | Other | Crustose | 0.97 | 0.433 |
| *Phaeophyscia endophoenicea* | Pha_endo | Indicator | Foliose | 0.03 | 0.002 |
| *Phlyctis agelaea* | Phl_agae | Indicator | Crustose | 0.16 | 0.011 |
| *Phlyctis argena* | Phl_arge | Other | Crustose | 1.00 | 0.520 |
| *Platismatia glauca* | Pla_glau | Other | Foliose | 0.03 | 0.002 |
| *Pseudosagedia aenea* | Pse_aene | Other | Crustose | 0.43 | 0.116 |
| *Psilolechia lucida* | Psi_luci | Other | Crustose | 0.03 | 0.002 |
| *Pyrenula nitida* | Pyr_nita | Red-listed | Crustose | 0.51 | 0.172 |
| *Pyrrhospora quernea* | Pyr_quer | Other | Crustose | 0.03 | 0.002 |
| *Rinodina cf efflorescens* | Rin_effl | Other | Crustose | 0.05 | 0.005 |
| *Ropalospora viridis* | Rop_viri | Other | Crustose | 0.43 | 0.067 |
| *Scoliciosporum pruinosum* | Sco_prui | Red-listed | Crustose | 0.03 | 0.002 |
| *Sphaerophorus globosus* | Sph_glob | Indicator | Fruticose | 0.03 | 0.002 |
| *Thelopsis rubella* | The_rube | Red-listed | Crustose | 0.11 | 0.009 |
| *Thelotrema lepadinum* | The_lepa | Indicator | Crustose | 0.19 | 0.030 |
| *Trapeliopsis gelatinosa* | Tra_gela | Other | Crustose | 0.03 | 0.002 |
| *Trapeliopsis granulosa* | Tra_gran | Other | Crustose | 0.05 | 0.004 |
| *Trapeliopsis pseudogranulosa* | Tra_pseu | Other | Crustose | 0.03 | 0.002 |
| *Vezdaea aestivalis* | Vez_aest | Other | Crustose | 0.03 | 0.002 |

| Scientific name | Abbreviation | Species group | Bryophyte group | Plots | Trees |
|---|---|---|---|---|---|
| *(B) Bryophytes (n = 52)* | | | | | |
| *Antitrichia curtipendula* | Anti_cur | Indicator | Moss | 0.35 | 0.040 |
| *Brachythecium rutabulum* | Brac_rut | Other | Moss | 0.57 | 0.089 |
| *Bryum capillare* | Bryu_cap | Other | Moss | 0.16 | 0.012 |
| *Bryum moravicum* | Bryu_mor | Other | Moss | 0.46 | 0.074 |
| *Campylopus flexuosus* | Camp_fle | Other | Moss | 0.03 | 0.002 |
| *Dicranella heteromalla* | Dicr_het | Other | Moss | 0.03 | 0.002 |
| *Dicranum fulvum* | Dicr_ful | Red-listed | Moss | 0.19 | 0.016 |
| *Dicranum fuscescens* | Dicr_fus | Other | Moss | 0.03 | 0.002 |
| *Dicranum majus* | Dicr_maj | Other | Moss | 0.49 | 0.091 |
| *Dicranum montanum* | Dicr_mon | Other | Moss | 0.86 | 0.303 |
| *Dicranum scoparium* | Dicr_sco | Other | Moss | 1.00 | 0.576 |
| *Frullania dilatata* | Frul_dil | Other | Liverwort | 0.89 | 0.247 |

**Table A1.** *(Continued).*

| Scientific name | Abbreviation | Species group | Bryophyte group | Plots | Trees |
|---|---|---|---|---|---|
| *Frullania fragilifolia* | Frul_fra | Other | Liverwort | 0.51 | 0.044 |
| *Frullania tamarisci* | Frul_tam | Other | Liverwort | 0.59 | 0.117 |
| *Homalia trichomanoides* | Homa_tri | Indicator | Moss | 0.08 | 0.005 |
| *Homalothecium sericeum* | Homa_ser | Indicator | Moss | 0.51 | 0.067 |
| *Hylocomium splendens* | Hylo_spl | Other | Moss | 0.19 | 0.016 |
| *Hypnum cupressiforme* | Hypn_cup | Other | Moss | 1.00 | 0.897 |
| *Isothecium alopecuroides* | Isot_alo | Other | Moss | 0.89 | 0.210 |
| *Isothecium myosuroides* | Isot_myo | Other | Moss | 0.89 | 0.382 |
| *Lejeuna cavifolia* | Leje_cav | Other | Liverwort | 0.24 | 0.019 |
| *Lepidozia reptans* | Lepi_rep | Other | Liverwort | 0.05 | 0.004 |
| *Leucobryum glaucum* | Leuc_gla | Other | Moss | 0.05 | 0.004 |
| *Lophocolea bidentata* | Loph_bid | Other | Liverwort | 0.03 | 0.005 |
| *Lophocolea heterophylla* | Loph_het | Other | Liverwort | 0.16 | 0.012 |
| *Metzgeria fruticulosa* | Metz_fru | Red-listed | Liverwort | 0.30 | 0.047 |
| *Metzgeria furcata* | Metz_fur | Other | Liverwort | 1.00 | 0.608 |
| *Mnium hornum* | Mniu_hor | Other | Moss | 0.86 | 0.289 |
| *Nardia scalaris* | Nard_sca | Other | Liverwort | 0.03 | 0.004 |
| *Neckera complanata* | Neck_com | Indicator | Moss | 0.59 | 0.105 |
| *Neckera crispa* | Neck_cri | Indicator | Moss | 0.05 | 0.004 |
| *Neckera pumila* | Neck_pum | Red-listed | Moss | 0.41 | 0.082 |
| *Orthotrichum diaphanum* | Orth_dia | Other | Moss | 0.03 | 0.004 |
| *Orthotrichum pulchellum* | Orth_pul | Red-listed | Moss | 0.16 | 0.030 |
| *Orthotrichum stramineum*[1] | Orth_sp. | Other | Moss | 0.65 | 0.184 |
| *Paraleucobryum longifolium* | Para_lon | Other | Moss | 0.08 | 0.005 |
| *Plagiochila asplenioides* | Plag_asp | Other | Liverwort | 0.32 | 0.054 |
| *Plagiomnium affine* | Plag_aff | Other | Moss | 0.11 | 0.011 |
| *Plagiomnium cuspidatum* | Plag_cus | Other | Moss | 0.08 | 0.005 |
| *Plagiothecium denticulatum* | Plag_den | Other | Moss | 0.97 | 0.338 |
| *Plagiothecium undulatum* | Plag_und | Other | Moss | 0.08 | 0.005 |
| *Pleurozium schreberi* | Pleu_sch | Other | Moss | 0.03 | 0.002 |
| *Polytrichastrum formosum* | Poly_for | Other | Moss | 0.84 | 0.215 |
| *Porella platyphylla* | Pore_pla | Indicator | Liverwort | 0.32 | 0.049 |
| *Ptilidium pulcherrimum* | Ptil_pul | Other | Liverwort | 0.08 | 0.019 |
| *Radula complanata* | Radu_com | Other | Liverwort | 0.78 | 0.212 |
| *Rhytidiadelphus loreus* | Rhyt_lor | Other | Moss | 0.46 | 0.081 |
| *Sciuro-hypnum reflexum* | Sciu_ref | Other | Moss | 0.41 | 0.095 |
| *Thuidium tamariscinum* | Thui_tam | Other | Moss | 0.05 | 0.004 |
| *Ulota crispa* | Ulot_cri | Other | Moss | 0.70 | 0.347 |
| *Zygodon conoideus* | Zygo_con | Red-listed | Moss | 0.16 | 0.012 |
| *Zygodon rupestris* | Zygo_rup | Indicator | Moss | 0.59 | 0.084 |

**App. 2**

**Table A2.** Correlation matrix (Pearson's $r$) between variables (A) in plots ($n = 37$) and (B) on trees ($n = 571$). Only significant correlations and variables are presented. Significance levels: $^{*}P < 0.05$; $^{**}P < 0.01$ and $^{***}P < 0.001$

| | Basal area | Elevation | Inclination | Latitude, $x$ | Layering | Longitude, $y$ | Recent forestry impact | Stem density |
|---|---|---|---|---|---|---|---|---|
| *(A) Plots* | | | | | | | | |
| Inclination | | $-0.38^{*}$ | | | | | | |
| Latitude, $x$ | | $0.77^{***}$ | | | | | | |
| Layering | | $-0.44^{**}$ | | $-0.35^{*}$ | | | | |
| Light | $-0.44^{**}$ | | | | | | | |
| Location | | | | | $-0.41^{*}$ | | | |
| Longitude, $y$ | | $-0.53^{**}$ | | $0.64^{***}$ | $-0.33^{*}$ | | | |
| Recent forestry impact | $-0.45^{**}$ | | $-0.52^{**}$ | | | $0.32^{*}$ | | |
| Rocks and stones | | | | | | $-0.34^{*}$ | $-0.38^{*}$ | |
| Stem density | $0.52^{**}$ | | $0.33^{*}$ | | | | $-0.62^{***}$ | |
| Surveyed bark area | | | | | | | | |
| Topography | | $0.51^{**}$ | | | | | | |
| Tree age, max | | | | | | | $-0.37^{*}$ | |
| Tree height, max | | | | | $0.37^{*}$ | | | |

| | Age | Bark diversity | Diameter (BH) | Inclination | Light |
|---|---|---|---|---|---|
| *(B) Trees* | | | | | |
| Bark diversity | $0.28^{***}$ | | | | |
| Diameter (BH) | $0.66^{***}$ | $0.42^{***}$ | | | |
| Inclination | | $-0.09^{*}$ | $-0.19^{***}$ | | |
| Light | $0.22^{***}$ | | $0.18^{***}$ | | |
| Moss Cover | $0.21^{***}$ | | $0.25^{***}$ | $-0.10^{*}$ | |
| Tree viability | $-0.10^{*}$ | $0.13^{**}$ | $0.17^{***}$ | $-0.22^{***}$ | $0.11^{**}$ |

**App. 3**

**Table A3.** Pearson correlation coefficients between variables, species groups and ordination axes in NMS ordinations of the tree-level data set. Results refer to ordinations of species abundances and species groups, respectively. Cumulative correlations are provided for each axis.

| | Species group – variables | | Species abundance – variables | | |
|---|---|---|---|---|---|
| | Axis 1<br>$R^2 = 0.20$ | Axis 2<br>$R^2 = 0.72$ | Axis 1<br>$R^2 = 0.16$ | Axis 2<br>$R^2 = 0.27$ | Axis 3<br>$R^2 = 0.31$ |
| Variables | | | | | |
| Bark diversity | – 0.11 | – 0.34 | – 0.25 | – 0.22 | – 0.14 |
| DBH | 0.01 | – 0.49 | – 0.58 | – 0.28 | – 0.38 |
| Inclination of trunk | 0.01 | – 0.06 | 0.16 | – 0.13 | – 0.05 |
| Light | – 0.19 | – 0.14 | – 0.26 | – 0.03 | – 0.05 |
| Moss cover | 0.34 | – 0.21 | – 0.17 | 0.03 | – 0.43 |
| Tree age | – 0.10 | – 0.59 | – 0.58 | – 0.49 | – 0.46 |
| Tree viability | – 0.04 | 0.08 | – 0.24 | 0.19 | 0.18 |
| Species groups | | | | | |
| Red-listed lichens | – 0.03 | – 0.52 | | | |
| Indicator lichens | – 0.04 | – 0.35 | | | |
| Other lichens | – 0.73 | – 0.62 | | | |
| Red-listed bryophytes | 0.28 | – 0.24 | | | |
| Indicator bryophytes | 0.15 | – 0.49 | | | |
| Other bryophytes | 0.36 | – 0.80 | | | |