

Article

Composition and Specialization of the Lichen Functional Traits in a Primeval Forest—Does Ecosystem Organization Level Matter?

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Abstract: Current trends emphasize the importance of the examination of the functional composition of lichens, which may provide information on the species realized niche diversity and community assembly processes, thus enabling one to understand the specific adaptations of lichens and their interaction with the environment. We analyzed the distribution and specialization of diverse morphological, anatomical and chemical (lichen secondary metabolites) traits in lichen communities in a close-to-natural forest of lowland Europe. We considered these traits in relation to three levels of forest ecosystem organization: forest communities, phorophyte species and substrates, in order to recognize the specialization of functional traits to different levels of the forest complexity. Traits related to the sexual reproduction of mycobionts (i.e., ascomata types: lecanoroid apothecia, lecideoid apothecia, arthonioid apothecia, lirellate apothecia, stalked apothecia and perithecia) and asexual reproduction of mycobionts (pycnidia, hyphophores and sporodochia) demonstrated the highest specialization to type of substrate, tree species and forest community. Thallus type (foliose, fruticose, crustose and leprose thalli), ascospore dark pigmentation and asexual reproduction by lichenized diaspores (soredia and isidia) revealed the lowest specialization to tree species and substrate, as well as to forest community. Results indicate that lichen functional trait assemblage distribution should not only be considered at the level of differences in the internal structure of the analyzed forest communities (e.g., higher number of diverse substrates or tree species) but also studied in relation to specific habitat conditions (insolation, moisture, temperature, eutrophication) that are characteristic of a particular forest community. Our work contributes to the understanding of the role of the forest structure in shaping lichen functional trait composition, as well as enhancing our knowledge on community assembly rules of lichen species.

Keywords: functional traits composition; substrates; phorophytes; forest communities; Białowieża Forest



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1. Introduction

Lichens are important and widely applied environmental indicators of the naturalness and quality of the environment, used inter alia to determine changes in forest ecosystems caused by management [1–3]. They are used to select the most valuable habitats for the protection of all biodiversity [4–7]. Traditionally, the assessment of the quality of the environment relied on taxonomic diversity metrics [3]. However, assessing the quality of the environment simply based on lichen species diversity is not sufficient due to the high site specificity and context dependency of the patterns revealed, thus affecting their low transferability into similar ecosystem types of different geographical zones. Current trends place emphasis on describing the functional composition that provides additional information about biodiversity patterns and community assembly processes [8–11]. Therefore,

application of the functional diversity approach in lichenological studies provides more mechanistic insights into the importance of environmental factors driving lichen biodiversity changes more accurately than the traditional approach based exclusively on species richness. For example, the high taxonomic diversity of lichens found in higher mountain elevations is not reflected by the high functional diversity of the lichen communities found there [8]. At higher elevations, species with fruticose and foliose thalli, benefiting from the high air humidity, and asexual reproductive structures facilitating faster establishment under unfavorable conditions have been found [8]. Conversely, at lower elevations, species with crustose thalli and reproducing sexually by large, pigmented or septate spores have been found [8]. High functional diversity, e.g., in natural forests or in forests with low human influence, may be an indication of the high microhabitat diversity available for lichens, while low functional diversity may express simplification of lichen community composition due to habitat homogenization, e.g., in intensively managed stands [3,10]. Functional traits enable us to more clearly understand the specific adaptations of lichens to environmental conditions [2,8,11–13] and, furthermore, to assess the degree of naturalness of the entire ecosystem or the degree of its anthropogenic transformation [2,9,10,14,15]. Understanding the patterns of occurrence of lichen functional traits in different microhabitats and forest communities can also help to assess changes in the lichen biota and across the entire forest ecosystem, resulting from forest management, pollution, changes in the structure of forests due to fires, insect outbreaks and tree diebacks [2,9,10,16,17]. For example, the higher abundance of lichens with small ascospores at lower mountain elevations is connected with their better adaptation to low precipitation [8], while the higher abundance of species with a vegetative reproduction in managed forests, compared to non-managed forests, may be explained by their better adaptation to colonization in habitats under human impact [10].

The use of lichen functional traits to assess the naturalness of the forest, or the degree of its transformation, is possible only if a reference ecosystem, which may be treated as a model for the distribution of lichen functional traits, is known. Therefore, forest areas protected from direct human influence deserve special attention; they are biodiversity hotspots [18–22] and model ecosystems for identifying and assessing the role of various environmental factors, e.g., climatic conditions (temperature, precipitation), type of forest stand or composition of tree species building the forest, in shaping lichen species diversity patterns and their functional traits [20,23,24]. Until now, model studies concerning the composition and distribution of lichen functional traits in well-preserved areas of the different regions of Europe, with various forest communities and diverse tree species composition, are rare and mostly conducted in mountain areas [8]. More common are studies comparing old forest stands with managed forests (e.g., [2,10,14,25,26]). However, in most cases, these works merely describe selected functional traits of lichens, e.g., thallus type, type of photobionts, type of ascomata or type of vegetative reproduction (e.g., [20,24]). Various functional traits of lichens from European lowland temperate forests of a primary character have not been analyzed so far (see [19]). In addition, there are no works on the functional composition and distribution of functional traits in relation to different levels of ecosystem organization, i.e., in relation to forest communities, tree species and types of substrates. The last remaining temperate primeval forest in Europe, which is valuable for studying the distribution of the functional traits of lichens, is the Białowieża Forest [27–29]. Here, one can find different forest communities of complex stand structure, shaped by various species of trees of different ages, and with a significant amount of deadwood and specific microclimate [27]. All these characteristics contribute towards shaping the composition of the lichen biota [7] and explain the differences in the grouping of lichens by different functional traits.

In the Białowieża Forest, two main ecological mechanisms shape the functional diversity of lichen communities: niche partitioning in deciduous forests (where lichens characterized by functional traits such as large ascomata and ascospores are dominant) and environmental filtering in coniferous forests (where lichens with small ascomata and

ascospores are dominant [30]). In this paper, we conducted a broad analysis of the diverse functional traits of lichen species analyzed in previous lichenological works: morphological, anatomical and chemical (lichen secondary metabolites) properties, which has not yet been conducted so far in the forest communities of primeval character in the European lowlands. Research on the distribution of lichen functional traits, which may be considered as adaptations to particular habitat properties, allows for a deeper understanding of the ecological mechanisms which shape lichen assemblage structure [20,31–34]. In our study, we considered three levels of forest ecosystem organization: forest communities, phorophyte species and substrates, in order to recognize specialization of lichen functional traits to different spatial scales. Application of this approach would provide detailed knowledge on the importance of particular spatial scales in shaping the distribution patterns of lichen functional traits, which, in turn, may be highly useful in the formulation of nature conservation priorities. More specifically, it may constitute a basis for the identification of the spatial scale(s) on which conservation of lichen species diversity should be focused in particular.

Our aims were to examine (i) patterns of distribution of lichen functional traits and the total functional composition of lichens in relation to forest communities, tree species and substrates, (ii) which functional traits dominated in the lichen community at the level of forests communities, tree species and substrates and (iii) whether lichen species' functional traits show specialization in relation to type of forest, species of tree or type of substrate.

2. Materials and Methods

2.1. Study Area and Data Collection

The study area was located in northeastern Poland in the Białowieża Forest, in the Białowieża National Park (52°46' N 23°52' E). The area of the Białowieża Forest is characterized by a transitional temperate climate dominated by continental influences and is referred to as a forest of the temperate zone [35]. This is one of the best-preserved forests in the European lowland [27–29,36]. The Białowieża National Park is characterized by a high structural and spatial forest complexity, as well as specific microclimate conditions, which is reflected in its high biodiversity. The long-term exclusion of this forest from direct human interference provides a high variety and abundance of substrates creating specific microhabitats for lichen species [37–39], i.e., deadwood in diverse stages of decomposition, dead standing and fallen trees, exposed roots of windthrown trees, various tree species of different ages and other microhabitats not found or rarely represented in managed forests.

The field survey was conducted in 2014–2015, on a set of 144 permanent plots, 100 × 100 m each, established in the 1980s [30,37–41]. This area is covered by the six most common forest communities of the Białowieża Forest distinguished on the basis of phytosociological characteristics, e.g., topography, soil moisture, groundwater level, forest canopy cover and species composition of the herb layer and trees building the stand. Mixed deciduous fertile oak–lime–hornbeam forest *Tilio-Carpinetum* (54 plots) is characteristic of flat areas of mesic soil moisture and a low groundwater level, with 80%–90% canopy cover. Floodplain streamside alder–ash forest *Circaeo-Alnetum* (22 plots) is characteristic of banks of rivers and streams developing on seasonally flooded and wet soils with a high groundwater level, with 60–70% canopy cover. Swamp alder carr *Carici elongatae-Alnetum* (18 plots) is characteristic of shallow depressions, developing on wet seasonally flooded soil with a high groundwater level, and with 50–60% canopy cover. Coniferous mesic (spruce)–pine forest *Peucedano-Pinetum* (27 plots) is characteristic of elevated parts of river terraces, developing on soils with mesic moisture and a low groundwater level, with 40–50% canopy cover. Coniferous pine–oak mixed forest *Pino-Quercetum* (18 plots) is characteristic of hillocks adjacent to river valleys, mostly occurring on moderately wet soil with a low groundwater level and 60% canopy cover. Coniferous moist oak–spruce forest *Quercu-Piceetum* (5 plots) is characteristic of local area depressions, developing on moderately wet soils with a low groundwater level, and 60–70% canopy cover. Among the 144 plots, 64 were homogenous and were covered entirely by only a single commu-

nity, whilst in the remaining plots, 2–3 different communities co-occurred, but invariably, one community dominated and covered at least 70% of the plot. The investigated forest communities were diverse in terms of structure (see also Table 1 in [38]) and tree species composition, which resulted in a high diversity of bark structure, hardness, water capacity, content of chemical compounds and pH [42], together with an abundance of various substrates, as well as microclimatic conditions [38,41,43]. These various components create specific microhabitat factors, which might influence the grouping of lichens with specific functional traits.

On each plot, all lichens (epiphytic, epixylic and epigeic) were recorded. For each lichen species, in each plot, the type of forest community, tree species and type of substrate were recorded. Only lichens growing on trees and wood-related substrates were considered in the analyses. The very low number of soil-dwelling lichens (less than 10 species) and their very low abundance did not allow carrying out analyses on all scales of ecosystem organization, and thus they were excluded from the dataset.

To minimize the load on the results, for each level of forest ecosystem organization, we selected only the six most common entities for analyses. We selected (i) all present types of forest communities, (ii) tree species: European alder *Alnus glutinosa* Gaertn., European ash *Fraxinus excelsior* L., European hornbeam *Carpinus betulus* L., European oak *Quercus robur* L., Norway spruce *Picea abies* (L.) H. Karst, small-leaved lime *Tilia cordata* Mill., and (iii) substrates: bark of trunks of living trees, branches of living trees, stems and branches of shrubs, bark of trunks and branches of fallen trees, wood of trunks and branches of fallen trees (e.g., logs) and wood of dead standing trees (stumps and snags).

The nomenclature of the lichen species follows Fałtynowicz and Kossowska [44] and, in some cases, the newest taxonomic papers, e.g., Sérusiaux et al. [45], Czarnota and Guzow-Krzemińska [46], Ertz et al. [47] and Boluda et al. [48]. The collected material is deposited in the lichen collections of the Jan Kochanowski University in Kielce (KTC) and the University of Gdańsk (UGDA).

2.2. Functional Traits

We evaluated three groups of functional traits of 313 species of lichens: (i) morphological and anatomical, (ii) reproduction and (iii) chemical (lichen secondary metabolites, Table S1). *Lichenomphalia umbellifera* and *Multiclavoula mucida*, recorded in our study area, were excluded from the analyses because they were the only two species of lichenized Basidiomycota in the whole dataset. Traits regarding the sexual and asexual reproduction of each species were considered when a species was found with those traits in the study area.

The functional traits were distinguished and data were completed for each species mainly on the basis of: Purvis [49], Smith et al. [50], Wirth et al. [51], Bässler et al. [8], Koch et al. [12], Malíček et al. [10] and the newest papers with original species descriptions, e.g., Aptroot et al. [52], Divakar et al. [53], Czarnota [54], Czarnota and Guzow-Krzemińska [46,55], Kukwa [56], Palice et al. [57], Guzow-Krzemińska et al. [58,59], Ertz et al. [47], Malíček et al. [60] and Launis et al. [61].

2.2.1. Morphological and Anatomical Traits Considered:

1. Thallus type (leprose, crustose, foliose, fruticose). Leprose and crustose lichen thalli (microlichens) and foliose and fruticose lichen thalli (macrolichens) were distinguished. Lichens with the placodioid thallus type were included in crustose lichens, and filamentous types (e.g., *Usnea*) in fruticose lichens. The morphological thallus types were used in determining the sensitivity of lichens to external factors and changes in the environment (bioindicator of environmental quality [2]), with crustose lichens being more resistant and fruticose lichens being the most sensitive [49].
2. Photobiont type. Four groups of species were distinguished: lichens containing green algae (*Asterochloris*, *Trebouxia*, *Stichococcus* and others), lichens with *Trentepohlia* s.l., lichens with cyanobacteria (*Nostoc*) and non-lichenized taxa lacking photobionts commonly examined by lichenologists, i.e., species of *Chaenothecopsis*, *Microcalicium*

and *Mycocalicium*. *Trebouxia* and other green algae are the most common photobionts in lichen symbioses [62,63], and they can colonize numerous environments and tolerate dry and insolated conditions [64]. *Trentepohlia* photobionts have a particular adaptation to environments with higher temperatures and humidity levels [65,66]. Cyanobacterial photobionts are desiccation-tolerant, but most of them require liquid water for rehydration [63,64].

3. Ascospore dark pigmentation (ascospores that are dark-pigmented; ascospores that are not pigmented). The wall of ascospores can include pigments and melanins, which may relate to specific microhabitats [8], e.g., habitats of higher insolation to which species with dark ascospores are adapted [8,11].
4. Ascospore septation (ascospores that are one-celled, two-celled, multi-celled with transverse septa only or muriform). This trait is probably connected with lichen dispersion and specialization to specific microhabitats [31], e.g., one-celled or two-celled ascospores are dominant in harsher environmental conditions such as higher insolation and temperature fluctuations, while multi-celled ascospores are dominant in milder environments [11].
5. Ascomata texture and pigmentation (ascomata without carbonized structures, ascomata with carbonized structures and/or ascomata with pruina). Dark pigments and melanins present in fungal cells protect ascomata against high solar irradiation and photoinhibition, and dark fruitbodies probably occur more often in environments with high levels of abiotic stress [67]. The presence of pruina, mainly on apothecia, is a physical protection against excessive light or other extreme environmental conditions [68].

2.2.2. Reproduction Traits

1. Ascomata type (generative structures formed by the fungus itself). Six types of ascomata, and their modifications, were distinguished: lecanoroid ascomata (i.e., with a thalline margin), lecideoid ascomata (with no algal cells in the margin), arthonioid ascomata, lirellate ascomata, stalked apothecia and perithecia [50,51]. The sexual reproduction of the fungal partner (mycobiont) ensures the retention of population genetic variability, allowing adaptation to new and changing habitat conditions [49,63,69]. Ascospores are able to disperse over long distances [70].
2. Asexual reproduction of mycobionts (pycnidia, hyphophores and sporodochia). Many species produce conidia or other structures, which are probably important for the effective distribution of mycobiont partners over long distances [10].
3. Asexual reproduction type of both bionts (mycobiont and photobiont) by vegetative diaspores. Soredia and isidia were distinguished as the most common among lichens. Granules present in some lichens (e.g., *Chrysothrix candelaris* and *Lepraria* species) are included in the soredia category. Phyllidia (present only in *Peltigera praetextata* in our study) are included in the isidia category. Vegetative propagules are the fast and efficient mode of co-dispersal of compatible partners [49,63,71], and their production seems to be an adaptation to stable habitats [69,70,72,73].

2.2.3. Chemical (Lichen Secondary Metabolites) Traits

Sixteen groups of the lichen secondary metabolites were distinguished: aliphatic (fatty) acids, antraquinones, benzyl esters, dibenzofurans, diphenyl ethers, orcinol depsides, β -orcinol depsides, orcinol depsidones, β -orcinol depsidones, orcinol tridepsides, pulvinic acid derivatives, terpenes (zeorin), usnic acid derivatives, xanthenes, naphthaquinones and other substances. We empirically confirmed by thin-layer chromatography data on the presence of secondary metabolites in the lichen thalli for most species, and for all these species that may show chemical variability [74–76]. Lichen secondary metabolites occur in various parts of lichen thalli (cortex, medullary layer, soredia and/or apothecial margins) and are easily detectable by thin-layer chromatography [74–76]. They can impact biotic interactions of lichens with their environment ([77] and literature cited within). Several

roles of lichen secondary metabolites have been recognized so far: (i) photoprotection from UVA and UVB light, e.g., anthraquinones, xanthenes, atranorin, usnic acid derivatives and pulvinic acid derivatives [74,77–80], (ii) allelopathic (antibacterial): orcinol and β -orcinol depsides, orcinol and β -orcinol depsidones, usnic acid, gyrophoric acid, lichesterinic acid and terpenes ([74] and literature cited within), (iii) anti-herbivore defense: terpenes, antraquinones, pulvinic acid derivatives, some depsides and depsidones [68,74] and (iv) antioxidant: atranorin, divaricatic acid, pannarin and lecanoric acid [77,80].

2.3. Data Analysis

The number of occurrences of each functional trait was estimated across the whole study area—we recorded the number of a given trait observed in an individual forest community, tree species and substrate, and this served to build a network of dependencies, enabling us to count and compare the specialization of functional traits. To explore the relationships between the chemical, morphological and reproduction traits of the lichen species and forest communities, tree species and substrates, we constructed nine quantitative interaction matrices, using the *plotweb()* function implemented in the *bipartite* package [81]. Thus, based on the frequency of each trait, one separate graphical visualization of the interaction matrix was performed for each of the three groups of functional traits in relation to the three levels of forest ecosystem organization. To assess the degree of specialization of the chemical, morphological and reproduction traits to forest communities, trees and substrates, for each functional trait in each of the nine networks, using the *bipartite::specieslevel()* function, we computed the Poisot et al. [82,83] paired difference index (PDI). A comparison of robustness of the six specialization indices (using empirical and simulated interaction matrices) performed by Poisot et al. [84] revealed that the PDI was a measure of the highest informativity in explaining community structure. The other measures of species specialization taken into consideration were, e.g., resource range (RR) [85], Kullback–Leibler distance (d') [86] and species specificity index (SSI) [87]. The PDI also minimalizes biases connected with the incompleteness of the sampling of all possible interactions in a community and works well with data representing a variety of statistical distributions [84]. The PDI is calculated as follows:

$$PDI = \frac{\sum_{i=2}^R (P_1 - P_i)}{R - 1}$$

where P_1 reflects the highest strength of an interaction, P_i is the interaction strength with the i th forest community, tree or substrate and R is the number of forests, trees and substrates. Strengths of interactions in the case of P_1 and P_i are frequencies of linkages occurring within a particular quantitative interaction matrix [83]. Thus, the PDI contrasts a species' (here functional traits') strongest interaction with one type of forest community, tree or substrate with those over all remaining types at each level of forest ecosystem organization. The PDI ranges from 0 to 1, where low values indicate low specificity (high generalization) and high values indicate high specificity (low generalization) of lichens' traits to the exact forest community, tree and substrate. To assess differences between the PDI of each of the three groups of lichen functional traits to communities, trees and substrates, we performed one-way analysis of variance (ANOVA), followed by a Tukey post hoc test (*agricolae::HSD.test()* function [88]). In order to avoid omitting results of potentially high ecological meaning, regardless of statistical significance, we also focused on size effects [89] and did not adjust p values from multiple tests (e.g., by Bonferroni correction [90]).

Table 1. The Poisot et al. [82,83] specialization index (PDI) of lichen species functional traits in relation to forest communities, tree phorophytes and substrates.

Functional Trait	Trait Id	Forest Community	Tree Phorophyte	Substrate
Chemical traits (lichen secondary metabolites)				
Aliphatic acids	Aliph. acids	0.384	0.491	0.568
Antraquinoses	Antraqu.	0.754	0.744	0.848
Beta-orcinol depsides	B-orc.dps	0.542	0.481	0.606
Beta-orcinol depsinodes	B-orc.dpsnds	0.611	0.643	0.674
Benzyl esters	Benzyl est.	0.585	0.840	0.742
Dibenzofurans	Dibenzof.	0.587	0.506	0.708
Diphenyl ethers	Diphenyl eth.	0.561	0.600	0.748
Naphthaquinones	Naphthaqu.	0.379	0.797	0.709
No substances	No subst.	0.725	0.634	0.823
Orcinol depsides	Orc. dps	0.522	0.368	0.612
Orcinol depsinodes	Orc. dpsnds	0.464	0.540	0.537
Orcinol tridepsides	Orc. tridps	0.473	0.384	0.679
Other substances	Other subst.	0.669	0.672	0.803
Pulvinic acid deriverates	Pulvinic acid	0.634	0.768	0.911
Terpenoids	Terpen.	0.661	0.568	0.782
Usnic acid deriverates	Usnic acid	0.560	0.500	0.608
Xanthones	Xanth.	0.642	0.502	0.793
Morphological and anatomical traits				
Photobiont type:				
Algae absent	Algae absent	0.350	0.684	0.809
Green	Green	0.572	0.497	0.649
Cyanobacteria	Cyanob.	0.775	0.781	0.762
Trentepohlia	Trentep.	0.784	0.683	0.906
Ascospore dark pigmentation:				
Spores not pigmented	Spores not pigm.	0.660	0.648	0.714
Spores pigmented	Spores pigm.	0.642	0.451	0.789
Ascospore septation:				
Spores one-celled	Spores 1-c.	0.582	0.531	0.672
Spores two-celled	Spores 2-c.	0.643	0.494	NA
Spores multi-celled	Spores multi-c.	0.753	0.675	0.855
Spores muriform	Spores murif.	0.660	0.773	0.587
Thallus type:				
Crustose	Crustose	0.663	0.636	0.768
Foliose	Foliose	0.510	0.459	0.649
Fruticose	Fruticose	0.398	0.559	0.494
Leprose	Leprose	0.623	0.364	0.867
Ascomata texture and pigmentation:				
Ascomata with carbonized structures	Ascom. carbo.	0.708	0.709	0.816
Ascomata with carbonized structures + Ascomata with pruina	Ascom. carbo. and pruina	0.625	0.497	0.818
Ascomata without carbonized structures	Ascom. no carbo.	0.641	0.654	0.628
Reproduction traits				
Ascomata type:				
No ascomata	No ascomata	0.702	0.439	0.675
Arthonia	Arthonia	0.551	0.476	0.925
Lecanora	Lecanora	0.726	0.804	0.671
Lecidea	Lecidea	0.566	0.540	0.576
Lirella	Lirella	0.793	0.727	0.888
Stalked	Stalked	0.503	0.687	0.849
Perithecia	Perithecia	0.880	0.919	0.877

Table 1. Cont.

Functional Trait	Trait Id	Forest Community	Tree Phorophyte	Substrate
Asexual reproduction of mycobiont:				
No asexual reproduction of mycobiont	No asex. repr. mycobiont	0.800	0.506	0.720
Hyphophores	Hyphophores	0.604	0.850	0.771
Pycnidia	Pycnidia	0.637	0.602	0.689
Sporodochia	Sporodochia	0.696	0.766	0.998
Asexual reproduction of both bionts:				
No asexual reproduction of both bionts	No asex. repr. both bionts	0.695	0.642	0.809
Isidia	Isidia	0.548	0.647	0.576
Soredia	Soredia	0.695	0.408	0.644

To explore patterns in the composition of functional traits among communities, trees and substrates, for each level of forest ecosystem organization, we performed one separate non-metric multidimensional scaling ordination (NMDS; *vegan::metaMDS()* function [91]) with the maximal number of iterations set to 999. We performed each NMDS using pairwise Bray–Curtis dissimilarity matrices. To ensure the repeatability of each NMDS result, we set the maximal number of random starts to 250. To check how well the NMDS results correspond with raw data, we used the *vegan::goodness()* function, which calculates the goodness of fit (GOF) statistics for ordination results. Following the rule of thumb, very high GOF values (>0.2) indicate a poor fit, while very low GOF (<0.001) values indicate an ideal fit. In addition, we evaluated the results of each NMDS by providing the stress values (SV), which measure the differences between distances in the reduced dimensional space (NMDS axes 1 and 2) compared to the complete multidimensional space. Very low (<0.001) SV indicate that the first two ordination axes explain most of the variability, while high SV (>0.2) point out the high randomness of the results [91]. To reduce the impact of outlier observations (i.e., functional traits rarely or substantially commonly represented in our dataset) on the ordination results, data were normalized prior to NMDSs, using the *vegan::decostand()* function [91]. To determine whether forest communities, trees or substrates were the most heterogeneous regarding the composition of the chemical, morphological and reproduction traits of lichens, for each level of forest ecosystem organization (regarding each of the three groups of functional traits), we calculated the mean Bray–Curtis dissimilarity index (BCI; *vegan::vegdist()* function [91]). All analyses were performed in R software [92].

3. Results

We discovered a similar number of interactions in the networks of lichen traits, at each studied level of ecosystem organization. There were 102 interactions in the network of chemical traits and forests communities, and chemical traits and trees, and 101 links in the network of chemical traits and substrates. Morphological traits were linked by 101, 100 and 93 interactions with forest communities, trees and substrates, respectively. The number of interactions for reproduction traits analyzed revealed 84 links with forest communities, 79 with trees and 77 with substrates (Table 1, Figures 1–3). Comparing the networks presented in Figures 1–3, we obtained quite similar numbers of interactions regarding each level of ecosystem organization and functional trait categories. However, at the same time, we identified different strengths of interactions of particular functional traits with particular ecosystem components, revealing high differences in different traits' association levels (reflected in PDI values; Table 1) with each forest community, tree phorophyte and substrate.

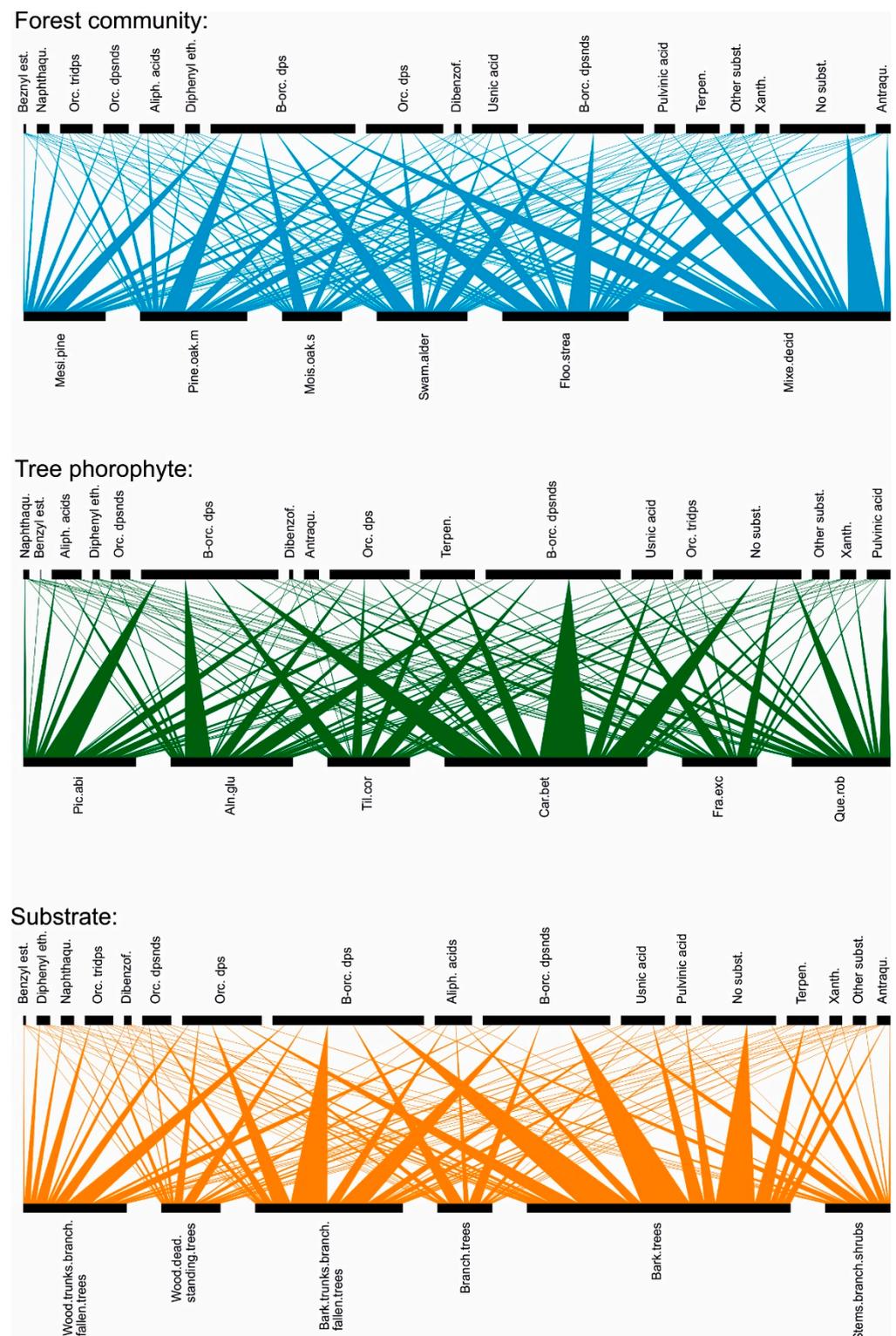


Figure 1. Networks based on the frequency of chemical traits of lichens with forest communities, tree phorophytes and substrates. For full names of functional traits, see Table 1. For full names of forest communities, tree species and substrates, see Section 2.

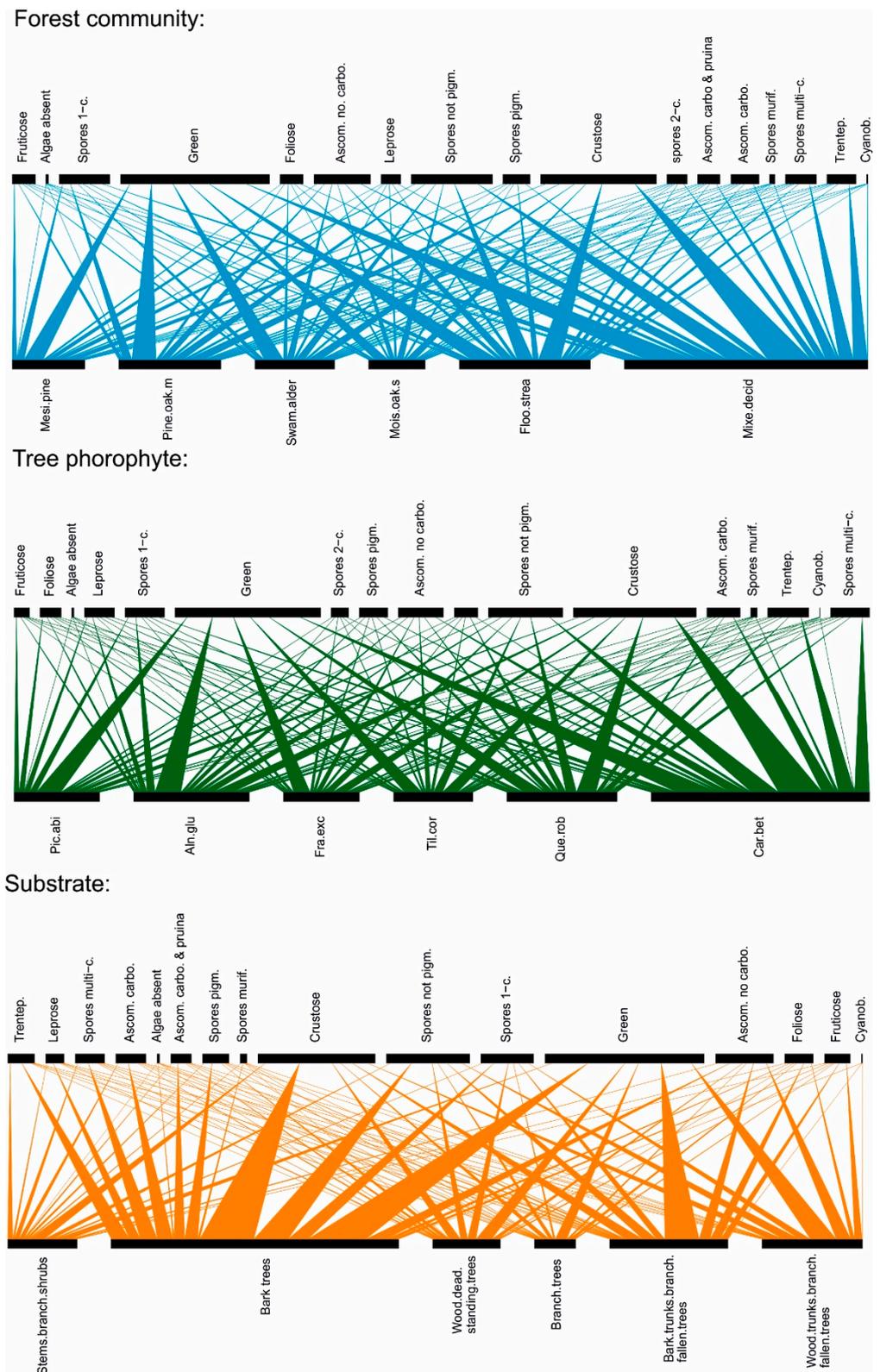


Figure 2. Networks based on the frequency of morphological traits of lichens with forest communities, tree phorophytes and substrates. For full names of functional traits, see Table 1. For full names of forest communities, tree species and substrates, see Section 2.

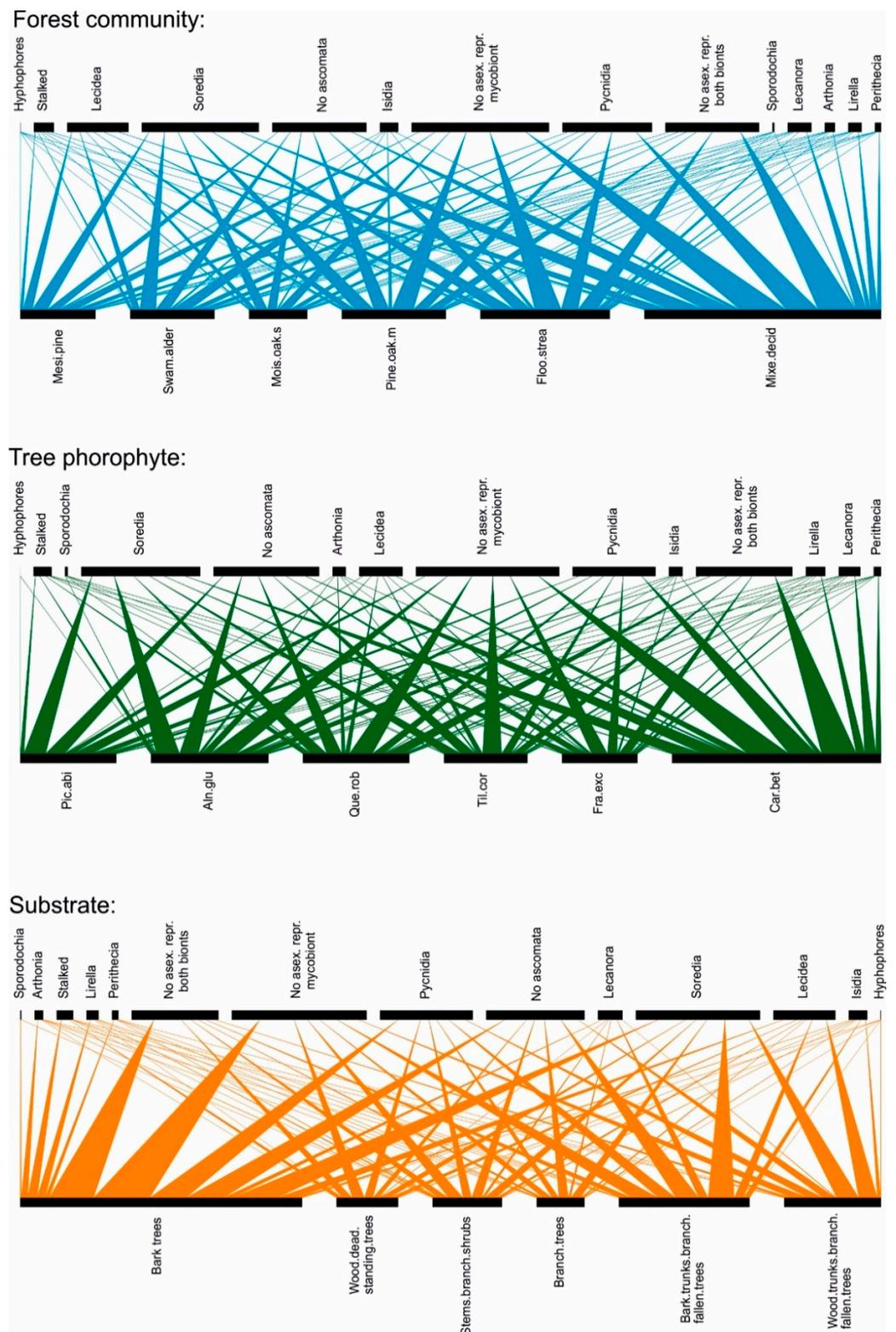


Figure 3. Networks based on the frequency of reproduction traits of lichens with forest communities, tree phorophytes and substrates. For full names of functional traits, see Table 1. For full names of forest communities, tree species and substrates, see Section 2.

The PDI indices of the specialization of the morphological and chemical traits to substrates were significantly higher than their PDI indices to communities and trees. Both of these groups of traits did not differ by PDI value. The PDI indices of the specialization of

the reproduction traits to forest communities, trees and substrates did not differ from each other, but the PDI of this trait group was different from both remaining groups (Figure 4a, Table 2).

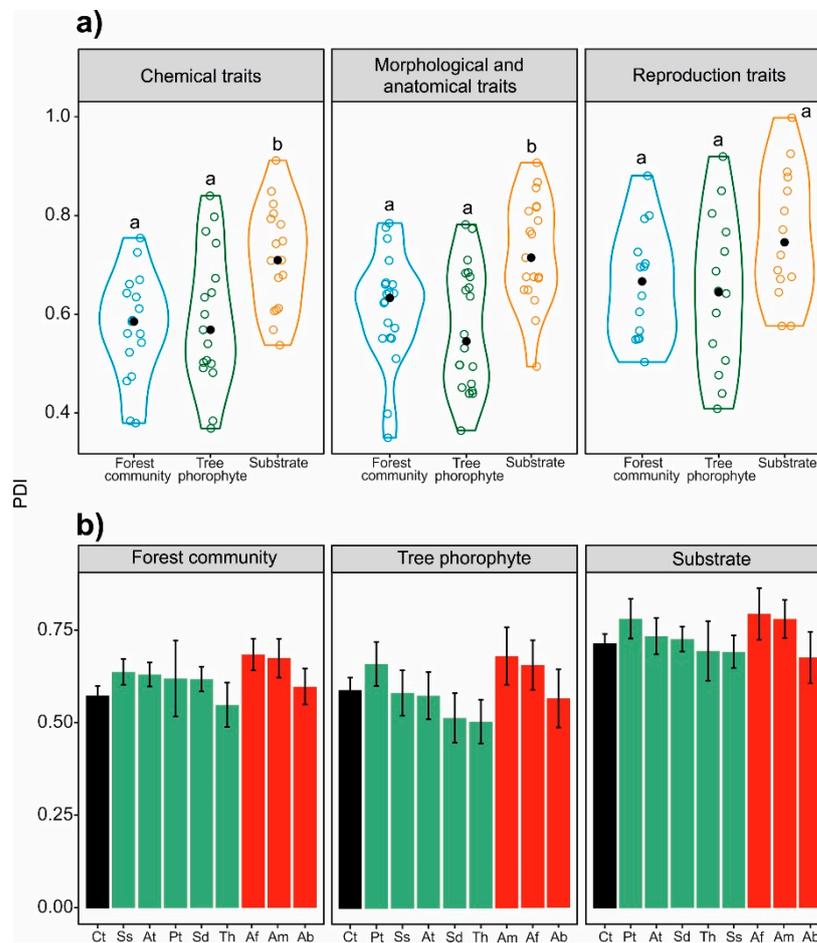


Figure 4. Differences in the Poiset et al. [82,83] specialization index (PDI) of chemical, morphological and anatomical and reproduction traits of lichens between forest community, tree phorophyte and substrate levels (a) and a comparison of the mean (\pm SE) PDI calculated for individual traits of lichens in respect to forest community, tree phorophyte and substrate levels (b). Empty points in (a) are sites and solid lines around sites are Kernel density plots. The black solid points in (a) are medians. Groups marked by the same letter in (a) do not differ statistically significantly at $p = 0.05$, according to Tukey's posteriori test. Black bars in (b) are chemical traits (Ct). Light green bars in (b) are morphological and anatomical traits: ascospore septation (Ss), ascomata texture and pigmentation (At), photobiont type (Pt), ascospore dark pigmentation (Sd) and thallus type (Th). Red bars in (b) are reproduction traits: ascomata type (Af), asexual reproduction of mycobiont (Am) and asexual reproduction of both bionts (Ab).

Considering the highest differences in the mean specialization of individual morphological traits to trees, the highest values of the PDI were reported for photobiont type, ascospore septation and ascomata type, and the lowest for thallus type and ascospore dark pigmentation. Regarding forests and substrates, only weak differences between the mean specialization of individual morphological traits were found, with slightly lower PDI values revealed for thallus type (regarding forest communities), and slightly higher levels of specialization reported for photobiont type (regarding substrates). When considering the PDI of individual reproduction traits, the asexual reproduction of both bionts was identified as the functional trait with the lowest degree of specialization for each of the three levels of forest ecosystem organization. In contrast, ascomata type formation and

asexual reproduction of mycobiont were the traits which demonstrated the highest levels of specialization with respect to forest community, tree and substrate levels (Figure 4b).

Table 2. Comparison of the Poisot et al. [82,83] specialization index (PDI) of chemical, morphological and reproduction traits of lichen species between forest community, tree phorophyte and substrate levels. *F* and *p* values calculated from ANOVA are shown. Groups marked by the same letter in a row do not differ significantly at *p* = 0.05, according to Tukey's posteriori test. The highest value is indicated in bold.

Parameter	Forest Community		Tree Phorophyte		Substrate		ANOVA	
	Mean	SE	Mean	SE	Mean	SE	<i>F</i>	<i>p</i>
Chemical traits	0.574a	0.106	0.590a	0.139	0.715b	0.105	7.212	<0.01
Morphological traits	0.612a	0.111	0.571a	0.124	0.727b	0.106	9.618	<0.001
Reproduction traits	0.661a	0.113	0.644a	0.157	0.762a	0.132	3.099	0.056

The NMDS ordination, performed for all groups of lichen functional traits and forest communities (GOF = 0.005; SV = 0.040), revealed compositional similarity between all types of communities, expressed in the almost equal distribution of most traits (Figure 5, forest community). However, some of the traits revealed a slightly higher association with a particular community, e.g., *Trentepohlia* photobiont, perithecia, lecanoroid and lirellate ascomata, ascomata with carbonized structures and/or with pruina, multi-celled and muriform ascospores, lack of asexual reproduction of both bionts (i.e., soredia and isidia), the presence of antraquinones, terpenes, pulvinic acid derivatives or usnic acid derivatives or lack of lichen secondary metabolites, were associated with mixed deciduous and floodplain streamside communities, which, in addition, was distinguished by the presence of lichens with a cyanobacteria photobiont, arthonioid apothecia and sporodochia and producing xanthenes. Only the photobiont absent functional trait revealed a slightly higher association with wet swamp alder carr than with the other forest communities.

A separate group included functional traits which revealed a higher association with coniferous communities (mesic (spruce)–pine forest, pine–oak mixed forest and moist oak–spruce forest), e.g., fruticose thalli, lecideoid and stalked types of ascomata, aseptate or two-celled ascospores, ascospores dark pigmented or ascomata lack, soredia, isidia and secondary metabolites aliphatic acids, benzyl esters, orcinol tridepsides, orcinol depsidones, naphthaquinones, diphenyl ethers, dibenzofurans, β -orcinol depsides and β -orcinol depsidones. Among the coniferous forests, the mesic (spruce)–pine community was distinguished by the highest presence of benzyl esters.

Whilst considering the composition of functional traits at the tree species level, we revealed a compositional continuum of traits among the studied phorophytes (GOF = 0.011; SV = 0.080). However, some traits revealed a higher association with oak and spruce, separating these two tree species from other trees (Figure 5, tree phorophyte). Stalked and arthonioid ascomata, apothecia with dark carbonization and pruina, sporodochia and non-lichenized fungi lacking photobionts, as well as some secondary metabolites, xanthenes and pulvinic acid derivatives, revealed a greater association with oak. In the case of spruce, secondary metabolites such as benzyl esters, naphthaquinones and dibenzofurans revealed the strongest association, while sorediate, isidiate, fruticose and foliose functional traits revealed a slightly lower association degree.

Regarding the composition of functional traits on substrates (GOF = 0.006; SV = 0.054), we identified several well-pronounced groups of traits assembled in specific substrates (Figure 5, substrate level). The most distinct group of traits, i.e., photobiont absent, stalked apothecia and secondary metabolites pulvinic acid derivatives, naphthaquinones, diphenyl ethers, dibenzofurans and benzyl esters, was represented by traits associated with the wood of dead standing trees (i.e., stumps and snags). The second distinct group of traits, e.g., hyphophores, lecideoid ascomata with carbonized structures and pruina, one-celled and pigmented ascospores and orcinol tridepsides, formed an assemblage that was associated with the wood of trunks and the branches of fallen trees. The remaining functional traits, e.g., multi-celled and not pigmented ascospores, isidia and soredia, were more associated

with the bark of trees, and the bark and branches of fallen trees. However, some traits, i.e., perithecioid, lirellate and lecanoroid ascomata, seem to be associated more with the stems and branches of shrubs.

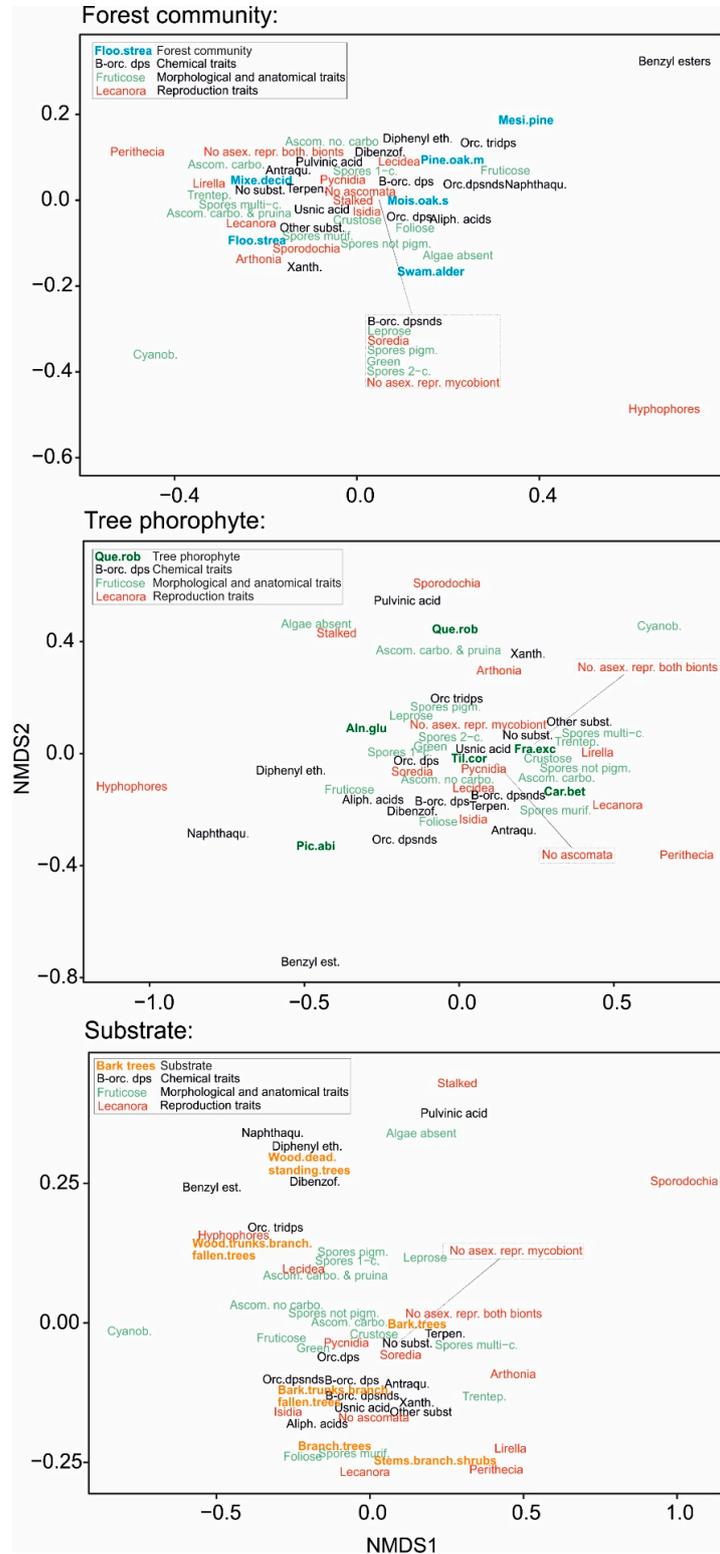


Figure 5. Results of NMDS ordination performed for functional traits of lichens regarding forest community, tree phorophyte and substrate levels. For full names of functional traits, see Table 1. For full names of forest communities, tree species and substrates, see Section 2.

The highest compositional heterogeneity (the highest BCI) of the morphological and reproduction traits was recorded at the substrate level, while BCI values for the forest community and tree species levels were lower and similar to each other. The mean BCI values of the composition of chemical traits were similar at all levels of forest ecosystem organization (Figure 6).

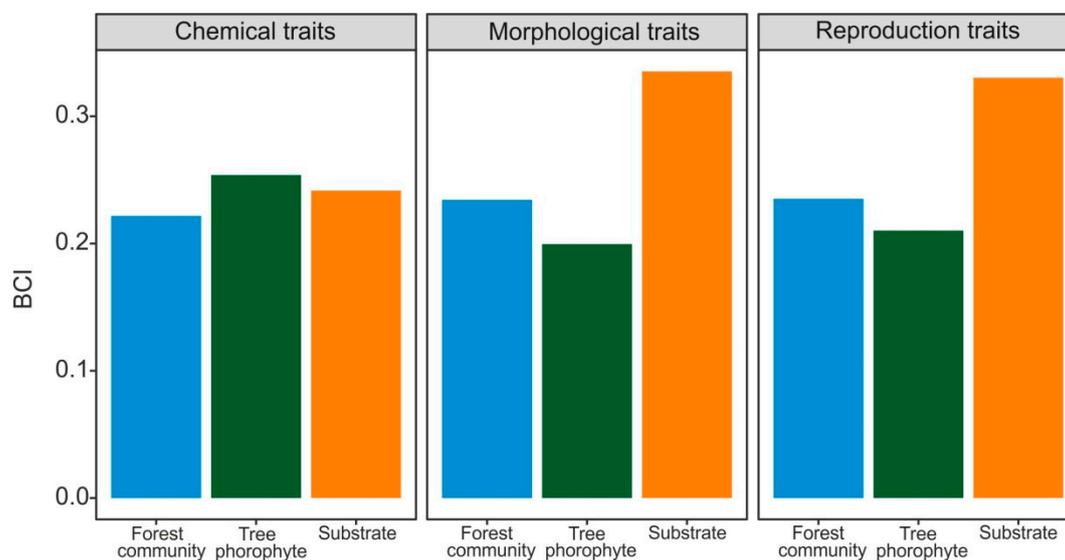


Figure 6. Mean Bray–Curtis compositional dissimilarity index (BCI) of chemical, morphological and anatomical and reproduction traits of lichens at forest community, tree phorophyte and substrate levels.

4. Discussion

4.1. Possible Limitations of the Study

Some species, despite being known for their ability to reproduce both generatively and vegetatively, may represent only one type of reproduction, i.e., producing only fruiting bodies, or forming only soredia/isidia (see [73]). Thus, analyzing selected functional traits (actually occurring in the study area) may be somewhat limiting in the interpretation of the results obtained in a broader context concerning the distribution of these traits in natural forests. However, the data used in our study represent the actual state of knowledge for lowland forest ecosystems of natural character in Central–Eastern Europe. Thus, we are aware of our study limitations and set another target for future works concerning the distribution of the analyzed functional traits in natural forests of other geographical zones.

We analyzed all distinguished functional traits as independent groups, but some of them may be correlated with each other as a result of functional or adaptive association, or due to evolutionary history (compare [93,94]), e.g., lichens forming small-stalked fruiting bodies produce small-sized, unicellular or bicellular spores with dark pigments—these traits are typical for calicioid lichens. However, small spores are not exclusively associated with small ascomata but can also be produced by species with medium-sized fruiting bodies. Similarly, dark-colored spores are not strictly associated with just stalked ascomata but also with lirellate and perithecioid ascomata. Analyses of individual functional traits in conjunction with phylogenetic diversity would certainly allow a deeper interpretation of these patterns in future studies.

4.2. Specialization to Substrates

The studied lichen functional traits, i.e., morphological and anatomical, reproduction and lichen metabolites, expressed the greatest specialization to substrates. We demonstrated that different types of substrates affect the grouping of lichens with similar functional traits. It was previously reported that lichens revealed selectivity to different substrates according to their moisture retention capacity, indicating the importance of the

physical properties of the substrate in shaping lichen associations [95]. Different substrates may also be a potential source of lichen photobionts involved in the lichenization process (formation of new lichens by symbiosis of the fungal partner and photobionts), as demonstrated by Zúñiga et al. [96]. The photobiont type trait revealed a high specialization to substrates, in comparison to other traits, e.g., *Trentepohlia* photobionts were associated with the bark of trees and the stems and branches of shrubs, whilst green algae were associated mainly with the bark of trees, cyanobacteria photobionts were associated with the wood of trunks and the branches of fallen trees and taxa lacking photobionts were associated with the wood of dead standing trees. All these substrates differ in structure and chemical and physical properties, which may result in greater preferences of photobionts for particular substrates.

The ascomata type and asexual reproduction of the mycobiont also revealed a high specialization to substrates. This was probably associated with the greater mycobiont preferences for a particular type of substrate, as fungal specificity to a substrate is a key determinant of evolution for the lichen symbiosis [97]. Among different ascomata types, lirellate, perithecioid and lecanoroid ascomata revealed an association with the branches of trees and the stems and branches of shrubs. It is surprising that lichens with perithecia grew abundantly on the stems and branches of shrubs, as the majority of such species are rare and their occurrence was reported to be associated usually with the presence of old trees [40,98,99]. Similarly, Koch et al. [12] reported that the presence of perithecia was related to older stages of forest succession. The close connection of the perithecia functional trait with the stems and branches of shrubs in our investigated area may indicate suitable microhabitat conditions present in the Białowieża Forest, facilitating rapid lichen colonization also on very young trees. In turn, lichens forming stalked apothecia showed greater specialization to deadwood. Deadwood is often mentioned as an important substrate for numerous lichen species in forest ecosystems [100–102]. In our research area, some lichen functional traits revealed a strong association with this type of substrate. Traits linked to the wood of dead standing trees, i.e., stumps and snags, and the wood of trunks and branches of fallen trees constituted a separate group composed of lecideoid and stalked ascomata, with carbonized structures and pruina, producing one-celled and pigmented ascospores. All these traits are related to calicioid lichens, many of which are often referred to as indicators of old-growth forests with long ecological continuity [100,101]. They indicated strong specialization to hard wood and old trees, especially those with hard bark, forming numerous and deep cracks [42,101]. The dark-pigmented ascospores trait was also connected with calicioid lichens, as they are typical for this group, as previously reported by Malíček et al. [10] from old-growth mountain spruce forests. This type of ascospore has pigments and melanins [8] which protect it against high insolation, similarly to how dark pigmentation protects ascomata [68]. This last trait, as well as lichen secondary metabolites, associated with deadwood in the study area, was linked with more insolated microhabitats in open places, mostly snags, which are remnants of broken trees. The large specialization of functional traits, including asexual reproduction (e.g., pycnidia, hyphophores) of the lichen mycobiont, is also consistent with the theory of mycobiont specificity to a particular type of substrate [97].

The conjoined asexual reproduction of both bionts, i.e., isidia and soredia, showed the lowest specialization to substrates. It is most unlikely to be the physical and chemical properties of the substrate but rather other factors that shape the distribution of these functional traits. Perhaps these are microclimatic factors, e.g., humidity, temperature or insolation, associated with specific microhabitats created on different substrates. These factors may also have an impact on other lichen functional traits' distribution, such as thallus types, or ascospore septation.

4.3. Specialization to Tree Species

Our research revealed the high specialization of photobiont type, ascomata type and asexual reproduction of mycobionts to tree species. This may indicate that, as in the case of

photobionts' and mycobionts' specialization to diverse types of substrates, these two bionts reveal selectivity to tree species. Although the green photobionts did not express clear preferences for a particular tree, *Trentepohlia* photobionts showed an association with ash, cyanobacteria photobionts with ash and oak and non-lichenized fungi lacking photobionts with oak. Both the asexual reproduction of mycobionts and the ascomata type produced by mycobionts were associated with a specific tree species. Stalked apothecia, arthonioid ascomata and sporodochia traits were clearly associated with oak. The remaining traits: asexual reproduction of mycobionts and ascomata type, were more or less associated with hornbeam, ash and lime. On these trees, a set of lichens with other specific traits was also found, which confirmed previous results on the similarity of the lichen biota growing on those phorophytes [39].

The lowest specialization to tree species was revealed for ascospore dark pigmentation and thallus type functional traits. The distribution of these functional traits was probably affected by other factors, e.g., insolation or humidity and availability of specific substrates. However, this requires further examination.

4.4. Specialization to Forest Communities

Among functional traits, ascomata types and asexual reproduction of mycobionts exhibited the highest specialization towards forest communities. In turn, the thallus type functional trait demonstrated the lowest specialization, although fruticose thalli appeared to be slightly more associated with coniferous communities. Most functional traits were similarly dispersed between forest communities, and only some of them revealed greater preferences for a specific community. Lichen assemblages with similar traits in different forest communities were often the sum of lichens' traits associated with the main tree species of such community, and they were associated with the substrates abundantly represented in this forest community. This indicates that it is not the forest community itself but rather the availability of specific phorophytes and substrates that influences the lichen functional traits' composition. Lichen communities of diverse traits were shaped by the internal structure of the forest, i.e., presence of various substrates and tree species. As an illustration, the lichen functional traits found in coniferous communities were similar to those associated with the wood of dead standing trees (snags), spruce and oak, as these substrates and trees were the main components of coniferous communities, or, similarly, functional traits found in mixed deciduous communities were associated with, e.g., the bark of trees, branches of trees, stems and branches of shrubs, hornbeam and lime, since these components were abundantly available there.

On the other hand, some functional traits, e.g., ascospore septation (one-celled, two-celled, multi-celled and muriform ascospores) and the asexual reproduction of both bionts (isidia and soredia), seemed to be more associated with a specific forest community than with a specific tree species. This may be due to the habitat conditions of the forest community: humidity, temperature, light and soil fertility. Lichens with small one-celled or two-celled ascospores were characterized by a slightly higher association with coniferous communities than with other community types or tree species. The production of small ascospores is usually associated with the isolation of specific microhabitats of lichens, e.g., snags or logs, and consequently with the need for long-distance spore dispersal. Small ascospores allow dispersal over long distances and colonization of new habitats [31]. On the contrary, multi-celled and muriform ascospores, which are larger in comparison to non-septate or one-septate ascospores, revealed a slightly higher association with mixed deciduous, alder carr and wet floodplain streamside communities than with coniferous communities. Mixed deciduous and wet communities provide a high availability of various microhabitats which assure a high colonization potential for lichens. Thus, they are not required to search for new suitable habitats at long distances and may invest in the production of large ascospores which disperse over short distances [11,31,103] to ensure faster development [104]. Similar results for the association of large ascospores with old forests were obtained by Malíček et al. [10]. The pool of resources in mixed deciduous and

wet communities, as well as humidity, is higher in comparison to coniferous communities, for both lichen components (photobionts and mycobionts), which increases the probability of co-occurrences and therefore the relichenization process [104].

Soredia and isidia traits revealed a slightly higher specialization to coniferous communities than to other community types or tree species. These propagules facilitate fast lichen spreading as they co-disperse both compatible partners capable of growing and developing a mature thallus [63,71,73], which probably enables a faster colonization of newly created microhabitats in coniferous forests, e.g., wood in the first stage of decomposition. Zarabska-Bożejewicz and Kujawa [17] reported a higher proportion of sorediate and isidiate lichens in coniferous forests in comparison to rural areas under the impact of human activities. Lichens reproducing by soredia are considered to be better adapted to stable habitats [14,69,70,72,73], but in our study, all types of forest communities, both coniferous and mixed deciduous, were old [27,73] and stable, i.e., not under human pressure. Nimis and Martellos [71] reported a higher proportion of sorediate lichens in humid-shaded habitats, and a lower share in dry habitats such as disturbed areas. In the case of the primeval Białowieża Forest, coniferous communities were certainly characterized by lower humidity and higher insolation than mixed deciduous and wet communities. A higher proportion of vegetative propagules in managed forests was reported by Malíček et al. [10], who interpreted this pattern as a better adaptation of asexual reproduction to local conditions, and a wider ecological amplitude.

Additionally, it appears that photobiont types (*Trentepohlia* and cyanobacteria) demonstrated a relatively high association with a specific forest community, which could be related to differences in temperature and humidity. The greater preferences of *Trentepohlia* photobionts for mixed deciduous communities were the result of specific microhabitat conditions and more stable temperature and humidity conditions, as revealed in an earlier report from the Białowieża Forest [37]. *Trentepohlia* photobionts are known for their particular adaptations to relatively higher temperatures and higher humidity conditions [65]. Similarly, the positive association of lichens with *Trentepohlia* photobionts and old lowland deciduous oak-dominated woodlands was demonstrated by Wolseley et al. [20]. In turn, it was reported that the cyanobacteria photobionts trait had a higher association with wet floodplain communities. Lichens with cyanobacteria photobionts require water for rehydration [33,63,64], which is supplied from the humid air due to the evaporation of water. At the same time, these lichens are tolerant to dryer conditions [63,64], which may occur with stronger sun exposure in a more open streamside alder–ash forest, compared to a deciduous forest. Cyanobacterial lichens are considered as late-successional species, restricted to wet microhabitats and old tree bark [33].

Our results indicate that lichen functional trait assemblage distribution should not only be considered at the level of differences in the internal structure of the analyzed forest communities, such as a higher number of diverse substrates or tree species. Functional traits should be also analyzed in relation to specific habitat conditions characteristic of a particular forest community, such as insolation, moisture, temperature and eutrophication, as they may affect the coexistence of lichens with specific traits [8,11,72].

5. Conclusions

We revealed that the overall composition of lichen functional traits in a forest community may be considered as an outcome of the high variety of different components forming the internal structure of the forest community, i.e., tree species and substrate diversity, as well as the high variety of specific microclimatic conditions, e.g., insolation, moisture, temperature and eutrophication, formed in different microhabitats. Overall, lichen functional traits demonstrated the highest specialization to substrate type, high specialization to tree species and low specialization to forest community, but this pattern differed between the studied traits. Sexual reproduction of mycobionts (lecanoroid apothecia, lecideoid apothecia, arthonioid apothecia, lirellate apothecia, stalked apothecia and perithecia) and asexual reproduction of mycobionts (pycnidia, hyphophores and sporodochia) demon-

strated the highest specialization to substrate type and tree species but lower specialization to forest community. The lowest specialization to all studied tree levels of ecosystem organization was characteristic of thallus type (foliose, fruticose, crustose and leprose thalli), ascospore dark pigmentation and asexual reproduction of two bionts (soredia and isidia).

The results of our study allow determining the distribution and specialization patterns of various lichen functional traits in relation to substrates, tree species and forest communities. It is apparent that there is a need for further investigation on lichen functional traits' specialization towards the different physical and chemical parameters of substrates and the bark of trees. This could provide a more thorough insight into the correlation of the distribution of some lichen secondary metabolites' traits towards certain specific chemical or physical parameters. Particular attention should be focused on obtaining precise measurements for microhabitat conditions (humidity, light, temperature, etc.) in which testing of substrates occurs. Consequently, this should provide a more cogent explanation for lichen community assemblages based on specific traits.

Supplementary Materials: The following are available online at <https://www.mdpi.com/article/10.3390/f12040485/s1>, Table S1. Lists of all lichen species recorded in the study area and their functional traits.

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