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The Role of Retention Trees in Providing a Habitat for Bryophytes and Lichens in Young Forest Stands: A Mid-Term Perspective

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Abstract: Retention of trees from the previous generation is one of the most widespread conservation practices in forests used for timber production. Despite the comparatively long history of this approach in Europe, there is a lack of long-term studies on the effectiveness of retention trees in preserving epiphyte communities. We compared the diversity of bryophyte and lichen species on retention trees in 20 young forest stands in Latvia in two assessments, 11 years and 18 years after clearfelling. Linear mixed-effects models showed that richness of both lichens and bryophytes remained stable during the assessment years, while bryophyte cover and diversity on retention trees increased over time. The main indicator of higher species richness, cover and diversity on retention trees in managed forests in hemi-boreal vegetation zone was the tree species, with deciduous trees playing the key role. They also provided essential habitat for rare species. Regarding bryophytes, ash, elm, and aspen can be suggested as more efficient retention trees, thus aiding the continuity of bryophyte succession in young forest stands. For lichens, lime could also be prioritised.

Keywords: retention forestry; bryophytes; lichens; species richness; species cover; species diversity; hemi-boreal forest

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1. Introduction

Biological diversity conservation is an essential aspect of forest management for long-term maintenance of healthy and resilient forests [1], especially as intensive forestry is known to cause the fragmentation and decline of habitats [2]. In the recent decades, retention of trees or tree groups from the previous generation has been one of the most widespread conservation practices in forests used for timber production [3]. Retention forestry preserves biodiversity [4] and integrates biodiversity structures in a managed forest landscape [5,6]. With the overarching goal of biodiversity preservation, retention forestry specifically aims to help species survive the regeneration phase, to increase the variation in forest structures in the regenerated stand, and to preserve structural continuity and connectivity in the managed forest landscape [7,8].

The structures related to the retention trees may be important for many species not only immediately after forest felling, but also during a prolonged period afterwards [9]. Specific old-growth structures may support epiphytic species' communities in afforested lands [10] and in managed forests [11,12], and recent studies suggest that even fine woody debris are able to support certain amount of cryptogamic species [13]. However, the effect of management may differ among taxonomical groups [14], with stronger effects observed for bryophyte species (especially liverworts) than for lichen species [15–17]. Epiphytic lichens appear more tolerant and display less significant reactions to environmental changes than mosses [15].

In the boreal and temperate forests of Europe, the method of tree retention is used over wide areas extensively [7]. At the same time, many uncertainties about its positive impact on species diversity [18] and importance in the preservation of biota in mid- and long term [5,9,19] still exist, due to scarce studies [15,20,21]. Epiphytic species are indicators to habitat conditions that support wide diversity of other organisms [22,23]. Accordingly, most studies refer to rare and/or red-listed species [9,20] and complete epiphytic vegetation surveys are seldom carried out [24]. Furthermore, many species are limited by regional distribution, therefore it is important to conduct studies in specific ecological conditions on different spatial scales. Due to differences in species' distribution each local case study contributes to better understanding of the efficiency of retention forestry [25].

The aim of this study was to assess mid-term efficiency of the living retention trees in maintaining lichen and bryophyte species diversity in young forest stands regenerated after clearfelling.

2. Materials and Methods

The study was performed in the eastern and central parts of Latvia in the boreo-nemoral vegetation zone [26] (Figure 1). The mean annual temperature (1991–2020) is +6.8 °C and the mean annual precipitation is 685.6 mm [27]. Forest covers 53% of the terrestrial land area, and the dominant tree species are Scots pine (*Pinus sylvestris* L.), Norway spruce (*Picea abies* (L.) H.Karst.), and silver and downy birch (*Betula pendula* Roth and *Betula pubescens* Ehrh., respectively) [28]. The dominant forest management system is uniform regeneration felling (clearfelling) in small areas. Biodiversity considerations are mandatory when performing forest management. One of the biodiversity preservation measures is to leave retention trees after felling: five to eight trees per each ha of the felling area have to be retained.

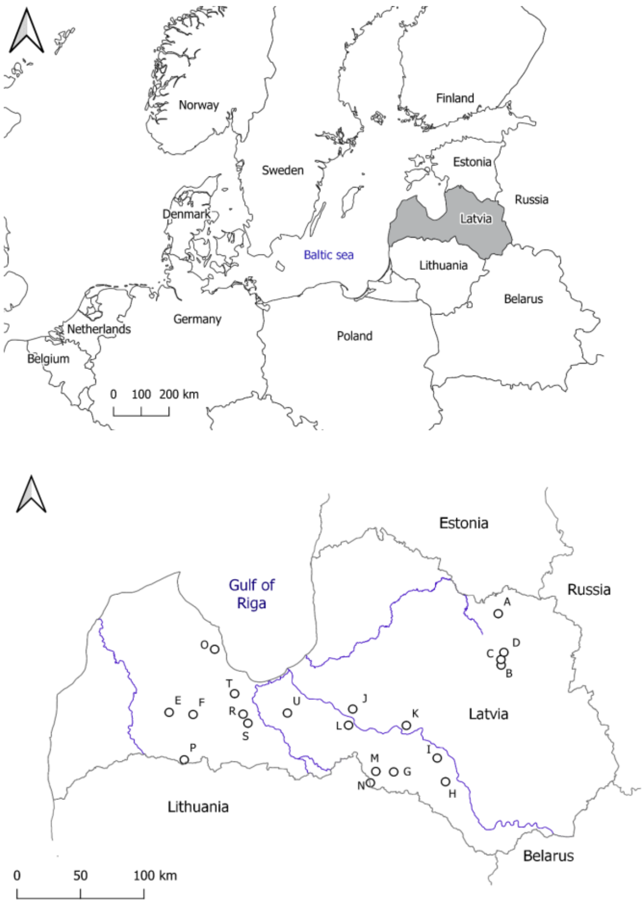

Figure 1. The location of the studied forest stands. The letters represent the studied plots.

In total, 20 forest stands, growing in similar lowland conditions (30–100 m a.s.l.), were chosen in randomised selection. The age of the selected forest stands varied from 10 to 12 years (with a mean age of 11 years) in 2014. The majority of forest stands were located on mineral soils (13 forest stands), with three stands representing wet conditions. The most common forest type was *Oxalidosa*, according to forest typology in Latvia. Latvian forest typology is based on soil characteristic and moisture conditions, reflected in dominant tree species and ground vegetation communities. Site types are named after the respective dominant ground vegetation species [29] (Table 1).

In the first survey year (2014), five retention trees in each forest stand were selected according to two criteria: preferably deciduous trees, and trees with higher survival potential in the future (based on the visual assessment), except one stand where only three retention trees were described (Table 1).

Table 1. Characteristics of the study plots. Abbreviations: Acpl: *Acer platanoides*, Algl: *Alnus glutinosa*, Bepe: *Betula pendula*, Frex: *Fraxinus excelsior*, Pisy: *Pinus sylvestris*, Potr: *Populus tremula*, Quro: *Quercus robur*, Ulgl: *Ulmus glabra*, Tico: *Tilia cordata*. The number of surveyed trees is shown. Coordinates are shown in ETRS89 TM Baltic93 system.

Study Plot	The Number of Surveyed Trees by Species	Year of Clearfelling	Forest Type/Fertility	Soil	Coordinates	
					E	N
A	1 Algl, 4 Bepe	2003	*Myrtillosa turf.mel*/mesotrophic	drained peat	487,543	6,365,430
B	2 Frex, 3 Potr	2003	*Oxalidosa*/eutrophic	dry mineral	488,020	6,323,578
C	5 Potr	2003	*Oxalidosa*/eutrophic	dry mineral	488,040	6,328,124
D	3 Ulgl	2003	*Aegopodiosa*/eutrophic	dry mineral	490,620	6,333,859
E	2 Potr, 3 Quro	2002	*Myrtilloso-polytrichosa*/mesotrophic	wet mineral	591,961	6,288,735
F	4 Potr, 1 Quro	2002	*Oxalidosa*/eutrophic	dry mineral	610,873	6,287,850
G	1 Bepe, 1 Frex, 3 Potr	2004	*Oxalidosa turf.mel.*/eutrophic	drained peat	399,666	6,240,728
H	1 Algl, 1 Frex, 1 Potr, 2 Quro	2004	*Myrtillosa turf.mel.*/mesotrophic	drained peat	440,062	6,230,958
I	1 Pisy, 4 Tico	2004	*Oxalidosa*/eutrophic	dry mineral	434,386	6,250,437
J	1 Frex, 3 Potr, 1 Tico	2002	*Dryopteriosa*/mesotrophic	wet mineral	369,643	6,293,094
K	3 Bepe, 2 Pisy	2004	*Oxalidosa*/eutrophic	dry mineral	411,258	6,277,966
L	3 Algl, 1 Bepe, 1 Potr	2002	*Mercurialiosa mel.*/eutrophic	drained mineral	365,764	6,280,126
M	3 Acpl, 1 Potr, 1 Quro	2004	*Aegopodiosa*/eutrophic	dry mineral	385,608	6,241,691
N	1 Bepe, 3 Quro, 1 Ulgl	2004	*Oxalidosa*/eutrophic	dry mineral	380,903	6,232,653
O	1 Algl, 1 Frex, 1 Potr, 2 Tico	2003	*Myrtillosa mel.*/mesotrophic	drained mineral	625,533	6,341,470
P	2 Bepe, 1 Potr, 2 Quro	2002	*Oxalidosa*/eutrophic	dry mineral	605,520	6,250,790
R	1 Potr, 4 Quro	2002	*Myrtillosa mel.*/mesotrophic	drained mineral	650,214	6,289,832
S	4 Potr, 1 Quro	2002	*Oxalidosa*/eutrophic	dry mineral	654,327	6,282,632
T	1 Potr, 4 Quro	2003	*Myrtilloso-polytrichosa*/mesotrophic	wet mineral	642,772	6,306,155
U	3 Algl, 1 Quro, 1 Tico	2002	*Mercurialiosa mel.*/eutrophic	drained mineral	318,092	6,292,116

For each retention tree the entire stem surface from ground level up to two m height (including stem, stem base and root collar) was surveyed, recording all bryophyte and lichen species, including epiphytes and facultative epiphytes. For each tree, the relative projective cover of each bryophyte and lichen species was determined on the entire stem surface area. The range of diameter at breast height (DBH) varied from 0.21 to 0.67 m, the described tree trunk surface from 1.3 to 4.2 m^2, respectively. All studied retention trees were mature and their age at least equalled the length of the rotation period for the specific species. The first collection of ecological data was carried out in the summer and autumn of 2014 [30]. In 2021, the bryophyte and lichen species in all studied stands were repeatedly evaluated on the same trees and according to the same methodology. The trees that had perished between the assessments and were in different forms of dead wood, were not sampled.

Some or all species under genera *Cladonia* P. Browne, *Lecanora* Ach., *Opegrapha* Ach., *Ramalina* Ach., *Lepraria* Ach., *Lecidella* Körb. were merged under one unit (e.g., *Lepraria* spp. and *Lecidella* spp.). Most lichens and bryophytes were identified in the field. Some species were collected and later identified in the laboratory, using microscopy to examine morphology for lichens and bryophytes and chemical reagents like 10% potassium hydroxyl solution, sodium hypochlorite solution (commercial bleach) and ethanol solution of para-phenylenediamine for lichens according to Smith et al. [31]. The nomenclature of Hodgetts et al. [32] was followed for bryophytes and that of Smith et al. [31] for lichens. The species specified as indicators included woodland key habitat indicator species and special biotope species considering local species pool, as in Āboliņa et al. [33] and Auniņš [34].

To describe diversity of epiphytes on the living retention trees, the Shannon diversity index was calculated based on the mean cover of species. Linear mixed-effects models were used to assess the effects of host tree species, DBH, forest type, as well as differences between surveys (year) on species richness, cover and diversity (Shannon diversity index) of bryophyte, lichen, indicator and all epiphyte species on living trees. To account for dependencies in data due to repeated measures, stand and tree were used as random effects. Random slope of year was allowed to evaluate the spatial stability of changes in epiphyte richness as well as to omit the pseudoreplication problem [35]. For count data (species richness), model residuals were adjusted according to Poisson distribution (log link function). The relationships between species composition of bryophytes and lichens and environmental variables and epiphyte community characteristics were explored by detrended correspondence analyses (DCA). The analyses were based on species cover. Canonical axes were rescaled and rare species were downweighed. The relationship between two canonical axes and lichen species richness and cover, bryophyte species richness and cover, and indicator species richness, as well as DBH of host trees, were assessed by Pearson correlation analyses. Successional vectors were drawn to assess temporal changes in epiphyte communities on retention trees. Data analysis was conducted in R v. 4.2.0 [36], using libraries "lme4" [37] and "vegan" [38].

3. Results

From the 98 trees previously surveyed in 2014, eight deciduous trees had perished and in the second assessment were in the form of snags (two), stumps (three), and fallen deadwood (three). Four trees could no longer be identified in the field. In total, 99 taxa have been determined, from which 43 were lichens and 56 bryophytes, representing a local species pool. Considering that ecotone (root collar) was included in the survey, the determined taxa represented different ecological groups, with the majority of epiphytes accompanied by several epigeids and epixyles (as facultative epiphytes).

Among the recorded taxa, ten species emerged, but four were absent in the second assessment (2021). Respectively, three lichen taxa had disappeared, e.g., *Lecanora varia* (Hoffm.) Ach., and six new taxa had emerged, e.g., *Phaeophyscia orbicularis* (Neck.) Moberg, *Chaenotheca ferruginea* (Turner) Mig. in 2021. For bryophytes, one species had disappeared (*Homalothecium sericeum* (Hedw.) Schimp.), and four taxa emerged, e.g., *Plagiothecium latebricola* Schimp. and *Sciuro-hypnum populeum* (Hedw.) Ignatov & Huttunen. The occurrence had decreased for half of species—23 lichens and 26 bryophytes, including six indicator species (two lichens and four bryophytes). For example, lichen species *Vulpicida pinastri (*Scop.) J.-E.Mattsson & M.J.Lai, *Melanelixia glabratula* (Lamy) Sandler & Arup and genus *Lecanora* spp. showed the highest decrease in occurrence (Supplementary Table S1). The relative cover had decreased for 18 lichen species and 15 bryophyte species. At the same time the relative cover for several indicator species had increased, e.g., for the lichens *Arthonia spadicea* Leight., *Arthonia vinosa* Leight., *Lobaria pulmonaria* (L.) Hoffm., *Pertusaria pertusa* (L.) Tuck. and bryophytes *Anomodontella longifolius* (Schleich. ex Brid.) Hartm., *Neoorthocaulis attenuatus* (Mart.) L.Söderstr., De Roo &Hedd., *Homalia trichomanoides* (Hedw.) Brid., *Syzygiella autumnalis* (DC.) K.Feldberg, Váňa, Hentschel & Heinrichs (Table S1). The majority of facultative epiphytes that have varying colonization abilities to other substrates like soil emerged, e.g., *Atrichum undulatum* (Hedw.) P. Beauv., *Ptilidium ciliare* (L.) Hampe, or increased in abundance, e. g. *Climacium dendroides* (Hedw.) F. Weber & D. Mohr, *Dicranum polysetum* Swartz (Table S1).

The richness of bryophytes, lichens and indicator species remained stable as indicated by non-significant differences between assessments, while the total cover and diversity of all species and bryophytes in particular had significantly increased (Figure 2, Table S2). However, at the tree level, the richness of bryophytes tended to increase, while that of lichens tended to decrease, and this tendency appeared stronger for bryophytes (Figure 2, Table S2).

Among the tested environmental variables, tree species was the main predictor of the species richness, cover, and diversity (represented by the Shannon index) as indicated by the highest χ^2 values, particularly for bryophytes (Figure 2, Table S2). The highest richness of bryophyte species was associated with the tree species *Fraxinus excelsior* L., *Populus tremula* L., and *Ulmus glabra* Huds.; however, such differences were significant for strongest contrasts (compared to *Pinus sylvestris*). The highest number of lichen species was estimated on *Tilia cordata*, *Fraxinus excelsior* and *Betula pendula* (Figure 2) with the strongest significant contrasts between *Tilia cordata* Mill. and *Quercus robur* L. These tree species, along with *Quercus robur* and *Alnus glutinosa* (L.) Gaertn., were estimated to have the strongest positive effect on the cover of bryophytes and lichens, in particular on the latter (Figure 2). The DBH of retained trees had moderate but significantly positive effect on the bryophyte species richness and cover (Figure 2, Table S2).

The composition of species was explained by continuous gradient that accounted for 66 of the total variation (eigenvalue = 0.660) (Figure 3). The main gradient along the first ordination axis was mainly related to host species and was distinguishing bryophyte and lichen communities. On the right side of ordination, the tree species with acid bark pH (*Betula pendula*, *Alnus glutinosa, Pinus sylvestris* and *Tilia cordata*) hosted larger lichen species community, as well as higher lichen cover and richness in contrast to broad-leaved trees and aspens and distinguished a group of more light demanding species, e.g., *Hypogymnia physodes* (L.) Nyl., *Parmelia sulcata* Taylor, *Parmeliopsis ambigua* (Wulfen) Nyl. According to the ordination scores of species, the species associated with alkaline bark pH (*Fraxinus excelsior* and *Populus tremula*) were located on the negative side of the first axis and related with high indicator and bryophyte species richness and cover, separating a group of bryophytes as *Homalia trichomanoides*, *Neckera pennata* Hedw., *Anomodontella longifolius*. The second gradient which accounted for 28% of the total variation (eigenvalue = 0.280) was difficult to explain, but probably related to local specific conditions (Figure 3).

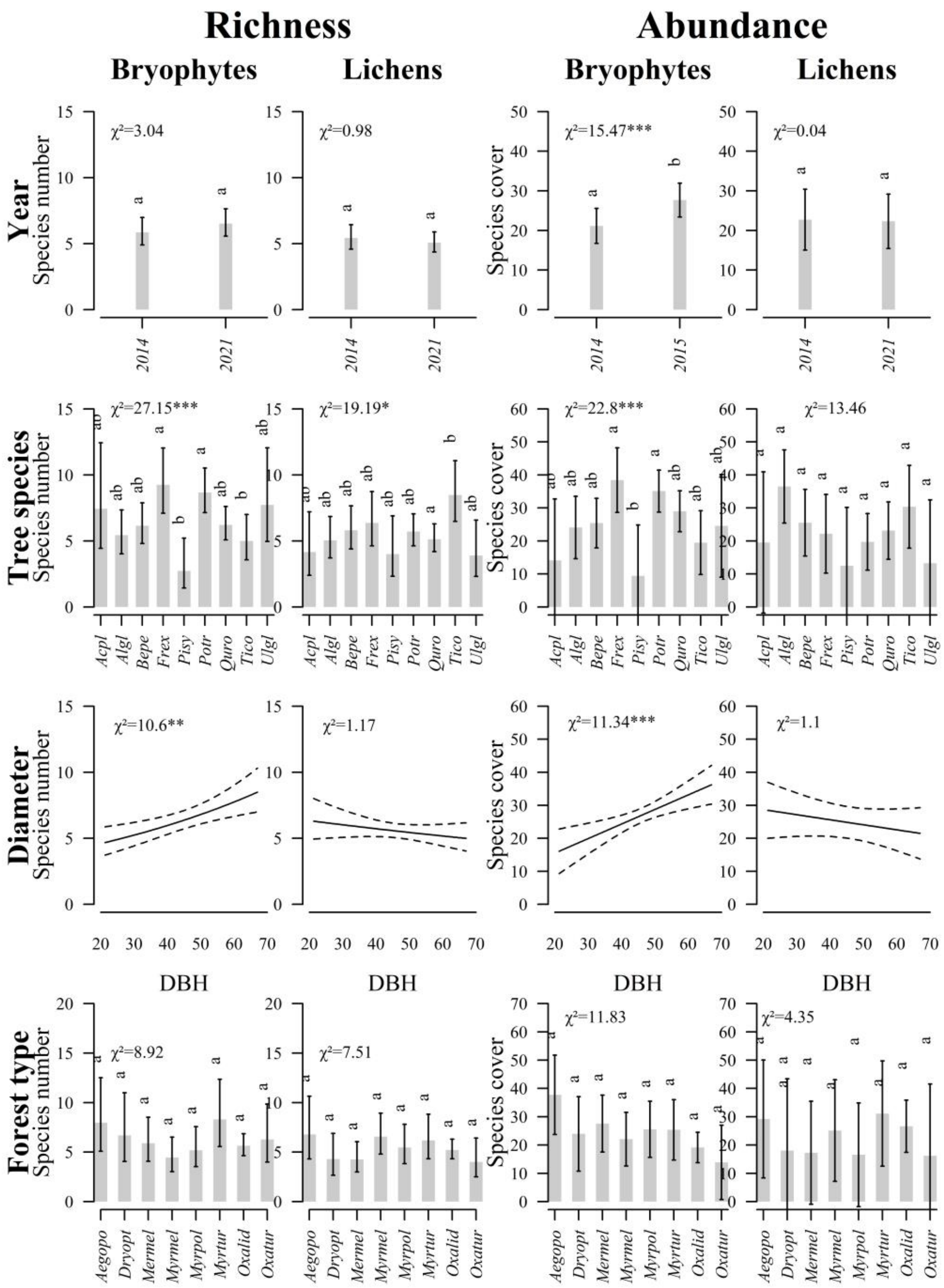

Figure 2. The estimated marginal effects of assessment year, tree species, diameter of breast height (DBH) and forest type (Table S2) on richness and abundance of bryophytes and lichens growing on retained trees 7 to 14 years since clearfelling. Whiskers indicate 95% confidence intervals. Similar letters above bars indicate lack of significant differences at $\alpha = 0.05$. Significance code, p–values "*" - <0.05, "**" - <0.01, "***" - <0.001. Abbreviations Acpl: *Acer platanoides*, Algl: *Alnus glutinosa*, Bepe: *Betula pendula*, Frex: *Fraxinus excelsior*, Pisy: *Pinus sylvestris*, Potr: *Populus tremula*, Quro: *Quercus robur*, Ulgl: *Ulmus glabra*, Tico: *Tilia cordata*; DBH: diameter at breast height, Aegopo: *Aegopodiosa*, Dryopt: *Dryopteriosa*, Mermel: *Mercurialiosa mel.*, *Myrmel: Myrtillosa mel.*, Myrpol: *Myrtilloso-polytrichosa*, Myrtur: *Myrtillosa turf.mel.*, Oxalid: *Oxalidosa*, Oxatur: *Oxalidosa turf.mel.*

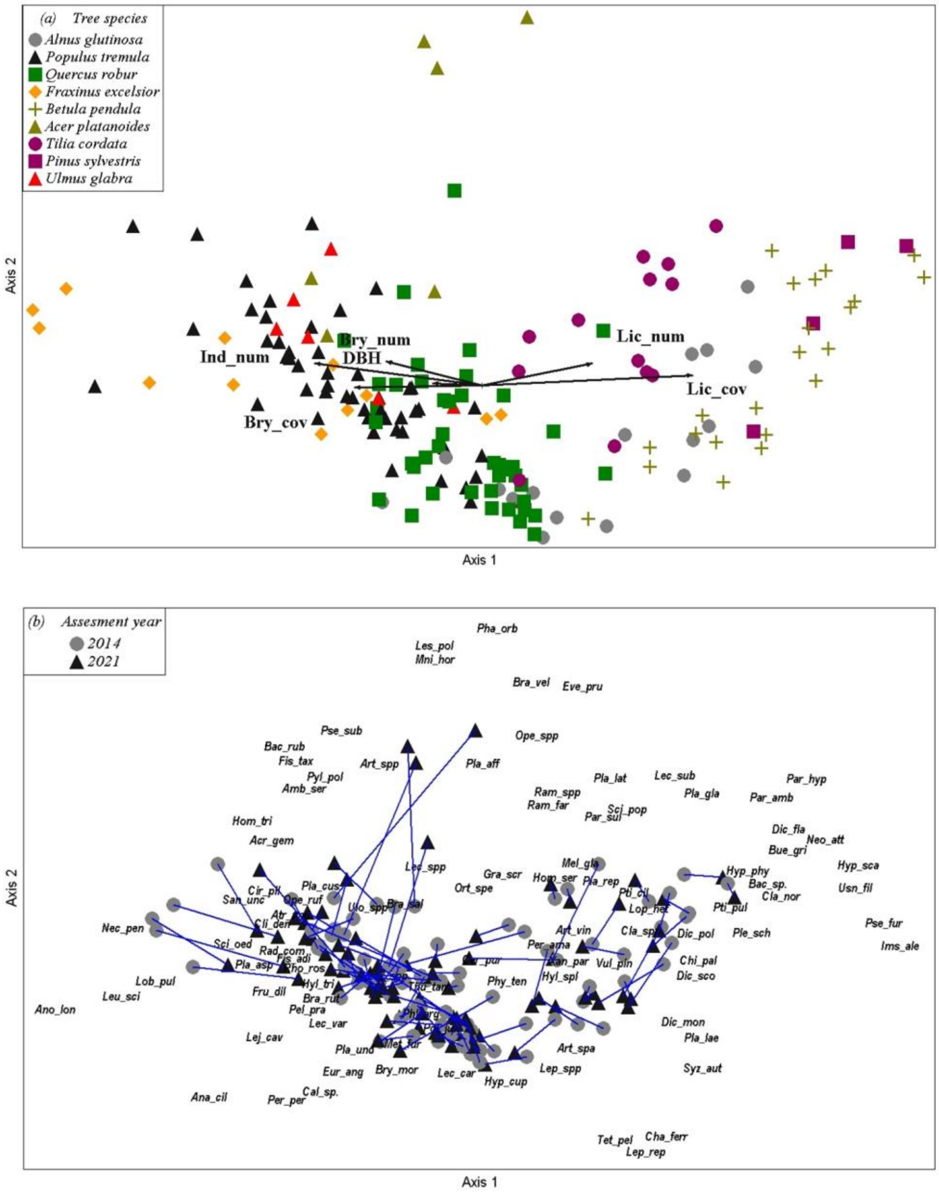

Figure 3. Detrended correspondence analysis **(**DCA) ordination of bryophyte and lichen species on retention trees 11 and 18 years after clearfelling (in 2014 and 2021, respectively). The first two canonical axes are shown. Panel (**a**) depicts tree ordination according to species, panel (**b**) shows species ordination with successional changes of trees. In (**a**), vectors show correlations between species community metrics, as well as diameter of breast height (DBH) of host trees and the first two canonical axes. Abbreviations Bry_num: number of bryophytes, Ind_num: number of indicators, Bry_cov: cover of bryophytes, Lic_num: number of lichens, Lic_cov: cover of lichens. Species abbreviations: see in Table S1.

The successional changes in species communities were small to moderate as indicated by relative length (according to respective gradient) of succession vectors, though the changes in bryophyte and lichen communities were specific to individual tree species and local conditions. According to the main gradient, successional changes on *Fraxinus excelsior* were expressed as an increase in species diversity, especially for lichens, e.g., *Lobaria pulmonaria*, *Phlyctis argena* (Ach.) Flot., *Lepraria* spp. and *Acrocordia gemmata* (Ach.) A.Massal. On the opposite side of main gradient, successional changes on trees *Pinus sylvestris*, *Betula pendula*, *Alnus glutinosa* and *Tilia cordata* with higher lichen species richness and abundance were smaller but related to increase in bryophyte richness and cover. Such changes indicate intensifying competition between bryophytes and lichens. In the middle part of gradient, related to tree species *Quercus robur*, *Populus tremula* and *Ulmus glabra* the changes were negligible and random, indicating stable bryophyte and lichen communities. However, regarding the second gradient, the successional changes were most explicit on trees (*Acer platanoides*, *Quercus robur*) for the eutrophic stand, which were comparable to the length of the entire gradient, as species *Phaeophyscia orbicularis*, *Leskea polycarpa* Hedw. emerged.

4. Discussion

The disturbance of a clearfelling is known to dynamically alter the epiphyte communities on retained trees with bryophytes being most sensitive [15,21,39], with often lichens favouring open conditions [18]. In longer period (18 years after clear felling) the species richness on retained trees was temporally stable over time as indicated by a non-significant effect of year (Table S2), supporting the efficiency of the applied retention practice for the preservation of epiphyte richness [39]. The overall richness of bryophytes and lichens on the retention trees, however, was moderate (Table S1) which might be related to stand history, as the retention trees were surveyed in conventionally managed commercial stands [23]. Also, some ambiguities regarding the difficult-to-identify genera may have caused slight underestimation of species' richness.

Furthermore, total species and bryophyte species cover and diversity had increased (Figure 2, Table S2), thus signifying the ongoing bryophyte recovery [21,39]. Concomitantly, bryophyte species richness tended to slightly increase over time as indicated by the marginal effects of year (Table S2). Such processes can be explained by stabilization of microclimate [40] with the development of new forest generation, especially regarding more balanced moisture regime, which is an important factor for bryophytes [41].

Similar to the results of previous studies [42,43], tree diameter of studied retention trees significantly affected the richness and cover of bryophytes. Larger trees hosted more diverse and abundant communities of epiphytes, due to a larger available surface for colonisation and higher diversity of available microhabitats [41]. Larger tree diameter is usually related to greater age of tree, thus providing a longer time for colonization [25]. In contrast, the richness and abundance of lichens was independent of DBH (Figure 2), which could be explained by higher environmental tolerance of this taxonomic group, particularly regarding tree size [25,44]. Furthermore, the fact that the cover of bryophytes was negatively correlated with lichen species richness and cover, but positively with tree size (Figure 3) indicates that in the case of competition lichens could be sensitive to tree DBH. Similar conclusions were drawn by Jüriado et al. [45] and Jüriado and Paal [46].

The tree species is the main driver of epiphytic species diversity, reflecting the host preference of the epiphytes [12,43,47,48]. Broad-leaved trees (*Ulmus glabra*, *Fraxinus excelsior* and *Acer platanoides*) and aspens, due to the alkaline reaction of the bark [49] are known to host high epiphytic bryophyte species richness in managed forest landscapes, and as individual deciduous trees in young forests [10–12]. This was also found in our study. Our data also highlighted the importance of broad-leaved trees and particularly aspens as a substrate for epiphytic indicator species in forests, similarly to the results by Hedenås and Hedström [50] and Rudolphi and Gustafsson [20]. These biological legacies of deciduous retention trees are important biodiversity structures and essential habitat for rare epiphytic species after forest harvest. In contrast, higher lichen species richness and cover were provided by tree species with more acidic bark like *Tilia cordata*, *Alnus glutinosa*, *Betula pendula* (Figure 2, Figure 3). This could be explained by higher lichen species tolerance [43] and favourable conditions for bryophytes on broadleaved trees [45].

As our sites included a rather wide array of site types with uneven distribution, and the highly diverse site conditions, combined with small number of studied trees and different host tree species, as well as limited height of sample plots, these could be reasons why the occurrence of some common epiphyte lichens, e.g., *Ramalina farinacea* (L.) Ach., *Imshaugia aleurites* (Ach.) S.L.F. Mey. was very low or some species were absent. For example, our study included only three *Pinus sylvestris* trees, which could lead to underestimation of richness of epiphytic lichen species associated specifically with pine.

In the studied stands, the number of common foliose lichen species, e.g., *Hypogymnia physodes* and *Parmeliopsis ambigua*, on pines, black alders, and birches showed the strongest changes in occurrence. These species are good colonisers after clearfelling [18], and the changes likely resulted from shifting light conditions as tree canopies close [6,51]. Such conditions are considered favourable for bryophytes, mainly on the lower part of the stem, where light availability is decreasing due to forest regeneration [45], and especially for species that positively react to forest cover increase, as *Pylaisia polyantha* (Hedw.) Schimp., *Amblystegium serpens* (Hedw.) Schimp., *Hypnum cupressiforme* Hedw. [52], also observed in studied stands. Furthermore, the increase in facultative epiphytes (Table S1) reflected higher and more balanced humidity [40].

This explains the observed substitutions of bryophytes and lichens, highlighting changes in competitiveness of the taxonomic groups [53]. Accordingly, the inverse relationships between lichen and bryophyte cover and richness (Figure 2) suggest explicit competition between bryophytes and lichens, as changes in microclimate intensify. This confirms the efficiency of retention trees for ensuring the continuity of epiphyte succession under intensive management.

Furthermore, forest regeneration with subsequent changes and stabilisation of the microclimate [40,54] provides suitable conditions for species favouring more stable and specific microclimatic conditions, including several indicator species [55]. At our sites, the occurrence of more sensitive lichen species, e.g., *Acrocordia gemmata*, *Arthonia vinosa* and *Lobaria pulmonaria* had increased over time, and also the richness of indicators was positively related to higher total bryophyte species abundance and richness. All bryophyte and lichen indicator species recorded on retention trees in the first assessment were still present in the second survey and indicator species' diversity remained stable. This is consistent with earlier findings that epiphytic species that are sensitive to intense disturbances may survive on retention trees for a longer time period [20,50].

Retention forestry is a viable conservation practice providing a live substrate for bryophyte and lichen species and thus ensuring their sustainable survival in intensively managed forests. In the present study, no data on the initial species richness and cover at the moment of felling were available, therefore we are currently unable to draw more specific conclusions on the "lifeboat" role of retention trees immediately after clearcutting. Still, the dynamics of indicator species confirms the importance of retention forestry in biodiversity conservation.

5. Conclusions

Deciduous retention trees in studied managed forests in hemi-boreal zone were sufficient to ensure lichen and bryophyte species diversity in mid-term, up to 19 years after felling. The host tree species had stronger impact on bryophyte and lichen diversity than tree size, with *Populus tremula, Fraxinus excelsior, Ulmus glabra* and *Tilia cordata* having the strongest positive effect, implying a wider array of options for retention forestry. Still, larger diameter trees supported higher bryophyte diversity. Successional changes of species were related to competition between bryophytes and lichens, developing better environmental conditions for higher abundance of bryophytes, while the richness of species did not change, indicating the stability of species accumulation. Accordingly, the efficiency of retention trees and their density in particular can be mentioned as prospect for further research assessing colonization of epiphytes on regenerating trees.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d15070870/s1, Table S1: The list of recorded lichen and bryophyte taxa on living retention trees in surveys 11 and 18 years after clear felling (in 2014 and 2021, respectively). The number of trees where each species was recorded and relative projective cover (trees without species excluded) of each species are shown. Indicator species are marked *, Table S2:

Strength (χ^2-value) and significances (p-value) of fixed effects of year, tree species, diameter, forest type on lichen and bryophyte species richness, cover, Shannon diversity index, as well as variance related to the random effects of tree and plot.

Author Contributions: Conceptualization, L.G.-I. and Z.L.; methodology, L.G-I. and D.J.; software, L.G-I. and R.M.; validation, L.G.-I., Z.L. and Ā.J.; formal analysis, L.G.-I.; investigation, L.G-I. and D.J.; resources, Z.L.; data curation, L.G-I.; writing—original draft preparation, L.G-I. and R.M.; writing—review and editing, L.G-I., R.M., Z.L., D.J. and Ā.J.; visualization, L.G-I. and R.M.; supervision, Z.L. and Ā.J.; project administration, Z.L.; funding acquisition, Z.L. and Ā.J. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement: The datasets are available upon reasonable request by contacting the corresponding author.

Conflicts of Interest: The authors declare no conflicts of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript; or in the decision to publish the results.

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