


Epiphytic communities of retention trees of *Fagus sylvatica*, a case study of SW Germany

Epiphytische Pflanzengesellschaften auf Habitatbäumen der Rot-Buche (*Fagus sylvatica* L.). Eine Fallstudie aus Südwest-Deutschland

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Abstract

Retention trees and retention tree groups are of great value for the conservation of biodiversity: They are home to plant and animal species that have almost disappeared from commercial forests due to forest management interventions. The common beech (*Fagus sylvatica* L.) is of particular importance here, as it is one of the most dominant deciduous tree species in Central European forests. The present study analyses the contribution of the different tree zones for the epiphytic biodiversity of old beech trees in the montane altitudinal belt zone in the southern Black Forest, SW Germany. Twenty-four large beech habitat trees from 24 different plots were systematically sampled from the base of the trunk to the canopy. All epiphytic plant species (bryophytes and lichens) as well as relevant environmental data were recorded representatively on sample plots of 20 × 30 cm in size, selected by means of specific criteria. A total of 170 species of epiphytes were recorded, including 88 lichens and 82 bryophytes. Using numerical classification, the sample areas were divided into six cluster groups. Five plant communities/associations could be identified: (1) *Ulotetum crispae* Ochs. 1928, (2) *Dicrano scoparii-Hypnetum filiformis* Barkm. 1958, (3) *Antitrichia curtispindula* community – within the alliance *Lobario-Antitrichion* Wirth 1968, (4) *Usnea dasopoga-Platismatia glauca* community – within the alliance *Usneion dasypogae* Barkm. 1958, (5) *Parmelietum furfuraceae* Hiltzer 1925. In addition, there were sample plots of dominant bark. This study thus makes a holistic contribution to the knowledge of epiphyte species and their communities on old beech trees, especially by including the little-researched tree crowns.

Keywords: Black Forest, bryophytes, lichens, epiphyte communities, phytosociological, tree canopies

Erweiterte deutsche Zusammenfassung am Ende des Artikels

1. Introduction

Within recent literature there has been increased emphasis on the importance of old growth retention structures for biodiversity, specifically for the species that depend upon these structures (STORCH et al. 2020). *Fagus sylvatica* L. is known to be a dominant broad-leaved tree species in forests within Central Europe (LEUSCHNER & ELLENBERG 2017). It has bark that is considered moderately acidic (BARKMAN 1958) with a pH of 5.5 (WALENTOWSKI

et al. 2010), but it has also been recorded as having a higher pH within areas surrounding bark wounds or areas of bark decay (FRITZ 2010). *Fagus sylvatica* is known for its smooth bark, but with increasing age and surface area, additional features develop such as porous to fissured substrate and loose bark, as well as a combination of extremely wet-shaded and highly exposed areas (WIRTH 2018). Thus, an increase in age allows more opportunities for species to become established, including epiphytes (HOFMEISTER et al. 2016).

Owing to the bark physiology of *F. sylvatica* there are epiphyte species that have high fidelity to *F. sylvatica*, many of which are shared only with *Carpinus betulus* (WIRTH 2010). These include *Graphis scripta*, *Ropalospora viridis* and *Pyrenula nitida*, *Pertusaria velata*, *P. hymenea*, *P. ultipunctata*, *P. trachythallina*, *P. constricta*, *Fuscisea cyathoides*, *Lecanora intumescens* (HOFMEISTER et al. 2016, WALENTOWSKI et al. 2010, WIRTH 2010), and *Belonia herculana*, known to occur exclusively on genus *Fagus* (WIRTH 2010). Equally, in the canopy, a greater abundance of specialist epiphytes, *Ulota crispa* and *Orthotrichum* species have been observed as being present more frequently on *F. sylvatica*, compared to other broad-leaved tree species (WALENTOWSKI et al. 2010, ÓDOR et al. 2013).

Phytosociological literature specific to the epiphytic species assemblages found on *F. sylvatica* in Western Europe has recorded successional patterns that are associated with the characteristic smooth bark of *F. sylvatica*. The successional patterns described are understood to be associated with both changes in the vegetation itself from chronosequence of the tree (FRITZ et al. 2009), and external factors from a change in the surrounding habitat (BARKMAN 1958). Successions of alliances found on the main stem of *F. sylvatica* in a forest environment include *Graphidion – Isothecion myosuroidis* at the bottom of the tree stem; *Graphidion – Ulotion – Antitrichion – Lobarion* for the lower-mid tree stem; and on the branches and upper stem, *Graphidion – Ulotion* (BARKMAN 1958).

Tree canopies are known to harbour a high proportion of epiphyte flora, specifically red list species, when compared with the first 2 m of the tree trunk, which is commonly sampled (BOCH et al. 2013, KIEBACHER et al. 2016). However, research is limited due to access restrictions, so many lower plant communities and species have been historically neglected (ZOTZ & BADER 2009, BOCH et al. 2013). From research to date it is clear that epiphyte communities in the upper sections of the tree are complex owing to the three-dimensional architecture of the tree crown (KIEBACHER et al. 2016, KAUFMANN et al. 2019). This creates completely different microclimates and phyto-chemical site conditions (KAUFMANN et al. 2019), with very different epiphyte assemblages (DITTRICH et al. 2022), when compared with that of the lower stem. Lichen communities are known to be more diverse in the upper stem and canopy, where there is increased light, whilst bryophyte communities are known to occupy the lower stem, where it is more humid (BOCH et al. 2013, KAUFMANN et al. 2019). Little is known about how environmental factors influence species and communities within the whole tree (KAUFMANN et al. 2019). Studying the whole tree and plot level environmental factors may therefore provide more complete data for sampling, and ultimately for bioindication and nature conservation objectives (DITTRICH et al. 2022).

Using the Southern Black Forest, Germany, as a case study site, this study contributes to fill the gaps of epiphytic phytosociological knowledge within the tree canopy; detailing epiphyte species and communities present in the tree canopy, and the ecological value of specific tree zones for epiphyte species and communities. We aim to answer the following research questions: 1) Which epiphytic plant species and communities are found on *F. sylvatica*? 2) How do different tree zones, exposure and light influence the occurrence of plant communities?

This study includes the identification of all epiphyte species sampled, where possible, from *F. sylvatica*, and recording them on sample plots from the base of the tree to the outer crown. The grouping of samples has been based on similarity and differences using multivariate numerical analysis. Environmental data was included to understand the drivers of the site demands of the different epiphyte communities. The communities have been compared, based upon floristic similarity, using existing phytosociological literature.

2. Study sites and tree selection

The study sites are illustrated in Figure 1, located in the Southern Black Forest in temperate montane forest, and are an integrated part of the “ConFoBi” (Conservation of Forest Biodiversity in Multiple-use Landscapes of Central Europe) project. ConFoBi is a research training group that focusses on the effectiveness of retention forestry, combining ecological studies on forest biodiversity with social and economic studies of biodiversity conservation across multiple spatial scales (STORCH et al. 2020).

The geology within the Southern Black Forest is dominated by granite and gneiss within the western and southern areas, and sandstone within the eastern and northern areas (STORCH et al. 2020). Typical stands include the tree species spruce (*Picea abies* [L.] H. Karst), silver fir (*Abies alba* Mill.) and *F. sylvatica*, and management practices include shelterwood, group shelterwood (“Femelschlag”), strip cutting, and single-tree selection (“Plenter” forest) (BAUHUS & PYTTEL 2015). Further details on the region and the plot selection criterion are presented in STORCH et al. (2020).

For sampling, plots with largest *F. sylvatica* individuals were selected within the montane elevation belt, with forest under regular management. Dominating species was *F. sylvatica*, mixed with silver fir. The criteria applied included (1) elevation, ranging between 700 m and 900 m, and (2) the presence of mature *F. sylvatica* trees. Within each plot, the *F. sylvatica* tree with the greatest diameter at breast height (DBH) was pre-selected. As DBH is not the only factor determining the maturity of the tree (DITTRICH et al. 2013), additional criteria were applied, including the size of the canopy, the number of large branches, and the number of microhabitats (KIEBACHER et al. 2016). Using the aforementioned criteria, a total of 24 plots (see Fig. 1) were suitable for sampling, and from each plot one beech tree was selected.

Within the 24 plots selected the mean annual temperature recorded for the plots in 2017 was 8.9 °C. Temperature data was collected using HoBologgers (Onset 1-800-LOGGERS) on all plots continuously, using a 1 h sampling interval, and annual precipitation for the plots was recorded at an average of 1141 mm/year (Deutscher Wetterdienst, Wetter und Klima aus einer Hand).

3. Material and methods

3.1 Data collection

Fieldwork was carried out from February to November 2017. Epiphytic species were recorded throughout each of the trees sampled. Sections of the tree that were not accessible from the ground were accessed using roped access techniques. Plots were sampled throughout the tree using a 20 × 30 cm plot size. A combination of microhabitats (as defined by KRAUS et al. 2016) and un-defined microhabitats, such as branches and bark were sampled. Branches with a circumference of less than 20 cm achieved

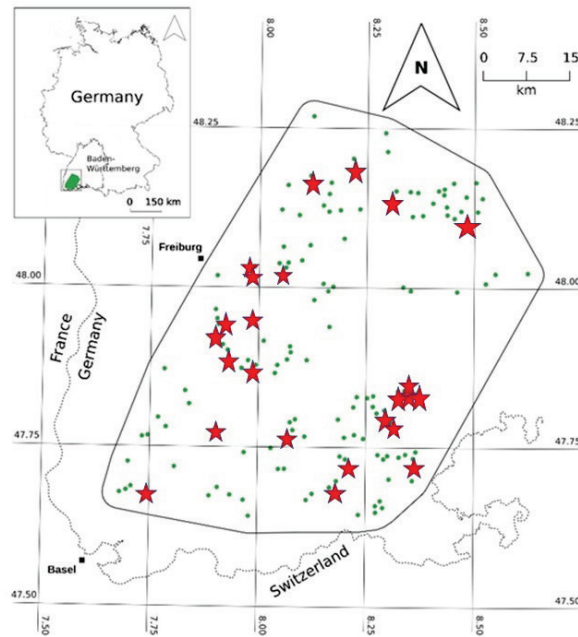


Fig. 1. Location of the study sites (red stars) and the ConFoBi study plots (green dots) in the Southern Black Forest, and in Germany, in the state of Baden-Württemberg (insert).

Abb. 1. Lage der Untersuchungsgebiete (rote Sterne) und der ConFoBi-Untersuchungsflächen (grüne Punkte) im Südschwarzwald und in Deutschland im Bundesland Baden-Württemberg (Einfügung)

the 20 × 30 cm plot size by using a greater length of the stem, therefore changing the shape of the plot but maintaining the total area. Repetitions were taken from all vertical zones, and from different aspects of the tree canopy (as detailed in Fig. 2 below).

The approach used for recording epiphyte species cover within each plot included the modified Braun-Blanquet scale (BRAUN-BLANQUET 1964, and modifications made by REICHELDT & WILMANN 1973). Species that could not be identified during fieldwork were referenced for the purpose of recording cover values for the plot, and taken for later identification with a microscope. Species that were difficult to identify, were confirmed or determined by Prof. Volkmar Wirth (lichens) and Michael Lüth (bryophytes). Species identification and nomenclature followed the published works of SMITH (2004) for bryophytes and PATON (1999) for liverworts, and WIRTH (1995), WIRTH et al. (2013) for lichen species. Methods used for lichen identification included chemical spot tests, using potassium hydroxide (K), sodium hypochlorite, paraphenylenediamine (Pd) and UV light to observe reactions on some species, both in the field and in the laboratory with a microscope.

During fieldwork environmental data collected from each plot included; zone on the tree, aspect on the tree, and solar radiation. The selected trees were divided into six different zones, the zones were defined by JOHANSSON (1974) (as illustrated in Fig. 2), but modified to include the different forest vegetation layers recorded on European trees (MUELLER-DOMBOIS & ELLENBERG 1974). Aspect (north, south, east and west) were recorded using a compass to determine the exposure at each plot location.

Further environmental data recorded included solar radiation. Due to there being no standard approach to sampling solar radiation on plots situated on tree structures, an approach was devised based on available solar radiation data, combined with tools used to sample plots at ground level, but adaptable to use within the tree structure. The amount of direct solar radiation was determined by using

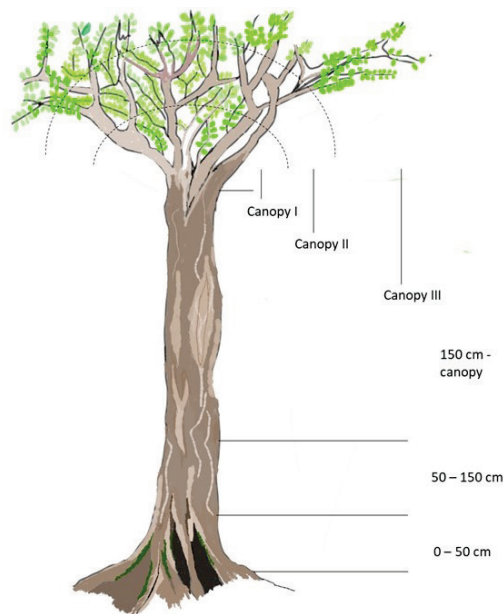


Fig. 2. Tree zones, from the base to the outer canopy. The zones are defined based on a modified version of JOHANSSON (1974).

Abb. 2. Baumzonen, von der Basis bis zum äußeren Blätterdach. Die Zonen werden basierend auf einer modifizierten Version von JOHANSSON (1974) definiert.

a model following Verein Deutscher Ingenieure (VDI 378-) (Beuth Publishing DIN, <https://www.beuth.de>) and using METEOSAT, based on the number of hours of sunlight in each month of the year recorded for each plot location, in combination with a solar compass (SonnenKompass, Grube) that enabled the recording of the number of hours of solar radiation received at each plot location (including the effect of the overhead canopy).

The calculation of the indirect solar radiation included data from direct solar radiation for each plot, and combined indirect solar radiation based on the approach used in SCARTAZZA et al. (2016). SCARTAZZA et al. (2016) used a ceptometer to measure light at different vertical levels within the tree canopies of *F. sylvatica*. The result of this study found that light intensity decreased from the top to the bottom of the tree, with measurements indicating an approximate 20% decrease between each of the three canopy layers. This approach was used to indicate the influence that the indirect light contributes to the direct solar radiation values at each of the plot locations.

3.2 Data analysis

To classify the epiphytic vegetation in a reproducible way, a stepwise procedure was applied. The samples were classified by hierarchical agglomerative clustering based on similarity of species and abundance values, using the Bray-Curtis coefficient (BRAY-CURTIS 1957). This method was favoured because it can be applied to semi-quantitative data and skips double absence. The flexible-beta clustering method was chosen for classification, as this method is compatible with semi-metric distance measurements (MCCUNE & GRACE 2002).

3.2.1 Pruning the dendrogram

There is no definitive means of pruning the dendrogram obtained from cluster analysis, therefore a quantitative and objective approach was used (DUFRENE & LEGENDRE 1997). This method includes using the Indicator Species Analysis (IndVal, in the Indicspecies package) to determine which cluster grouping has either the highest sum of species indicator values that are significant or, the highest number of significant indicator species, using this approach the optimum number of groups was obtained.

3.2.2 Indicator species analysis

The Indicator Species Analysis (Indicspecies package (1.7.8); DE CÁCERES 2020) was used to find the best match between the clusters groups and further divide the dendrogram into subgroups based on species composition. To separate the species and plot groups present, a Cutree method was used (from the hclust function, stats package).

To relate species to plot groups a Chi-Squared test was performed to determine if a relationship exists between the two groups. The results of the Chi-Squared test were then used to create a contingency table to establish where the matching groups were located.

The indicator species analysis helped to determine which species were differentiating between plot groups. Species with a high level of fidelity based on abundance and frequency (GLAVAC 1996) were sorted and listed as indicator species for each plot cluster group. The results of the Contingency table along with the results of the Indicator Species Analysis were then used to build the vegetation table.

3.2.3 Ordination

In order to understand the relationship that the plot groups have within one and other and to understand the influence that the environmental factors have on the plot groups, Non-Metric Multi-dimensional Scaling (NMDS) (using metaMDS from the vegan package) was used (MCCUNE & GRACE 2002). Furthermore, NMDS allows the use of distance measurement, and as such Bray-Curtis was selected to ensure compatibility with the Cluster Analysis. The environmental factors were added using a regression on the NMDS axis. To determine if certain species were driving the plot distribution pattern, intrinsic variables were plotted using statistical measurements on the NMDS axis.

Data analysis was undertaken using R, version 3.6.3 (R CORE TEAM 2020).

3.2.4 Phytosociological grouping

Phytosociological ordering of the groups was undertaken using the step-wise procedure, using statistical measurements to form plot groups. Statistical measurements were also used to determine species that are representative of the groups at different hierarchical levels and therefore represented as diagnostic species and further to be used to as community/association names. Vegetation units that were named communities and community groups related to described associations, alliances and higher hierarchical levels (MUELLER-DOMBOIS & ELLENBERG 1974), due to different levels of species saturation of the plots sampled. Some communities were in the rank of associations, based on the similarity of their species composition.

Communities from this study, using both species and environmental factors were then compared with existing phytosociological descriptions of related syntaxa, using species and environmental descriptions from published works (BARKMAN 1958, WIRTH 1966, WILMANN & WIRTH 1968, JAMES et al. 1977, MARSTALLER 2006, 2015).

4. Results

4.1 Sample results

A total of 170 species of epiphyte were recorded, 88 lichen and 82 bryophyte species (see Supplement E1, for a complete list of species). A total of 194 plots were sampled from the selected 24 trees.

There are two main groups in the dendrogram, and the dendrogram is further divided into six clusters, representing six plot groups (Fig. 3). The six plot groups were named according to the dominant species found with the Indicator Species Analysis. Table 1 presents the plot groups and their diagnostic epiphyte species, following the step-wise procedure of the sampled plots.

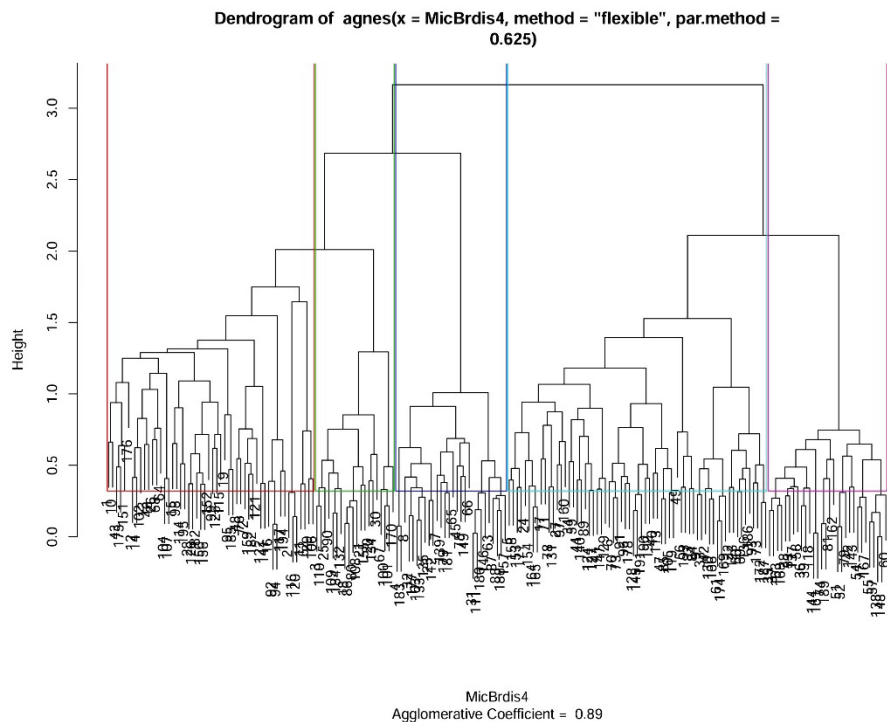


Fig. 3. Dendrogram illustrating the result of Cluster Analysis based on their floristic dissimilarity (Agglomerative Coefficient = 0.89). The six different colour boxes represent the six different plot groups.

Abb. 3. Dendrogramm zur Veranschaulichung des Ergebnisses der Clusteranalyse basierend auf ihrer floristischen Unähnlichkeit (Agglomerationskoeffizient = 0,89). Die sechs verschiedenen Farbfelder repräsentieren die sechs verschiedenen Plot-Gruppen.

The patterns illustrated on the ordination diagram in Figure 4 indicate that the strongest factors appear to be light (light peak) and vertical locations (Comp.) based on the length of the arrows and p -values of 0.001 for both factors; aspect (sin and cos) were found to be not significant (see Supplement E2 for more detail). The variable which is the most strongly related to the first two ordination axes is vertical location, whilst light is strongly related to the first ordination axis and vertical location to the second one. The *Parmelietum furfuraceae* association can be seen primarily where light is most abundant, whilst the *Ulotetum crispae* association is found on the opposite gradient, in the more shaded sections of the tree (the ordination diagram with eclipses further illustrates this in Supplement E3). The vertical locations largely follow the same pattern.

Figure 5 illustrates the species that drive the distribution of each of the communities/associations. The patterns on this figure allow us to see that there are two opposite gradients from the top right to the bottom left of the diagram; with species typical of humid environments (*Hypnum andoi* and *Platismatia glauca*) found in the top left, whilst at the opposite gradient, bare bark is dominant suggesting a more exposed environment. The two figures (Fig. 4 and 5) together provide an indication of environmental factors; light, vertical location and humidity in which the communities / associations are found.

Table 1. Communities and associations using the results of the Cluster Analysis and the Indicator Species Analysis.

Tabelle 1. Gesellschaften und Verbände unter Verwendung der Ergebnisse der Clusteranalyse und der Indikatorartenanalyse.

Plot groups	Community groups	Communities/ associations	Diagnostic species
1	<i>Hypnum cupressiforme</i>	<i>Ulotetum crispae</i> Ochn. 1928	<i>Hypnum cupressiforme</i> , <i>Parmelia saxatilis</i> s.l.
2		<i>Dicrano scoparii-Hypnetum filiformis</i> Barkm. 1958	<i>Hypnum filiforme</i> , <i>Isothecium myosuroides</i> , <i>Eurhynchium striatum</i> , <i>Lepraria finkii</i> , <i>Pertusaria albescens</i>
3		<i>Antitrichia curtipendula</i> community	<i>Antitrichia curtipendula</i> , <i>Metzgeria furcata</i> , <i>Orthotrichum affine</i> , <i>Isothecium alopecuroides</i> , <i>Homalothecium sericeum</i>
4		<i>Usnea dasopoga-Platismatia glauca</i> community	<i>Platismatia glauca</i> , <i>Usnea dasopoga</i> , <i>Hypnum andoi</i> , <i>Pertusaria amara</i>
5	<i>Melanohalea exasperatula</i>	<i>Parmelietum furfuraceae</i> Hilitzer 1925	<i>Pseudevernia furfuracea</i> , <i>Physcia tenella</i> , <i>Melanohalea exasperatula</i> , <i>Buellia griseovirens</i> , <i>Hypogymnia tubulosa</i>
6			Predominating bark

4.2 Flora and ecology of the epiphytic associations and communities

Based on the 194 epiphyte samples collected from the base to the outer crown of *F. sylvatica*, we were able to distinguish six different epiphyte ecological groups, representing five floristic epiphytic plant communities (Supplement E4, running number 1–165), and one “group” representing unvegetated bark (Supplement E4, 166–195). The vegetation table in Supplement E4 is composed of a list of the species, the plot groups, and the epiphytic plant communities. The below syntaxonomical descriptions include detail of the similarities that the plot groups have with communities or associations described in phytosociological literature (BARKMAN 1958, WIRTH 1966, WILMANN & WIRTH 1968, JAMES et al. 1977, MARSTALLER 2006, 2015), based on the comparison of species and ecological variables.

***Ulotetum crispae* Ochn. 1928 (Supplement E4, running number 1–28)**

The **indicator species** of *Ulotetum crispae* recorded for this study include: *Hypnum cupressiforme* and *Parmelia saxatilis*. Species with a high fidelity include: *Coenogonium pineti*, *Frullania dilatata*, *Lepraria rigidula*, *Ulota bruchii*, *U. crispa* and *Usnea* sp.

In this study, *Ulotetum crispae* was recorded primarily at the base and mid-trunk, within conditions that are shaded to partial shade, i.e. related to microsites with higher humidity. It occurs in dense carpets in the most humid, partial-shaded conditions where bryophytes and

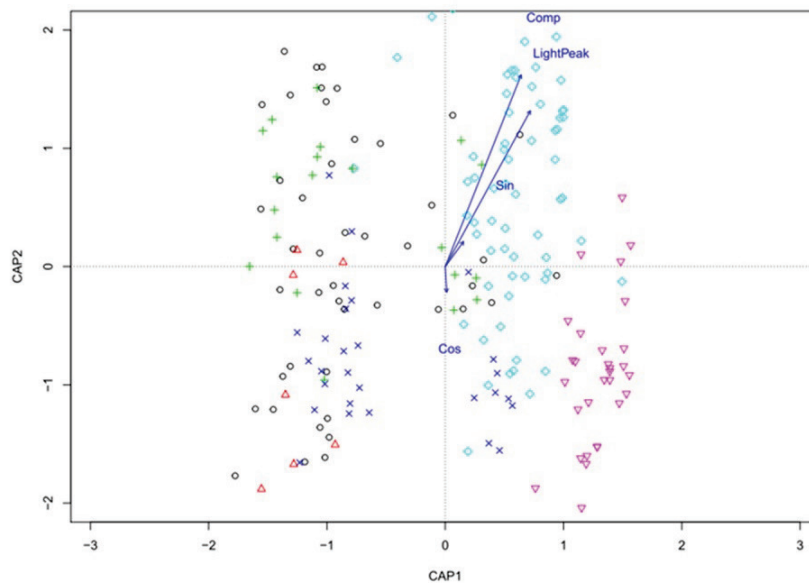


Fig. 4. Ordination diagram of Non-Metric multi-dimensional Scaling (NMDS) with projections of the environmental variables as vectors, including solar radiation (light peak), tree zones, from the base to the top of the canopy (Comp) and aspect (sin and cos). The coloured symbols indicate the different plot groups formed by the cluster analysis. Dark blue crosses: *Ulotetum crispae*, Red triangles: *Dicrano scoparii-Hypnetum filiformis*, Black circles: *Antitrichia curtispindula* community, Green plus signs: *Usnea dasopoga-Platismatia glauca* community, Turquoise diamonds: *Parmelietum furfuraceae*, Pink up-side down triangles: Predominating bark.

Abb. 4. Ordinationsdiagramm der nichtmetrischen mehrdimensionalen Skalierung (NMDS) mit Projektionen der Umgebungsvariablen als Vektoren, einschließlich Sonneneinstrahlung (Lichtspitze), Baumzonen, von der Basis bis zur Spitze des Blätterdachs (Comp) und aspect (sin und co). Die farbigen Symbole kennzeichnen die verschiedenen Plot-Gruppen, die durch die Clusteranalyse gebildet wurden. Dunkelblaue Kreuze: *Ulotetum crispae*, rote Dreiecke: *Dicrano scoparii-Hypnetum filiformis*, schwarze Kreise: *Antitrichia curtispindula*-Gesellschaft, grüne Pluszeichen: *Usnea dasopoga-Platismatia glauca*-Gesellschaft, türkise Rauten: *Parmelietum furfuraceae*, rosa umgedrehte Dreiecke: vorherrschende Rinde.

foliose lichens thrive. This community therefore differs from the other communities/associations found in this study in both appearance and form, as it creates large areas of lush coverings within the base and creeping up to the mid-section of the tree.

The floristic composition found in this study relates to the *Ulotetum crispae*, variant *typicum* Marstaller 2015, including *Ulotetum bruchii*, *U. crispa*, *Frullania dilatata*, *Hypnum cupressiforme*, *Lepararia* sp., and there is also reference to *Parmelia* species, albeit *Parmelia sulcata*. A similar microclimate has also been recorded, with conditions including high humidity. MARSTALLER (2015) also refers to *H. cupressiforme* pushing the cushioned species into the background, which further resembles the group found in this study. There is also some resemblance with the species recorded in this study to the *Ulotetum bruchii* Barkman 1958, but much fewer species show the floristic relation with this description.

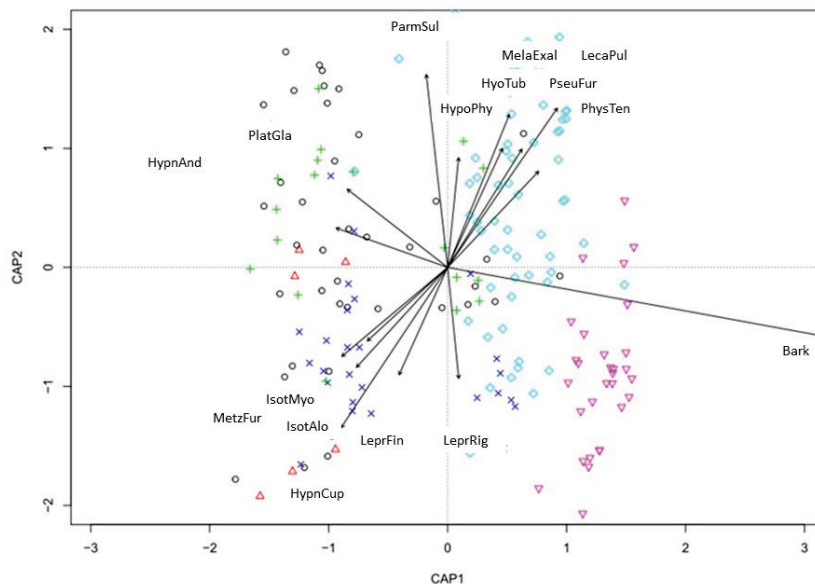


Fig. 5. Ordination diagram of Non-Metric multi-dimensional Scaling (NMDS) with Intrinsic Species (with P -values of < 0.001) as vectors, illustrating the species that are driving the plot distribution. A full species list has been provided in Supplement E1. The symbols indicate the different plot groups formed by the cluster analysis. The coloured symbols indicate the different species groups formed by the cluster analysis. Dark blue crosses: *Ulotetum crispae*, Red triangles: *Dicrano scoparii-Hypnetum filiformis*, Black circles: *Antitrichia curtipendula* community, Green plus signs: *Usnea dasopoga-Platismatia glauca* community, Turquoise diamonds: *Parmelietum furfuraceae*, Pink up-side down triangles: Predominating bark.

Abb. 5. Ordinationsdiagramm der nichtmetrischen mehrdimensionalen Skalierung (NMDS) mit intrinsischen Arten (mit P -Werten von $< 0,001$) als Vektoren, das die Arten veranschaulicht, die die Diagrammverteilung bestimmen. Eine vollständige Artenliste findet sich in Anhang E1. Die Symbole geben die verschiedenen Plotgruppen an, die durch die Clusteranalyse gebildet wurden. Die farbigen Symbole zeigen die verschiedenen Artengruppen an, die durch die Clusteranalyse gebildet wurden. Dunkelblaue Kreuze: *Ulotetum crispae*, rote Dreiecke: *Dicrano scoparii-Hypnetum filiformis*, schwarze Kreise: *Antitrichia curtipendula*-Gesellschaft, grüne Pluszeichen: *Usnea dasopoga-Platismatia glauca*-Gesellschaft, türkise Rauten: *Parmelietum furfuraceae*, rosa umgedrehte Dreiecke: vorherrschende Rinde.

***Dicrano scoparii-Hypnetum filiformis* Barkm. 1958 (Supplement E4, 29–35)**

Diagnostic species include *Isothecium myosuroides*, *Hypnum cupressiforme* var. *filiforme*, *Eurhynchium striatum*, *Lepraria finkii*, and *Pertusaria albescens*. The association was represented with seven plots. The species recorded in this plot group match the *Dicrano scoparii-Hypnetum filiformis* Barkm. 1958 as described by MARSTALLER (2015), including a dominance of *Hypnum cupressiforme* var. *filiforme*, and faithful taxa *Isothecium myosuroides* and *Lepraria* sp. It also has been recorded on *F. sylvatica*, and the three-layered growth form recorded this study also resembles the growth form of *Dicrano scoparii-Hypnetum filiformis*. A new sub-variant has been suggested for this syntaxon in MARSTALLER (2006, 2015), however the species recorded in this study do not match this variant adequately.

The *Dicrano scoparii-Hypnetum filiformis* differs from the other communities in being principally recorded in the lower – mid section of the tree in humid and shaded positions, with species that are similarly associated with locations of high humidity. BARKMAN (1958) similarly describes the *Dicrano scoparii-Hypnetum filiformis* as being located on the lower – mid stem with a N-W exposure.

***Antitrichia curtispindula* community (Supplement E4, 36–80)**

Indicator species include: *Metzgeria furcata*, *Orthotrichum affine*, and the characteristic *Antitrichia curtispindula* has high fidelity for this group. Other species recorded as having high fidelity include *Isothecium alopecuroides*, *Homalothecium sericeum*, *Radula complanata*, *Orthotrichum lyellii*, *O. striatum*, *Platygyrium repens*, *Parmelia sulcata*, *Evernia prunastri* and *Melanelixia glabratula*. This community has a floristic similarity with the *Dicrano scoparii-Hypnetum filiformis*, as some species are shared between the communities, such as *Isothecium* sp. and *Hypnum* sp.

The *Antitrichia curtispindula* community differs from the other communities recorded due to its position and growth form. The ecological parameters associated with this community within this study include a prevalence within the N-NW aspect, and within humid locations on the tree. It was further recorded primarily within the lower sections of the tree, but also within the tree canopy.

The *Antitrichia curtispindula* community belongs to the alliance *Lobario-Antitrichion* Wirth 1966, with *Antitrichia curtispindula*, *Metzgeria furcata*, *Homalothecium sericeum* and *Radula complanata* as common diagnostic species (WIRTH 1966, WIRTH & WILMANN 1968). The positioning and some species of the *Antitrichia curtispindula* community are also comparable to *Antitrichietum curtispindulae* Hiltner 1925, but floristically they were not as well connected.

***Usnea dasopoga-Platismatia glauca* community (Supplement E4, 81–100)**

Indicator species include: *Hypnum andoi*, *Platismatia glauca*, *Pertusaria amara*, *Usnea dasopoga*, along with high fidelity species *Dicranum scoparium*, *Graphis scripta*, *Hypogymnia physodes* and *Lepraria* sp. The diagnostic species for this community differs from the other syntaxa, with lichen species being the dominant indicator species.

Within this study the *Usnea dasopoga-Platismatia glauca* community prevailed in the upper tree trunk and the lower and mid tree canopy, but not in direct sunlight, and includes species that are known to occur in environments of high humidity, e.g. *Hypnum andoi* was recorded in every sample, indicating high humidity (BLOCKEEL et al. 2014).

The *Usnea dasopoga-Platismatia glauca* community has a strong resemblance to the species and the ecology of the alliance *Usneion dasypogae* Barkman 1958 indicated by the presence of *Usnea dasopoga*, *Platismatia glauca* and *Hypogymnia physodes*. Within this alliance, there was some resemblance with the *Cladonieta-Usneetum tuberculatae* Barkman 1958, however the location on the tree differs. The *Cladonieta-Usneetum tuberculatae* association has largely been recorded at the very base of the tree, thus containing other species typical of a forest floor-tree base interface, including *Hypnum cupressiforme*, *Cladonia* species and *Trapeliopsis* species. WILMANN & WIRTH (1968) described *Usneion dasypogae* from humid environments within the upper sections of the trunk and the tree canopy, but not in exposed positions with direct contact to rainfall. This compares well with the *Usnea dasopoga-Platismatia glauca* community found in this study.

***Parmelietum furfuraceae* Hilitzer 1925 (Supplement E4, 101–165)**

The **indicator species** recorded include: *Melanohalea exasperatula*, *Pseudevernia furfuracea*, *Physcia tenella*, *Buellia griseovirens* and *Hypogymnia tubulosa*. Whilst the species with high fidelity include *Brachythecium velutinum*, *Candelariella efflorescens*, *Lecanora chlorotera*, *Orthotrichum speciosum*, *Physcia adscendens* and *P. stellaris*.

In this study, the *Parmelietum furfuraceae* was recorded in well-lit positions within the lower to upper canopy, with moderate to high solar radiation on the medium – smaller outer branches. It differs from the other groups described in both its position and floristic composition, e.g. it contains many species typical of dry and exposed conditions. The position on the host tree, the floristic composition found in this study, including a dominance of *Pseudevernia furfuracea*, *Hypogymnia tubulosa*, and *Melanohalea exasperatula*, and the three-layered growth structure make this group comparable to the association.

BARKMAN (1958) describes the *Parmelietum furfuraceae* as one of the best studied epiphyte associations, but with many fragmentary records. There are five sub-associations described for the association, none of the sub-associations correspond well with the association found in this study as the species composition described are different. It is possible that the *Parmelietum furfuraceae* found in this study is a new variant.

4.3 Niches on *Fagus sylvatica*

The epiphyte communities recorded on *F. sylvatica* each occupy specific niches on the tree. Some niches overlap and some have clear boundaries. As illustrated on Figure 4 and 5, the plot groups are driven by environmental factors. Figure 6 further illustrates examples of the different communities/associations recorded.

The position on *F. sylvatica* where a majority of the communities are found is within the central trunk zone (Zone 3, see Fig. 2), on the North-West facing side of the tree (see Fig. 7), with communities/associations *Antitrichia curtispindula*, *Usnea dasopoga-Platismatia glauca*, *Dicrano scoparii-Hypnetum filiformis* and *Ulotetum crispae* being recorded. The zones of the tree with unvegetated bark and reduced epiphyte species and communities include the North-East facing sides of the tree, from zones 1–3.

The *Parmelietum furfuraceae* association occupies areas of high solar radiation primarily in the canopy and the upper sections (zones 4 and 5) of the trunk, on the East-facing side of the tree. The plot group described as “Dominant bark”, has some overlap with the *Parmelietum furfuraceae* association, but Dominant bark is located more on the North-Eastern facing side, and associated with areas of high exposure on the lower to upper main trunk, typical of locations where wind movement increases, as described in SILLETT & ANTOIRE (2004).

The *Dicrano scoparii-Hypnetum filiformis* and the *Ulotetum crispae* are located at the opposite end of the gradient to that of the communities described above (see Fig. 4 and 5), recorded on sections of the tree with the least amount of light, positioned at the bottom of the tree and on the north and west-facing sides. Niches with high humidity, but increased illumination, also play a role in the distribution of the plot groups with the *Usnea dasopoga-Platismatia glauca* and *Antitrichia curtispindula* communities being located on the south-facing side of the tree within the mid-lower canopy, and the lower sections of the tree on the north-facing side.



Fig. 6. **a)** *Ulotelum crispae*, **b)** *Dicrano scoparii-Hypnetum filiformis*, **c)** *Antitrichia curtispindula* community, **d)** *Usnea dasopoga-Platismatia glauca* community, **e)** *Parmelietum furfuraceae*, **f)** Predominating bark (with very few epiphytes and dominant bark) (Photos: D. Stevenson, 2017).

Abb. 6. **a)** *Ulotelum crispae*, **b)** *Dicrano scoparii-Hypnetum filiformis*, **c)** *Antitrichia curtispindula*-Gesellschaft, **d)** *Usnea dasopoga-Platismatia glauca*-Gesellschaft, **e)** *Parmelietum furfuraceae*, **f)** Vorherrschende Rinde (mit sehr wenigen Epiphyten und dominanter Rinde) (Fotos: D. Stevenson, 2017).

5. Discussion

This study aimed to discover epiphyte communities within montane forest conditions, within plots located in the Southern Black Forest, selecting favourable climatic zones and locating optimal *Fagus sylvatica* trees within typical forest stands. The sampling and analysis approach to this study aimed to further discover a “true” understanding of epiphyte communities throughout *F. sylvatica* and also to establish if certain zones within the tree have higher ecological value.

Many epiphytic studies have been undertaken on the substrate and bark (CRITES et al. 1998, JOHANSSON et al. 2007, MEŽAKA et al. 2008, RANIUS et al. 2008, FRITZ et al. 2009 & 2010, DITTRICH et al. 2022, etc.), this study focusses on the climatic conditions and not the substrate. Different climatic conditions are found throughout the tree which better reflect the site demands of the communities/associations described (BARKMAN 1958).

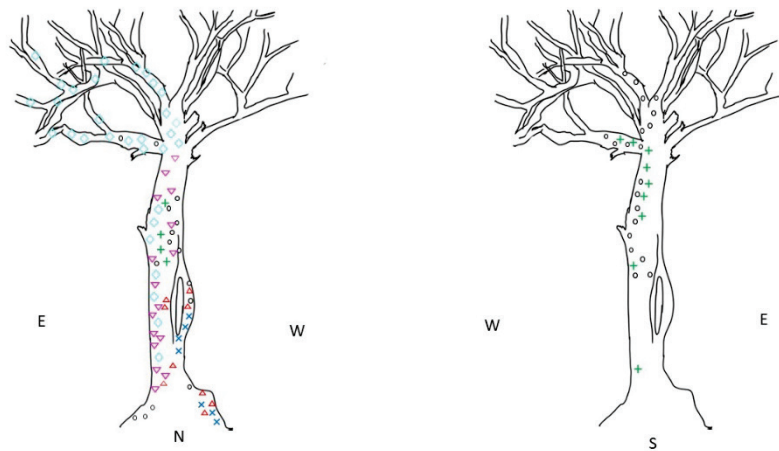


Fig. 7. Tree diagram illustrating the different communities and their specific niches on *F. sylvatica*. The cardinal points are illustrated, N: North, E: East, W: West, S: South. The coloured symbols indicate the different communities/ associations formed by the cluster analysis. Dark blue crosses: *Ulotetum crispae*, Red triangles: *Dicrano scoparii-Hypnetum filiformis*, Black circles: *Antitrichia curtispindula* community, Green plus signs: *Usnea dasopoga-Platismatia glauca* community, Turquoise diamonds: *Parmelietum furfuraceae*, Pink up-side down triangles: Predominating bark.

Abb. 7. Baumdiagramm, das die verschiedenen Gesellschaften und ihre spezifischen Nischen auf *F. sylvatica* veranschaulicht. Die Himmelsrichtungen sind dargestellt: N: Norden, E: Osten, W: Westen, S: Süden. Die farbigen Symbole kennzeichnen die verschiedenen Gemeinschaften/Verbände, die durch die Clusteranalyse gebildet wurden. Dunkelblaue Kreuze: *Ulotetum crispae*, rote Dreiecke: *Dicrano scoparii-Hypnetum filiformis*, schwarze Kreise: *Antitrichia curtispindula*-Gesellschaft, grüne Pluszeichen: *Usnea dasopoga-Platismatia glauca*-Gesellschaft, türkise Rauten: *Parmelietum furfuraceae*, rosa umgedrehte Dreiecke: vorherrschende Rinde.

Separating and determining the differences between the plot groups recorded on *F. sylvatica* required insight into their species composition and specific environmental requirements. Characterisation of the different epiphytic assemblages was challenging, as epiphytes are largely influenced by solar radiation and humidity for their distribution (WILL-WOLF et al. 2002), however both solar radiation and humidity are difficult to obtain from the tree canopy (BARKMAN 1958).

It was clear when comparing the floristic analysis and the ecological niches of the communities for this study to that of the phytosociological literature, that there are communities that match and others that have similarities but also divergences, specifically relating to species composition or position on the tree. The primary reason for these differences is a combination of factors, including; climate and micro-climate (ZOTZ et al. 2009), as well as the use of different sampling approaches, including sampling the whole tree, and the use of statistical multivariate analysis.

Differences between this study and the literature was evident for the *Parmelietum furfuraceae* association. The indicator species and the upper-canopy position connected well with the association, however the five sub-associations described in this association were not comparable. BARKMAN (1958) describes differences occurring in species composition, along with position on the host as being driven by climatic factors. *Parmelietum furfuraceae* has further been described as very variable association with other sub-associations being

recognised as a result of species differentiation (JAMES et al. 1977). The differences in species composition recorded within *Parmelietum furfuraceae* found within this study to that of the phytosociological literature is therefore likely to have been due to climatic differences, but also due access difficulties, as a result of its location in the upper stem and tree canopy.

Climate was also seen influencing the differences in species composition for *Dicrano scoparii-Hypnetum filiformis*. The association connected well to that of the study, but the three sub-associations described were again not comparable. When comparing the climatic factors of *Dicrano scoparii-Hypnetum filiformis* found in this study to that of the literature, the association in this study was recorded within the Black Forest, within temperate montane forest, however in BARKMAN (1958) it was recorded and described primarily in northern European lowlands. BARKMAN (1958) further supports this possibility as he describes climatic difference, including elevation, where elevations of greater than 350 m result in a slightly different species assemblage to that typically found in the association (the plots sampled for this study ranged from 700–900 m in elevation). MARSTALLER (2006, 2015) presents further variations of the *Dicrano scoparii-Hypnetum filiformis*, including variations found in more mountainous regions, further supporting the difference in species within this association as a consequence of climatic differences due elevations.

To obtain a true understanding of the epiphyte communities found on *F. sylvatica*, this study used data from statistical analysis to determine the different diagnostic species within the plot groups. The whole tree was accessed and environmental data was recorded during fieldwork. Much of the phytosociological literature on epiphyte communities did not have access to statistical analysis, nor sampling beyond 2 m on the stem (this remains a limitation in studies conducted today; DITTRICH et al. 2022), and communities and ecological conditions would have been established during excursions (BARKMAN 1958), where there would have been a level of bias when sampling. The plot groups in this study, therefore do not all fit neatly into the phytosociological descriptions. These factors were considered when comparing the study groups to that of the phytosociological literature.

When establishing which zones of the tree have the most ecological value both community/association diversity and syntaxa that have connection with old-forest habitats were considered (HUMPHREY et al. 2002). It was clear that the central trunk on the North-West facing side housed the most epiphyte communities/associations (including *Antitrichia curtispindula* community, *Usnea dasopoga-Platismatia glauca* community, *Dicrano scoparii-Hypnetum filiformis* association and *Ulotetum crispae* association). Furthermore, these groups are communities/associations that contain obligate-epiphyte species (epiphytes only found on tree habitats), further increasing their ecological value due to being less ubiquitous. Additionally, the *Antitrichia curtispindula* community, described in the North-Western zones is a community viewed as being in successional transition to the *Nephrometum belli* association within the *Lobario-Antitrichion* alliance (WIRTH 1966), a syntaxon associated with old forest habitat, containing many species limited to old growth forests.

It can therefore be concluded that the zones of the tree that appear to be of greatest ecological value include the North-West side of the central trunk (zone 3); the poorest zones on the *F. sylvatica* sampled appeared to be the North-East main trunk (zones 1–3) facing side of the tree with increased bark surface and fewer species and communities/ associations being recorded in these zones.

In summary, this study has been able to identify five epiphyte communities recorded on *F. sylvatica* within the Black Forest. Similarities to existing association/communities from phytosociological literature have been identified, and differences have been highlighted.

This study provides additional insights into the “true” floristic composition and niches of the epiphyte communities found on *F. sylvatica*, providing both an insight into the communities that are found on *F. sylvatica*, and their environmental conditions, and further providing evidence of zones, on the tree, of ecological value. This study contributes to existing phytosociological systems to help explain community response.

Erweiterte deutsche Zusammenfassung

Einleitung – Obwohl viele Studien über epiphytische Arten und Pflanzengesellschaften existieren (BARKMAN 1958, WIRTH 1966, WILMANN & WIRTH 1968, MARSTALLER 2006, 2015), sind repräsentative Daten über ihre Einnischung innerhalb des ganzen Baumes kaum vorhanden. Diese Fallstudie analysiert die Epiphytenvegetation zwischen Stammfuß und Kronenbereich auf 24 großen Rot-Buchen (*Fagus sylvatica* L.) im Südschwarzwald. Durch numerische Analysen floristischer und standörtlicher Daten werden folgende Forschungsfragen beantwortet: 1) Welche epiphytischen Pflanzenarten und -gesellschaften finden sich auf Rot-Buche? 2) Wie beeinflussen die Lage in verschiedenen Baumkompartimenten, Exposition und Lichtversorgung ihr Vorkommen?

Untersuchungsgebiet – Das Untersuchungsgebiet liegt im Südschwarzwald in der Höhenstufe des montanen Bergmischwalds. Die Böden sind aus Gneisverwitterung hervorgegangene Braunerden. Das Klima ist durch eine mittlere Jahresmitteltemperatur von 8,9 °C (Onset 1-800-LOGGERS) und 1141 mm Jahresniederschlag gekennzeichnet.

Methoden – In dieser Fallstudie werden die epiphytisch vorkommenden Arten und Pflanzengesellschaften auf Rot-Buche inventarisiert und klassifiziert. Die Datenanalyse wurde mit R, Version 3.6.3 (R CORE TEAM 2020) durchgeführt. Die Probestellen wurden anhand des Bray-Curtis-Koeffizienten (BRAY-CURTIS 1957) durch hierarchisches agglomeratives Clustering, basierend auf der Ähnlichkeit von Arten und Häufigkeitswerten, klassifiziert. Durch die Indikatorartenanalyse (Indic-species-Paket (1.7.8); DE CÁCERES 2020) wurden die diagnostischen Arten der jeweiligen Clustergruppe zugeordnet. Durch Anwendung von Non-Metric Multidimensional Scaling (NMDS; hier als metaMDS aus Vegan; MCCUNE & GRACE 2002) wurde der Einfluss von Umweltfaktoren auf die Vegetation ermittelt. Die resultierenden Pflanzengesellschaften wurden mit beschriebenen Syntaxa (vgl. BARKMAN 1958, WIRTH 1966, WILMANN & WIRTH 1968, MARSTALLER 2006, 2015, ELLIS et al. 2015) in Beziehung gebracht.

Ergebnisse – Insgesamt wurden 170 epiphytische Pflanzenarten erfasst, darunter 88 Flechten und 82 Moose. Die Clusteranalyse ergab zwei floristisch und ökologisch sehr verschiedene Gesellschaftsgruppen mit fünf Gesellschaften/Assoziationen. Hinzu kommen Probestellen auf Rinde, also ohne Bewuchs. Zur Gesellschaftsgruppe von *Hypnum cupressiforme* gehören das *Ulotetum crispae* mit den diagnostischen Arten *Hypnum cupressiforme* und *Parmelia saxatilis* s.l. und das *Dicrano scoparii-Hypnetum filiformis* mit *Hypnum filiforme*, *Isothecium myosuroides*, *Eurhynchium striatum*, *Lepraria finkii* und *Pertusaria albescens* als diagnostischen Arten. Zur Gesellschaftsgruppe von *Melanohalea exasperatula* zählen die *Antitrichia curtispindula*-Gesellschaft mit den diagnostischen Arten *Antitrichia curtispindula*, *Metzgeria furcata*, *Orthotrichum affine*, *Isothecium alopecuroides* und *Homalothecium sericeum*, die *Usnea dasopoga-Platismatia glauca*-Gesellschaft, gekennzeichnet durch *Platismatia glauca*, *Usnea dasopoga*, *Hypnum andoi* und *Pertusaria amara*, sowie das *Parmelietum furfuraceae* mit *Pseudevernia furfuracea*, *Physcia tenella*, *Melanohalea exasperatula*, *Buellia griseovirens* und *Hypogymnia tubulosa* als diagnostischen Arten.

Die NMDS ergab, dass Licht und vertikale Lage entscheidende Umweltfaktoren sind (vgl. Abb. 4 und 5; Länge der Pfeile und p-Werte von 0,001 für beide Faktoren). Das *Parmelietum furfuraceae* besiedelt die hellsten, das *Ulotetum crispae* die schattigen Kronenkompartimente. Hinzu kommt ein Feuchtigkeitsgradient, mit *Hypnum andoi* und *Platismatia glauca* in den feuchteren Bereichen, und unbesiedelter Rinde in den exponierten, trockeneren Bereichen.

Die in dieser Studie beschriebenen Gesellschaften wurden mit existierenden Beschreibungen (BARKMAN 1958, WIRTH 1966, WILMANN & WIRTH 1968, JAMES et al. 1977, MARSTALLER 2006, 2015) verglichen und teilweise benannt:

Ulotetum crispae Ochn. 1928

Dicrano scoparii-Hypnetum filiformis Barkm. 1958

Antitrichia curtispindula-Gesellschaft (*Lobario-Antitrichion* Wirth 1968)

Usnea dasopoga-Platismatia glauca-Gesellschaft (*Usneion dasypogae* Barkm. 1958)

Parmelietum furfuraceae Hilitzer 1925

Diskussion – Diese Studie beschreibt und analysiert die Arten und Vergesellschaftungen von Epiphyten sowie Umweltfaktoren an großen Buchen im Südschwarzwald. Dadurch konnten Schwerpunkte ihres Vorkommens innerhalb der Kronenkompartimente von der Stammbasis bis zur Krone ermittelt werden. Fünf epiphytische Kryptogamengesellschaften wurden unterschieden, hinzu kamen Probestellen auf fast unbewachsener Baumrinde. Die Benennung der Syntaxa richtet sich nach der pflanzensoziologischen Literatur. Die spezifischen Charakteristika in der vorliegenden Studie sind auf Unterschiede im Gesamtklima und in den jeweiligen Erfassungsmethoden zurückzuführen. Die vorliegenden Ergebnisse wurden durch Erfassung aller oberirdischen Kompartimente erzielt, also nicht eine selektive Beschränkung auf Stammbasis oder abgebrochene Kronenteile. Hinzukamen multivariate statistische Analysen zur Klassifikation der Aufnahme- und Artengruppen. Dem mittleren Stammbereich (Zone 3) in Nordwest-Exposition wurde die höchste naturschutzfachliche Wertigkeit zuerkannt, basierend auf der Anzahl der vorkommenden Syntaxa, der Anzahl an obligaten Epiphyten-Arten und der Anwesenheit der *Antitrichia curtispindula*-Gesellschaft, welche floristisch oder sukzessional den Übergang zum *Lobario-Antitrichion* darstellt und tendenziell alte Waldlebensräume benötigt (WIRTH 1966). Die geringste Wertigkeit wurde den unteren Stammbereichen (Zone 1 bis 3) in Nordost-Exposition zugesprochen. Insgesamt liefert die vorliegende Studie vertiefte, quantifizierende Kenntnisse über die floristische Zusammensetzung und Standortsansprüche der epiphytischen Syntaxa auf *Fagus sylvatica*, ihrer Kronenkompartimente und naturschutzfachlichen Wertigkeit.

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Author contribution statement

DS conducted this study within the “ConFoBi” (Conservation of Forest Biodiversity in Multiple-use Landscapes of Central Europe) project. DS undertook all field work, species identification and analysis under the supervision of both SG and AR as part of her doctorate degree. All authors contributed and revised drafts, and agreed on the manuscript before being submitted for publication.

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Supplements

Additional supporting information may be found in the online version of this article.

Zusätzliche unterstützende Information ist in der Online-Version dieses Artikels zu finden.

Supplement E1. Species list of bryophytes and lichens in the relevés.

Anhang E1. Artenliste der Moose und Flechten in den Vegetationsaufnahmen.

Supplement E2. R outputs.

Anhang E2. R-Ausgaben.

Supplement E3. Ordination diagram of Non-Metric multi-dimensional Scaling (NMDS) plot with ellipses.

Anhang E3. Ordinationsdiagramm des NMDS-Diagramms (Non-Metric Multi-Dimensional Scaling) mit Ellipsen.

Supplement E4. Epiphyte communities vegetation table.

Anhang E4. Vegetationstabelle der epiphytischen Pflanzengesellschaften.

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Supplement E1. Species list (bryophytes and lichens) in the relevés.

Anhang E1. Artenliste (Moose und Flechten) in den Vegetationsaufnahmen.

Bryophytes / Moose:

<i>Amblystegium humile</i>	<i>Isothecium myosuroides</i>	<i>Plagiothecium laetum</i>
<i>Amblystegium serpens</i>	<i>Lejeunea cavifolia</i>	<i>Plagiothecium succulentum</i>
<i>Amblystegium subtile</i>	<i>Leucodon sciuroides</i>	<i>Plagiothecium undulatum</i>
<i>Anomodon attenuatus</i>	<i>Lophocolea bidentata</i>	<i>Platygyrium repens</i>
<i>Antitrichia curtispindula</i>	<i>Lophocolea heterophylla</i>	<i>Porella platyphylla</i>
<i>Blepharostoma trichophyllum</i>	<i>Metzgeria furcata</i>	<i>Pseudobryum cinclidioides</i>
<i>Brachythecium rutabulum</i>	<i>Metzgeria tempera</i>	<i>Pseudoleskeella nervosa</i>
<i>Brachythecium salebrosum</i>	<i>Metzgeria violacea</i>	<i>Pterigynandrum filiforme</i>
<i>Brachythecium velutinum</i>	<i>Microlejeunea ulicina</i>	<i>Ptilidium pulcherrimum</i>
<i>Bryum capillare</i>	<i>Neckera complanata</i>	<i>Pylaisia polyantha</i>
<i>Cephalozia leucantha</i>	<i>Neckera pennata</i>	<i>Radula complanata</i>
<i>Dicranella heteromalla</i>	<i>Neckera pumila</i>	<i>Rhynchostegiella curviseta</i>
<i>Dicranodontium denudatum</i>	<i>Orthotrichum affine</i>	<i>Rhynchostegiella litorea</i>
<i>Dicranoweisia cirrata</i>	<i>Orthotrichum diaphanum</i>	<i>Rhynchostegiella tenella</i>
<i>Dicranum montanum</i>	<i>Orthotrichum lyellii</i>	<i>Syntrichia papillosa</i>
<i>Dicranum scoparium</i>	<i>Orthotrichum obtusifolium</i>	<i>Thuidium tamariscinum</i>
<i>Dicranum uncinatum</i>	<i>Orthotrichum pallens</i>	<i>Ulota bruchii</i>
<i>Eurhynchium striatum</i>	<i>Orthotrichum patens</i>	<i>Ulota coarctata</i>
<i>Frullania dilatata</i>	<i>Orthotrichum rogeri</i>	<i>Ulota crispa</i>
<i>Frullania tamarisci</i>	<i>Orthotrichum speciosum</i>	<i>Ulota crispula</i>
<i>Habrodon perpusillus</i>	<i>Orthotrichum stramineum</i>	<i>Ulota drummondii</i>
<i>Herzogiella seligeri</i>	<i>Orthotrichum striatum</i>	<i>Ulota intermedia</i>
<i>Homalothecium lutescens</i>	<i>Orthotrichum tenellum</i>	<i>Weissia</i> sp.
<i>Homalothecium sericeum</i>	<i>Oxyrrhynchium hians</i>	<i>Zygodon conoideus</i>
<i>Hypnum andoi</i>	<i>Plagiochila porelloides</i>	<i>Zygodon rupestris</i>
<i>Hypnum cupressiforme</i>	<i>Plagiomnium affine</i>	<i>Zygodon viridissimus</i>
<i>Hypnum cupressiforme</i> var. <i>filiforme</i>	<i>Plagiothecium denticulatum</i>	
<i>Isothecium alopecuroides</i>	<i>Plagiothecium elegans</i>	

Lichens / Flechten:

<i>Agonimia tristicula</i>	<i>Lecanora pulicaris</i>	<i>Pertusaria pupillaris</i>
<i>Arthonia punctiformis</i>	<i>Lecanora sambuci</i>	<i>Phaeophyscia endophoenicea</i>
<i>Bacidia biatorina</i>	<i>Lecidella elaeochroma</i>	<i>Phaeophyscia orbicularis</i>
<i>Bacidia epixanthoides</i>	<i>Lecidella flavosorediata</i>	<i>Phlyctis agelaea</i>
<i>Bacidia subincompta</i>	<i>Lepraria finkii</i>	<i>Phlyctis argena</i>
<i>Buellia disciformis</i>	<i>Lepraria incana</i>	<i>Physcia adscendens</i>
<i>Buellia griseovirens</i>	<i>Lepraria rigidula</i>	<i>Physcia aipolia</i>
<i>Caloplaca cerina</i>	<i>Loxospora elatina</i>	<i>Physcia stellaris</i>
<i>Candelariella efflorescens</i>	<i>Melanelixia glabratula</i>	<i>Physcia tenella</i>
<i>Candelariella reflexa</i>	<i>Melanelixia subaurifera</i>	<i>Platismatia glauca</i>
<i>Candelariella xanthostigma</i>	<i>Melanohalea elegantula</i>	<i>Porina leptalea</i>
<i>Chaenotheca furfuracea</i>	<i>Melanohalea exasperata</i>	<i>Protoparmelia hypotremella</i>
<i>Cladonia chlorophaea</i>	<i>Melanohalea exasperatula</i>	<i>Protoparmelia oleaginea</i>
<i>Cladonia fimbriata</i>	<i>Micarea prasina</i>	<i>Pseudevernia furfuracea</i>
<i>Coenogonium pineti</i>	<i>Normandina pulchella</i>	<i>Punctelia jeckeri</i>
<i>Evernia prunastri</i>	<i>Ochrolechia androgyna</i>	<i>Pyrenula nitida</i>
<i>Flavoparmelia caperata</i>	<i>Ochrolechia microstictoides</i>	<i>Ramalina farinacea</i>
<i>Fuscidea cyathoides</i>	<i>Ochrolechia turneri</i>	<i>Ramalina</i> sp.
<i>Fuscidea lightfootii</i>	<i>Opegrapha vulgata</i>	<i>Rinodina sophodes</i>
<i>Graphis scripta</i>	<i>Parmelia saxatilis</i> s.l.	<i>Ropalospora viridis</i>
<i>Hypogymnia physodes</i>	<i>Parmelia sulcata</i>	<i>Tephroma atra</i>
<i>Hypogymnia tubulosa</i>	<i>Parmotrema perlatum</i>	<i>Thelotrema lepadium</i>
<i>Hypotrachyna afrorevoluta</i>	<i>Parmotrema arnoldii</i>	<i>Tuckermannopsis chlorophylla</i>
<i>Hypotrachyna revoluta</i>	<i>Peltigera praetextata</i>	<i>Usnea dasopoga</i>
<i>Lecania naegelii</i>	<i>Pertusaria albescens</i>	<i>Usnea intermedia</i>
<i>Lecanora argentata</i>	<i>Pertusaria amara</i>	<i>Violella fucata</i>
<i>Lecanora carpinea</i>	<i>Pertusaria borealis</i>	<i>Xanthoria parietina</i>
<i>Lecanora chlarotera</i>	<i>Pertusaria coccodes</i>	<i>Xanthoria polycarpa</i>
<i>Lecanora expallens</i>	<i>Pertusaria coronata</i>	
<i>Lecanora intumescens</i>	<i>Pertusaria leioplaca</i>	

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Supplement E2. R outputs.

Anhang E2. R-Ausgaben.

***VECTORS

	CAP1	CAP2	r2	Pr(>r)
LightPeak	0.48006	0.87724	0.3716	0.001
Comp	0.36942	0.92926	0.4983	0.001
Sin	0.59510	0.80365	0.0107	0.424
Cos	0.04389	-0.99904	0.0079	0.468

LightPeak ***

Comp ***

Sin

Cos

Signif. codes:

0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1
' ' 1

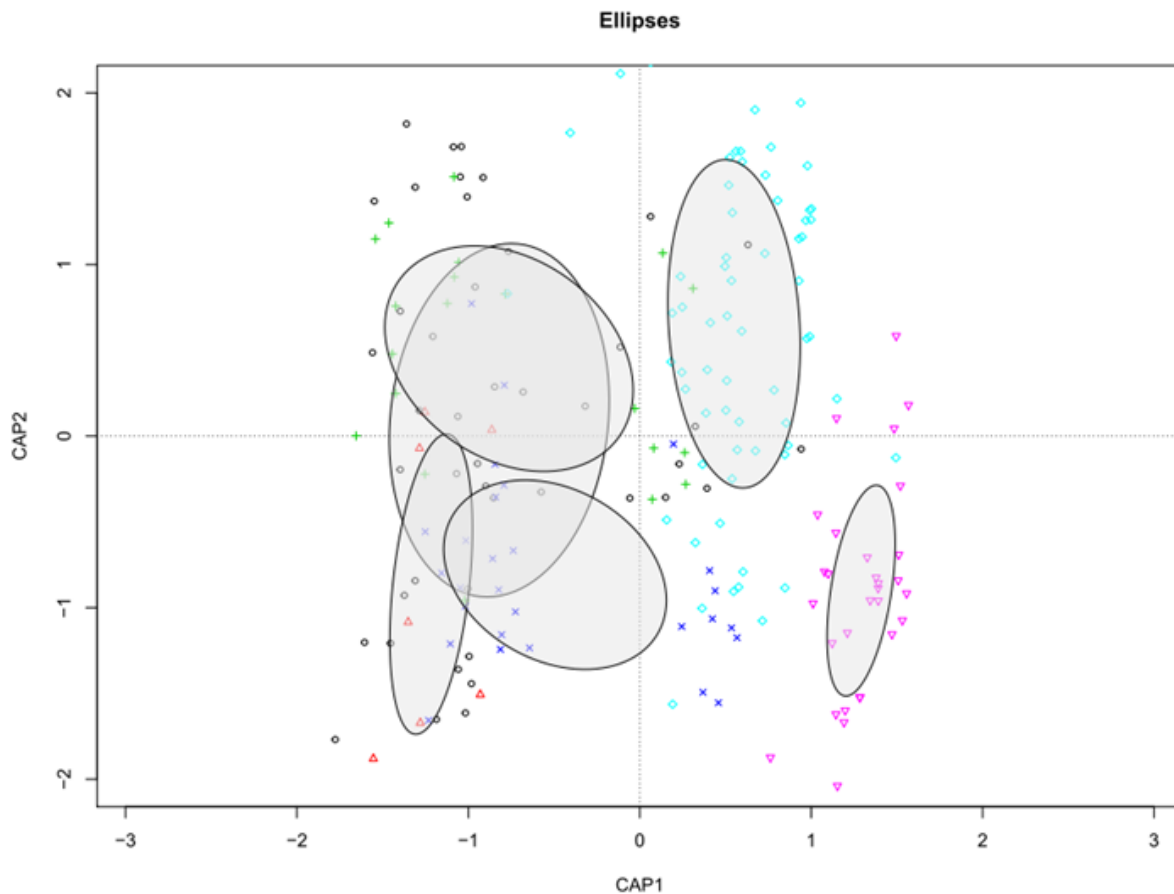
Permutation: free

Number of permutations: 999

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Supplement E3. Ordination diagram of Non-Metric multi-dimensional Scaling (NMDS) plot with ellipses. The different symbols represent the different communities/ associations formed by the cluster analysis. Dark blue crosses: *Ulotetum crispae*, Red triangles: *Dicrano scoparii-Hypnetum filiformis*, Black circles: *Antitrichia curtispindula* community, Green plus signs: *Usnea dasopoga-Platismatia glauca* community, Turquoise diamonds: *Parmelietum furfuraceae*, Pink up-side down triangles: Predominating bark.

Anhang E3. Ordinationsdiagramm des NMDS-Diagramms (Non-Metric Multi-Dimensional Scaling) mit Ellipsen. Die verschiedenen Symbole repräsentieren die verschiedenen Gesellschaften/Verbände, die durch die Clusteranalyse gebildet wurden. Dunkelblaue Kreuze: *Ulotetum crispae*, rote Dreiecke: *Dicrano scoparii-Hypnetum filiformis*, schwarze Kreise: *Antitrichia curtispindula*-Gesellschaft, grüne Pluszeichen: *Usnea dasopoga-Platismatia glauca*-Gesellschaft, türkise Rauten: *Parmelietum furfuraceae*, rosa umgedrehte Dreiecke: vorherrschende Rinde.



Supplement E4. Epiphytic plant communities on European Beech (*Fagus sylvatica* L.). Indikatorarten sind in Grün schattiert.

Anhang E4. Epiphytische Pflanzengesellschaften auf der Rotbuche (*Fagus sylvatica* L.). Indikator species are shaded in green.

Running number	Plot number	Location: Latitude	Location: Longitude	Altitude (m)	Cluster group	Position on tree (Tree zone)	Aspect (cardinal)	Direct irradiation (W/m ²)	Indirect irradiation (W/m ²)	Total irradiation (W/m ²)
7841	7497	346								
10352	9994	359								
10577	9944	383								
902	628	364								
7884	7881	3								
10512	10507	5								
7046	6044	1002								
9209	6472	2757								
12828	9707	3121								
15067	12942	2124								
14824	13431	1392								
7099	6855	244								
7286	6855	411								
7859	7144	715								
7430	7319	111								
11765	7319	2004								
10422	6621	10422								
13809	13241	568								
11298	9281	2009								
2105	700	1495								
8729	8397	331								
12309	10585	1724								
14074	11059	3015								
13390	11059	2331								
11895	7373	4482								
13800	11059	1871								
14538	11059	3479								
848	848	0								
778	778	0								
7335	6236	1302								
9339	9339	0								
10625	9338	1286								
14160	12451	1706								
11618	10048	1570								
12560	0	12560								
504	504	0								
631	6044	487								
9089	8059	1030								
8858	6471	2387								
12598	10074	2525								
17467	13431	4035								
12805	10481	2123								
10930	9141	1790								
4337	2417	1920								
1461	5953	8654								
5092	5953	930								
8175	7144	1031								
5561	610	6817								
1809	0	1160								
8272	648.8	486.6								
8896	7785	1111								
10085	7785	304.2								
10462	10380	82								
9915	6402	213								
10733	9602	1131								
12428	9282	3147								
11440	11196	2517								
3426	2859	566.5								
9633	7057	2576								
15176	12376	2800								
1022	9216	1001.2								
3776	3686	289.2								
15359	11059	4300								
18510	14245	3765								
14529	13574	7549								
10698	0	10698								
4997	4997	0								
14333	12452	1881								
13381	12452	1409								
15119	12452	2607								
9251	7516	1715								
5254	5254	0								
15227	12943	2284								
7879	7860	19								
1545	571.3	973.7								
10746	9141	1606								
7425	7144	281.7								
8303	4880	1184								
14296	0	14296								
15380	14245	634.4								

Note: Rare species were excluded from the analysis, with only species that exceeded 5% within all sampled plots (collectively) included. Also, all species that did not fit into a plot group were removed from this table. A full species list can be found in E1.