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Invasive *Prunus cerasifera* Ehrh. hosts more lichens than native tree species – does quantity reflect quality?

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ABSTRACT

The impact of nonnative trees on epiphytic lichen diversity is one of the most significant knowledge gaps in invasion ecology. One notable invader, *Prunus cerasifera* Ehrh., has been identified as a rapidly spreading nonnative into forest ecosystems, potentially influencing the diversity of epiphytic lichens. The objective of this study was to determine whether the taxonomic and functional diversity of lichens colonizing *P. cerasifera* bark differs from that observed on native trees composing early successional oak-hornbeam forest. We conducted our study in the surroundings of the Białowieża National Park by surveying epiphytes inhabiting four native trees (*Carpinus betulus*, *Tilia cordata*, *Quercus robur*, and *Populus tremula*), and non-native *P. cerasifera*, varying in diameter at breast height (DBH). Using ordination and linear regression, we found that *P. cerasifera* hosted the highest taxonomic and functional diversity of lichens. For *Q. robur* and *T. cordata* we observed a positive relationship between increasing DBH and lichen taxonomic and functional diversity. Similarly, the epiphyte richness increased with DBH in *P. cerasifera*, but we did not find any relationship between lichen functional diversity and DBH. This suggests that even small *P. cerasifera* individuals can support a high epiphyte functional diversity, surpassing that of native trees. We provided novel evidence of invasive tree impact on the least analysed group of dependent organisms, broadening functional and phylogenetic range of assessed nonnative trees. In this context, *P. cerasifera* appears to play a specific function as a host of particular importance for restoring epiphytic biota in transformed ecosystems.

1. Introduction

Epiphytic lichens are an essential component of forest ecosystems and constitute a crucial element of their proper structural integrity (Brunialti et al., 2010; Ellis, 2012; Schievenin et al., 2024). Their occurrence and diversity depend on the forest environment, like the type of forest community, quality, and internal structure (Łubek et al., 2020; Marini et al., 2011). The ecological and spatial complexity of a forest, along with a tree species diversity, determines the range of microhabitats for epiphytic organisms. Thereby, these factors enhance epiphytes taxonomic (Wierzcholska et al., 2024) and functional diversity (Felton et al., 2010; Łubek et al., 2020, 2019). The number of factors influencing the species composition of epiphytic biota is significantly affected by external conditions, particularly the intensity of human impacts. The most severe negative effects are observed in cases of forest transformation associated with intensive forestry practices, timber extraction, and pollution (Friedel et al., 2006; Matos et al., 2015). Anthropogenic global change has recently accelerated the transformations in the species composition of epiphytic biota, leading to the decline of some lichen species (Herk et al., 2002; Łubek et al., 2018; Marini et al., 2011) and the expansion of others (Herk et al., 2002; Rubio-Salcedo et al., 2017).

Invasive tree species are one of the biggest threats to biodiversity and ecosystem functioning (Dyderski and Jagodziński, 2021; Roy et al., 2024; Wohlgemuth et al., 2022). Broadleaved invasive tree species are increasingly colonizing native forests, and their spread will intensify under a changing climate (Camenen et al., 2016; Puchałka et al., 2023). The spread of invasive trees significantly contributes to the displacement

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of native tree species, alterations in habitat conditions, depletion of forest flora, and a biodiversity reduction (Bury and Dyderski, 2025; Dyderski and Jagodziński, 2021; Gentili et al., 2019; Slabejová et al., 2023; Stanek et al., 2024). However, their impact on various components of ecosystems is unevenly recognized. Most studies focused on invasive tree species impact on vascular plants, microorganisms, and arthropods, while lichens remain the least recognized group (Wohlgemuth et al., 2022).

Two recent literature reviews (Vilà et al., 2024; Wohlgemuth et al., 2022) revealed only a few examples of studies documenting impacts on lichen species richness or diversity, comparing native and non-native trees. Three studies assessed the effects of *Robinia pseudoacacia* in Italy. These studies found higher lichen species richness in non-native forests than in native oak forests, but most of the species in *R. pseudoacacia* forests were those tolerating air pollution and eutrophication, indicating a shift in community composition (Nascimbene and Marini, 2010). Comparing successional stages of *R. pseudoacacia* forests with native forests, Nascimbene et al. (2015), (2012) found lower species richness and a higher proportion of nitrophilous species in invasive species stands, revealing that even mature *R. pseudoacacia* forests did not recover their epiphytic lichen community. That way *R. pseudoacacia* led to a decrease in lichen β-diversity and contributed to biotic homogenization (Nascimbene et al., 2015). In contrast, a comparison of the lichen composition of native laurel forests and introduced groves of *Castanea sativa* in the Canary Islands revealed that introduced species hosted a similar number of species, but more species with high conservation values (González-Montelongo and Pérez-Vargas, 2021). A comparison of *Eucalyptus globulus* plantations with native oak and pine forests in Spain (Calviño-Cancela et al., 2013; González-Montelongo and Pérez-Vargas, 2019) revealed lower lichen species richness and diversity in stands of invasive species.

Besides the Mediterranean region, only two studies compared native and non-native trees in terms of lichen diversity in the temperate climate zone. In Sweden, Gustafsson et al. (2023) found that invasive *Quercus rubra* trees host a similar number of species as native oaks, but more species were exclusive to native phorophytes, and lichen communities of *Q. rubra* were more homogenous than those of native oaks. In Germany, Möller et al. (2021) found almost twice the number of species on native *Acer platanoides* than non-native *A. saccharinum*, and on native *Q. robur* than *Q. rubra*. They also found a similar number of species on native and non-native *Tilia* spp. Besides these studies, there are few more works have assessed the species composition of the lichen biota growing on the bark of invasive trees but not comparing with native trees (e.g. Kubiak, 2013).

Previous studies on nonnative tree species impacts on epiphytic lichens focused solely on lichen taxonomic diversity and species composition, omitting functional diversity. Only González-Montelongo and Pérez-Vargas (2021) analyzed the distribution of lichen traits, indicating differences in functional composition. Also, they did not account for tree size, which is known to be a significant driver of lichen diversity (Lie et al., 2009; Marmor et al., 2011; Nascimbene et al., 2009). The limited representation of studies, both in terms of geographic and functional scope, leads to a bias in the interpretation of non-native trees' impact on lichens (Hulme et al., 2013).

The Białowieża Forest, despite some human-driven impacts, is the only forest in the European lowlands that retains the characteristics of a primeval forest. Invasive plant species that have appeared in this area are spreading at different rates, forming numerous populations in some places. Their presence is most evident in rural areas, forest edges, and abandoned meadows or agricultural areas. Increasingly, invasive plants, including shrubs and trees, are being observed in forest communities, becoming their components (Adamowski et al., 2002). In the case of the species diversity of epiphytic lichens, which are directly associated with substrates such as tree bark, the appearance of invasive tree species in the Białowieża Forest can exert a substantially negative impact on them. As the object of study, we chose the invasive *Prunus cerasifera*, recently found even in the Strict Reserve of the Białowieża National Park (BNP) (Czortek et al., 2024). Now, *P. cerasifera* spreads in the initial stages of oak-hornbeam forests in the surroundings of the BNP.

Non-native species, by changing the structure in the stand, can promote certain lichen species with specific functional traits and inhibit other species. Despite the limited number and scope of previous studies, we know something about the impact of invasive tree species on lichen taxonomic diversity. However, we do not understand how invasive tree species can affect the functional composition and diversity of lichens. Therefore, we hypothesized that: (1) *P. cerasifera* hosts a lower lichen taxonomic and functional diversity than native trees, as it is known that invasive tree species have a negative impact on epiphyte diversity (e.g. Calviño-Cancela et al., 2013; Möller et al., 2021; Nascimbene et al., 2015, 2012); (2) the species richness and functional diversity of lichens on *P. cerasifera* increases with tree size, which is based on the knowledge that larger trees are characterised by a greater diversity of epiphytes (e.g. Marmor et al., 2011; Nascimbene et al., 2009); (3) *P. cerasifera*, as an invasive tree species, provides low capacity of ecosystem services for epiphytes compared to native trees – the lichen biota growing on *P. cerasifera* consists only of common and most frequent species occurring on neighbouring native trees.

2. Materials and methods

2.1. Invasive tree species studied

P. cerasifera can grow either as a shrub or a rapidly developing tree, attaining a maximum height of approximately 15 m. Its natural range extends across SE Europe, as well as SW and Central Asia, where it thrives in a broad altitudinal gradient, reaching elevations of up to 2200 m a.s.l. Within its introduced range, *P. cerasifera* can naturalize across diverse habitat types, including Scots pine monocultures, secondary woodlands, and even old-growth forests (see literature review in Czortek et al., 2024). *P. cerasifera* is recognized as a nonnative species in multiple temperate regions worldwide (Rejmánek and Richardson, 2013). Its introduced range includes N Africa, both W and E North America, SW South America, and New Zealand (POWO, 2022; Weber, 2017). In NW and NE Europe, *P. cerasifera* is classified as an invasive neophyte (Czortek et al., 2024). In Poland, according to Tokarska-Guzik et al. (2012) is classified as locally naturalized, but our previous study (Czortek et al., 2024) revealed that *P. cerasifera* fulfils criterion of invasive species, according to Richardson et al. (2000), spreading over 100 m in less than 50 years. However, its impact on native species have been not yet recognized. The exact date of its introduction to Poland remains uncertain (Tokarska-Guzik et al., 2012). However, the earliest documented occurrence in the Białowieża Forest traces back to the 1960s, when its cultivation was reported in the Belarusian part of this ecosystem (Smirnov, 1965). The first documented occurrences of *P. cerasifera* on the Białowieża Clearing date back to the late 1970s (data from herbarium of the Białowieża Geobotanical Station).

2.2. Study area

Our study was done in the northern part of the Białowieża Clearing, between the Białowieża village, the biggest settlement in the Polish part of the Białowieża Forest and the BNP (Fig. 1). This area had been in agricultural use since the 17th/18th century, up to the second half of the 20th century. Abandonment of agricultural activities greatly accelerated after 1989. Nowadays, this part of the Białowieża Clearing is a mosaic of mostly abandoned fields, mesic meadows and pastures, as well as initial stages of oak-hornbeam forest (*Tilio-Carpinetum*), dominated by spontaneous brushwoods of *Betula pendula*, *Populus tremula*, *Salix caprea* with *Carpinus betulus*, *Quercus robur* and *Tilia cordata* admixture, thickets of willows (*Salix cinerea* and *S. aurita*), savannah-like groups of spontaneous apple trees *Malus domestica* and *P. cerasifera*, as well as plantations of *Pinus sylvestris*, *Picea abies*, and *Alnus glutinosa*. *P. cerasifera* is most

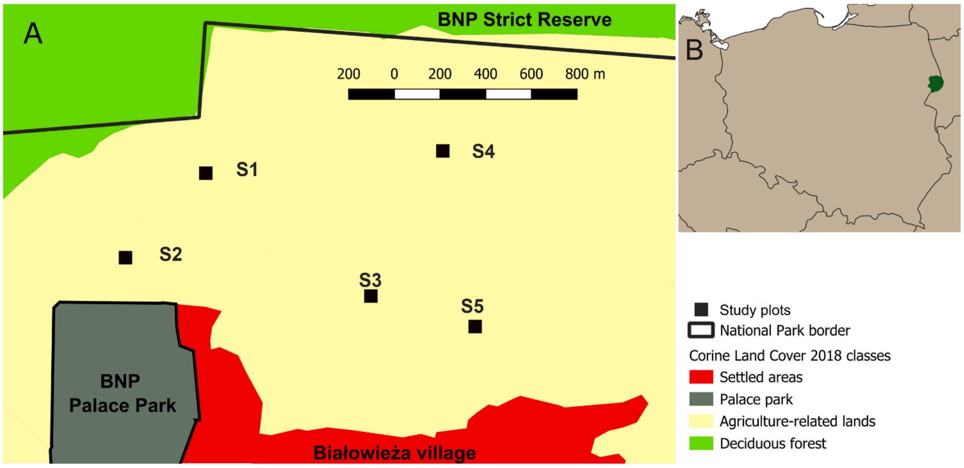

Fig. 1. Area of study with five study sites representing early successional stages of oak-hornbeam forest located on the Białowieża Clearing in the surrounding of the Strict Reserve of the Białowieża National Park (BNP).

common in open shrubland or loose brushwoods, locally reaching up to 90 % cover in the shrub and tree layer.

2.3. Data collection

We conducted the study in 2023, in five study sites of comparable size (S1: ~4.1 ha, S2: ~3.5 ha, S3: ~3.8 ha, S4: ~4.1 ha, and S5: ~3.1 ha), each sharing a similar history of land-use, corresponding to the land-use history of the entire Białowieża Clearing (Fig. 1). The species composition of the lichen biota was analyzed on the main tree species (hosts, phorophytes) that build mixed deciduous oak-lime-hornbeam forest, and already occur in the initial stages of this forest type: native *C. betulus*, *T. cordata*, *Q. robur*, *P. tremula*, and nonnative *P. cerasifera* (the nomenclature of vascular plants follows POWO, 2022). The abovementioned native tree species have a wide range of ecological variability of microhabitats for epiphytic lichens as the bark of these trees differs in texture, sculpture, and pH, which allows it to be inhabited by high taxonomical and functional diversity of lichen species (Barkman, 1958; Gustafsson and Eriksson, 1995; Hedenås and Ericson, 2004; Kuusinen, 1994; Łubek et al., 2021a, 2019; Lundström et al., 2013).

We selected 30 sample trees for *C. betulus*, *P. cerasifera*, and *T. cordata*, 29 trees for *P. tremula*, and 28 trees for *Q. robur* in three different classes of diameter at breast height (DBH): 1) up to 10 cm, 2) 10.1–20 cm, and 3) above 20.1 cm. Lichens were surveyed up to 250 cm above the ground. Lichen species were identified in the field, with specimens that were difficult to determine collected for laboratory identification. Standard lichenological methods were employed, including chemical spot tests on thalli, microscopic examination of apothecial sections for morphological and spore analysis, and thin-layer chromatography (TLC) to detect secondary metabolites. The abundance of each lichen species on each sample tree was estimated using a four-degree scale, where zero stands for lack of lichens, one for low abundance (to 3 occurrences in the plot), two for intermediate (4–10 occurrences), and three for the highest (over 11 occurrences). The lichen nomenclature follows Fałtynowicz et al. (2024), and the collected lichenological material is deposited at the Jan Kochanowski University in Kielce (KTC).

2.4. Lichen species and functional diversity characteristics

To assess the taxonomical diversity of epiphytic lichens, for each sample tree we calculated the species richness and Shannon index. To account for functional diversity of epiphytes we compiled a set of 12 lichen functional traits: thallus type, photobiont type, asexual reproduction type of both bionts (i.e., photo- and mycobiont), ascomata type formation, asexual reproduction of mycobiont, ascomata texture and pigmentation, ascomata area, spore pigmentation, septation, shape, volume, and lichen secondary metabolites (Table 1). Functional traits of lichen species were extracted from Łubek et al. (2020), Ertz et al. (2018), Giordani et al. (2012), Smith et al. (2009), Nimis and Martellos (2003), Orange et al. (2010), and Purvis (2000). Some trait values regarding ascomata area, spore shape, and spore volume were missing (Table 1). However, instead of excluding them from analyses we imputed missing trait values using the random forest-based imputation, provided in the *missForest::missForest()* function (Penone et al., 2014; Stekhoven and Bühlmann, 2012). Using the imputed trait dataset, we calculated the community-weighted mean (CWM) values of numerical lichen functional traits (i.e. ascomata area, spore shape, and spore volume) for each sample tree, applying species abundance as a weighting factor. In addition, for each sample tree, we calculated the percentage contribution of species producing soredia.

Based on the imputed dataset of functional traits and employing the *FD::dbFD()* function (Laliberté et al., 2023; Laliberté and Legendre, 2010), we computed two metrics of lichen functional diversity for each sample tree: functional richness and functional dispersion. Low functional richness, which measures the volume of occupied niche hyperspace by particular lichen species' trait value combinations (Hedberg et al., 2014), may suggest that species utilize a small part of the available niche hyperspace. This may imply a strong influence of environmental filtering in shaping the community assembly processes, often associated with pioneer habitats or stressful and extreme habitat conditions (Chesson, 2000). In contrast, high values of functional richness may indicate that most of the available niche hyperspace are occupied by species, expressing the prevalence of niche differentiation in shaping the structure of species assemblages due to the presence of substantial heterogeneity of microhabitats (Busch et al., 2019; Czortek et al., 2021; Łubek et al., 2020; Villéger et al., 2008). Functional dispersion measures the dissimilarities in trait composition within a community, represented by the mean distance of each species from the centroid of the trait hyperspace (Hedberg et al., 2014). Low functional dispersion values may indicate the dominance of species with trait values close to the centroid (occurring in either low or high abundances), suggesting that environmental filtering is key in structuring the species assemblages (Chesson, 2000; Grime, 2006). Conversely, high values of functional dispersion may reflect greater functional trait diversity and higher functional dissimilarities among species, indicating that niche differentiation is likely the primary driver of species coexistence within the community (Carroll et al., 2011; Czortek et al., 2021; Łubek et al., 2020; Tilman et al., 1997).

Table 1

Lichens' functional traits used in this study. their ranges. standard deviation (SD) and completeness.

Numeric traits	Min	Max	Mean	SD	Completeness [%]
Ascomata area [mm^2]	0.017	12.560	0.936	2.075	61.538
Spore shape [μm/μm]	1.000	25.714	4.471	5.390	61.538
Spore volume [μm^3]	23.570	4634.210	405.150	664.467	61.538
Categorical traits	**Number of main classes**	**Classes**			**Completeness [%]**
Thallus type	4	Crustose; Foliose; Fruticose; Leprose			100 %
Photobiont type	2	Clorococcoid and other green; Trentepohlia			100 %
Asexual reproduction of both bionts	3	Isidia; Soredia; No asexual reproduction			100 %
Ascomata type formation	6	Arthonioid; Lecanora; Lecidea; Lirella; Perythecia; No ascomata			100 %
Asexual reproduction of mycobiont	2	Pycnidia; No asexual reproduction			100 %
Ascomata texture pigmentation	3	With carbonized structures; Without carbonized structures; No ascomata			100 %
Spores dark pigmentation	3	Pigmented; Not pigmented; No spores			100 %
Spore septation	5	1-celled; 2-celled; Multi-celled; Muriform; No spores			100 %
Secondary metabolites	16	Aliphatic acids; Antraquinoses; Atranorin; Diphenyl ethers; Orcinol depsides; β-orcinol depsides; Orcinol depsidones; β-orcinol depsidones; Orcinol tridepsides; Pulvinic acid derivatives; Terpenoids; Usnic acid; Usnic acid derivatives; Xanthones; Other substances; No metabolites			100 %

2.5. Statistical analyses

To explore differences in lichen species composition amongst the sample tree representing five phorophyte species we employed the Non-Metric Multidimensional Scaling (NMDS) ordination using the *vegan::metaMDS()* function (Oksanen et al., 2025). For NMDS analysis, we applied the default parameters for data transformation and constructed the Bray-Curtis dissimilarity matrix, using the midpoint values of species abundance. To illustrate the relationships between the primary gradients of species composition identified through the usage of NMDS, we performed a passive projection of lichen biota characteristics, including DBH, components of taxonomical (i.e. species richness and Shannon index) and functional diversity (i.e. functional richness and functional dispersion), the proportion of species producing soredia, as well as CWMs of lichen functional traits (i.e. spore shape, spore volume, and ascomata area; Table 2), and tree host species identity as categorical factor, using the *vegan::envfit()* function (Oksanen et al., 2025). We tested the accuracy of this fit using a permutation test with 999 iterations.

To assess differences in lichen biota characteristics amongst five tree host species and depending on DBH (Table 2), we used linear (LMM) and generalized mixed-effect models (GLMM), implemented in the *glmmTMB:glmmTMB()* function (Brooks et al., 2017), with tree host identity, DBH, and interaction between DBH and tree host identity adopted as fixed predictors, and study site identity chosen as a random factor (accounting for lichen biota survey design and potential differences in abiotic habitat heterogeneity, and land-use history). To account for species richness we used GLMM with the Poisson distribution of the response variable, as indicated by dispersion parameter $= 0.71$ and P-value $= 0.06$ provided by the dispersion test implemented in the *DHARMa::testDispersion()* function (Hartig, 2025). To examine the Shannon index, functional richness, functional dispersion, and three CWMs of lichen functional traits, we employed LMMs with a Gaussian distribution, assuming the close-to-normal distribution of response variables. To investigate differences in the proportion of lichens producing soredia, we used GLMM with the beta distribution of the response variable. For each characteristic of lichen biota, we constructed global models including all three hypothesized fixed predictors. Next, we simplified global LMMs and GLMMs by reducing them to minimize AICc using the *MuMIn::dredge()* function (Bartoń, 2025), and selected the final models based on the lowest AICc values. We used the *MuMIn::r.squaredGLMM()* function (Bartoń, 2024) to calculate marginal and conditional coefficients of determination (R^2_m and R^2_c, respectively) for all final models. The R^2_m represents the variance explained exclusively by the fixed effects, while R^2_c indicates the variance explained by both fixed and random effects. The difference between R^2_c and R^2_m reflects the fraction of variance attributed solely to the random factor.

In evaluating the significance of results and visualizing final LMMs and GLMMs, we prioritized effect sizes over P-values. We adopted this approach because P-values are highly sensitive to sample size, and focusing on them exclusively may lead to biologically relevant patterns being wrongly interpreted as statistically not significant (Wasserstein and Lazar, 2016). To account for effect sizes of DBH and interaction between tree host species identity and DBH, we illustrated the results of final models using marginal responses, i.e., predicted values assuming all other explanatory variables at a constant level using the *ggeffects::ggpredict()* function (Lüdecke, 2018). To evaluate the effect sizes of tree host species identity, we calculated the marginal means for each LMM and GLMM, and conducted Tukey's *posteriori* test with studentized adjustment for multiple hypothesis testing, using the *emmeans::emmeans()* function (Lenth, 2025).

We employed the IndVal method, implemented in the *labdsv* package (Roberts, 2023) to identify lichen species statistically significantly affiliated to particular tree species. This method (based on the species' average abundance data) allowed us to assess whether a particular epiphyte species is more abundant in a particular tree host species by providing parameters informing on the strength and statistical significance of association (Roberts, 2023).

Table 2

Descriptive statistics of variables used in this study. Abbreviations: CWM – community weighted mean.

Variable	Min	Max	Mean	SD
Species richness	4.0	31.0	13.3	6.2
Shannon index	1.277	3.359	2.393	0.498
Functional richness	0.051	0.959	0.632	0.216
Functional dispersion	0.195	0.364	0.310	0.037
CWM of ascomata area	0.417	2.181	1.209	0.397
CWM of spore shape	1.954	6.675	3.043	0.850
CWM of spore volume	245.6	851.3	428.2	103.2
Proportion of lichens with soredia	0.00	0.70	0.32	0.14
Tree diameter at breast height [cm]	2.2	38.0	16.1	8.9

3. Results

On the surveyed phorophytes we found 89 lichen species (both macro- and microlichens). We found the highest number of species on the bark of *P. cerasifera* (76 species), while less species on the other trees: *Q. robur*, *T. cordata*, *P. tremula*, and *C. betulus*, with 51, 50, 44, and 44 species, respectively. In the total lichen biota we found 22 species common to all tree species, 13 common to two tree hosts, 15 to three, and 13 to four hosts. The highest number of exclusive species was recorded on the bark of *P. cerasifera* (16 species), and the lowest on *T. cordata* and *Q. robur* (only one species each).

The NMDS ordination revealed distinct differences in lichen species composition amongst the tree hosts investigated (stress value = 0.171), indicating a fair representation of the compositional dissimilarities in the reduced NMDS space (Fig. 2). We identified *T. cordata*, *C. betulus*, and *P. tremula* as tree hosts with the largest compositional heterogeneity of lichen assemblages, while *P. cerasifera* and *Q. robur* were the most homogenous regarding the epiphytes' composition. The structure of lichen assemblages inhabiting *T. cordata* was described by the high contribution of species producing large spores (vector representing the CWM of spore volume; Fig. 2; Table 3). The species composition of lichens occurring on *C. betulus* and *P. tremula* was shaped by high values of the spore shape CWM and large DBH, respectively (Fig. 2; Table 3). The structure of lichen assemblages occurring on *P. cerasifera* was characterized by high species richness and Shannon index, high values of functional richness and functional dispersion, as well as high contribution of species producing soredia and taxa with large ascomata area (Fig. 2; Table 3).

For species richness, Shannon index, functional richness, functional dispersion, and CWM of spore shape, final models included all predictors from global models (Table 4). Regarding the CWM of spore volume and the proportion of lichens with soredia, both final models consisted of single effects of tree host species identity and DBH. Considering the final model built for the CWM of the ascomata area, it included only a single effect of tree host species. Taking into account almost all parameters mentioned above, most of the variance was explained by fixed predictors (ranging from 27.0 % to 78.7 %), while the effect of the random factor (linked with the study site identity) on the results obtained was generally weak (ranging from 1.7 % to 9.6 %). Only in the case of ascomata area and spore shape CWMs, the random factor explained about 18.6 % and 28.0 % of variability, while the fixed effect 36.0 % and 13.2 %, respectively (Table 4).

The mean lichens' species richness in sample trees representing *P. cerasifera* (22.6 ± 1.5 SE taxa) was about 13.6, 8.2, 11.1, and 13.2 species higher than in plots representing *T. cordata*, *Q. robur*, *P. tremula*, and *C. betulus*, respectively (Fig. 3**a**). Single effect of DBH on species richness was similarly weak as compared to *P. tremula* and *C. betulus* sample trees (Figs. 3**b**-3**c**). While in sample trees representing *T. cordata* and *Q. robur* the species richness increased from 4.6 and 10.1–24.3 and 24.4 taxa, respectively, in *P. cerasifera* it increased from 19.0 to 29.1 species at DBH ranging from 2.2 cm to 38.0 cm (Fig. 3**c**). We identified sample trees representing *P. cerasifera* as having the highest mean values of Shannon index (3.05 ± 0.08 SE). In *T. cordata*, *Q. robur*, *P. tremula*, and *C. betulus* sample trees values of this index were about 0.97, 0.52, 0.69, and 0.95 lower, respectively, compared to *P. cerasifera* (Fig. 3**d**). Alongside increasing the DBH, the Shannon index increased slightly from 1.97 at 2.2 cm to 2.29 at 38.0 cm (Fig. 3**e**). Similarly gentle impact of DBH on Shannon index we reported for *P. cerasifera* and *C. betulus* (an increase from 2.89 and 1.97 at 2.2 cm to 3.30 and 2.29 at 38.0 cm, respectively; Fig. 3**f**). Considering *T. cordata* and *Q. robur*, this relationship was strongly positive: the values of Shannon index increased from 1.54 and 2.11 at 2.2 cm to 2.88 and 3.15 at 38. 0 cm, respectively (Fig. 3**f**).

We reported the *P. cerasifera* sample trees as having the highest mean

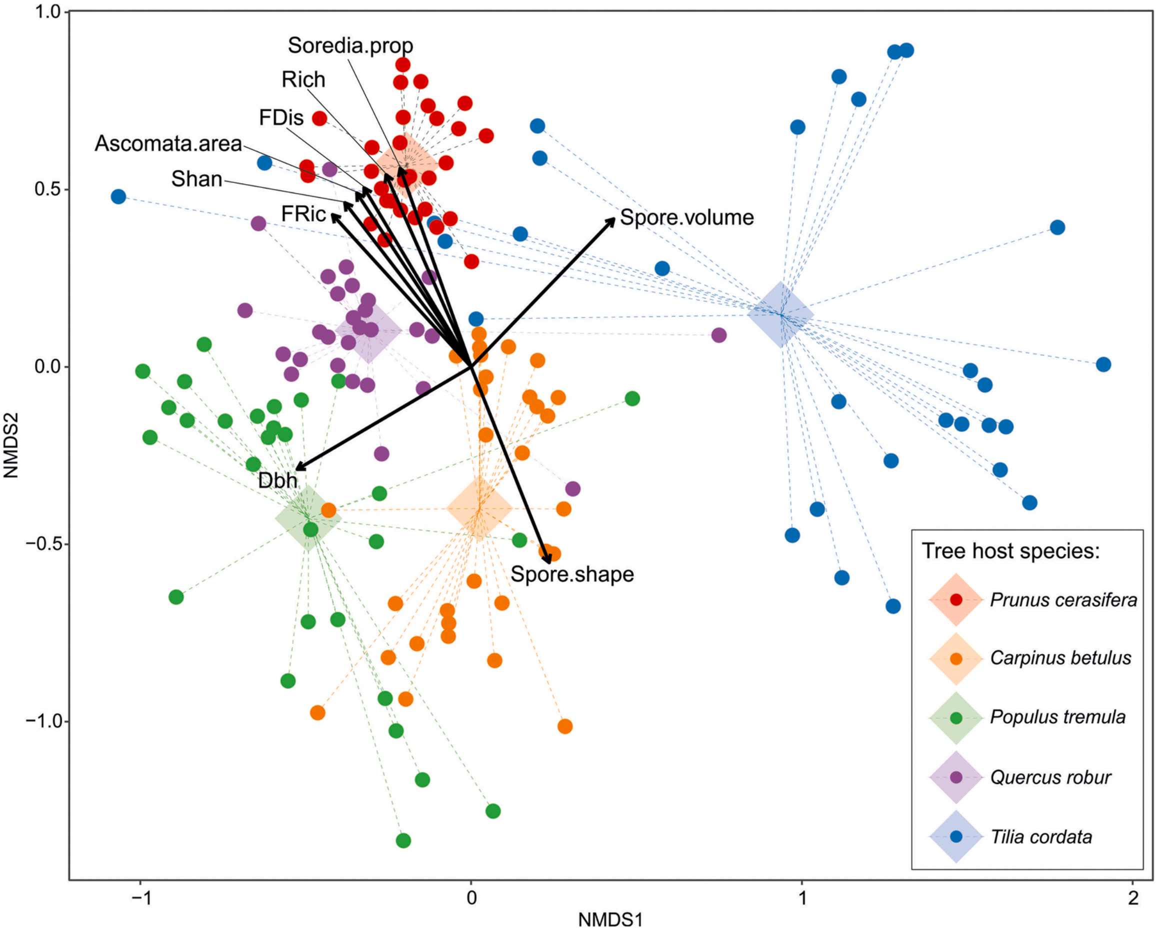

Fig. 2. Visualisation of NMDS ordination showing dissimilarities in species composition of lichens amongst five tree host species differing in regards to diameter at breast height (DBH) with passive projection of characteristics of epiphytes' species diversity (shown as black arrows; Table 3): Rich – species richness, Shan – Shannon diversity index, FRic – functional richness, FDis – functional dispersion, Ascomata.area – community weighted mean (CWM) of ascomata area, Spore.shape – CWM of spore shape, Spore.volume – CWM of spore volume, Soredia.prop – proportion of lichens with soredia. Points represent coordinates of plots (tree hosts representing particular tree species). Diamonds represent centroids of species composition of epiphytic lichens in plots.

Table 3

Parameters of epiphytic lichens biota characteristics passively fitted to the results of the NMDS ordination visualizing dissimilarities in lichen species composition amongst five tree host species differing in regards to the diameter at breast height. Determination coefficients R^2 and P-values were computed through the usage of permutation tests with 999 iterations. Abbreviations: CWM – community-weighted mean.

Variable		Acronym	NMDS1	NMDS2	R^2	P
Species richness		Rich	−0.539	0.841	0.588	0.001
Shannon index		Shan	−0.662	0.749	0.623	0.001
Functional richness		FRic	−0.698	0.715	0.231	0.001
Functional dispersion		FDis	−0.576	0.817	0.166	0.001
CWM of ascomata area		Ascomata.area	−0.636	0.771	0.530	0.001
CWM of spore shape		Spore.shape	0.393	−0.919	0.122	0.001
CWM of spore volume		Spore.volume	0.718	0.695	0.185	0.001
Proportion of lichens with soredia [%]		Soredia.prop	−0.357	0.933	0.299	0.001
Tree diameter at breast height [cm]		DBH	−0.876	−0.481	0.060	0.015
Tree host:	*Prunus cerasifera*	-	−0.196	0.568	0.589	0.001
	Carpinus betulus	-	0.025	−0.399		
	Populus tremula	-	−0.491	−0.427		
	Quercus robur	-	−0.310	0.102		
	Tilia cordata	-	0.935	0.147		

functional richness of lichen assemblages (0.84 ± 0.04 SE). In comparison, mean functional richness in sample trees representing *T. cordata*, *Q. robur*, *P. tremula*, and *C. betulus* was about 0.24, 0.19, 0.22, and 0.35 lower, respectively, than in *P. cerasifera* (Fig. 3**g**). Lichen functional richness increased prominently alongside increasing the DBH from 0.38 at 2.2 cm to 0.67 at 38.0 cm (Fig. 3**h**), with *Q. robur* and *T. cordata* recognized as revealing the highest increases in values of this metric from 0.43 and 0.29 at 2.2 cm to 0.98 and 1.06 at 38.0 cm (Fig. 3**i**). *P. cerasifera*, *P. tremula*, and *C. betulus,* in turn, demonstrated the lowest increases in functional richness depending on DBH (Fig. 3**i**). The mean values of lichens' functional dispersion did not differ considerably amongst the studied phorophytes (Fig. 3**j**). A single effect of DBH on this parameter was similarly low as reported for plots representing *P. cerasifera*, *P. tremula*, and *C. betulus* but regarding *Q. robur* and *T. cordata* sample trees, it increased substantially from 0.28 and 0.27 at 2.2 cm to 0.37 and 0.38 at 38.0 cm, respectively (Figs. 3**k**-3**l**).

The mean values of spore shape CWM differed slightly among the studied tree hosts (Fig. 4**a**). Likewise, a single effect of DBH on spore shape CWM remained similarly gentle (a decrease from 3.34 μm/μm at 2.2 cm to 2.03 μm/μm at 38.0 cm; Fig. 4**b**) as for sample trees representing almost all hosts (apart from *C. betulus* plots; Fig. 4**c**). The mean values of spore volume CWM showed gentle differences across the examined phorophytes, with *T. cordata* identified as having the highest (509.00 ± 21.50 SE μm^3), and *C. betulus* having the lowest values of this parameter (350.00 ± 20.70 SE μm^3; Fig. 4**d**). A single effect of DBH on spore volume CWM was negligible (Fig. 4**e**). We identified *P. cerasifera* sample trees as having the highest mean proportion of sorediate lichens (∼44.0 % ± 2.4 % SE of species), which was about 8.9, 6.5, 15.3, and 25.5 % higher than reported for *T. cordata*, *Q. robur*, *P. tremula*, and *C. betulus*, respectively (Fig. 4**f**). The single influence of DBH on the proportion of lichens with soredia remained weak (Fig. 4**g**). Considering the CWM of ascomata area, mean value of this parameter was the highest in *P. cerasifera* (1.60 ± 0.08 SE mm^2), and the lowest in *C. betulus* sample trees (0.89 ± 0.09 SE mm^2; Fig. 4**h**).

Analysis of indicator species revealed 29 lichen taxa statistically significantly affiliated to *P. cerasifera* plots, with the highest strength of association reported for nitrophilous species (e.g. *Rinodina sophodes*, *Hypogymnia physodes*, or *Physcia aipolia*; Table 5), early succession species (e.g. *Lecanora symmicta* or *Melanelixia subaurifera*) and forest species (e.g. *Opegrapha niveoatra* or *Platismatia glauca*). Additionally, we found 15 exclusive, very rare species growing only on *P. cerasifera*, and mostly all of them represented the forest species (e.g. *Cetrelia cetrarioides*, *Fellhanera gyrophorica*, *Flavoparmelia caperata*, *L. thysanophora*, *O. vulgata*, or *Pertusaria coccodes*; Table 6). We identified nine epiphyte species statistically significantly associated with *P. tremula* plots that demonstrated the strongest affiliations, such as nitrophilous species (e.g. *Phaeophyscia orbicularis* or *Athallia pyracea*; Table 5) and forest species (e.g. *Acrocordia gemmata* or *L. argentata*). For this tree we found additionally two very rare exclusive species (e.g. *Bacidia rubella* or *Myriolecis sambuci;* Table 6). Five forest lichen taxa were statistically significantly affiliated to *T. cordata* (e.g. *Arthonia ruana*, *Graphis scripta*, or *Porina aenea*; Table 5). Five nitrophilous species each demonstrated significant associations with *C. betulus* (e.g. *Lecania naegelli*, *Lecidella elaeochroma*, or *R. pyrina*) and *Q. robur* plots (e.g. *L. chlarotera*, or *Bacidina mendax*). For *C. betulus* three rare exclusive forest species were also found (e.g. *A. didyma* or *Pyrenula nitidella*; Table 6), and only one for *Q. robur* (*B. biatorina*).

4. Discussion

4.1. Differences in epiphytic lichen diversity amongst tree hosts

The species composition of the epiphytic lichen assemblages inhabiting the invasive *P. cerasifera* was characterized by higher species richness and Shannon index. Additionally, this nonnative revealed higher values of functional richness and functional dispersion, compared to the lichen communities of native tree species composing the early successional stages of the temperate deciduous forest ecosystem. These patterns contradict Hypothesis 1, which assumed that *P. cerasifera* would host a lower lichen taxonomic and functional diversity than native trees. Our findings contrast with those reported for other invasive trees, e.g. *Q. rubra* (Gustafsson et al., 2023) and *R. pseudoacacia* (Nascimbene et al., 2015, 2012; Nascimbene and Marini, 2010). Compared to native trees (*Q. robur* and *Q. petraea*), these nonnatives support lower epiphyte species diversity than natives, which has been attributed to differences in their bark's physical properties, particularly bark fissure depth (Gustafsson et al., 2023). Moreover, in the case of *R. pseudoacacia*, Nascimbene et al. (2015) observed biotic homogenization in terms of β-diversity components of the lichen biota inhabiting this nonnative phorophyte. The authors attributed this phenomenon to the prevalence of environmental filtering in determining the lichen assemblages structure, which may promote the spread of competitive, nitrogen-demanding species (Nascimbene et al., 2015).

Among surveyed phorophytes, the epiphytic lichen biota of *P. cerasifera* and *Q. robur* revealed the lowest similarities in species composition. In contrast, for *T. cordata*, *P. tremula*, and *C. betulus* we demonstrated the highest dissimilarities in the lichen assemblages structure. This may suggest that regarding *Q. robur* and *P. cerasifera*, the epiphyte composition was highly consistent and shaped by a core species group demonstrating high affinities to occur on them (e.g. *P. glauca* or *Melanohalea exasperatula*; see Table 5). In contrast, on other tree hosts, lichen species composition appeared to be more random, potentially indicating a high species turnover among trees representing particular host species. Contrasting findings, indicating a high similarity between

Table 4
Parameters of final mixed effect models chosen based on model selection procedure and AICc criterion (with site identity as a random factor) testing for the influence of tree host species (Tree). tree diameter at breast height (DBH). and interaction (marked in the table by colons) between tree host species and tree diameter at breast height on the diversity of epiphytic lichen species. RE – SD of random effects; AICc – AICc of the final model; AICc$_0$ – AIC of the null (intercept-only) model; CWM – community-weighted mean. Statistically significant results are in bold.

Response	Predictor	Estimate	SE	*t/z*	*P*	RE SD	AICc	AICc$_0$	R^2_m	R^2_c
Species richness	(Intercept)	2.140	0.160	13.335	**< 0.001**	0.120	774.401	1019.412	0.636	0.696
	Tree=*P. cerasifera*	0.804	0.178	4.509	**< 0.001**					
	Tree=*P. tremula*	0.339	0.194	1.749	0.080					
	Tree=*Q. robur*	0.173	0.174	0.997	0.318					
	Tree=T. cordata	−0.623	0.228	−2.726	**0.006**					
	DBH	0.005	0.008	0.731	0.465					
	Tree=*P. cerasifera*: DBH	0.004	0.009	0.496	0.620					
	Tree=*P. tremula*: DBH	−0.008	0.009	−0.849	0.396					
	Tree=*Q. robur*: DBH	0.015	0.009	1.671	0.094					
	Tree=T. cordata: DBH	0.035	0.011	3.097	**0.001**					
Shannon index	(Intercept)	1.972	0.140	14.042	**< 0.001**	0.154	54.402	198.859	0.643	0.739
	Tree=*P. cerasifera*	0.914	0.158	5.777	**< 0.001**					
	Tree=*P. tremula*	0.387	0.161	2.396	**0.016**					
	Tree=*Q. robur*	0.142	0.152	0.935	0.349					
	Tree=T. cordata	−0.434	0.168	−2.587	**0.009**					
	DBH	0.007	0.006	1.182	0.237					
	Tree=*P. cerasifera*: DBH	0.002	0.008	0.283	0.777					
	Tree=*P. tremula*: DBH	−0.008	0.008	−0.994	0.320					
	Tree=*Q. robur*: DBH	0.017	0.008	2.110	**0.034**					
	Tree=T. cordata: DBH	0.025	0.009	2.814	**0.004**					
Functional richness	(Intercept)	0.376	0.079	4.755	**< 0.001**	0.053	−92.832	−31.555	0.436	0.494
	Tree=*P. cerasifera*	0.439	0.099	4.434	**< 0.001**					
	Tree=*P. tremula*	0.199	0.098	2.015	**0.043**					
	Tree=*Q. robur*	0.057	0.093	0.611	0.541					
	Tree=T. cordata	−0.086	0.106	−0.813	0.416					
	DBH	0.007	0.004	1.759	0.078					
	Tree=*P. cerasifera*: DBH	−0.005	0.005	−1.101	0.271					
	Tree=*P. tremula*: DBH	−0.004	0.004	−0.890	0.373					
	Tree=*Q. robur*: DBH	0.006	0.005	1.247	0.212					
	Tree=T. cordata: DBH	0.011	0.005	2.120	**0.034**					
Functional dispersion	(Intercept)	0.268	0.013	19.821	**< 0.001**	0.007	−605.685	−547.295	0.432	0.472
	Tree=*P. cerasifera*	0.066	0.017	3.818	**< 0.001**					
	Tree=*P. tremula*	0.032	0.017	1.916	0.055					
	Tree=*Q. robur*	0.014	0.016	0.906	0.364					
	Tree=T. cordata	0.005	0.018	0.308	0.758					
	DBH	< 0.001	< 0.001	0.416	0.677					
	Tree=*P. cerasifera*: DBH	< −0.001	< 0.001	−0.063	0.949					
	Tree=*P. tremula*: DBH	< 0.001	< 0.001	0.260	0.794					
	Tree=*Q. robur*: DBH	0.001	< 0.001	2.139	**0.032**					
	Tree=T. cordata: DBH	0.002	< 0.001	2.385	**0.017**					
CWM of ascomata area	(Intercept)	0.877	0.092	9.605	**< 0.001**	0.167	48.158	113.890	0.368	0.554
	Tree=*P. cerasifera*	0.707	0.074	9.460	**< 0.001**					
	Tree=*P. tremula*	0.469	0.077	6.026	**< 0.001**					
	Tree=*Q. robur*	0.366	0.071	5.132	**< 0.001**					
	Tree=T. cordata	0.264	0.081	3.248	**0.001**					
CWM of spore shape	(Intercept)	3.342	0.372	8.978	**< 0.001**	0.453	333.838	340.052	0.132	0.412
	Tree=*P. cerasifera*	−0.941	0.403	−2.335	**0.019**					
	Tree=*P. tremula*	−0.426	0.413	−1.033	0.301					
	Tree=*Q. robur*	−0.597	0.393	−1.521	0.128					
	Tree=T. cordata	−0.334	0.426	−0.783	0.433					
	DBH	−0.032	0.017	−1.900	0.057					
	Tree=*P. cerasifera*: DBH	0.060	0.021	2.742	**0.006**					
	Tree=*P. tremula*: DBH	0.057	0.020	2.742	**0.006**					
	Tree=*Q. robur*: DBH	0.027	0.021	1.243	0.213					
	Tree=T. cordata: DBH	0.031	0.023	1.338	0.181					
CWM of spore volume	(Intercept)	327.128	24.540	13.330	**< 0.001**	26.930	1741.596	1768.891	0.270	0.339
	Tree=*P. cerasifera*	101.672	23.371	4.350	**< 0.001**					
	Tree=*P. tremula*	83.900	24.143	3.475	**< 0.001**					
	Tree=*Q. robur*	62.823	22.727	2.764	**0.005**					
	Tree=T. cordata	158.473	24.946	6.353	**< 0.001**					
	DBH	1.450	0.817	1.775	0.075					
Proportion of lichens with soredia	(Intercept)	−1.643	0.145	−11.257	**< 0.001**	0.103	−190.788	−151.684	0.787	0.804
	Tree=*P. cerasifera*	1.237	0.143	8.641	**< 0.001**					
	Tree=*P. tremula*	0.575	0.150	3.820	**< 0.001**					
	Tree=*Q. robur*	0.972	0.141	6.871	**< 0.001**					
	Tree=T. cordata	0.868	0.165	5.233	**< 0.001**					
	DBH	0.009	0.004	2.030	**0.042**					

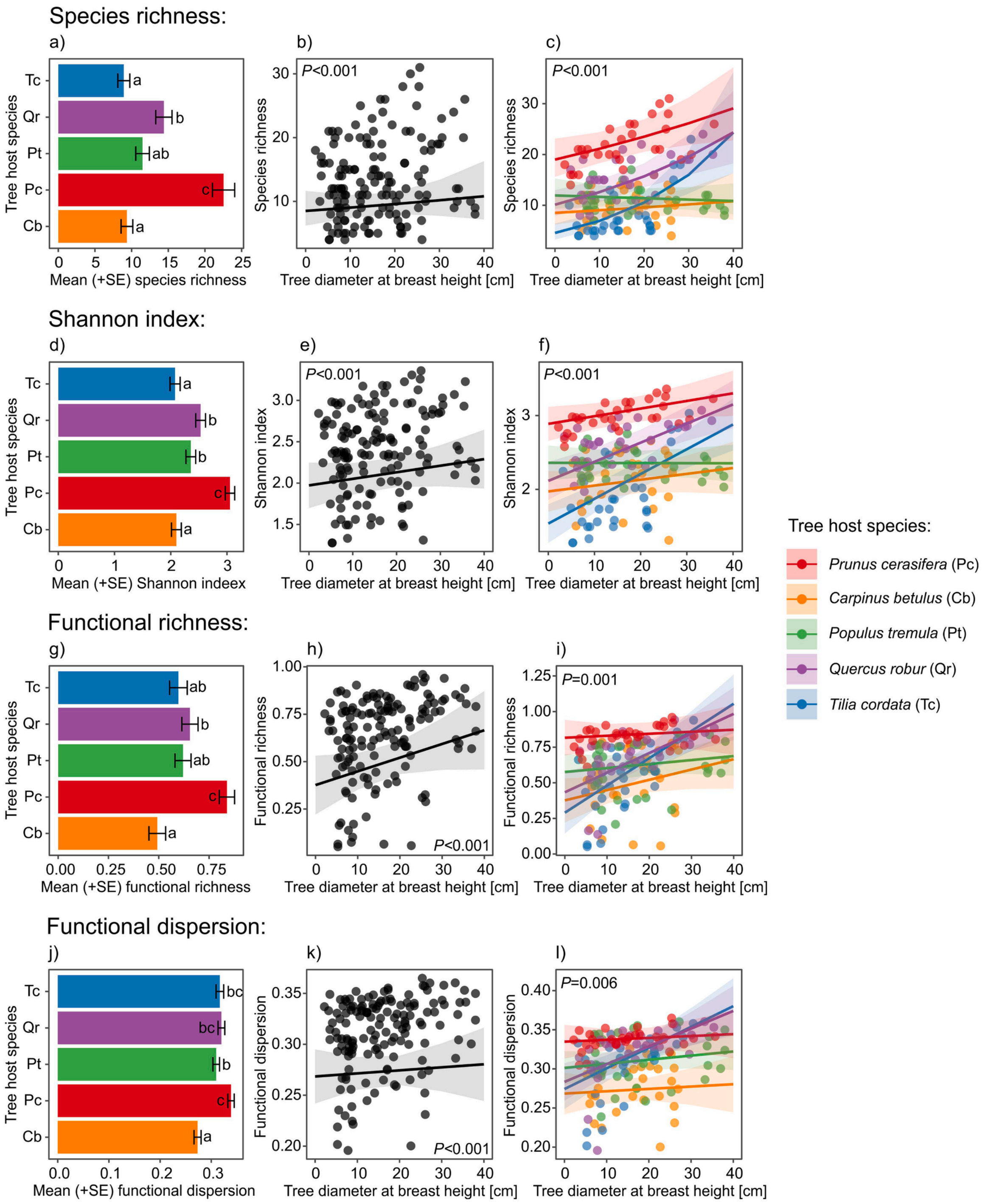

Fig. 3. Partial regression plots visualising final mixed effect (with site identity as random factor) models (chosen based on model selection procedure and AICc criterion) testing for effects of tree host species, tree diameter at breast height, and interaction between tree host species and tree diameter at breast height on: species richness (a-c), Shannon index (d-f), functional richness (g-i), and functional dispersion (j-l) of epiphytic lichens. Groups marked by the same letter do not differ statistically significantly at $P = 0.05$, according to Tukey's posteriori test. Statistical significance of the impacts of tree diameter at breast height, and the interaction between tree host species and tree diameter at breast height on lichen species' diversity characteristics were evaluated using ANOVA. For model parameters see Table 4.

T. cordata and *C. betulus*, with slightly lower similarities of these species to *Q. robur* and *P. tremula*, we obtained for the epiphytic lichens diversity of dominant forest-forming trees in the Strict Reserve of BNP (Łubek et al., 2021a, 2021b, 2019).

Epiphytic biota on *P. cerasifera*, and to some extent on *Q. robur*, revealed the highest both taxonomic and functional diversity, compared to other hosts. These results do not align with our initial assumptions about the negative impact of nonnative *P. cerasifera* on lichen taxonomic and functional diversity formulated in Hypothesis 1. For *C. betulus* we observed the lowest species and functional diversity, differing substantially from the patterns obtained from previous studies conducted in the BNP Strict Reserve (e.g. Łubek et al., 2019, 2020). There, we analysed the mechanisms shaping the functional diversity of lichen biota, identifying high values of functional dispersion as one of the key factors

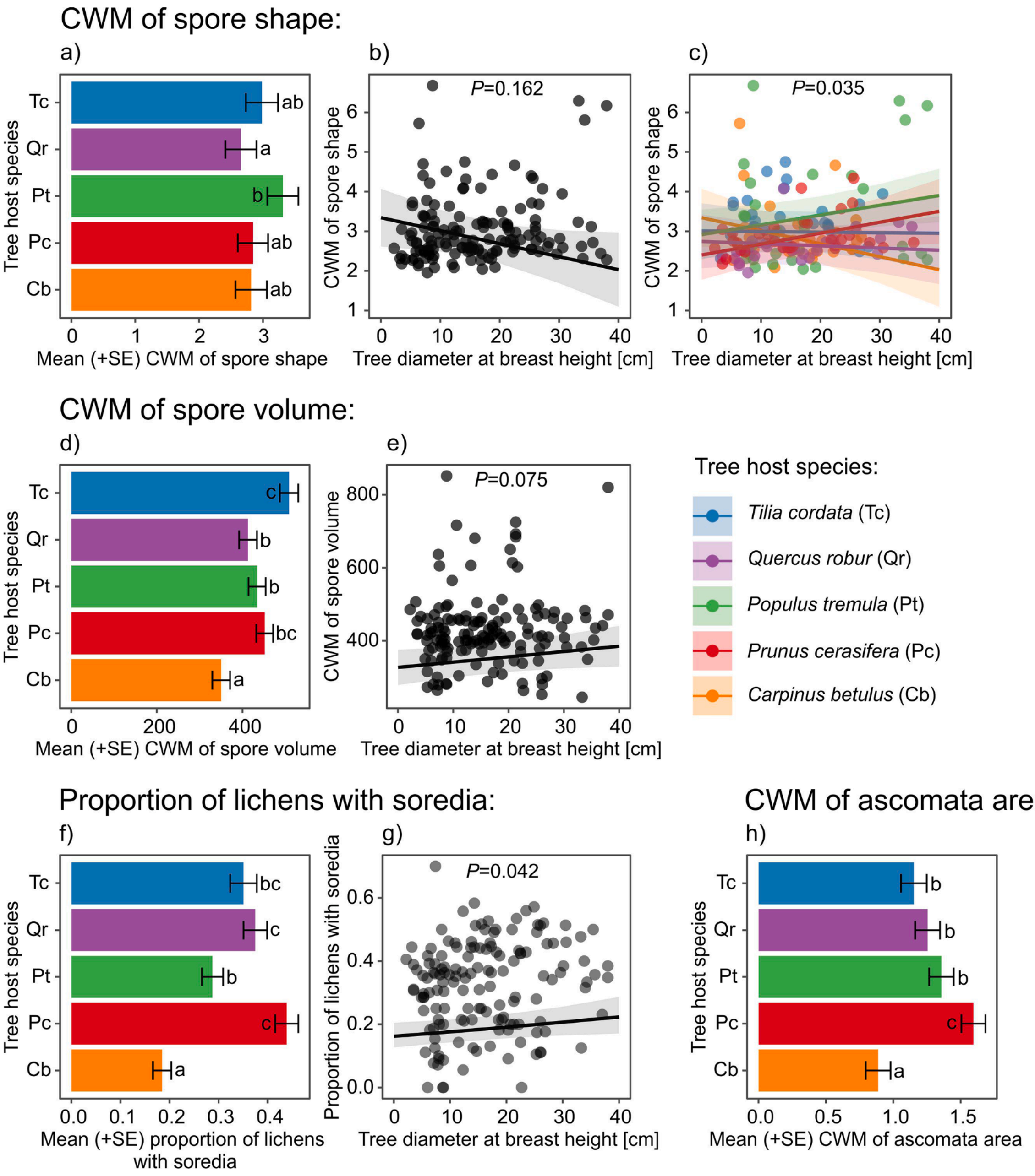

Fig. 4. Partial regression plots visualising final mixed effect (with site identity as random factor) models (chosen based on model selection procedure and AICc criterion) testing for effects of tree host species, tree diameter at breast height, and interaction between tree host species and tree diameter at breast height on lichen species' functional traits: community weighted mean (CWM) of spore shape (a-c), CWM of spore volume (d-e), proportion of lichens with soredia (f-g), and CWM of ascomata area (h). Groups marked by the same letter do not differ statistically significantly at $P = 0.05$, according to Tukey's posteriori test. Statistical significance of the impacts of tree diameter at breast height, and the interaction between tree host species and tree diameter at breast height on functional traits of lichen species were evaluated using ANOVA. For model parameters see Table 4.

driving the high functional diversity of epiphytes on *C. betulus* and *F. excelsior* (Łubek et al., 2020). This may suggest that the species composition of lichens on *C. betulus* in our case, one of the key tree species forming oak-hornbeam forests (Faliński, 1986), was not yet fully established in the initial stages of this forest type succession. This hypothesis may be further supported by the observed high heterogeneity of the lichen biota composition linked with the potential species turnover taking place on this tree host continuously. Considering *P. cerasifera*, despite its species composition being relatively homogeneous, numerous epiphyte species occurred exclusively on this tree, as indicated by high affinities to inhabit *P. cerasifera* reported for *P. glauca, Lepraria elobata, Ramalina fraxinea*, and *Usnea subfloridana.*

4.2. *Effects of tree size on diversity of epiphytes*

The impact of DBH on the lichen species richness, functional richness, and functional dispersion varied substantially across the phorophyte species surveyed. In regards to *C. betulus* and *P. tremula*, we identified no effect of DBH on lichen species diversity. This may be related to the varying colonization dynamics of different lichen species, which may lead to the rapid disappearance of some pioneer species (e.g. *L. symmicta* or *M. subaurifera*), and the appearance of others adapted to more stable conditions (e.g. *A. didyma* or *B. arceutina*). We found the strongest positive influence of DBH on lichen species richness and functional diversity for *T. cordata* and *Q. robur*. This can be explained by

Table 5
Relative abundance of epiphytic lichen species with the total number of occurrences over five and their indicative values regarding the studied tree hosts. The IndVal statistics and *P*-values of species' association with particular tree host species were calculated using the IndVal method. Relative abundance (fraction of plots with the species occurrence) of species statistically significantly ($P < 0.05$) associated with particular tree hosts are marked in **bold**.

Species	Relative abundance					IndVal	*P*	Total number of occurrences
	Carpinus betulus	*Prunus cerasifera*	*Populus tremula*	*Quercus robur*	*Tilia cordata*			
Acrocordia gemmata (Ach.) A. Massal.	0.000	0.000	**1.000**	0.000	0.000	0.207	0.001	6
Anisomeridium biforme (Borrer) R.C. Harris	0.000	0.000	**0.554**	0.446	0.000	0.095	0.039	8
Anisomeridium polypori (Ellis & Everh.) M.E. Barr	0.000	0.000	**0.538**	0.343	0.120	0.167	0.003	16
Arthonia ruana A. Massal.	0.000	0.000	0.000	0.000	**1.000**	0.433	0.001	13
Athallia pyracea (Ach.) Arup, Frödén & Søchting	0.000	0.000	**0.959**	0.041	0.000	0.397	0.001	13
Bacidia arceutina (Ach.) Arnold	0.203	0.000	**0.797**	0.000	0.000	0.330	0.001	15
Bacidina mendax Anzi	0.020	0.301	0.166	**0.473**	0.040	0.236	0.001	29
Bacidina modesta (Zwackh ex Vain.) S. Ekman	0.000	**0.800**	0.000	0.000	0.200	0.133	0.005	7
Buellia griseovirens (Turner & Borrer ex Sm.) Almb.	0.000	**0.820**	0.000	0.063	0.117	0.164	0.001	9
Candelariella efflorescens R.C. Harris & W.R. Buck	0.105	0.105	0.000	**0.789**	0.000	0.197	0.001	9
Cladonia coniocraea (Flörke) Spreng.	0.000	0.094	0.098	**0.808**	0.000	0.173	0.002	8
Coenogonium pineti (Ach.) Lücking & Lumbsch	0.304	0.087	0.000	0.000	**0.609**	0.243	0.001	20
Evernia prunastri (L.) Ach.	0.013	**0.546**	0.014	0.325	0.101	0.510	0.001	59
Graphis scripta (L.) Ach. s.l.	0.000	0.174	0.000	0.000	**0.826**	0.330	0.001	15
Gyalecta fagicola (Arnold) Kremp.	0.221	0.000	0.000	**0.632**	0.147	0.113	0.019	8
Hypogymnia physodes (L.) Nyl.	0.000	**0.880**	0.000	0.082	0.038	0.557	0.001	23
Hypogymnia tubulosa (Schaer.) Hav.	0.000	**0.949**	0.000	0.051	0.000	0.316	0.001	11
Lecania naegelii (Hepp) Diederich & van den Boom	**0.527**	0.087	0.138	0.236	0.013	0.491	0.001	64
Lecanora argentata (Ach.) Malme	0.150	0.023	**0.632**	0.161	0.035	0.567	0.001	46
Lecanora carpinea (L.) Vain.	0.266	**0.288**	0.145	0.254	0.047	0.259	0.002	106
Lecanora chlarotera Nyl.	0.134	0.258	0.224	**0.364**	0.021	0.221	0.004	45
Lecanora leptyrodes G.B.F. Nilsson	0.166	**0.432**	0.019	0.365	0.018	0.303	0.001	57
Lecanora pulicaris (Pers.) Ach.	0.200	**0.357**	0.025	0.100	0.318	0.345	0.001	91
Lecanora symmicta (Ach.) Ach.	0.000	**0.684**	0.024	0.122	0.171	0.592	0.001	44
Lecanora varia (Hoffm.) Ach.	0.000	**0.775**	0.115	0.000	0.111	0.077	0.035	5
Lecidella elaeochroma (Ach.) M. Choisy	**0.259**	0.215	0.213	0.246	0.068	0.259	0.001	127
Lepraria incana (L.) Ach.	0.077	**0.769**	0.000	0.000	0.154	0.103	0.019	6
Lepraria rigidula (B. de Lesd.) Tønsberg	0.000	**0.683**	0.079	0.163	0.076	0.091	0.039	8
Melanelixia glabratula (Lamy) Sandler & Arup	0.109	**0.544**	0.017	0.179	0.151	0.435	0.001	57
Melanelixia subaurifera (Nyl.) O. Blanco, A. Crespo, Divakar, Essl., D. Hawksw. & Lumbsch	0.013	**0.779**	0.026	0.055	0.128	0.623	0.001	35
Melanohalea exasperatula (Nyl.) O. Blanco, A. Crespo, Divakar, Essl., D. Hawksw. & Lumbsch	0.000	**0.903**	0.000	0.097	0.000	0.120	0.013	5
Mycobilimbia epixanthoides (Nyl.) Vitik., Ahti, Kuusinen, Lommi & T. Ulvinen	**0.667**	0.000	0.000	0.000	0.333	0.111	0.015	8
Myriolecis hagenii (Ach.) Śliwa, Zhao Xin & Lumbsch	0.000	0.074	**0.651**	0.238	0.037	0.202	0.002	17
Opegrapha niveoatra (Borrer) J.R. Laundon	0.000	**0.560**	0.000	0.300	0.140	0.112	0.015	9
Parmelia barrenoae Divakar, M.C. Molina & A. Crespo	0.006	**0.507**	0.065	0.322	0.100	0.473	0.001	60
Parmelia sulcata Taylor	0.000	**0.516**	0.092	0.286	0.107	0.223	0.001	28
Phaeophyscia nigricans (Flörke) Moberg	0.061	0.000	**0.939**	0.000	0.000	0.259	0.001	9
Phaeophyscia orbicularis (Neck.) Moberg	0.136	0.085	**0.544**	0.236	0.000	0.375	0.001	36
Physcia adscendens (Fr.) H. Olivier	0.090	**0.360**	0.207	0.289	0.055	0.312	0.001	79
Physcia aipolia (Ehrh. ex Humb.) Fürnrohr subsp. *aipolia*	0.000	**0.842**	0.071	0.018	0.069	0.505	0.001	23
Physcia dubia (Hoffm.) Lettau	0.305	**0.437**	0.051	0.141	0.066	0.291	0.001	50
Physcia tenella (Scop.) DC.	0.082	**0.303**	0.233	0.300	0.082	0.293	0.001	106
Platismatia glauca (L.) W.L. Culb. & C.F. Culb.	0.000	**1.000**	0.000	0.000	0.000	0.233	0.001	7
Polycauliona polycarpa (Hoffm.) Frödén, Arup & Søchting	0.064	**0.654**	0.000	0.171	0.112	0.501	0.001	42
Porina aenea (Wallr.) Zahlbr.	0.059	0.000	0.000	0.000	**0.941**	0.314	0.001	11
Pseudoschismatomma rufescens (Pers.) Ertz & Tehler	**0.563**	0.047	0.316	0.050	0.023	0.188	0.003	20
Ramalina farinacea (L.) Ach.	0.050	**0.577**	0.026	0.309	0.038	0.423	0.001	46
Rinodina pyrina (Ach.) Arnold	**0.498**	0.137	0.071	0.276	0.017	0.216	0.004	31
Rinodina sophodes (Ach.) A. Massal.	0.000	**0.817**	0.021	0.043	0.120	0.572	0.001	27
Ropalospora viridis (Tønsberg) Tønsberg	0.067	0.399	0.000	0.036	**0.499**	0.183	0.005	20
Scoliciosporum sarothamni (Vain.) Vězda	0.147	**0.659**	0.057	0.137	0.000	0.374	0.001	28
Usnea dasopoga (Ach.) Röhl.	0.000	**0.833**	0.000	0.000	0.167	0.111	0.020	5
Xanthoria parietina (L.) Th.Fr.	0.084	**0.372**	0.284	0.195	0.065	0.372	0.001	95

the gradual colonization of these trees by epiphytes attributed to the more advanced stages of lichen assemblages succession.

Regarding the invasive *P. cerasifera*, we observed only a slight impact of DBH on species richness, functional richness, and functional dispersion of the lichen biota. This differs totally from our initial expectations formulated in Hypothesis 2, which stated that the species richness and functional diversity of lichens on *P. cerasifera* would increase with its DBH. Previous studies on other invasive tree species, such as *Q. rubra* in Sweden (Gustafsson et al., 2023), have also shown no effect of DBH on lichens' species richness, while also reporting lower species richness compared to native trees. The high species richness and functional diversity of epiphytes inhabiting *P. cerasifera* may be linked with the presumably easy colonization rates revealed by epiphytes from neighbouring host trees, as well as hosts from more distant areas of the BNP, supported by the presence of some ancient forest indicator species that occurred exclusively on *P. cerasifera* trees (e.g. *C. cetrarioides, F. caperata,*

Table 6
Rare and exclusive lichen species found on individual trees (species very rare, occurring in fewer than 5 plots, not included in the IndVal analysis), exclusive to particular phorophytes.

Lichen species	*Carpinus betulus*	*Prunus cerasifera*	*Populus tremula*	*Quercus robur*	*Tilia cordata*	Total number of occurrences
Arthonia didyma Körb.	+					1
Bacidia biatorina (Körb.) Vain.				+		2
Bacidia rubella (Hoffm.) A. Massal.			+			2
Cetrelia cetrarioides (Delise) W.L. Culb. & C.F. Culb.		+				1
Cladonia coniocraea (Flörke) Spreng.		+				1
Fellhanera gyrophorica Sérus., Coppins, Diederich & Scheidegger		+				1
Flavoparmelia caperata (L.) Hale		+				1
Lecanora conizaeoides Cromb.		+				1
Lecanora thysanophora R.C. Harris		+				1
Lecidea nylanderi (Anzi) Th. Fr.		+				1
Lepraria elobata Tønsberg		+				2
Micarea micrococca (Körb.) Gams ex Coppins		+				1
Myriolecis sambuci (Pers.) Clem.			+			2
Opegrapha vulgata Ach.		+				1
Pertusaria coccodes (Ach.) Nyl.		+				1
Protoparmelia hypotremella van Herk, Spier & V. Wirth	+					2
Pseudevernia furfuracea (L.) Zopf		+				1
Pyrenula nitidella (Flörke) Müll. Arg.	+					1
Ramalina fraxinea (L.) Ach.		+				3
Trapeliopsis flexuosa (Fr.) Coppins & P. James		+				1
Usnea subfloridana Stirt.		+				2

O. vulgata, *P. coccodes*, *R. fraxinea*, *U. dasopoga* or *U. subfloridana*). Thus, invasive *P. cerasifera* appeared highly similar in terms of the functional diversity of epiphytes found on *C. betulus* and *P. tremula*, suggesting that these trees, regardless of their size, can serve as trees hosting high functional diversity of lichens. Moreover, lichen assemblages inhabiting these three host trees may be characterized both by the notable contribution of pioneer species, typical of the early stages of epiphyte succession, and lichen taxa typical of mature trees, indicative of the old-growth forest ecosystem. The obtained results contradict Hypothesis 3, which assumed that the lichen biota growing on *P. cerasifera* would consist only of common and most frequent species occurring on neighbouring native trees. Similar results were reported for *P. spinosa*, where lichen species assemblages hosted by this phorophyte expressed a wide range of ecological strategies, from pioneer species to late colonizers (Ferry and Lodge, 1996). This particular characteristic of *P. cerasifera* – its ability to be colonized by ecologically diverse groups of lichens – can be explained by its strong resemblance to other phylogenetically-close Rosaceae species, such as *Malus domestica*, which is known to be a suitable host for rare and stenotopic lichen species (Ginszt et al., 2022; Matwiejuk, 2017). Similar patterns were identified for the invasive *Castanea sativa* on the Canary Islands. The lichen biota of this invasive tree differed considerably from the biota of native tree species, yet it also served as a habitat for rare species associated with old and well-preserved forests (González-Montelongo and Pérez-Vargas, 2021).

Interpreting the results obtained for the CWMs of lichen functional traits, the lack of differences in spore shape among tree species and the absence of an effect of increasing DBH on epiphyte diversity can be explained by the presence of species with both small and large spore shapes. Early-successional epiphytes (e.g. *L. symmicta*), which colonize trees with small DBH, and forest-specialist species (e.g., *P. nitidella*), characteristic of larger trees, could both contribute to this pattern. The highest spore volume CWM values were associated with *T. cordata*, likely due to the presence of forest-specialist species adapted to stable microhabitat conditions (e.g. *A. ruana* or *G. scripta*). These taxa may take advantage of the diverse range of microhabitats available on this tree, and therefore do not need to disperse over long distances, which would otherwise require the production of smaller, lighter spores (e.g. Pentecost, 1981; Johansson et al., 2012). Contrary, the results for *C. betulus* indicate that it was characterized by the presence of epiphyte species with small spore volume (e.g. *L. naegelii*) and ascomata area (e.g. *L. cyrtella* or *R. pyrina*). This may suggest a relatively low availability of suitable microhabitats for lichens developing on this phorophyte in the initial stages of oak-hornbeam forest succession.

The highest contribution of sorediate lichens was associated with *P. cerasifera* and, to a lesser extent, with *Q. robur* and *T. cordata*. Lichens producing soredia can spread rapidly and colonize new substrates, which may explain their ubiquity (e.g. Nimis and Martellos, 2003). However, this asexual reproduction strategy is also considered typical for lichen taxa better adapted to stable environments offered by old-growth forest ecosystems (e.g. Ronnås et al., 2017; Ertz et al., 2018). Thus, the high proportion of sorediate species (e.g. *H. tubulosa* or *R. farinacea*) on *P. cerasifera* may confirm both the wide spectrum and relatively large stability of the microhabitats this tree provides. Based on the abovementioned patterns we reject Hypothesis 2, assuming a positive impact of increasing the DBH on lichen functional diversity, and Hypothesis 3, assuming that epiphytes assemblages inhabiting *P. cerasifera* would be composed only of common and most frequent species occurring on neighbouring native trees.

4.3. Mechanisms explaining the assembly processes of lichen communities

The highest functional richness values recorded for *P. cerasifera* may suggest that the diversity of realized niches and the volume of the filled niche hyperspace were the greatest on this tree. This indicates that *P. cerasifera* may provide a wider range of specific microhabitats, which are effectively colonized and extensively utilized by various functional types of lichens, including pioneer and ancient forest indicator species. These include, for instance, sorediate species (e.g. *Buellia griseovirens*), epiphytes with large and small ascomata area (e.g. *U. subfloridana* or *Micarea micrococca,* respectively), species with large and small spore volumes (e.g. *P. aipolia* or *M. micrococca*, respectively), as well as lichen taxa producing large and small spores shapes (e.g. *B. modesta* or *L. varia*, respectively). Therefore, niche differentiation (i.e. high heterogeneity of the species' realized niches) would be considered one of the key mechanisms shaping the community assembly processes of epiphytic lichens on *P. cerasifera* trees under the DBH gradient of the trees surveyed. These patterns contradict Hypothesis 3, which predicted that *P. cerasifera* as an invasive tree species would provide a low capacity of ecosystem services for epiphytes compared to native trees. Although niche differentiation appears to play an important role in shaping lichen communities on *P. cerasifera*, we acknowledge that this interpretation is based on indirect evidence from functional diversity parameters assessment and should be treated with a caution. Further studies involving direct tests of niche differentiation versus neutral or habitat filtering mechanisms are needed to confirm this.

Regarding native phorophytes, the functional richness of lichens was lower than on *P. cerasifera*. This indicates a lower diversity of niches realized by epiphytes, a lower degree of niche hyperspace occupancy, and likely a stronger influence of habitat filtering in shaping the epiphytic biota structure on native phorophytes. This potentially high importance of habitat filtering in shaping the lichen community assembly on native host species may be explained by the lack of suitable microhabitats on the bark of smaller trees, which have not yet developed the appropriate pH, physical structure, nutrient content, water-holding capacity, and light availability (e.g. Barkman, 1958; Lie et al., 2009; Benítez et al., 2015). As a result, individual lichen species can colonize only a low number of small-size microhabitats with particular properties, continuously developing alongside increasing the DBH. A positive relationship between DBH and functional richness, strongly influenced by tree species identity, may confirm these patterns. Regarding tree hosts such as *T. cordata* or *Q. robur*, only larger specimens can host a higher diversity of more dissimilar lichen realized niches. However, for *P. cerasifera*, even small trees can offer a wide spectrum of niches for colonization early in the life stages of this host species.

5. Conclusion

Our study provided the first assessment of invasive tree species impact on lichen functional diversity, and one of few studies describing the invasive tree impact on the taxonomic diversity of epiphytes. Understanding the mechanisms shaping the species and functional diversity of lichen biota on native phorophytes forming the early-successional temperate deciduous forest, as well as on the co-occurring invasive *P. cerasifera*, enabled us to assess this tree's impact on epiphytic lichen assemblages. We revealed higher taxonomic and functional diversity on invasive *P. cerasifera* than on four native tree species. Surprisingly, lichen communities on *P. cerasifera* were similarly distant to pioneer and late-successional species, and the exception was closer similarity of *P. cerasifera* to late-successional *Q. robur.* The lichen biota inhabiting *P. cerasifera* included both early-successional pioneer species and late-successional, ancient forest indicator species. It also comprised epiphytes with contrasting functional traits and taxa not recorded on native phorophytes, with niche differentiation identified as a likely key mechanism shaping the assembly rules of lichen communities. In this context, *P. cerasifera* appears as a phorophyte with a great potential for supporting the restoration and maintenance of high epiphyte species diversity. At the same time, it may serve as an effective refuge and an important source of propagules for numerous lichen species inhabiting trees in urban landscapes and forest monocultures. However, to determine the precise role of *P. cerasifera* in the restoration of human-transformed ecosystems through the recovery of lichen diversity, further detailed studies are necessary. These would benefit from considering not only the microscale of specific substrates or *P. cerasifera*'s bark properties but also the level of the entire ecosystem and landscape context.

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Ethical statement

The study did not involve human or animal participants as study subjects.

CRediT authorship contribution statement

Wojciech Adamowski: Writing – review & editing, Writing – original draft, Investigation. **Dyderski Marcin Krzysztof:** Writing – review & editing, Writing – original draft, Visualization, Formal analysis. **Anna Łubek:** Writing – review & editing, Writing – original draft, Visualization, Resources, Methodology, Investigation, Data curation, Conceptualization. **Sylwia Wierzcholska:** Writing – review & editing, Writing – original draft, Investigation, Conceptualization. **Patryk Czortek:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Resources, Methodology, Formal analysis, Data curation, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Raw data are deposited in the "figshare" repository under the following link: https://doi.org/10.6084/m9.figshare.28692680.v1

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