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Tree species identity modifies the efficiency of habitat tree retention for conserving epiphytes in temperate mountain forests



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ABSTRACT

Forest ecosystems play an outstanding role in supporting diverse bryophyte and lichen communities. However, intensive forest management has led to a considerable decline of epiphyte communities, which are sensitive to the simplification of forest stands and the interruption of stand continuity. Retention forestry, which originally aimed to conserve important structural elements for biodiversity after clearcut, has more recently also been incorporated into continuous-cover forestry in temperate European forests. As both management systems differ from each other, it is difficult to transfer findings to the efficiency of retention measures for biodiversity conservation from clearcut to continuous-cover management systems. Therefore, we studied how habitat trees retained in continuous-cover forestry in temperate mountain forests of Germany dominated by Fagus sylvatica, Picea abies, and Abies alba would benefit epiphytic bryophytes and lichens. We analysed the epiphyte vegetation on 1254 trees in 132 forest stands. We compared large-sized habitat retention trees (HT) and smaller-sized average trees (AT). We detected a significantly higher species richness on HT, which was more strongly driven by lichens than by bryophytes. Even stronger increases in Simpson and Shannon diversity suggested that these increases in richness were due to increased population sizes of several species and not due to the addition of few individuals of few species. Strong variability in the response of epiphyte diversity occurred between tree species, with bryophytes being particularly favored by F. sylvatica and lichens by A. alba. Retention of HT is thus a suitable tool to conserve epiphytes in Central European temperate forests, even after blind selection of HT without consideration of the epiphyte vegetation before tree selection.

1. Introduction

The simplification of the structure and tree species composition of forests stands due to forest management can have negative impacts on biodiversity (Hilmers et al., 2018; Paillet et al., 2010). The influence of management is most radical, where forests are clearcut, because this results in structurally strongly simplified and homogeneous even-aged forest stands (Rosenvald and Lõhmus, 2008). Savilaakso et al. (2021), reviewing studies from boreal forests in Fennoscandia and European Russia, investigated the effects of age class forestry on various taxonomic groups in comparison to uneven-aged managed forests and unmanaged natural forests. The key findings were that the number of

ous even-aged to mitigate the negative impacts of intensive forestry on biodiversity, is retention forestry. This method was first introduced in the boreal forest bians advantation of the second formula for the second formula formula for the second formula for the second formula for the second formula formula for the second formula formula for the second formula formula for the second formula formula formula for the second formula for the second formula f

(Savilaakso et al., 2021).

biome, where clearcut forestry is dominant (Gustafsson et al., 2012; Shorohova et al., 2019), and is now widely implemented in clearcutting systems all over the world (Martínez Pastur et al., 2020). Saving single individuals or small patches of large-diameter trees or deadwood is the

forest-dependant species was higher under uneven-aged management, and that even-aged forests were less species rich than natural forests

How important structural diverse forests are for biodiversity has

widely been recognized (Hekkala et al., 2023; Tinya et al., 2021). One

silvicultural measure that aims to maintain structural richness in order

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key characteristics of retention forestry (Gustafsson et al., 2020; Lindenmayer et al., 2012) and is done to facilitate the recovery of the species pool and ecosystem processes after harvest (Bauhus et al., 2009). So far, comprehensive overviews exist that deal with the efficiency of retention measures in forests, which emerged from clearcut-based management systems (Fedrowitz et al., 2014; Mori and Kitagawa, 2014; Rosenvald and Lõhmus, 2008). However, only little is known about the benefits of retention forestry on biodiversity, when introduced to continuous-cover forestry.

Continuous-cover forestry is most often practised in temperate forests (Bauhus et al., 2013) and has become popular in large parts of Central Europe (Gustafsson et al., 2020). Unlike clearcutting, continuous-cover forestry relies on the selective logging of individual trees or small groups of trees, thereby gradually transforming even-aged stands into uneven-aged forests (Eyvindson et al., 2021). Retention measures incorporated in continuous-cover forestry should focus on the retention of large-diameter habitat trees and deadwood, which are supposed to be highly relevant for conserving biodiversity (Gustafsson et al., 2020), and organic carbon stocks (Hauck et al., 2023).

In contrast to boreal forests, where studies of the ecological effects of retention forestry focus on the more widespread clearcut forests (Fedrowitz et al., 2014; Mori and Kitagawa, 2014), several studies dealt with the effects of retention measures in continuous-cover forestry in temperate forests of Europe. These studies documented the promotional effect of retention forestry on the abundance of tree-related microhabitats (TreMs) (Asbeck et al., 2020; Frey et al., 2020; Spînu et al., 2022). Retention measures and high TreM abundance were associated with increasing diversity of bats, birds, and insects (Basile et al., 2020; Hendel et al., 2023; Rappa et al., 2023).

Effects of the retention of habitat trees on epiphytic bryophytes and lichens in temperate forests under continuous-cover management have been scarcely addressed (Kaufmann et al., 2021), even though they are important components of the overall species diversity of temperate forests (Coppins and Coppins, 2005) and are known to respond more sensitively to forest management than, for instance, vascular plants (Kaufmann et al., 2018; Paillet et al., 2010). This high sensitivity is caused by the fact that epiphytes depend much more directly on structural traits of the trees and on tree species identity than the ground vegetation (Dittrich et al., 2014, 2013; Kaufmann et al., 2017).

Tree aging does usually not result in the complete replacement of bryophyte and lichen communities that would result in high species turnover (Ellis and Ellis, 2013; Fritz et al., 2009). Aside from some pioneer species of the smooth bark of young trees (Gustafsson et al., 2023), epiphyte succession in temperate forests primarily consists of the gain in species on large-diameter trees in the overmature and decay stages of the forest development cycle compared to medium-sized trees in the optimum stage that before harvest (Dittrich et al., 2013; Hauck et al., 2012; Kaufmann et al., 2018). Comparing the diversity of epiphytic bryophytes and lichens between trees before or at the rotation age with that of overmature large-diameter trees thus expect an increase in epiphyte species richness, but a limited change in species composition.

In concert with air pollution, widespread stand simplification, decreasing the number of potential host trees species and the removal of large sized trees and deadwood, which have been identified to be crucial for epiphyte assemblages (Hofmeister et al., 2015; Király et al., 2013; Mežaka et al., 2008), has led to substantial decreases of forest epiphytes in temperate Europe (Hauck et al., 2013). Hence, the retention of habitat trees that offer microhabitats that are important for epiphytes could have beneficial effects on the diversity of epiphytic bryophytes and lichens.

Only little is known on which bases habitat trees should be selected in continuous-cover forestry to promote epiphytes. In general, broadleaved trees are recognized to enhance bryophyte and lichen diversity (Gerra-Inohosa et al., 2023; Király et al., 2013; Mežaka et al., 2008; Ódor et al., 2013) but their role as habitat trees in continuous-cover forests remains unclear. Kaufmann et al. (2021) gave a little insight whether habitat trees would provide epiphytes the opportunity to recover and disperse after logging. However, Kaufmann et al. (2021) focused only on habitat trees of a single tree species, *Abies alba*. In a more recent study, Emrich et al. (2025) provided a first comprehensive overview about the performance of different habitat tree species identities in different broadleaved and conifer-dominated forest types in southwest Germany.

The aim of the present study is to investigate whether habitat trees (HT) with above-average stem diameter have a higher bryophyte and lichen diversity than non-habitat, average trees (AT), and thus, if they would be appropriate to facilitate the colonization of epiphytes after harvest in temperate continuous-cover forestry. Therefore, we conducted a comparative study between HT and AT of the three most dominant tree species (Abies alba, Picea abies and Fagus sylvatica) in the study area, the Black Forest in southwest Germany, and also included four rare tree species (Pseudotsuga menziesii, Acer pseudoplatanus, Fraxinus excelsior and Quercus petraea) in order to reveal the role of tree species identity. In general, we assumed a higher value to large-diameter trees as HT for epiphyte diversity due to the availability of more microhabitats and a longer colonization time and test the hypothesis (1) that HT harbor more diverse bryophyte and lichen assemblages compared to smaller sized AT across all studied tree species. However, we also assumed that tree size alone is not the most important criterion according to which habitat trees should be selected and hypothesized (2) that tree species identity exerted an even stronger influence on epiphytic bryophyte and lichen diversity than stem diameter.

2. Methods

2.1. Study area

The study was carried out in southwestern Germany in the southern part of the Black Forest, a forested mountain range in the federal state of Baden-Württemberg (Fig. 1). Geologically, the bedrock of the Black Forest mainly consists of gneiss and granite, which is overlain by red bed and bunter at most places and has resulted in the formation of acidic and nutrient-poor soils. During the Pleistocene, the geomorphology of the southern Black Forest has been modified by glaciation (Hofmann et al., 2024). Mean annual temperature ranges from 5 to 7 $^\circ \mathrm{C}$ and mean annual precipitation from 1500 to 2100 mm (Reklip, 1995), and both are influenced by an elevational gradient ranging from 120 to 1493 m a.s.l. The forested area of the Black Forest is dominated by Norway spruce (Picea abies (L.) H. Karst., 42% of the total forest area), silver fir (Abies alba Mill., 18%), and European beech (Fagus sylvatica L., 15%) (Kändler and Cullmann, 2016). Forests are dominantly managed in continuous-cover forestry, creating uneven-aged forest stands (Bauhus and Pyttel, 2015). However, the co-occurrence of even-aged monocultures of Norway spruce witness former management as age class forests after clearcut, which are gradually transferred into uneven-aged stands in state-owned forest. Retention of large-diameter trees and deadwood is performed in the legal scope of the old and deadwood program of the state of Baden-Württemberg (ForstBW, 2016), where groups of habitat trees consisting of about 15 trees per 3 ha are excluded from logging.

2.2. Study design and sample tree selection

We used 1 ha plots that had been established in 135 forest stands of the southern Black Forest prior to our field work in the framework of the project "Conservation of forest biodiversity in multiple-use landscapes of Central Europe ("ConFoBi", Storch et al., 2020) in continuous-cover forests in 2016. The study plots are located between 500 and 1400 m a.s.l. with a minimum distance between the plot centers of 750 m. Plots were subjected to different silvicultural treatments before 2016 and represented partly uneven-aged stands and partly even-aged stands in transition to uneven-aged stands, where continuous-cover forestry had



Fig. 1. Location of the study area in the southern Black Forest, southwestern Germany with the studied forest stands (N = 135, orange dots).

been implemented more recently. Other stands were unmanaged for at least 40 years. Since 2016, all plots were excluded from forest operations to ensure constant conditions for the ConFoBi project. The plot selection was based on two environmental gradients: firstly, structural richness, which was expressed by the amount of standing deadwood detected via aerial images and, secondly, forest connectivity measured as the forest fraction in a 25 km² area around the plot center (Storch et al., 2020). Forest connectivity was used for the analyses in our study. More detailed information about the study design, plot selection, and categorization of stand structure has been provided by Storch et al. (2020). Due to major disturbances, only 132 out of originally 135 ConFoBi plots could be included in our study (Tab. A1 in the Appendix A), where field work was conducted in 2019 and 2020.

The selection of study trees was based on an earlier inventory conducted within the ConFoBi project, in which the 15 trees with the largest crown sizes per plot were identified on aerial images with a ground sampling distance of 40 cm (Asbeck et al., 2019) after automatized delineation of the tree crowns with TreeVis software (Weinacker et al., 2004). Following this preselection by remote sensing, we selected the 5 trees with the largest diameter at breast height (DBH) per plot as habitat trees (HT), irrespective of the tree species. Furthermore, we selected 5 trees of the dominant tree species in the 1 ha plot as average tree (AT) based on complete stand surveys from the plot. AT should represent the mean DBH (\pm 15 %). of the dominat tree species on the sample plot. We chose 5 AT per plot, by selecting 1 AT in the vicinity of each HT. This was done by selecting the closest candidate tree that met the DBH and tree species criteria from each AT; the maximum distance between a HT and its corresponding AT was 60 m. The DBH did differ significantly between HT (6616 cm) and AT (29 \pm 8 cm).

In total, we investigated 1254 trees for epiphytes. Norway spruce (N = 675 trees), silver fir (N = 219), and European beech (N = 270) were dominating compared to the less common tree species Douglas fir

(*Pseudotsuga menziesii*, N = 59), sycamore maple (*Acer pseudoplatanus*, N = 17), European ash (*Fraxinus excelsior*, N = 11), and sessile oak (*Quercus petraea*, N = 3), referred in the following as spruce, silver fir, beech, Douglas fir, maple, ash and oak.

2.3. Sampling of epiphytic bryophytes and lichens

The cover of all individual bryophyte and lichen species was recorded from the lower tree trunks surveying the complete stem surface from 0-2 m above the ground. Cover was estimated in percent classes (0.1 %, 0.5 %, 1 %; 5-100 % in 5 % steps). Unknown bryophytes and lichens were collected and identified in the laboratory using light microscopy. For lichens, thin-layer chromatography (TLC) following Elix and Ernst-Russell (1993) was performed, if the analysis of secondary metabolites was required for species identification. Secondary metabolites were identified by using LIAS metabolites (Elix et al., 2012). Nomenclature follows Hodgetts and Lockhart (2020) for bryophytes and Wirth et al. (2013) for lichens.

2.4. Statistics

All statistical analyses were conducted in R 4.3.0 (R Core Team, 2023) and all graphs were rendered using the R package "ggplot2" 3.4.4 (Wickham, 2016).

2.4.1. Species richness

Differences in species richness (α -diversity) between samples were tested for significance with a Tukey's HSD test. Therefore, we calculated marginal means for each sample group with the package "emmeans" 1.10.7 (Lenth, 2025) from Poisson GLMMs, following the equation species richness (epiphytes, bryophytes, lichens) ~ tree species*tree category + (1| Plot). For visualization of differences between groups, we used the letter display method (cld) from the package "multcomp" 1.4–25 (Hothorn et al., 2008).

Differences in landscape-scale species richness (y-diversity) between HT and AT (and between each tree species), were identified by calculating sample-based rarefaction and extrapolation curves based on the species frequencies with 95 % confidence intervals (overlapping confidence intervals reveal no significant difference) using the R package "iNEXT" 3.0.0, (Hsieh et al., 2022). To account for differences in the number of sampled trees per tree species, we compared Hill numbers of different orders, i.e. species richness (q = 0), Shannon diversity (q = 1), and Simpson (q = 2) diversity at the same sample size, which was the double of the lowest reference sample size (N = 96; Abies alba). Extrapolating species richness (q = 0) beyond this level would provide unreliable results (Chao et al., 2014; Colwell et al., 2012). The analysis with Hill numbers has the advantage of expressing measures of diversity on a uniform scale using the Hill-Simpson index the reciprocal of Simpson's index and for the Hill-Shannon index the exponential of Shannon's entropy index, both expressing increasing diversity with increasing index values (Hill, 1973).

We used the R packages "lme4" 1.1-34 (Bates et al., 2015) and "glmmTMB" 1.1.8 (Brooks et al., 2017) to calculate generalized linear mixed models (GLMM) to analyse the influence of environmental predictors on species richness. Elevation, DBH, tree species and tree category (HT vs. AT) were used as fixed effects, as was the plot as a random effect. Separate models were run for common and uncommon tree species (for definitions see Table 1). Continuous variables were standardized prior to analyses with the "scale" function. Environmental variables in the models were tested for multicollinearity by calculating the variance inflation factor (VIF) (function "multicollinearity") implemented in the R-package "performance" 0.10.5 (Lüdecke et al., 2021). Predictors with VIF > 5 were excluded from the models, as a VIF less than 5 indicates a low correlation of that predictor with other predictors (James et al., 2013). For model selection, we assumed a Poisson distribution, as the response variable was the number of species. Model fit and

Table 1

Environmental variables used in general linear mixed models (GLMM) and canonical correspondence analysis (CCA).

Variable	Unit	Range (mean \pm SD)
Elevation DBH Tree species	m a.s.l. cm -	Continuous: $443-1334$ (826 ± 182) Continuous: $12-137$ (46 ± 22) Categorial: 3 levels / 7 levels Common tree species (3 levels) <i>Abies alba</i> (Ab.al) <i>Fagus sylvatica</i> (Fa.sy) <i>Picea abies</i> (Pi.ab)
		Common and rare tree species (7 levels) rare Acer pseudoplatanus (Ac.ps) Fraxinus excelsior (Fr.ex) Pseudotsuga menziesii (Ps.me) Quercus petraea (Qu.pe)
Tree category	-	Categorial: 2 levels average tree (AT) habitat tree (HT)
Tree species*Tree category		Categorial: 13 levels Ab.alAT, Ab.alHT Fa.syAT, Fa.syHT Pi.abAT, Pi.abHT Ac.psAT, Ac.psHT Fr.exAT, Fr.exHT Ps.meAT, Ps.meHT Qu.peHT

dispersion were checked by using the R package "DHARMa" 0.4.6 (Hartig, 2022). As underdispersion was detected in all models, we change to a generalized Poisson distribution (Harris et al., 2012) using the R package "glmmTMB" 1.1.8. In order to find the best model, we subsequently removed single terms from the full model as long as a decrease of the Akaike Information Criterion (AIC) > 2 was detectable by using the "drop1" function (R package "stats"). After each step, we tested the fit of the residuals and the distribution as stated above. The final models for both taxonomic groups followed the equation: Species $richness \sim DBH + Elevation + Tree species$ (common; common plus rare tree species) + Tree category + (1 | Plot). Since the bryophyte data contained many zero values, we applied a zero-inflated hurlde model with a truncated generalized Poisson distribution as implemented in the "glmmTMB" package. We also tested the effect of the combination tree species and tree category in separate models for bryophytes and lichens, following the steps stated above, resulting in the final model: Species richness ~ $DBH + Elevation + Tree species \times Tree category + (1 | Plot).$

2.4.2. Species composition

We used canonical correspondence analysis (CCA) to identify how environmental predictors affect the individual epiphyte species by using the "cca"-function implemented in the R package "vegan" 2.6-4 (Oksanen et al., 2022). Prior to the CCA, we applied a detrended correspondence analysis (DCA) to calculate the length of the first axis, which exceeded four standard deviations (SD) and thus confirmed the application of the CCA, which assumes an unimodal response of species along an ecological gradient. We were interested in whether the predictors used in the GLMMs would also affect epiphyte communities, for which reason our CCA-model followed the equation: cover species data ~ *DBH* + *elevation* + *tree species* + *tree category (AT, HT)*. We used the raw species cover percentages and removed species with less than five occurrences from the community matrix. We used the function 'anova.cca' with a permutation test using 999 permutations to test the significance of the model, the individual axis (by="axis") and the environmental predictors (by="term"). Additionally, significant associations of epiphyte species and HT, AT, or individual tree species or HT and AT were detected using indicator analyses with the function "signassoc" in the R package "indicspecies" 1.7.14 (de Cáceres and Legendre, 2009).

3. Results

3.1. Differences between average trees (AT) and habitat trees (HT)

In total, we found 53 bryophyte and 100 lichen species (γ -diversity). HT harbored 48 bryophyte and 98 lichen species and AT, 40 bryophyte and 84 lichen species. On common tree species (N = 1164 sampled trees) 52 bryophyte species and 96 lichen species were recorded. On rare tree species with a total of only 90 sample trees, we found as many as 31 bryophyte and 43 lichen species (Tables B1, B2).

Tukey's HSD test revealed a significantly higher epiphyte species richness on HT compared to AT (5 \pm vs. 4 \pm species; $p \leq 0.05$) when all tree species were pooled (Fig. 2). When the two taxonomic groups were treated separately, significantly higher species richness on HT than AT was also found for lichens (Fig. 2), but not for bryophytes.

However, the Kruskal-Wallis test results were only partly supported by the rarefaction-extrapolation species-area curves (Fig. 3) for species richness, Shannon diversity, and Simpson diversity. Confidence intervals for HT and AT did not overlap for Shannon and Simpson diversities, as long as all epiphyte data were analysed together (Fig. 3). Furthermore, there was no overlap for the interpolated (rarefaction) part of the species-area curves for species richness, but for the extrapolated curve sections (Fig. 3), indicating a weak difference.

Bryophytes and lichens behaved differently if species-area curves were calculated for these groups separately for common and rare tree species (Fig. B1). For the common tree species, the species-area curve for HT attained greater values than for AT for species richness in bryophytes and lichens, but only for the interpolated curve sections. Shannon and Simpson diversities were higher in HT than AT for lichens, but not for bryophytes. For the rare tree species, there was no difference in species richness between HT and AT for bryophytes and lichens. Shannon and Simpson diversities were significantly higher on HT than AT in bryophytes, but not in lichens, though the latter showed a similar insignificant tendency.

3.2. Importance of tree species identity for epiphyte species richness on AT and HT $\,$

We used different approaches to examine the effect of tree species identity on epiphyte species richness: Generalized linear mixed models (GLMM) that compared spruce AT as the most common tree group with all trees (HT and AT) of beech and silver fir showed that beech generally had a positive effect on bryophyte and lichen species richness, whereas such effect was only found for lichens in the case of silver fir (Table 2). Among the rare tree species, maple, ash, and oak increased both bryophyte and lichen species richness (Table 2). Douglas fir, however, had no effect on bryophyte species richness and a negative effect on lichen species richness in comparison with spruce AT (Table 2).

In another approach, we investigated effects on species richness separately for AT and HT of the individual tree species, again with spruce AT as a baseline (Table 3). Here, we found increased species richness on beech AT and HT in bryophytes, but only on beech AT (but not HT) in lichens (Table 3). Spruce HT had higher species richness of bryophytes and silver fir HT had higher species richness of lichens compared to spruce AT (Table 3). These results for spruce and silver fir were confirmed by a Tukey's HSD test, but in this test the difference between spruce AT and HT became only significant for lichens (Fig. 4). Maple, ash, and oak increased bryophyte species richness both for HT and AT compared to spruce AT in the GLMM (Table 3; oak AT were lacking in the dataset). For lichen species richness, such promotional effects by rare tree species were only found for maple AT, ash HT, and oak HT. The negative effect of Douglas fir on lichen species richness was only significant for HT (Table 3). In addition to tree species and tree category (HT vs. AT), elevation and DBH had significant positive effects on species richness in lichens, but not in bryophytes (Tables 2, 3).



Fig. 2. Species richness on average trees (AT) and habitat trees (HT) across all tree species for all epiphytes, bryophytes and lichens. Black diamonds indicate mean species richness. Asterisks (***) indicate significant differences $p \le 0.05$; n.s., not significant at $p \le 0.05$ (according to the Tukey's HSD test, calculated from marginal means extracted from GLMMs).



Fig. 3. Rarefraction (solid line) and extrapolation (dashed line) curves of epiphytes on habitat trees (HT, blue) and average trees (AT, orange) for Hill-number q = 0 (species richness), Hill number q = 1 (Shannon index) and Hill number q = 2 (inverse simpson index). Confidence intervals are shaded. Not intersecting confidence intervals show a significant difference (p < 0.05).

3.3. Effects of AT/HT and tree species on Simpson and Shannon diversity

Compared to species richness that only refers to the presence of species, some of the differences in epiphyte diversity between tree categories (AT vs. HT) and tree species became more pronounced if diversity indices are regarded that take into account species numbers and relative species abundances (Fig. 5). The higher species richness in bryophytes on beech than on spruce and fir (Figs. 4c, 5a) was associated with even stronger differences in inverse Simpson diversity (Fig. 5c) and

in Shannon diversity (Fig. 5e). The higher Simpson and Shannon indices evidence that the higher number of bryophyte species on beech was not due to the addition of rare species that occurred only with few individuals, but due to a higher number of co-dominant species compared to spruce and fir (Fig. 5). Bryophyte Simpson and Shannon diversities for spruce and fir were generally lower than for beech and thus also showed lower variation in dependence of tree species and tree category (Fig. 5c, e). Nevertheless, both Simpson and Shannon bryophyte diversities were higher for spruce HT than spruce AT and higher for fir HT than fir AT

Table 2

Regression models (GLMM) predicting bryophyte and lichen species richness on common and rare tree species^a.

	Bryophyte only	es: common tree	e species	Bryophytes: all tree species			Lichens: common tree species only			Lichens: all tree species		
Predictors	Estimates	CI	р	Estimates	CI	р	Estimates	CI	р	Estimates	CI	р
(Intercept)	-0.53	-0.73 - -0.32	< 0.001	-0.53	-0.720.33	< 0.001	0.67	0.56 - 0.78	< 0.001	0.68	0.58 - 0.79	< 0.001
Elevation	0.06	-0.04 - 0.16	0.249	0.07	-0.03 - 0.17	0.164	0.41	0.33 - 0.49	< 0.001	0.38	0.31 - 0.46	< 0.001
DBH	0.07	-0.01 - 0.16	0.089	0.07	-0.01 - 0.15	0.107	0.15	0.09 - 0.21	< 0.001	0.16	0.10 - 0.22	< 0.001
Silver fir	-0.07	-0.27 - 0.14	0.526	-0.05	-0.25 - 0.15	0.627	0.10	0.00 - 0.20	0.050	0.09	-0.01 - 0.19	0.07
Beech	1.47	1.27 – 1.66	< 0.001	1.46	1.27 – 1.65	< 0.001	0.14	0.03 - 0.25	0.010	0.12	0.01 - 0.23	0.031
HT	0.19	0.01 - 0.36	0.035	0.18	0.02 - 0.35	0.027	0.08	-0.04 - 0.19	0.179	0.05	-0.06 - 0.17	0.35
Maple				1.67	1.34 - 2.00	< 0.001				0.36	0.10 - 0.62	0.006
Ash				1.38	0.96 - 1.80	< 0.001				0.46	0.06 - 0.86	0.02
Douglas fir				-0.01	-0.37 - 0.36	0.971				-0.30	-0.510.08	0.007
Oak				1.32	0.62 - 2.02	< 0.001				0.61	0.01 - 1.21	0.05
Zero inflation r	nodel											
(Intercept)	-3.63	-3.99 - -3.27	< 0.001	-3.61	-3.96 - -3.27	< 0.001						
Random Effects	3											
σ^2	1.12	1.13	0.27	0.28								
τ_{00}	0.23	0.23	0.19	0.18								
ICC	0.17	0.17	0.41	0.40								
Marginal R ²	0.21	0.22	0.31	0.29								
Conditional R ²	0.34	0.35	0.59	0.57								

^a Estimates represent logarithmized means. Baseline: Spruce, AT. CI = 95 %-confidence intervals, σ^2 = residual variance, τ_{00} = intercept variance, ICC = intra-class correlation coefficient [ICC = $\tau_{00} / (\tau_{00} + \sigma^2)$

Table 3

Regression models (GLMM) predicting bryophyte and lichen species richness on tree species categories^a.

	Bryophytes			Lichens		
Predictors	Estimates	CI	р	Estimates	CI	р
(Intercept)	-0.57	-0.790.34	< 0.001	0.68	0.57 – 0.78	< 0.001
DBH	0.07	-0.02 - 0.15	0.130	0.16	0.10 - 0.22	< 0.001
Elevation	0.06	-0.04 - 0.16	0.220	0.38	0.30 - 0.46	< 0.001
Spruce HT	0.24	0.02 - 0.47	0.030	0.07	-0.05 - 0.19	0.261
Silver fir AT	-0.26	-0.71 - 0.20	0.272	-0.08	-0.30 - 0.14	0.499
Silver fir HT	0.20	-0.07 - 0.47	0.146	0.18	0.03 - 0.33	0.020
Maple AT	1.70	1.25 – 2.14	< 0.001	0.49	0.14 - 0.84	0.006
Maple HT	1.89	1.44 – 2.35	< 0.001	0.28	-0.09 - 0.66	0.137
Beech AT	1.53	1.29 – 1.77	< 0.001	0.15	0.02 - 0.28	0.020
Beech HT	1.66	1.40 - 1.93	< 0.001	0.14	-0.03 - 0.31	0.113
Ash AT	1.51	1.02 - 1.99	< 0.001	0.40	-0.09 - 0.88	0.108
Ash HT	1.35	0.62 - 2.07	< 0.001	0.62	0.02 - 1.22	0.044
Douglas fir AT	-0.14	-1.13 - 0.85	0.787	-0.07	-0.60 - 0.46	0.790
Douglas fir HT	0.22	-0.20 - 0.63	0.313	-0.27	-0.520.02	0.036
Oak HT	1.53	0.80 - 2.25	< 0.001	0.63	0.02 - 1.24	0.042
Zero inflation model						
(Intercept)	-3.61	-3.963.27	< 0.001			
Random Effects						
σ^2	1.14			1.05		
τ_{00}	0.23			0.18		
ICC	0.17			0.15		
Marginal R ²	0.23			0.13		
Conditional R ²	0.36			0.26		

^a Estimates represent logarithmized means. Baseline: Spruce AT. CI = 95 %-confidence intervals, σ^2 = residual variance, τ_{00} = intercept variance, ICC = intra-class correlation coefficient [ICC = τ_{00} / (τ_{00} + σ^2)]

with low absolute differences, but at narrow confidence intervals indicating significance (Fig. 5c, e).

The significant higher species richness on fir HT than fir AT that was observed for lichens (Figs. 4e, 5b) was associated with a much greater difference for Simpson and Shannon diversities (Fig. 5d, f), showing that

the increase in species was driven by several species with high relative abundance on fir HT. Though the means of Simpson and Shannon indices for HT also attained higher values than for AT in beech and spruce for lichens, there were overlaps in the confidence intervals indicating the lack of statistical significance (Fig. 5d, f).



Fig. 4. Species richness (α -diversity) on average trees (AT) and habitat trees (HT) for epiphytes (a,b), epiphytic bryophytes (c,d) and lichens (e,f) on common (a,c,e) and rare tree species (b,d,f). Gray (a,c,e) and black(b,d,f) diamonds indicate mean species richness of each group. The following tree species are represented: *Picea abies* (Pi.ab, AT: N = 404, HT: N = 271), *Fagus sylvatica* (Fa.sy, AT: N = 168, HT: N = 102), *Abies alba* (Ab.al, AT: N = 48, HT: N = 171), *Pseudotsuga menziesii* (Ps.me, AT: N = 12, HT: N = 47), *Acer pseudoplatanus* (Ac.ps, AT: N = 11, HT: N = 6), *Fraxinus excelsior* (Fr.ex, AT: N = 8, HT: N = 3) and *Quercus petraea* (Qu.pe, HT: N = 3). Samples sharing a common capital letter do not differ significantly ($p \le 0.05$, Tukey's HSD test, calculated from marginal means extracted from GLMMs).

3.4. Relative importance of common and rare tree species for total epiphyte diversity

The importance of tree species identify is also represented in the γ -diversity of epiphytes on specific host trees, which was not a function of sample tree numbers per tree species. On beech, 81 % and 61 % of all bryophyte and lichen species were found, respectively, which contrasts to spruce (59 % and 75 %) and silver fir (40 % and 66 %), even though the number of sampled spruce trees was 2.5 times higher and the number of sampled fir trees was only slightly lower than that of beech trees. Maple and ash represented only 2 % (28 trees) of all sample trees, but these two tree species harbored as much as 44 % and 24 % of all bryophytes, and 29 % and 12 % of all lichen species, respectively. Only 3 oak trees were sampled, but they harbored 11 % of the total bryophytes and 9 % of the lichen species. On Douglas fir (N = 59 trees), 11 % and 19 % of the total bryophyte and lichen species found in our study were detected.

3.5. Species composition

Despite the differences in Shannon and Simpson diversities shown between HT and AT for individual tree species (Fig. 5), there was no general difference in epiphyte species composition detectable between HT and AT in the CCA (Fig. B2). Rather, overall species composition was strongly influenced by the tree species, with a clear difference between spruce and beech, but the epiphyte vegetation of fir having ties to the epiphyte vegetation of both spruce and beech (Fig. B2). The CCA showed a strong influence of elevation and a weaker influence of DBH on species composition. In agreement with the intermediate position of fir in the CCA (Fig. B2), indicator species analysis (Table B3) yielded the highest number of indicator species for beech and the second-highest for spruce, but no bryophyte and only few lichen species as indicator species of fir. No indicator species could be found for HT or AT.



Fig. 5. Rarefaction (solid line) and extrapolation (dashed line) curves of bryophytes (a,c,e) and lichens (b,d,f) on the most common tree species: a and b show the curves for Hill number q = 0 (species richness), c and d show the curves for Hill number q = 2 (inverse simpson index) and e and f show the curves for Hill number q = 1 (Shannon index). Confidence intervals are shaded. Vertical gray dotted line indicates the doubled least reference sample size (N = 96) at which the effective number of dominant species is compared. Not intersecting confidence intervals show a significant difference ($p \le 0.05$).

4. Discussion

Habitat trees (HT), i.e. large-diameter trees that are spared from logging for biodiversity conservation (Lindenmayer, 2017) and additionally to increase forest carbon stocks (Hauck et al., 2023), are an important tool in forest management to conserve forest biota, but few studies have so far systematically evaluated their conservation value in direct comparison with average-sized trees (AT) that are subjected to forest management and are dedicated to be logged during their optimal stage at one point in time. In agreement with the target of selecting HT for biodiversity conservation, we found higher epiphyte species richness on HT than AT when studying bryophyte and lichen diversity on as much as > 1200 trees. This was found for species richness of all epiphytic bryophytes and lichens when jointly analysed in a merged

dataset, confirming our first hypothesis. We found the same result for lichens when analysed separately, but not for bryophytes. Bryophyte species richness on HT was only significantly higher when compared to spruce AT, which represented the most common group of AT, but not compared to all AT regardless of the tree species. In general, we found that the effectiveness in increasing epiphyte diversity by HT is strongly modified by the identity of the tree species that are selected as HT, which has great practical implications for forest conservation practice and confirms our second hypothesis.

The stronger stimulation of Simpson and Shannon diversities than of species richness by HT suggests that the promotion of epiphyte diversity by HT is not only due to the addition of few individuals or cover percentages to the poorer epiphyte vegetation of AT. Rather, it suggests that several epiphyte species are favored by HT, which can increase in cover and become co-dominant. If the increase in species richness would be driven by only few individuals of species that lack on AT, both the inverse Simpson index and the Shannon index would not have shown even stronger increases on HT compared to AT than species richness (Gregorius and Gillet, 2008; Keylock, 2005).

The overall higher epiphyte species diversity on large old trees (i.e. HT) compared to younger trees of lower stem diameter (i.e. AT) is driven by the greater microhabitat diversity of large old trees (Paillet et al., 2017), by changes in microclimate (Kovács et al., 2017) and bark and stemflow chemistry that depend on tree size, canopy shape, and bark structure (Hauck, 2011; Levia and Frost, 2003; Schooling et al., 2017) and by the longer habitat continuity that favors epiphytes with dispersal limitations (Hilmo and Såstad, 2001; Sillett et al., 2000). These age- and diameter-dependent changes are generally well-known and are the cause why many forest epiphytes have declined in managed forests (Dittrich et al., 2016; Hauck et al., 2013). The CCA results show that in our case altered site conditions on HT primarily resulted in changes in frequency and population sizes, but not in species composition.

Our data demonstrate that the effectiveness of HT selection depends on the tree species. In the studied forests, which were dominated by Picea abies, Fagus sylvatica, and Abies alba, and thus three of main temperate tree species of Central Europe, bryophytes were more strongly favored by beech than by any other HT, whereas fir HT only increased lichen, but not bryophyte species richness. Spruce HT increased species richness compared to spruce AT, according to mixed modeling in bryophytes, but only based on the pairwise mean comparison in lichens. Tree species that were rare in our dataset, like Acer pseudoplatanus, Fraxinus excelsior, and Quercus petraea, contributed disproportionally highly to total epiphyte species richness. The effect of these tree species on epiphytic bryophyte and lichen diversity is generally well-known (Gerra-Inohosa et al., 2023; Király et al., 2013) and depends on species-specific differences in structural, microclimatic and chemical microhabitat traits (Mežaka et al., 2012; Ódor et al., 2013).

Interestingly, lichen species richness on beech was more strongly promoted on AT than on HT. This can be attributed to the preference of several crustose lichen species (like Graphis scripta, Porina aenea and several Lecanora and Arthonia species) for the smooth periderm of lowdiameter beech trees, whereas otherwise both lichen and bryophyte species richness mostly increases with increasing stem diameter and increasing tree age. Douglas fir was the only tree species, which exerted a negative effect on lichen species richness in our study, while it not influenced bryophyte diversity. Since Douglas fir was among the rare species in our analysis (N = 59 trees), it might be too early to generally discourage from the cultivation of this species from the perspective of epiphytic lichen conservation. However, this result gives reason to intensify the research on potential effects of more widespread Douglas fir introduction into European temperate forests, as this is discussed as a measure the climate change adaptation of forest management, while the effects on different groups of organisms are insufficiently known (Bärmann et al., 2023; Glatthorn et al., 2023). However, we have to state that the selection of habitat trees suitable for epiphytes has to be made against the background of climate change and the associated increased frequency of heat and drought periods. Especially the three dominating tree species Abies alba, Picea abies and Fagus sylvatica are considered to be less drought and heat tolerant compared to other rarer tree species (Hauck et al., 2025) surveyed in our study, which is why they could no longer be considered as habitat trees in certain areas.

Appendix A

The strong modification of the effect of tree category (HT vs. AT) on epiphyte diversity by tree species identity, on the one hand, and the different responses of bryophytes and lichens, on the other hand, suggest that it is not possible to conserve all forest epiphytes with a limited number and variety of HT. However, as long as HT are selected in large numbers like currently done in Germany due to certification and governmental funding schemes (Asbeck et al., 2021), our results suggest that, even without surveying the epiphyte vegetation beforehand, there is a high probability that saving HT from logging in temperate forests of Central Europe increases epiphytic lichen and (to a lesser, but still significant degree) epiphytic bryophyte diversity.

5. Conclusion

The retention of large old trees as habitat trees, which is increasingly practiced in continuous-cover management systems of Central Europe clearly contributes to the conservation of epiphytic lichens and bryophytes by increasing species diversity and is thus a suitable tool for maintaining high biodiversity in managed forests. It surely does not replace the high conservation value of completely unmanaged oldgrowth forests for forest epiphytes, but can be an effective measure for the integration of epiphyte conservation on large spatial scales into managed forests. Our data also highlight the importance of tree species identity in the effectiveness of habitat tree retention for epiphyte conservation and suggest that in the studied mountain forests especially the retention of beech, of rare tree species and (especially for lichens) also of silver fir increases the conservation value for epiphytes.

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CRediT authorship contribution statement

Emrich Dina: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis. **Kaufmann Stefan:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Gustafsson Lena:** Writing – review & editing, Supervision. **Hauck Markus:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization.

Declaration of Competing Interest

We confirm that this manuscript has not been published elsewhere and is not under consideration by any other journal. All of the authors agree with submission to *Forest Ecology and Management*. We have no conflicts of interest to declare.

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Table A1
Study plot characteristics

10

PlotID DBH	DBH [sd]	Elevation [m]	Basal area [m²/ha]	Basal area	Basal area	Basal area silver fir [%]	Main tree species	Habitat tree species	Management	Tree species richness
							w. 1.			_
CFB001 40	19	1247	51,93	14	82	1	Picea abies	Picea abies (4), Acer pseudoplanatus (1)	strict-	5
077000000	10	070	17.00	0	<i>(</i> 1	0	D: 1:		protection	
CFB002 24	13	873	17,92	0	61	3	Picea abies	Fagus sylvatica (2), Picea abies (3)	uneven-aged	4
CFB003 35	21	1226	16,53	17	74	7	Picea abies	Picea abies (4)	strict-	4
									protection	
CFB005 36	22	806	38,95	13	39	48	Fagus sylvatica,	Abies alba (4), Picea abies (1)	even-aged	6
CFB007 32	13	1334	9,38	0	63	0	Acer pseudoplatanus	Picea abies (4)	strict-	2
									protection	
CFB008 28	11	1295	31,85	2	98	0	Picea abies	Picea abies (5)	mixed	2
									management	
CFB009 23	15	716	22,14	12	30	43	Picea abies	Abies alba (2), Fagus sylvatica (2), Picea abies (1)	even-aged	10
CFB010 40	22	713	35,40	7	76	17	Picea abies	Abies alba (4), Fagus sylvatica (1)	strict-	4
									protection	
CFB011 29	16	904	30,25	18	29	33	Fagus sylvatica, Abies alba	Abies alba (2), Pseudotsuga menziesii (2), Fagus sylvatica (1)	mixed	6
									management	
CFB014 37	16	512	34,90	16	10	23	Pseudotsuga menziesii, Fagus	Pseudotsuga menziesii (4), Fagus sylvatica (1)	even-aged	5
			-				sylvatica		0	
CFB015 24	21	1069	29.63	19	44	35	Picea abies. Fagus sylvatica.	Abies alba (4). Fagus sylvatica (1)	even-aged	4
			,				Abies alba			
CFB016 29	25	947	32 32	72	9	18	Fagus sylvatica	Fagus sylvatica (4) Abies alba (1)	even-aged	4
CFB017 47	17	1069	37 38	0	100	0	Picea abies	Picea abies (5)	even-aged	2
CFB018 26	21	947	43 59	1	76	8	Picea abies	Picea abies (4) Abies alba (1)	even aged	4
CFB010 20	16	1014	32.04	49	11	40	Fagus sylvatica	Abies alba (4) Fagus sylvatica (1) Dicea abies (1)	even-aged	4
CEB020 41	15	002	30.40	1	77	-10 22	Picea abies	Abies alba (4), Pieza abies (1)	even aged	4
CFB020 41 CFB021 28	14	1092	27.92	2	02	1	Picea abies	Diese abies (4). Abies alba (1)	even-aged	
CFB021 36	14	715	57,62	3	92	4	Piceu ubles	Picea ables (4), Ables alba (1)	even-aged	5
CFB022 20	15	/15	04,58	14	10	5	Pseudoisuga menziesii, Fagus	Pseudoisuga menziesii (4), Fugus sylvalica (1)	even-aged	0
CED000 40	16	1006	24.44	01	24	40	Sylvalica	Abias alles (A) Disas abias (1)	arran a sad	4
CFB028 48	10	1020	34,44	21	34	43	Pagus sylvanca	Ables alba (4), Picea ables (1)	even-aged	4
CFB030 24	17	510	31,04	12	4	4	Pseudotsuga menziesu, Fagus	Pseudotsuga menziesti (5)	even-aged	10
00001 00	10	F 43	00.05	0.0	60		sylvatica		,	-
CFB031 38	13	541	29,05	30	62	1	Picea ables, Fagus sylvatica	Fagus sylvatica (3), Piced ables (2)	even-aged	5
CFB033 16	12	985	14,96	12	67	19	Picea abies	Picea abies (3), Abies alba (2)	even-aged	4
CFB034 33	13	928	28,76	7	79	0	Picea abies	Larix decidita (3), Picea abies (2)	even-aged	3
CFB035 43	14	533	32,44	62	24	13	Fagus sylvatica	Fagus sylvatica (4), Picea abies (1)	even-aged	5
CFB036 36	11	1050	42,77	0	98	0	Picea abies	Picea abies (5)	even-aged	4
CFB037 40	11	1056	44,93	92	0	8	Fagus sylvatica	Fagus sylvatica (4), Abies alba (1)	even-aged	2
CFB038 31	14	904	41,48	0	81	3	Picea abies	Picea abies (2), Pinus sylvestris (2), Abies alba (1)	even-aged	4
CFB039 39	15	649	28,52	32	31	8	Fagus sylvatica	Fagus sylvatica (2), Pseudotsuga menziesii (1), Fraxinus excelsior (1), Abies alba (1)	even-aged	6
CFB044 43	10	835	62,31	4	83	13	Picea abies	Abies alba (3), Fagus sylvatica (2)	mixed	5
									management	
CFB045 30	16	587	33,28	5	54	1	Picea abies	Pinus sylvestris (3), Picea abies (2)	even-aged	10
CFB046 18	9	502	22,93	13	31	1	Fraxinus excelsior, Fagus	Acer pseudoplatanus (1), Fagus sylvatica (2), Pinus sylvestris (1), Picea abies (1)	even-aged	12
							sylvatica			
CFB047 20	15	744	22,55	20	58	11	Picea abies, Fagus sylvatica	Fagus sylvatica (2), Picea abies (1), Abies alba (2)	even-aged	8
CFB048 22	16	704	29,27	10	52	1	Picea abies	Picea abies (4), Pinus sylvetris (1)	even-aged	14
CFB050 23	21	775	44,48	0	15	84	Picea abies	Abies alba (4), Picea abies (1)	uneven-aged	6
CFB052 18	10	945	30,61	0	52	0	Picea abies, Pinus sylvestris	Picea abies (5)	uneven-aged	4
CFB053 27	20	950	43,19	0	83	10	Picea abies	Picea abies (5)	uneven-aged	4
CFB054 14	8	734	26,46	17	29	21	Fagus sylvatica	Fagus sylvatica (3), Picea abies (2)	even-aged	11
CFB055 20	13	767	37,60	0	54	34	Picea abies, Abies alba	Picea abies (2), Pinus sylvestris (2). Abies alba (1)	mixed	8
	-				-				management	
CFB056 21	11	443	25.97	9	20	60	Abies alba	Pinus sylvestris (3). Larix decidua (2)	mixed	8
512000 21	**		_0,,,,	-	20				management	-
CFB057 24	18	640	35.72	1	63	9	Picea abies. Abies alba	Picea abies (5)	even-aged	7
			,	-		-			(4 an nav: :
									conuntile	и он нелі раде)

Table A1 (continued)

PlotID DBH [cm]	DBH [sd]	Elevation [m]	Basal area [m²/ha]	Basal area beech [%]	Basal area spruce [%]	Basal area silver fir [%]	Main tree species	Habitat tree species	Management	Tree species richness
CFB058 19	13	694	25,61	0	64	3	Fraxinus excelsior, Picea abies	Picea abies (3), Salix sp. (1), Fraxinus excelsior (1)	mixed management	10
CFB059 24	10	634	33,37	21	57	0	Picea abies, Fagus sylvatica	Picea abies (3), Fagus sylvatica (1), Pinus sylvestris (1)	even-aged	8
CFB060 26	20	613	31,55	2	33	55	Acer pseudoplatanus	Abies alba (2)	even-aged	8
CFB061 35	17	515	25,31	71	0	0	Fagus sylvatica	Fagus sylvatica (4), Pseudotsuga menziesii (1)	even-aged	6
CFB063 28	19	566	24,39	55	18	13	Fagus sylvatica	Fagus sylvatica (4), Abies alba (1)	even-aged	10
CFB064 19	13	717	22,72	46	3	39	Fagus sylvatica	Fagus sylvatica (4), Acer pseudoplatanus (1)	even-aged	6
CFB065 21	14	684	23,83	3	81	14	Picea abies	Picea abies (3), Abies alba (2)	even-aged	6
CFB066 35	8	748	23,27	19	75	0	Picea abies	Picea abies (3), Larix decidua (2)	even-aged	4
CFB067 32	11	740	31,90	0	74	6	Picea abies	Abies alba (3), Picea abies (2)	even-aged	3
CFB068 14	10	792	24,13	40	18	42	Fagus sylvatica, Abies alba	Fagus sylvatica (3), Abies alba (2)	even-aged	5
CFB069 27	22	794	29,11	4	28	68	Picea abies, Abies alba	Abies alba (4), Picea abies (1)	even-aged	6
CFB071 30	13	678	33,92	1	48	0	Picea abies	Picea abies (4), Pinus sylvetris (1)	even-aged	9
CFB072 18	14	713	30,49	0	31	59	Picea abies	Abies alba (5)	even-aged	8
CFB073 24	18	871	36,42	42	25	34	Fagus sylvatica	Abies alba (3), Picea abies (2)	uneven-aged	3
CFB075 20	15	885	20,96	40	42	14	Picea abies, Fagus sylvatica	Abies alba (3), Picea abies (2)	even-aged	5
CFB076 29	17	504	11,03	87	0	0	Fagus sylvatica	Fagus sylvatica (5)	even-aged	7
CFB077 26	13	778	35,58	0	56	0	Picea abies	Picea abies (5)	even-aged	3
CFB078 25	17	697	35,48	46	20	22	Fagus sylvatica	Abies alba (3), Picea abies (1), Tilia cordata (1)	mixed	7
									management	
CFB079 43	16	922	32,47	0	83	10	Picea abies	Picea abies (4), Abies alba (1)	even-aged	4
CFB083 35	14	971	40,01	14	80	0	Picea abies	Picea abies (5)	even-aged	5
CFB084 21	15	754	39,84	0	77	20	Picea abies	Picea abies (3), Abies alba (2)	even-aged	5
CFB085 24	13	769	37,77	0	53	15	Picea abies	Pinus sylvestris (5)	even-aged	5
CFB086 38	8	713	35,21	0	91	0	Picea abies	Picea abies (5)	even-aged	5
CFB087 38	12	1018	35,50	1	88	0	Picea abies	Picea abies (5)	even-aged	4
CFB089 48	19	701	49,46	5	44	50	Picea abies	Abies alba (4), Picea abies (1)	even-aged	6
CFB091 22	21	1082	30,82	30	49	15	Fagus sylvatica	Picea abies (4), Abies alba (1)	even-aged	5
CFB093 36	21	665	33,65	20	42	24	Picea abies, Fagus sylvatica	Abies alba (3), Fagus sylvatica (1), Picea abies (1)	strict- protection	6
CFB094 12	9	1000	18,88	32	46	20	Picea abies, Fagus sylvatica	Abies alba (3), Picea abies (2)	even-aged	6
CFB096 23	12	750	36,25	45	3	39	Fagus sylvatica, Abies alba	Fagus sylvatica (3), Abies alba (2)	uneven-aged	5
CFB098 32	16	1120	35,32	0	93	6	Picea abies	Picea abies (5)	uneven-aged	4
CFB101 28	19	986	32,07	7	66	23	Picea abies	Picea abies (5)	uneven-aged	4
CFB102 38	10	877	43,30	0	86	0	Picea abies	Pseudotsuga menziesii (3), Picea abies (2)	even-aged	5
CFB104 32	17	580	16,25	11	51	1	Acer pseudoplatanus, Fagus sylvatica, Picea abies	Fagus sylvatica (2), Picea abies (1), Abies alba (1), Fraxinus excelsior (1)	mixed	8
CFB105 27	15	833	38.40	0	63	10	Picea abies	Picea abies (2). Abies alba (2). Larix decidua (1)	even-aged	6
CFB106 28	15	774	23.53	75	18	0	Fagus sylvatica	Fagus sylvatica (3). Pseudotsuga menziesii (2)	even-aged	7
CFB107 24	13	733	32.32	23	35	33	Fagus sylvatica	Abies alba (3) Fagus sylvatica (1) Pinus sylvestris (1)	even-aged	6
CFB108 24	15	1126	18.15	29	24	47	Picea abies	Abies alba (3), Picea abies (1), Fagus sylvatica (1)	even-aged	3
CFB109 21	16	888	24.26	6	29	62	Picea abies	Abies alba (5)	even-aged	6
CFB110 37	12	930	33.44	1	95	0	Picea abies	Picea abies (4). Larix decidua (1)	even-aged	5
CFB111 24	16	682	14.73	10	59	15	Acer pseudoplatanus. Picea	Fagus sylvatica (3). Acer pseudoplatanus (1). Picea abies (1)	even-aged	7
CED112 20	10	1160	22 50	0	02	2	abies Disea abies	Disea abise (E)	aven agod	E
CFD113 28	12	F16	33,38	0	93	3	Piceu ables	Piceu ables (5)	even-aged	5
CEB117 04	12	857	30.00	5	20 90	19	r seduoisugu menziesii Dicea abies	r scuurisuzu illeitziesii (3) Abias alba (2) Dinus subiatris (1) Famis subiation (1)	even-aged	5
CEP110 45	12	83/ 657	39,08 41.60	4	02	9 20	Fileu ables	Abies alba (2), Fillus sylvetris (1), Fugus sylvatica (1)	even-aged	5 7
CEB110 97	23 10	00/ 997	41,08 22,57	JI 41	1	38 49	rugus sylvatica Fagus sylvatica	Ables alba (A). Fagus sylvalica (2)	uneven-aged	/
CEB101 01	19	00/ 632	33,37 27.09	71 53	10	72	Fugus sylvatica	Totes unu (4), rugus sylvancu (1) Fague subvatica (2) Quarcus patraga (1) Degudatoura manniacii (1)	even aged	+
CEB122 20	15	03Z 527	27,08 68.07	33 97	56	1	Fugus sylvatica	rugus sylvatica (3), quercus per ueu (1), Pseudolsugu menziesii (1)	even-aged	5
CEB122 30	15	54/ 646	00,97 24 51	5	20	1	rugus sylvullu Abias alba	rugus sylvullu (3), rseluloisugu mentslesil (2)	even-aged	5
CEB123 31	10	040	24,31	5	22	1	Dicea abies	Dicea abies (5)	even-aged	5
GIDI27 20	10	747	20,01	-1	74	1	1 ICCU UDICS	1 iccu units (3)	management	5
									management	

Forest Ecology and Management 585 (2025) 122616

(continued on next page)

Table A1 (continued)

PlotID DBH [cm]	DBH [sd]	Elevation [m]	Basal area [m²/ha]	Basal area beech [%]	Basal area spruce [%]	Basal area silver fir [%]	Main tree species	Habitat tree species	Management	Tree species richness
CFB125 37	18	533	22,12	12	65	3	Picea abies, Abies alba	Picea abies (2), Larix decidua (2), Acer pseudoplatanus (1)	even-aged	7
CFB127 38	16	516	38,59	6	45	46	Picea abies, Abies alba	Abies alba (3), Picea abies (1), Pseudotsuga menzeisii (1)	even-aged	6
CFB128 32	16	982	40,32	11	86	0	Picea abies	Picea abies (3), Fagus sylvatica (1), Pseudotsuga menziesii (1)	even-aged	5
CFB129 29	20	549	32,15	36	2	44	Fagus sylvatica, Abies alba	Quercus petraea (2), Pseudotsuga menziesii (2), Fagus sylvatica (1)	even-aged	9
CFB130 33	16	978	39,15	15	34	43	Picea abies, Fagus sylvatica	Abies alba (3), Pseudotsuga menziesii (2)	even-aged	7
CFB131 52	10	1033	42,35	0	99	1	Picea abies	Picea abies (5)	even-aged	2
CFB132 37	11	862	37,99	0	68	0	Picea abies	Picea abies (5)	mixed	3
			,						management	
CFB133 39	18	743	38.35	33	21	46	Fagus sylvatica	Fagus sylvatica (3) Abies alba (2)	mixed	4
		, 10	,					- 48-44 - 59-57 - 41-54 - 41-56 - 41-54	management	
CFB134_31	12	898	43.01	1	52	17	Picea abies	Abies alba (3) Pinus sylvestris (1) Fagus sylvatica (1)	even-aged	7
CFB135 29	10	569	49 39	3	68	26	Picea abies	Picea abies (3) Abies alba (2)	uneven-aged	, 6
CFB136 20	10	787	30.30	0	72	26	Picea abies	Abies alba (3) Picea abies (2)	uneven ugeu	5
CFB137 24	20	815	33.66	0	59	20	Picea abjes Abjes alba	Dicea abies (3). Abies alba (2)	uneven-aged	5
CFB138-28	10	853	36.86	0	80	11	Picea abies	Picea abies (4) Abies alba (1)	uneven-aged	4
CEB140 33	11	744	40.00	2	68	2	Picea abies	Degudateuga mangiacii (2) Dicea abias (1) Abias alba (1) Dinus subjectris (1)	even aged	4
CEP140-33	14	744	22.80	2	41	11	Piccu ubies	Diruce colucettic (2), Ficed ables (1), Foles abla (1), Fillus Sylvesitis (1)	even-ageu	5
CFD141 24	14	730	33,69	1	41	11	Piceu ubles	Pullus sylvesuis (5), Piceu ables (2)	managament	5
CED140.06	14	0.01	21.60	14	66	17	Diana akina Farma mikurting	Diana akies (2) Akies alka (2)	management	4
CFB148 26	14	831	31,68	14	66	17	Picea ables, Fagus sylvatica	Picea ables (3), Ables alba (2)	even-aged	4
CFB151 33	15	851	32,94	0	44	27	Picea abies, Abies alba	Pseudotsuga menziesii (4), Abies alba (1)	even-aged	6
CFB152 34	16	994	73,11	3	78	17	Picea abies	Picea abies (5)	even-aged	6
CFB153 46	15	1063	49,76	1	99	0	Picea abies	Picea abies (5)	even-aged	3
CFB156 35	12	797	30,83	12	85	2	Picea abies	Picea abies (5)	even-aged	6
CFB159 31	19	529	34,27	9	74	5	Picea abies, Abies alba	Picea abies (3), Fagus sylvatica (2)	even-aged	7
CFB160 26	18	878	29,68	33	56	30	Picea abies, Fagus sylvatica	Abies alba (4), Fagus sylvatica (1)	mixed	3
									management	
CFB161 41	13	951	46,16	6	82	0	Picea abies	Picea abies (2), Pseudotsuga menzeisii (2), Abies alba (2)	even-aged	6
CFB162 21	9	848	34,10	0	61	0	Picea abies	Pinus sylvestris (5)		2
CFB163 37	13	765	37,73	2	58	39	Abies alba	Picea abies (3), Abies alba (2)	even-aged	9
CFB164 30	13	955	40,19	0	88	10	Picea abies	Abies alba (3), Picea abies (2)		5
CFB165 29	12	924	30,09	26	72	1	Picea abies, Fagus sylvatica	Fagus sylvatica (4), Picea abies (1)	even-aged	7
CFB167 28	9	813	38,00	8	92	0	Picea abies	Picea abies (5)	even-aged	3
CFB168 43	10	1001	33,12	0	94	2	Picea abies	Picea abies (4), Abies alba (1)		5
CFB171 24	13	953	40,91	31	63	6	Fagus sylvatica	Picea abies (4), Abies alba (1)		3
CFB172 31	13	950	34,32	17	74	9	Picea abies, Fagus sylvatica	Picea abies (4), Abies alba (1)		3
CFB173 30	16	858	28,97	6	94	0	Picea abies	Picea abies (5)		4
CFB176 34	14	749	50,48	8	64	0	Picea abies	Pinus sylvestris (3), Picea abies (2)	even-aged	3
CFB177 40	10	972	37,34	0	97	0	Picea abies	Picea abies (4), Larix decidua (1)	even-aged	4
CFB178 18	11	663	34,54	85	13	1	Fagus sylvatica	Fagus sylvatica (3), Picea abies (2)	strict-	6
									protection	
CFB179 27	16	1003	38,94	1	91	0	Picea abies, Pseudotsuga menziesii	Pseudotsuga menziesii (2), Picea abies (2), Acer pseudoplatanus (1)	even-aged	5
CFB180 30	12	959	32.38	7	75	18	Picea abies. Abies alba	Abies alba (3). Picea abies (2)		3
CFB181 29	13	903	42,49	0	65	21	Picea abies	Abies alba (5)	mixed	7
			,	-					management	
CFB182 27	18	878	35.71	34	7	60	Fagus sylvatica	Abies alba (5)	mixed	3
510102 2/	10	0,0	55,71	<u> </u>	,		- upun officiality	1000 000 (0)	management	0
CEB194 21	17	004	32 21	2	50	30	Dicea abjes Abjes alba	Dicea ahies (3) Ahies alba (2)	inanagement	3
CEB195 25	1/	7719	32,21 41.60	∠ 1	01	0	Dicea abies	Dicea abias (2) Decudateura manajacii (1) Larix dacidus (1)	even aged	2
CEB186 22	12	797	71,09	1 20	20	0	Ficea abjes Fravinus	FILE UNES (3), FSEUDOISUSU MENZIESII (1), LUIX UELIUU (1) Fagus subvatica (A) Dicea abias (1)	even aged	6
GFD100 23	13	/0/	22,70	27		U	excelsior		even-ageu	-
CFB188 43	15	852	38,62	3	93	1	Picea abies	Picea abies (4), Abies alba (1)		7

12

Appendix B

Table B1

Species list of bryophytes with abbreviations, and occurrence in the two data sets, one for the analysis of common tree species (CTS) and one for the analysis of rare tree species (RTS)

Species	Abbreviation	CTS	RTS
Liverworts:			
Bazzania trilobata (L.) Gray	Baz_tri	х	х
Blepharostoma trichophyllum (L.) Dumort.	Ble_tri	х	х
Frullania dilatata (L.) Dumort.	Fru_dil	х	х
Frullania tamarisci (L.) Dumort.	Fru_tam	х	х
Lophocolea heterophylla (Schrad.) Dumort.	Lop_het	х	х
Metzgeria furcata (L.) Dumort.	Met_fur	х	х
Metzgeria violacea (Ach.) Dumort.	Met_vio	х	х
Plagiochila porelloides (Torrey ex Nees) Lindenb.	Pla_por	х	х
Porella platyphylla (L.) Pfeiff.	Por_pla	х	х
Radula complanata (L.) Dumort.	Rad_com	х	х
Mosses:			
Alleniella complanata (Hedw.) S. Olsson, Enroth & D. Quandt	All_com	х	х
Anomodon viticulosus (Hedw.) Hook. & Taylor	Ano_vit	х	х
Antitrichia curtipendula (Hedw.) Brid.	Ant_cur	х	х
Brachytheciastrum velutinum (Hedw.) Ignatov & Huttunen	Bra_vel	х	
Brachythecium rutabulum (Hedw.) Schimp.	Bra_rut	х	х
Brachythecium salebrosum (Web. & Mohr) Schimp.	Bra_sal	х	х
Dicranum fuscescens Sm.	Dic_fus	х	x
Dicranum montanum Hedw.	Dic_mon	х	х
Dicranum scoparium Hedw.	Dic_sco	х	х
Dicranum tauricum Sapjegin	Dic_tau	х	х
Eurynchium striatum (Spruce) Schimp.	Eur_str	х	х
Exsertotheca crispa (Hedw.) S. Olsson, Enroth & D. Quandt	Exs_cri	х	х
Homalia trichomanoides (Hedw.) Brid.	Hom_tri	х	х
Homomallium incurvatum (Schrad. ex Brid.) Loeske	Hom_inc	х	х
Hypnum andoi A.J.E. Sm.	Hyp_and	х	х
Hypnum cupressiforme Hedw.	Hyp_cup	х	х
Isothecium alopecuroides (Lam. ex Dubois) Isov.	Iso_alo	х	х
Lepidozia reptans (L.) Dumort.	Lep_rep	х	х
Leucodon sciuroides (Hedw.) Schwägr.	Leu_sci	х	х
Lewinskya affinis (Brid.) F. Lara, Garilleti & Goffinet	Lew_aff	х	х
Lewinskya striata (Hedw.) F. Lara, Garilleti & Goffinet	Lew_str	х	х
Neckera pumila Hedw.	Nec_pum	х	х
Orthotrichum pumilum Sw. Ex anon.	Ort_pum	х	х
Orthotrichum sp.	Ort_spe	х	х
Orthotrichum stramineum Hornsch. ex Brid.	Ort_str	х	x
Paraleucobryum longifolium (Hedw.) Loeske	Par_lon	х	х
Plagiomnium affine (Blandow ex Funck) T. J. Kop	Pla_aff	х	х
Plagiomnium undulatum (Hedw.) T. J. Kop	Pla_und	х	х
Plagiothecium laetum Schimp.	Pla_lae	х	х
Plagiothecium latebricola Schimp.	Pla_lat	х	х
Platygyrium repens (Brid.) Schimp.	Pla_rep	х	х
Polytrichum formosum Hedw.	Pol_for	х	х
Pseudoamblystegium subtile (Hedw.) Vanderp. & Hedenäs	Pse_sub	х	х
Pterigynandrum filiforme Hedw.	Pte_fil	х	х
Ptilidium pulcherrimum (Weber) Vain.	Pti_pul	х	х
Pulvigera lyellii (Hook. & Taylor) Plášek, Sawicki & Ochyra	Pul_lye	х	х
Pylaisia polyantha (Hedw.) Schimp.	Pyl_pol	х	х
Rhytidiadelphus loreus (Hedw.) Warnst.	Rhy_lor	х	х
Sciuro-hypnum populeum (Hedw.) Ignatov & Huttunen	Sci_pop	х	x
Thuidium tamariscinum (Hedw.) Schimp.	Thu_tam	х	х
Ulota bruchii Hornsch. ex Brid.	Ulo_bru	х	х
Ulota crispa (Hedw.) Brid.	Ulo_cri	х	x

Table B2

Species list of lichens with abbreviations, and occurrence in the two data sets, one for the analysis of common tree species (CTS) and one for the analysis of rare tree species (RTS)

Species	Abbreviation	CTS	RTS
Alyxoria varia (Pers.) Ertz & Tehler	Aly_var	х	x
Arthonia didyma Körb.	Art_did	х	x
Arthonia radiata (Pers.) Ach.	Art_rad		x
Arthonia spadicea Leight.	Art_spa	х	х
Arthopyrenia punctiformis (Pers.) A. Massal.	Art_punc	х	х
Bacidia viridifarinosa Coppins & P. James	Bac_vir	х	x
Bacidina adastra (Sparrius & Aptroot) M.Hauck & V.Wirth	Bac_ada	х	х
Bacidina sulphurella (Samp.) M.Hauck & V. Wirth	Bac_sul		x
Bryora capillaris (Ach.) Brodo & D. Hawksw.	Bry_cap	х	х
Bryoria fuscescens (Gyeln.) Brodo & D. Hawksw.	Bry_fus	х	х
Bryoria sp.	Bry_sp	х	х
Buellia griseovirens (Turner Borrer ex. Sm.) Almb.	Bue_gri	х	х
Calicium glaucellum Ach.	Cal_gla	х	х
Candelariella reflexa (Nyl.) Lettau	Can_ref	x	x
Canaelariella xantnostigma (Pers. ex Ach.) Lettau	Can_xan	x	x
Characteria characteriala (Turner ex Ach) Th Fr	Cer_cer	X	x
Chaenotheca brunneola (Ach.) Tibell	Cha bru	X	x
Chaenotheca ferruginea (Turner ex Sm.) Mig	Cha fer	x	x
Chaenotheca furfuracea (L.) Tibell	Cha fur	x	x v
Chrysotrix candelaris (L) LB Laundon	Chr can	x	x
Cladonia coniocraea (Flörke) Spreng.	Cla con	x	x
Cladonia digitata (L.) Hoffm.	Cla dig	x	x
Cladonia fimbriata (L.) Fr.	Cla fim	x	x
Cladonia glauca Flörke	Cla gla	х	x
Cladonia pleurota (Flörke) Schaer.	Claple	х	x
Cladonia polydactyla (Flörke) Spreng.	Cla_pol	x	x
Cladonia pyxidata subsp. chlorophaea (Flörke ex Sommerf.) V.Wirth	Cla_pyx	х	х
Cladonia ramulosa (With.) J.R. Laundon	Cla_ram	х	х
Cladonia sp.	Cla_sp.	х	x
Cladonia squamosa (Scop.) Hoffm.	Cla_squ	х	x
Coenogonium pineti (schrad.) Lücking & Lumbsch	Coe_pin	х	х
Dictyocatenulata alba Finley & E.F. Morris	Dic_alb	х	x
Evernia prunastri (L.) Ach.	Eve_pru	х	х
Graphis scripta (L.) Ach.	Gra_scr	х	х
Hypocenomyce scalaris (Ach. Ex Lilj.) M.Choisy	Hyp_sca	х	х
Hypogymnia farinacea Zopf	Hyp_far	х	х
Hypogymnia physodes (L.) Nyl.	Hyp_phy	x	х
Imsnaugia aleurites (Ach.) S.L.F. Mey.	Ims_ale		
Lecanaciis abielina (Ach.) Korb.	Lec_abi	x	x
Lecanora argeniala (Acii.) Maline	Lec_arg	x	x
Lecanora chlarotera Nyl	Lec_cal	X	x
Lecanora compallens Herk & Aptroot	Lec_com	x	x
Lecanora conizaeodides Nyl ex Cromb	Lec con	x	x
Lecanora expallens Ach.	Lec exp	x	x
Lecanora intumescens (Rebent.) Rabenh.	Lec int	x	x
Lecanora pulicaris (Pers.) Ach.	Lec pul	х	x
Lecanora sp.	Lec_sp.	х	x
Lecanora subrugosa Nyl.	Lec_sub	х	х
Lecidea nylanderi (Anzi) Th. Fr.	Lec_nyl	х	x
Lecidella elaeochroma (Ach.) M. Choisy	Lec_ela	х	x
Lepraria eburnea J.R. Laundon	Lep_ebu	х	х
Lepraria elobata Tonsberg	Lep_elo	х	x
Lepraria finkii Nyl.	Lep_fin	х	х
Lepraria incana (L.) Ach.	Lep_inc	х	х
Lepraria jackii Tonsberg	Lep_jac	х	х
Lepraria rigidula (B. de Lesd.) Tonsberg	Lep_rig	х	х
Lepraria vouauxii (Hue) R.C. Harris	Lep_vou	х	х
Lobaria pulmonaria (L.) Hoffm.	Lob_pul		х
Loxospora elatina (Ach.) A. Massal.	Lox_ela	х	х
Melanelixia glabratula (Lamy) Sandler & Arup	Mel_gla	x	X
meiunonaiea elegantilla (Zanibr.) O. Blanco et al.	iviei_ele	х	х

(continued on next page)

Table B2 (continued)

Species	Abbreviation	CTS	RTS
Melanohalea exasperatula (Nyl.) O. Blanco et al.	Mel_exa	х	x
Micarea nitschkeana (J. Lahm ex Rabenh.) Harm	Mic_nit	х	х
Micarea prasina Fr.	Mic_pra	х	х
Mycoblastus sanguinarius (L.) Norman	Myc_san	х	х
Ochrolechia androgyna (Hoffm.) Arnold	Och_and	х	х
Ochrolechia microstictoides Räsänen	Och_mic	х	х
Ochrolechia turneri (Sm.) Hasselrot	Och_tur	х	х
Opegrapha vermicellifera (Kunze) J.R. Laundon	Ope_ver	х	х
Opegrapha vulgata (Ach.) Ach.	Ope_vul	х	х
Parmelia saxatilis (L.) Ach.	Par_sax	х	х
Parmelia serrana A. Crespo, M.C. Molina & D. Hawksw.	Par_ser	х	х
Parmelia sulcata Taylor	Par_sul	х	х
Parmeliopsis ambigua (Wulfen) Nyl.	Par_amb	х	х
Parmeliopsis hyperoptera (Ach.) Arnold	Par_hyp	х	х
Pertusaria albescens (Huds.) M. Choisy & Werner	Per_alb	х	х
Pertusaria amara (Ach.) Nyl.	Per_ama	х	х
Pertusaria coccodes (Ach.) Nyl.	Per_coc	х	х
Pertusaria coronata (Ach.) Th. Fr.	Per_cor	х	х
Pertusaria flavida (DC.) J.R. Laundon	Per_fla	х	х
Pertusaria leioplaca DC.	Per_lei	х	х
Pertusaria pertusa (Weigel) Tuck.	Per_per	х	х
Phlyctis argena (Spreng.) Flot.	Phl_arg	х	х
Physcia dubia (Hoffm.) Lettau	Phy_dub	х	х
Platismatia glauca (L.) W.L. Culb & C.F. Culb	Pla_gla	х	х
Porina aenea (Wallr.) Zahlbr.	Por_aen	х	х
Pseudevernia furfuracea (L.) Zopf	Pse_fur	х	х
Pyrenula nitida (Weigel) Ach.	Pyr_nit	х	х
Ramalina farinacea (L.) Ach.	Ram_far	х	х
Ropalospora viridis (Tonsberg) Tonsberg	Rop_vir	х	х
Schismatomma pericleum (Ach.) Branth & Rostr.	Sch_per	х	х
Thelotrema lepadinium (Ach.) Ach.	The_lep	х	х
Trapeliopsis flexuosa (Fr.) Coppins & P.James	Tra_fle	х	х
Usnea dasypoga (Ach.) Nyl.	Usn_das	х	х
Varicellaria hemisphaerica (Flörke) I. Schmitt & Lumbsch	Var_hem	х	х
Violella fucata (Stirt.) T.Sprib.	Vio_fuc	х	х
Vulpicida pinastri (Scop.) JE. Mattson & M.J. Lai	Vul_pin	х	x
Zwackhia viridis (Ach.) Poetsch & Schied	Zwa_vir	х	х

Table B3

Significant association between common tree species (Abies alba, Fagus sylvatica, Picea abies) and epiphytic lichens and bryophytes, determined via species indicator analysis. Only species with $p \le 0.05$ are given (in brackets).

Tree species	epiphytes
Abies alba	Lichens:
	Lecanora compallens (0.01), Parmelia saxatilis (0.01), Usnea dasypoga (0.01)
	Bryophytes:
	-
Fagus	Bryophytes:
sylvatica	Pseudoamblystegium subtile (0.01), Dicranum scoparium (0.01), Lewinskya striata (0.01), Plagiothecium latebricola (0.01), Pterigynadrum filiforme (0.01)
	Lichens:
	Chaenotheca chrysocephala (0.01), Chaenotheca ferruginea (0.01), Cladonia digitata (0.01), Cladonia polydactyla (0.01), Lecanora allophana (0.02), Lecanora subrugosa
	(0.01), Melanohalea elegantula (0.01), Micarea prasina (0.01),
Picea abies	Bryophytes:
	Brachythecium rutabulum (0.01), Exsertotheca crispa (0.01)
	Lichens:
	Evernia prunastri (0.01), Fuscidea pusilla (0.01), Lecanactis abietina (0.02), Lecanora intumescens (0.01), Pertusara amara (0.01), Thelotrema lepadinium (0.02)



Fig. B1. Rarefraction (solid line) and extrapolation (dashed line) curves of (a) bryophytes and (b) lichens on habitat trees (HT) and average trees (AT) for Hillnumbers q = 0 (species richness), q = 1 (Shannon index) and q = 2 (inverse Simpson index) including common and rare trees, N = 1254). Confidence intervals are shaded. Not intersecting confidence intervals show a significant difference ($p \le 0.05$)



Fig. B2. CCA ordination of (a) habitat trees (HT) and average trees (AT) of the common tree species *Picea abies, Fagus sylvatica,* and *Abies alba* (N = 1164) and (b) epiphytic lichens (red) and bryophytes (blue). Environmental variables and both axes are significant (p = 0.001). Species abbreviations are available in Appendix A Tab. A1, Tab. A2. CCA1 explains 30.5 % of the variation and CCA2 15.6 %. Note: Axes do not have the same scale

Data availability

Data will be made available on request.

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