



Light availability and phorophyte identity drive epiphyte species richness and composition in mountain temperate forests

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ABSTRACT

Bryophytes and lichens are the most species-rich groups of epiphytes in temperate forests. They colonise different tree species that create a wide variety of microhabitats, and conditions in these microhabitats are modulated by different factors. We assessed drivers that create and maintain epiphyte species richness and diversity of bryophytes and lichens along tree species composition gradients. We hypothesised that tree species composition influences the diversity of lichens and bryophytes. The study was conducted on 31 plots along the Kudowski Potok River (SW Poland). Each plot was a 500 m² circle ($r = 12.62$ m), along the banks of the stream. These sites are among the best-preserved remnants of a mountain landscape with a high diversity of forest types, representing a transition from the planted *Picea abies* secondary communities to broadleaved forests (potential natural vegetation). We analysed the tree species composition gradient using PCA, and we measured diffuse light availability. We assessed differences in epiphyte species richness among tree species using generalized linear mixed-effects models and species composition gradients of epiphytes using redundancy analysis. We found that tree species composition and light availability affected the composition of both bryophyte and lichen species. Moreover, lichen and bryophyte species richness were positively correlated. Broadleaved trees such as *Acer pseudoplatanus* and *Fraxinus excelsior* clearly increase the number of epiphytic bryophytes and lichen species in spruce stands. Deciduous trees left in management forests serve as a reservoir for epiphytic bryophytes and lichens. Our results indicate the importance of refuges composed of diverse deciduous trees that increase the biodiversity in commercial forests.

1. Introduction

The bryophytes and lichens that grow on trees are an important component of forest biodiversity, and in temperate forests, they form the main epiphytic assemblages (Barkman, 1958; Leuschner and Ellenberg, 2017; Rose, 1992). Epiphytic diversity and composition of bryophytes and lichens is affected by different factors from natural to anthropogenic, proceeding at different scales (e.g. Frego, 2007; Gustafsson and Hallingbäck, 1988; Király et al., 2012; Nascimbene et al., 2014; Paillet et al., 2010; Sales et al., 2016). At the tree level, identity of the tree species is crucial for epiphytic colonisation, since for numerous bryophytes and lichens trees are the only growth substrates, including for

very rare, endangered and ancient forest relic species, obligatorily connected with different tree species (e.g. Barkman, 1958; Brunialti et al., 2010; Cieśliński et al., 1996; Wierzcholska et al., 2018).

Studies under different environmental conditions revealed the role of host tree species on the composition of epiphytic communities (e.g., Jüriado et al., 2009; Thor et al., 2010; Király et al., 2012; Benítez et al., 2018), which is mainly related to host traits such as chemical and physical characteristics of the bark (Gustafsson and Eriksson, 1995; Jüriado et al., 2009; Fritz and Heilmann-Clausen, 2010; Benítez et al., 2018). Trees have also a wide variety of microhabitats – the specific niches on the trees known as TreMs (Tree-related microhabitats; Kraus et al., 2016; Larrieu et al., 2018), and conditions in these microhabitats

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are modulated by light intensity, relative humidity, and the proximity of other trees.

At the stand level, forest structure, such as diversity of tree species, age of trees and diversity of ages, as well as canopy structure, plays a crucial role in shaping the species composition of epiphytes (Esseen and Ekström, 2023; Felton et al., 2010; Hofmeister et al., 2015; Király et al., 2012; Mežaka et al., 2012). Thus, forests with different tree species composition harbour diverse assemblages of bryophytes and lichens (Király et al., 2012; Nascimbene et al., 2014). Among the main abiotic factors, the strongest influence on composition of epiphytes is light, which modulates the occurrence of light demanding and shade-tolerant species (Esseen and Ekström, 2023; Friedel et al., 2006; Jagodziński et al., 2018; Marschall and Proctor, 2004). Canopy structure, more or less openness, shapes access to light and also water availability, from which lichens and bryophytes benefit, as they are poikilohydric organisms (Marschall and Proctor, 2004). Despite the fact that both bryophytes and lichens grow as epiphytes, they exhibit distinct morphological, anatomical, and physiological characteristics (Ligrone et al., 2000; Purvis, 2000), which allows them to occupy different trees and microhabitats within a single tree in the forest community (Barkman, 1958; Ellis, 2012; Ódor et al., 2013).

Patterns of the composition of bryophyte and lichen diversity are known from well-preserved and semi-natural forests, but in most cases have been studied separately (Ellis, 2012; Lubek et al., 2018; Lubek et al., 2020; Nascimbene et al., 2013; Zin and Obidziński, 2011). Therefore, studies covering both bryophyte and lichen epiphytes, using the same methods allowing for quantitative comparisons, are few (Friedel et al., 2006; John and Dale, 1995; Loppi et al., 1999; Rose, 1992). Numerous studies have focused on sites altered by human activity, but still assessing only one epiphytic group (Bardat and Aubert, 2007; Hofmeister et al., 2016; Jagodziński et al., 2018; Nascimbene et al., 2013; Ódor et al., 2013; Wierzycholska et al., 2018). The co-occurrence of bryophytes and lichens is best recognised within primary forests (Cieśliński et al., 1996), and in the same type of forest with varying degrees of anthropogenic influence, as reported by Friedel et al. (2006). To date, there is scarce data on the relationships of both bryophytes and lichens along gradients of human-transformed mountain forest stands. Therefore, we conducted our research in mature mountain forests that, as a result of former intensive management, have been afforested (*Picea abies* predominance), and natural forests: such as beech forests (*Fagus sylvatica* dominated forests) and riparian to ravine forests (*Acer pseudoplatanus* and *Fraxinus excelsior* mixed forests) that constitute small enclaves of potential vegetation. The novelty of our study is that it covers the explanations for how habitat diversity in mountain regions, tree species effects and environmental factors, affect bryophyte and lichen species pools in temperate ecosystems. In many biological aspects, both groups are similar, but they also differ in their choice of microhabitats with different parameters within the same forest habitat. These two groups of epiphytes are crucial in forest ecology and the results of our study can serve as a useful tool for monitoring the effects of forest management and conservation. Therefore, we assessed the species richness and composition of epiphytic bryophytes and lichens along a gradient of forest communities, to explore niche overlap. Study on plant populations has gained increasing significance, particularly within the contemporary framework of environmental transformations (Chang, 2023). The utilization of presence/absence sampling emerges as a valuable and comparatively uncomplicated approach for the surveillance of the condition and dynamics of plant communities (Gozé et al., 2023).

Our aim was to assess the species richness and composition of epiphytic bryophytes and lichens along a tree species composition gradient with a similar level of humidity (all plots at the same distance from the stream). We hypothesised that (a) the species composition changes, and richness of bryophytes and lichens increases, along the forest gradient from secondary stands to remnants of natural forests, and (b) light affects the species composition and richness of bryophytes and

lichens differently.

2. Methods

2.1. Study area

We conducted our study in valleys of three streams in the Stołowe Mountains National Park (SMNP; SW Poland; 50.47°N, 16.35°E): Kudowski Potok River and its two main tributaries (Fig. 1). These sites are among the remnants of a mountain landscape with a high diversity of forest types, representing a transition from the planted *Picea abies* secondary communities through broadleaf forests dominated by *Fagus sylvatica* (potential natural vegetation) to riparian and ravine forests with *Acer* spp. and *Fraxinus excelsior* (Dyderski et al., *under review*). Since the 19th century *P. abies* has been widely cultivated as a fast-growing tree producing valuable timber. Such forest management caused an extensive elimination of deciduous species (e.g. beech) and the mass introduction of *P. abies* plantations (Barzdajn et al., 1999; Caudullo et al., 2016; Felton et al., 2010; Naudts et al., 2016). The average age of the forest within the plots is 85 years (Table A1). The anthropogenic effects led to long-term changes in vegetation, which we can still observe nowadays within the lower part of the mountain landscape. In the investigated area of SMNP, due to their inaccessibility, these forests have been less transformed than many other forests in low-elevation mountains, and we can observe the transition from anthropogenic to natural forest communities.

Along three streams, we systematically established 31 study plots, every 200 m of stream course (Fig. 1), with the exception of three sites: two with young forest patches and one dominated by *Alnus glutinosa*, which had outlying (significantly different) tree species composition, resulting in the inability to compare them with other plots that had appropriate representativeness.

The research plots were located in forest communities at elevations ranging from 449 m to 717 m above sea level (Table A1), with a temperate climate (mean annual temperature of 8.6 ± 0.2 °C and mean annual precipitation of 603.5 ± 41.0 mm measured in 2010–2020 in Kłodzko). The bedrock in the study areas is usually turonian marls and sandstones (Migoń et al., 2011), that supported the development of cambisols, gleysols, and luvisols (Kabała et al., 2011). The research sites represented a transect gradient along the type of forest from spruce monocultures (15 plots), to remnants of natural forest, which in this area are represented by beech forest (8 plots), and ravine forest characterised by ash-sycamore (8 plots).

2.2. Data collection

Each plot was a 500 m² ($r = 12.62$ m) circle, tangent to the stream course; each plot investigated had the same distance from the stream (adherent). In each plot, we measured the diameter at breast height of all living trees and calculated their biomass using allometric models. As stand species composition continuously shifted from spruce to beech to ash-sycamore forests, without clear distinction into forest types, we decided to reflect vegetation continuity (Austin, 2013) using principal components as a multivariate analysis. We used these measurements for the assessment of the tree species composition gradient using Principal Components Analysis (Dyderski et al., *under review*; Fig. 2), with tree species biomass as species scores and study plots as sites (Table A2). We separately included living and dead trees, as their proportions varied across the study plots. Based on PCA results we identified the PC1 axis as a complex variable reflecting transition from spruce-dominated forests through forests with decreasing shares of spruce and increasing beech shares, to stands with the highest shares of ash and sycamore (Dyderski et al., *under review*).

We collected data regarding the forest type (stand) and phorophyte (host tree) species within the plots, and bryophytes and lichens that grow on each species of phorophyte in the plots. We analysed the base

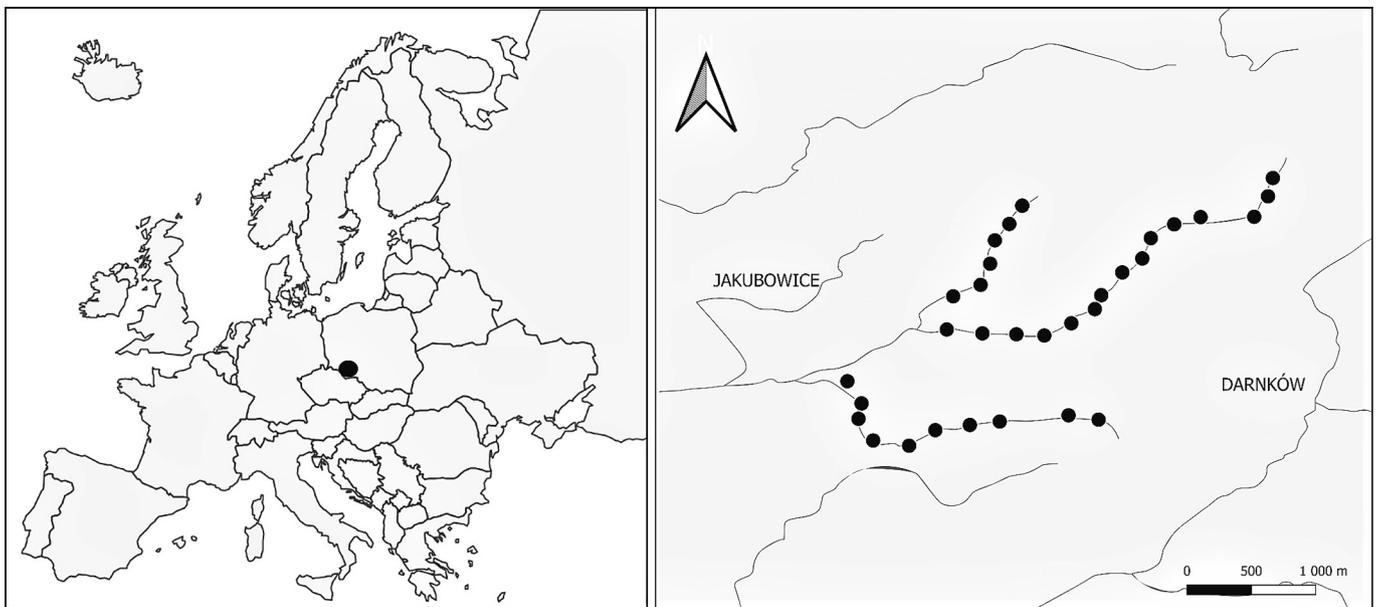


Fig. 1. The study area, including 31 plots situated along three streams in the Stolowe Mountains National Park (SW Poland).

and trunk of each living tree up to 2 m height. We determined bryophyte species based on field and microscopic examination. Bryological nomenclature follows Hill et al. (2006) for mosses and Szwejkowski (2006) for liverworts. We identified lichens in the field, and if necessary we collected samples for anatomical and chemical analyses in the laboratory. The nomenclature of lichen species follows Index Fungorum (2023).

We also measured diffuse light availability using a LAI-2270 device (Li-Cor Inc., Lincoln, NE, USA; <http://www.licor.com>). The LAI-2270 measures photon flux density at two sites – in the study site and a reference site (open-sky area) and we used the study site/open sky ratio as diffuse non-interceptance (DIFN), an approximation of light availability (Machado and Reich, 1999). As DIFN is the ratio of two measurements with the same units [$\text{mmol m}^{-2} \text{s}^{-1}$], it is dimensionless (Table A2). That method has been widely used as an approximation of diffusive light availability in numerous studies (Jagodziński et al., 2019; Machado and Reich, 1999; Parker, 1997). Within each plot, in mid-summer, when the canopy leaf area was at its peak, we sampled DIFN at a height of 0.5 m by eight series of ten measurements at randomly selected points.

2.3. Data analysis

We conducted all analyses using R software (R Core Team, 2022). Due to continuity of stand species composition we decided to not divide it into categories, but instead, to reduce the number of variables describing tree species composition using Principal Components Analysis (PCA). In PCA we used each plot as a ‘site’ and the living or dead biomass of each species as a variable (Dyderski et al., *under review*; Fig. 2). We conducted PCA using the vegan package (Oksanen et al., 2016). Before analyses we centred and scaled variables using the `stats::scale()` function.

We explored the species composition of epiphytes recorded on all individuals of particular tree species within study plots using ordination. There, records of all epiphytes noted on particular tree species within the study plot served as a single observation. To assess the effects of tree species composition and DIFN on bryophyte and lichen species composition we used Redundancy Analysis (RDA), implemented in the vegan package (Oksanen et al., 2016), despite longer gradients of species composition, causing small artefacts due to the presence of species-poor samples. We tested alternative ordination methods that did not provide

ecologically interpretable outcomes or, in the case of multidimensional scaling, had stress values that were too high. We used two environmental constraints: tree species composition (PC1, Fig. 2) as a quantitative index of stand species composition and DIFN as a proxy of light availability. We tested the parsimony of RDA against a null model (unconstrained ordination, i.e. principal components analysis) based on Akaike’s Information Criterion (AIC). We tested the importance of constraints using the permutation analysis of variance (PERMANOVA).

We assessed effects of host trees and DIFN on species richness using Generalized Linear Mixed-Effects Models (GLMMs) assuming the Poisson distribution of dependent variables. We developed models using the lme4 package (Bates et al., 2015) and the lmerTest package (Kuznetsova et al., 2017) to provide statistical significance of variables using z-values. For these models we used only phorophytes present for both bryophytes and lichens in at least five plots, i.e. *A. platanoides*, *A. pseudoplatanus*, *F. sylvatica*, *F. excelsior*, and *P. abies*. Firstly, we ensured a lack of collinearity using variance inflation factors, and we developed full models, including host tree species and DIFN. Then we reduced the models based on AIC. We also provided AIC0 – AIC of models with intercept and random effects only. We validated models ensuring a lack of overdispersion and inspecting distributions of residuals using diagnostic formal tests implemented in the DHARMa package (Hartig, 2021): dispersion test, outlier test, and residual normality test. We evaluated differences among host tree species assuming a constant (mean) value of other predictors using Tukey posteriori tests implemented in the emmeans package (Lenth, 2019). We also calculated two coefficients of determination: marginal (R2m) and conditional (R2c), which express the amount of variance explained by fixed-effects only and by both fixed and random effects jointly, respectively (Nakagawa and Schielzeth, 2013). We used the MuMIn package (Bartoń, 2017) for these calculations.

We assessed how the richness of one group affected the second using the same framework to evaluate relationships between bryophytes and lichens, with the interaction with phorophyte species. To obtain effect sizes of particular variables we calculated the marginal responses of models, i.e., predicted richness assuming a constant (mean) level of all remaining predictors, using the ggeffects package (Lüdtke, 2018).

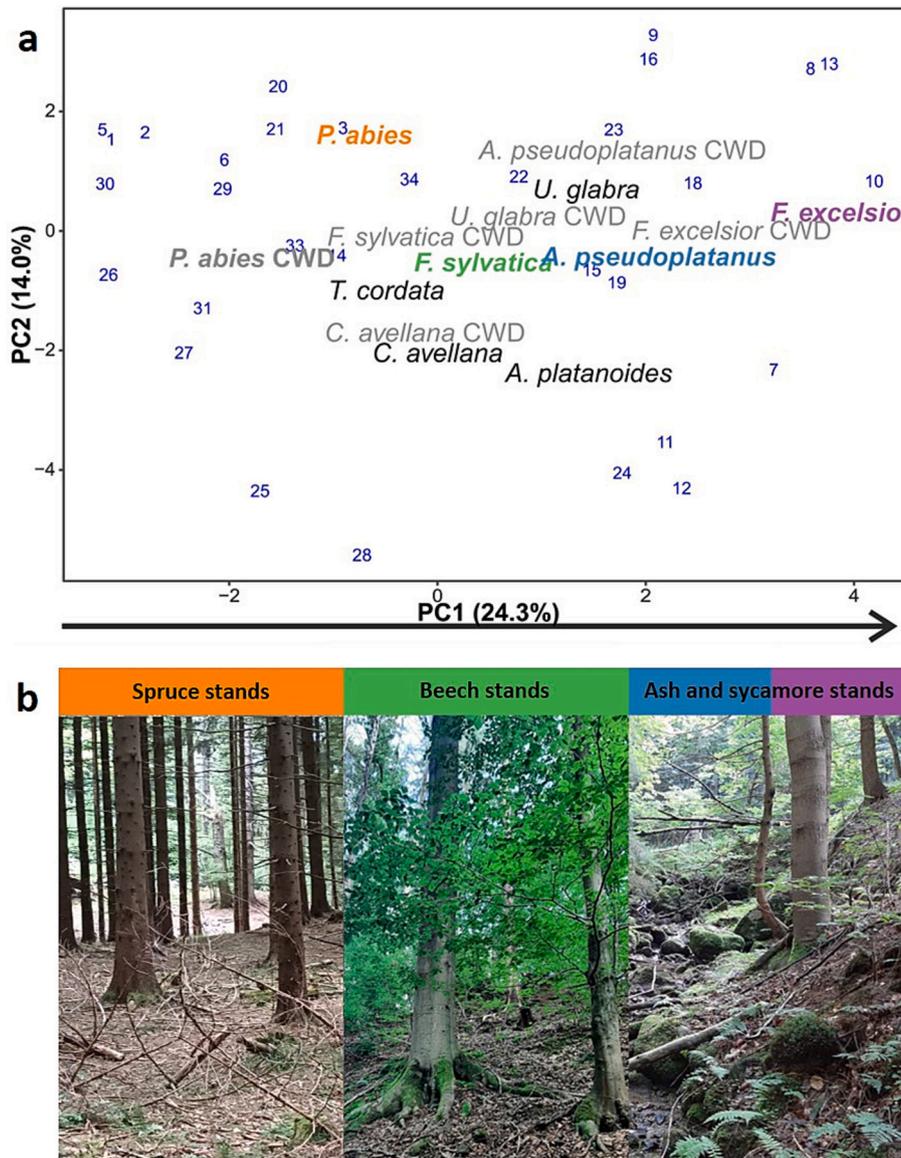


Fig. 2. Result of Principal Components Analysis of tree species composition (a) and photographical representation of the PC1 gradient (b). Blue numbers in (a): plot numbers, black names in (a): represent other important live tree species, tree species names in color in (a): represent the dominant live species (as shown by colors at the top of part b) – PCA scores of living trees, and grey names represent dead trees – PCA scores of dead trees. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

3. Results

3.1. Tree species composition affects the species composition of bryophytes and lichens

RDA revealed that both stand species composition and DIFN affected bryophyte and lichen species composition (Table 1). For bryophytes, constraints (i.e. DIFN and tree species composition) explained 7.3% of variability, and the first two axes explained 21.5% while for lichens, 6.7% and 27.1%, respectively. For bryophytes, tree species composition and DIFN were correlated with the main compositional gradients. Along the RDA1 axis bryophyte communities shifted from coniferous stands of *P. abies* through stands enriched by *F. sylvatica*, *Larix decidua*, and *Betula pendula* to broadleaf stands of *Acer pseudoplatanus*, *Acer platanoides*, *F. excelsior*, and *Tilia cordata*. Tree species with a low bark pH (Fig. 3a) such as *P. abies*, *B. pendula*, and *F. sylvatica*, were concentrated in the left side of the diagram, while those species with neutral to alkaline pH bark were on the right. Furthermore, epiphytes in the upper left part of the

Table 1

PERMANOVA test results for the influence of environmental constraints on epiphyte species composition in the RDA reduced space. Stand PC1 – a measure of stand species composition (low values of PC1 indicate spruce-dominated, intermediate – beech dominated, high values – ash-sycamore dominated, Fig. 2), DIFN – a proxy for light availability.

Variable	Df	Variance	F	Pr(>F)
Bryophytes				
DIFN	1	0.1737	4.7267	<0.001
Stand PC1	1	0.1381	3.7592	<0.001
Residual	107	3.9316	–	–
Lichens				
DIFN	1	0.1151	6.0809	<0.001
Stand PC1	1	0.0559	2.9531	<0.001
Residual	126	2.3860	–	–

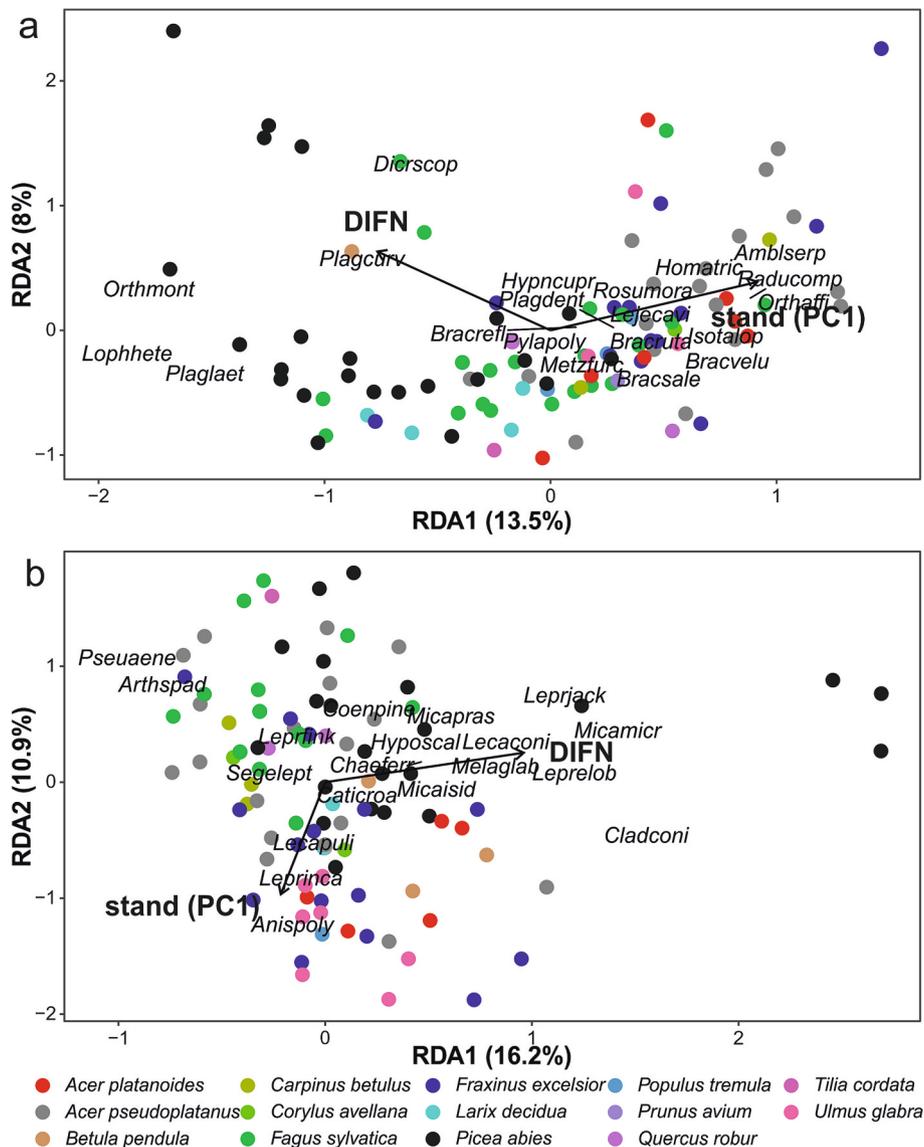


Fig. 3. Redundancy analysis of the epiphytic bryophyte (a) and lichen (b) communities. Each dot represents a single species in a particular study plot. PC1 – a measure of stand species composition (low values of PC1 indicate – spruce-dominated, intermediate – beech dominated, high values – ash-sycamore dominated, Fig. 2), DIFN – a proxy for light availability.

graph showed a positive correlation with high DIFN. Four stands with *P. abies* (well separated from other stands, in the upper left; Fig. 3a) were positively correlated with the most light-demanding (DIFN) epiphytes. RDA1 presents a compositional gradient that is based on the pH of the bark of the tree species and the light requirement. The left part of the diagram shows acidic hosts which attract poor and specific flora including invasive bryophytes like *Orthodontium lineare*. These stands were occupied primarily by acidophilus bryophytes such as *Dicranum scoparium*, *Plagiothecium curvifolium*, and *Dicranodontium denudatum*. The middle part of the graph is occupied by *F. sylvatica* stands with admixtures of *P. abies* and *L. decidua*. These hosts are characterised by common forest species like *Ortodicranum montanum*, *Lophocolea heterophylla*, and *Ptilidium pulcherrimum* that are observed within other types of forest stands. From the middle towards the right part of the graph, there is a predominance of broadleaved tree species. This transition shows constant and continuous compositional gradients along the RDA1 axis with a decrease of DIFN. The right part of the graph concentrates tree species with neutral to alkaline bark, such as *A. pseudoplatanus*, *A. platanoides*, *F. excelsior*, and *T. cordata* with decreasing shares of widespread *F. sylvatica*. These broadleaved stands were occupied by

bryophytes with strong affiliations from neutral to basic tree bark, such as *Metzgeria furcata*, *Radula complanata*, and *Orthotrichum affine*.

For lichens, the main compositional gradient of RDA was the DIFN gradient, mainly driven by three plots with *P. abies*, with lower variability along the tree species composition gradient and among tree species. Species such as *Cladonia coniocraea*, *Lepraria jackii*, *L. elobata*, *Micarea micrococca*, and *Lecanora conizaeoides*, on the right side of the diagram (Fig. 3b), were strongly associated with greater access to light and were simultaneously associated with the acidic bark of *P. abies*. Their occurrence was mainly associated with strongly overexposed spruce stands. Similarly, species such as *Melanelixia glabrata*, *Chaenotheca ferruginea*, *Coenogonium pineti*, *Hypocenomyce scalaris*, and *Micarea prasina* were located in the ordination space related to high DIFN, and were at the same time dependent on the presence of *P. abies* in the stand. These lichens grew mainly in mixed stands with *P. abies*, *F. sylvatica*, and *A. pseudoplatanus*. The group of species that prefer the most shade, in the graph on the left, were lichens such as *Diarthonia spadicea*, *Pseudosagedia aenea*, and *Segestria leptalea*. These species preferred the hard bark of the alkaline pH reaction of trees such as *F. sylvatica* and at the same time were associated with beech stands with admixtures of other broadleaved

trees, e.g., *Carpinus betulus* and *A. pseudoplatanus*. Analysing the influence of tree species composition on the compositional diversity of lichen species, a clear transition was marked from lichens, e.g. *Lepraria jackii* and *Micarea micrococca*, occurring exclusively in spruce stands or stands with a higher proportion of spruce, via the group of lichens, e.g. *Diatrionis spadicea*, *Pseudosagedia aenea*, which occurred in forests dominated by *F. sylvatica* and *A. pseudoplatanus*, and then to a group of lichens preferring deciduous forests with *T. cordata*, *F. excelsior*, and *A. pseudoplatanus*, e.g. *Anisomeridium polyporii*, *Lepraria incana*, *Lecanora pulicaris*, and *Lecania croatica*.

3.2. Drivers of epiphyte species richness

The final model of bryophyte species richness consisted of host tree species identity and DIFN (AICc = 457.6, AICc₀ = 476.7, R_m² = 0.260, R_c² = 0.307). An increase of DIFN from 0.01 to 0.11 increased the richness of bryophyte species from 5.1 to 10.4 (Table 2, Fig. 4). We found the highest estimated species richness of epiphytic bryophytes on *F. excelsior* (7.9 ± 0.8) and *A. pseudoplatanus* (8.6 ± 0.7), while the lowest on *F. sylvatica* (4.9 ± 0.4) and *P. abies* (5.4 ± 0.5; Fig. 3). The final model of lichen species richness consisted of host tree species identity and DIFN (AICc = 436.8, AICc₀ = 453.5, R_m² = 0.367, R_c² = 0.415). An increase of DIFN from 0.01 to 0.11 increased the richness of lichen species from 3.7 to 12.7 (Table 2, Fig. 4). The estimated lichen species richness was the lowest on *F. sylvatica* (3.1 ± 0.4) and the highest on *F. excelsior* (5.4 ± 0.7) and *A. pseudoplatanus* (5.3 ± 0.5) (Fig. 4).

We found positive relationships between epiphytic lichen and bryophyte species richness (Table 3, Fig. 5), accounting for host tree species identity. However, host tree species identity was statistically insignificant, according to the posteriori pairwise test. Lichen species richness (AICc = 391.5, AICc₀ = 439.0, R_m² = 0.404, R_c² = 0.465) increased with increasing bryophyte species richness – in plots with three bryophyte species estimated lichen species richness was 2.3, with ten – 5.9, and with 15–11.5 (Fig. 5).

4. Discussion

Our study revealed differences in species composition between bryophytes and lichens on phorophytes along the forest gradient. The lowest species richness was observed in secondary spruce forests, which subsequently increased in natural beech forests, reaching its highest value in ash-sycamore stands. Despite the high frequency of spruce in most study plots, we found that presence of deciduous trees, such as *F. excelsior* and *A. pseudoplatanus*, clearly increased the diversity of

Table 2

Generalized mixed-effects linear models of epiphyte species richness assuming the Poisson distribution.

Variable	Estimate	SE	z	P
Bryophytes (random effects SD: plot nested in river = 0.100, river <0.001)				
(Intercept)	1.668	0.164	10.149	<0.001
(Intercept)	1.632	0.172	9.480	<0.001
DIFN	0.065	0.030	2.135	0.033
host tree = <i>Acer pseudoplatanus</i>	0.386	0.183	2.108	0.035
host tree = <i>Fagus sylvatica</i>	-0.171	0.188	-0.908	0.364
host tree = <i>Fraxinus excelsior</i>	0.309	0.192	1.605	0.109
host tree = <i>Picea abies</i>	-0.064	0.189	-0.340	0.734
Lichens (random effects SD: plot nested in river = 0.198, river <0.001)				
(Intercept)	1.195	0.176	6.774	<0.001
DIFN	0.123	0.034	3.659	<0.001
host tree = <i>Acer pseudoplatanus</i>	0.219	0.187	1.176	0.239
host tree = <i>Fagus sylvatica</i>	-0.295	0.197	-1.502	0.133
host tree = <i>Fraxinus excelsior</i>	0.248	0.196	1.265	0.206
host tree = <i>Picea abies</i>	0.051	0.190	0.266	0.790

epiphyte species. Here *A. pseudoplatanus* and *F. excelsior* hosted the highest epiphytic bryophyte and lichen richness – up to 76% of the epiphytic bryophytes, and 67% of recorded lichen species, respectively. *Fraxinus excelsior* and *A. pseudoplatanus* are well known sources of microhabitats for many specialised groups of organisms (Cundall et al., 1998; Ellis et al., 2013; Jönsson and Thor, 2012; Lúbek et al., 2019; Mitchell et al., 2016; Moning et al., 2009). In addition, we found other deciduous trees (e.g. *Acer platanoides*) hosted endangered and protected species (e.g. *Orthotrichum lyellii*, *O. pallens*, *Agonimia flabelliformis*, *Arthonia radiata*, and *Naevia dispersa*), exclusively associated with these trees. These phorophytes maintain a plethora of epiphytes and play a crucial role for conservation and dispersion of epiphytes among degraded forest patches. The importance of deciduous trees in the diversity of the epiphytic biota and flora protection in temperate forest was reported in other studies (Mežaka et al., 2012; Thor et al., 2010). That is why tree species stand composition (diverse composition of deciduous trees) has also been highlighted as an important factor shaping epiphytic species diversity within temperate forests of different management regimes (Jagodźiński et al., 2018; Lúbek et al., 2020; Rose, 1992; Thomas et al., 2001; Wierzcholska et al., 2018; Wysocki et al., 2023).

In the case of *F. sylvatica* stands we did not find species diversity of epiphytes to be as high as in ravine and riparian forest. Despite some works pointing to large-diameter living *F. sylvatica*, as a ‘lifeboats’ for lichen species diversity (Hofmeister et al., 2016), in our study, the species richness of lichens was not high. This could be a result of low dendrometric properties of the analysed trees. For bryophytes and lichens we found that *F. sylvatica* had the lowest species richness. However, beech forest composed of diverse tree species (i.e. *P. abies* and *A. pseudoplatanus*) was distinguished by a higher richness of epiphytes than spruce forests.

In our study secondary forests composed of *P. abies* do not comprise the richness of epiphytic species, despite the significant dominance of these trees. These trees are predominantly occupied by facultative epiphytic bryophytes typical of coniferous forest litter, such as *Dicranum scoparium*, *Pohlia nutans*, and *Plagiothecium curvifolium*. Moreover, we observed that the epiphytic bryophytes connected with spruce grow mainly on the basal part of the tree trunk, while lichens, e.g. *Chaenotheca ferruginea*, *Hypocomyce scalaris* and *Lecanora conizaeoides*, inhabit the higher part of the spruce trunk.

Some lichen species are known to be associated with naturally acidic bark of the spruces, and associated with primary mountain spruce forests, which form species-rich assemblages including many threatened species (e.g. Langbehn et al., 2021; Malíček et al., 2019). Our survey did not show species clearly attached to spruce bark. In the spruce forest we observed a lack of obligatory species (that occur only on living trees) among bryophytes, as they are represented by multisubstrate taxa. The same patterns were detected for lichens, which are typical epiphytes that can also grow on decaying wood as epixylic species. This may stem from impoverished stand structure of the investigated forest. Similar results indicating low species diversity of cryptogam epiphytes in transformed monoculture stands were also reported by others (e.g. Felton et al., 2010; Hofmeister et al., 2015; Zin and Obidziński, 2011). Among the spruce forests we detected four markedly distinct plots (outliers) indicating species composition distinctiveness of bryophytes and lichens growing within these plots. These areas were characterised by higher light availability (DIFN) and a specific structure such as the presence of saplings, and lack of young understory trees, with only a few mature trees observed.

We found that, in addition to tree species composition, light intensity (expressed by DIFN) also had an impact on the species diversity of epiphytes. For lichens we found that higher light exposure exhibited a stronger positive correlation with their species richness compared to bryophytes, which also show a positive correlation. That phenomenon is mostly related to the three outlier plots within the secondary spruce forest where DIFN values vary from 0,1 to 0,06, whilst the rest of plots

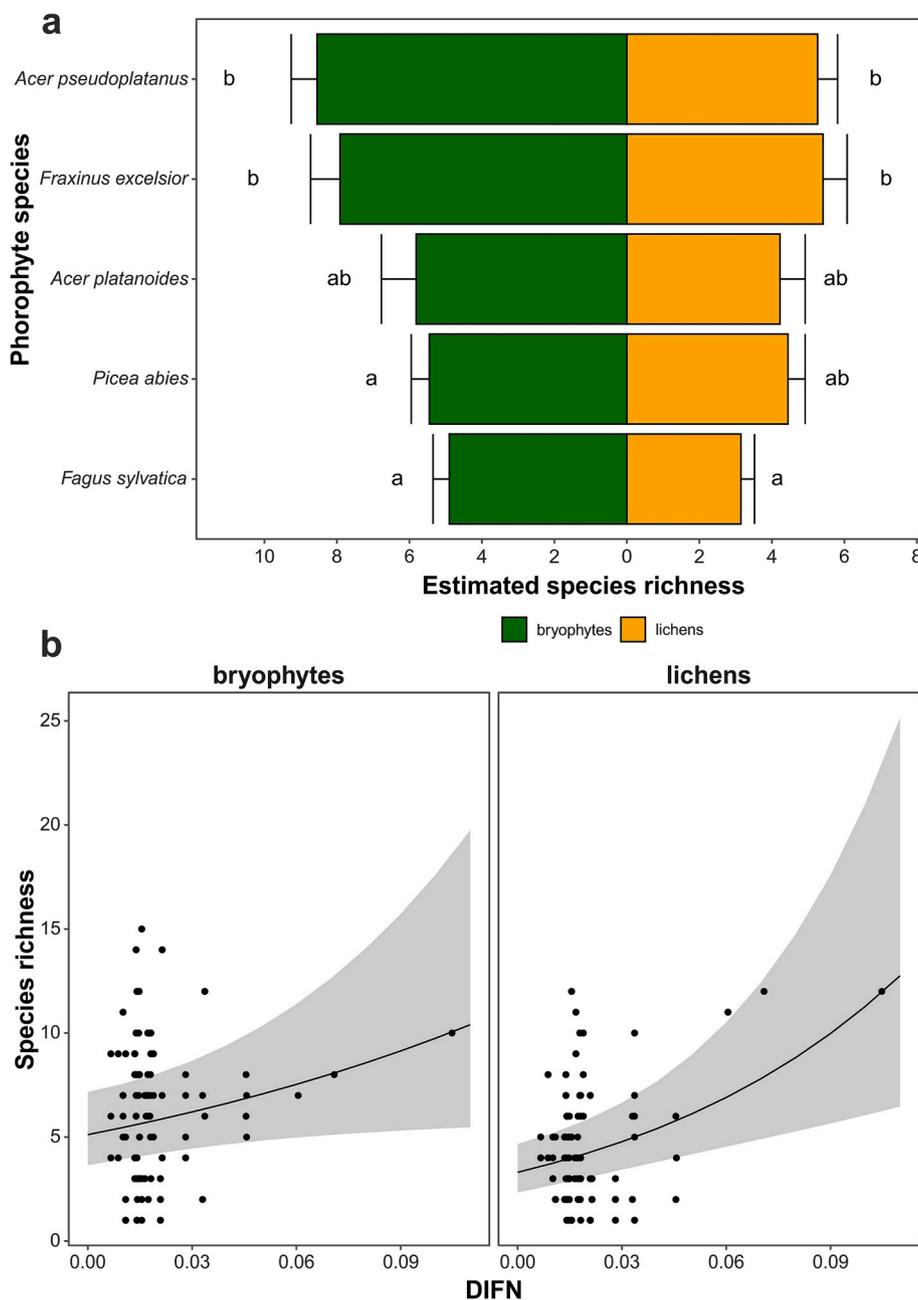


Fig. 4. Epiphyte species richness estimated for host tree species assuming a constant level of DIFN by marginal means (a) and marginal responses of epiphyte species richness to DIFN (b). Species denoted with the same letter in (a) did not differ at $p \leq 0.05$, according to a Tukey’s posteriori test.

Table 3
Relationships between lichen and bryophyte species richness assessed using generalized mixed-effects linear models assuming the Poisson distributions.

Variable	Estimate	SE	z	p
Lichen species richness (random effects SD: plot nested in river = 0.298, river <0.001)				
(Intercept)	0.432	0.261	1.657	0.098
Bryophyte species richness				
host tree = <i>Acer pseudoplatanus</i>	-0.060	0.240	-0.250	0.803
host tree = <i>Fagus sylvatica</i>	-0.051	0.241	-0.213	0.831
host tree = <i>Fraxinus excelsior</i>	0.046	0.247	0.187	0.852
host tree = <i>Picea abies</i>	0.282	0.233	1.210	0.226

vary from 0,04 to 0,006. This was related to the highest canopy openness, lack of young trees and presence of single mature trees. Despite the fact that spruce stands have been reported to have a low bryophyte and lichen species richness, light access increased the number of epiphyte species in these forests. The same result that light has shaped bryophyte and lichen associations was confirmed in previous studies (Friedel et al., 2006; Hilmo et al., 2009; Nirhamo et al., 2021; Ódor et al., 2013; Osyczka and Myśliwa-Kurdziel, 2023; Pharo and Vitt, 2000).

Based on our study the high species diversity of epiphytic bryophytes increases the diversity of epiphytic lichens, and vice versa. Although in ecology (Kerr, 1997), some approaches to evaluate the biodiversity and fine-scale marginal habitats for threatened species, like: vascular plants, bryophytes and birds (Wuczyński et al., 2014) and also for other groups, like: lichens, bryophytes, macrofungi and invertebrates (Hofmeister et al., 2019) have been proposed. According to Pakeman et al. (2022),

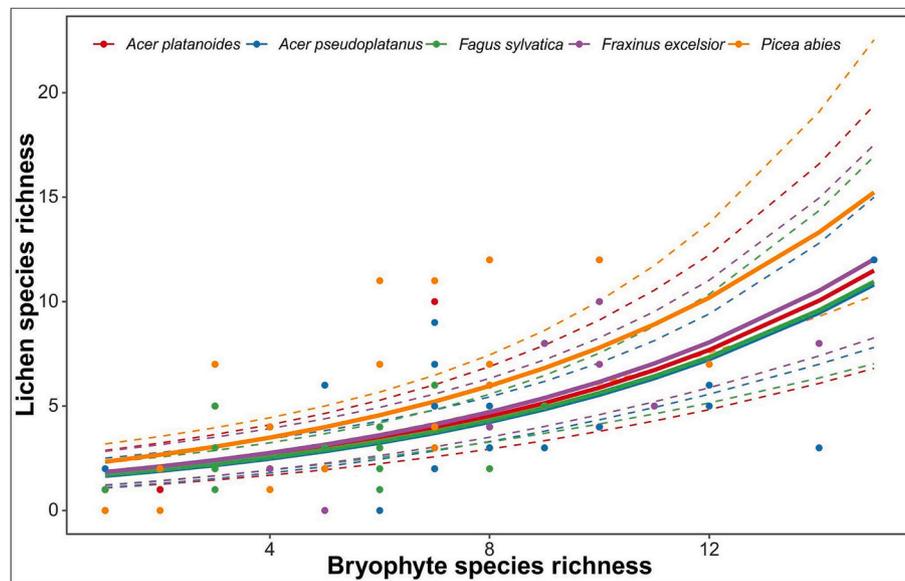


Fig. 5. Marginal responses of the relationship between lichen and bryophyte species richness, mediated by phorophyte species, derived from generalized mixed-effects linear models assuming Poisson distributions (Table 3). Solid lines indicate marginal responses, dashed lines – 95% confidence intervals.

studies on bryophytes and lichens show that in some habitats these groups represent the same patterns in species richness dependencies. In diverse temperate forest stands both groups of epiphytes can exploit accessible niches from acidic to neutral tree bark, and from overexposed sites to moderate and shaded ones. Our results indicate that high species diversity of epiphytic bryophytes can be a good objective criterion indicating high species diversity of epiphytic lichens in the mixed forests. This could be important in practice for the quick designation of areas for protection (see also [Oliver and Beattie, 1993](#)), since the lack of adequate tools to quickly identify the full biodiversity of an area can lead to abandonment of the decision to protect it and the loss of a valuable area.

We have shown that the heterogeneity of habitats that are created by a mixed stand of trees significantly affects the species richness of epiphytes. Environmental heterogeneity stands out as a principal factor linked to biodiversity, as regions characterised by pronounced environmental diversity have the potential to accommodate a greater number of species. This is attributed to the increased availability of niches in such environments. These relationships have been confirmed in other studies on species richness estimation ([Rocchini et al., 2010](#)).

5. Conclusions

Our study revealed that the composition of the stand and the availability of light shape the composition and richness of the epiphytic species. Any enrichment of spruce stands with deciduous trees significantly increases the species richness of epiphytic bryophytes and lichens. We claim that deciduous trees in spruce-dominated stands, serve as a reservoir for epiphytic bryophytes and lichens. In forests, the preservation of high species diversity of trees increases the chances of preserving species diversity of epiphytes. Deciduous trees left in management stands with a high proportion of conifers can be a source of propagules for faster recovery of the epiphytic flora and biota. Therefore, it is important that in managed forests or other human-affected forests, the high species diversity of phorophytes is maintained as much as possible, as they form specific microhabitats that allow a high species diversity of epiphytes. As a novelty we stated that species richness of both groups is positively correlated. When studying the species diversity of epiphytic bryophytes or lichens and assessing their species richness, e.g. in terms of the need for an area for conservation, in the absence of access to a suitable specialist like a bryologist or

lichenologist, it is possible to focus on one epiphytic group (bryophytes or lichens), as the result of one group could potentially indicate the result of the other group.

CRediT authorship contribution statement

Sylwia Wierzcholska: Conceptualization, Data curation, Investigation, Methodology, Supervision, Writing – original draft, Writing – review & editing. **Anna Łubek:** Conceptualization, Data curation, Investigation, Methodology, Writing – original draft, Writing – review & editing. **Marcin K. Dyderski:** Conceptualization, Formal analysis, Investigation, Methodology, Validation, Visualization, Writing – original draft, Writing – review & editing. **Paweł Horodecki:** Investigation, Methodology, Writing – original draft, Writing – review & editing. **Mateusz Rawlik:** Investigation, Methodology, Writing – original draft, Writing – review & editing. **Andrzej M. Jagodziński:** Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Writing – original draft, Writing – review & editing.

Declaration of competing interest

We declare no conflict of interest.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecoinf.2024.102475>.

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