



The response of lichens inhabiting exposed wood of spruce logs to post-hurricane disturbances in Western Carpathian forests

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ARTICLE INFO

Corresponding Editor: Peter D Crittenden

Keywords:

Lichen ecology
Wood-inhabiting lichens
Lichen succession
Hurricane winds
Coarse woody debris
Natural forest disturbances
Spruce mortality
Permanent study plots

ABSTRACT

We investigated which of the following environmental factors: the number of years since the windthrow of the tree (the age of dead wood), the phytocenosis (the type of forest community), altitude, exposure, wood hardness and the spatial scale of forest disturbances (small gaps with a few fallen spruces vs large-area windthrows) contributed to the diversity and abundance of lichens inhabiting the exposed wood of windthrown spruce trees in Polish Western Carpathian forests. Both Shannon H index and sum of coverage coefficients rose with increasing age of the wood, levelling off after 11–14 y (diversity) and 14–17 y (abundance). This factor appeared to be the most important for this group of lichens, but the significant positive impact of large-area windthrows on the lichen abundance was also demonstrated by using a GLM model. The age of the wood we precisely determined on the basis of data on Norway spruce mortality collected annually in permanent plots of the Gorce National Park since 2000. Using the Shore durometer we linked the course of the wood-inhabiting lichen succession with wood decay more precisely than before. The largest number of species was associated with medium hard wood, i.e., $51 < x \leq 80$ on the Shore scale. Based on the NMDS analysis, we distinguished four age groups of logs, differing in lichen abundance and defined by the dominance of distinctive species. A large number of usually corticolous lichen species used the wood of windthrown spruce logs as an optional habitat to survive large-scale, post-hurricane forest disturbances.

1. Introduction

Recurrent, violent windstorms in mountains constitute one of the main elements which translate into the large-scale recovery of dead-wood resources (Schelhaas et al., 2003; Kulakowski et al., 2017; Paluch and Jastrzębski, 2022). Unlike the natural dieback of single, old trees, storms can create larger gaps in standing wood, or even large-area windthrows that cause the diversification of microclimatic conditions on the landscape scale (Chen et al., 1999; Mitchell 2013).

Disturbances caused by severe winds can be exceptionally widespread in stands of the shallow-rooted Norway spruce *Picea abies* (e.g., Ulanova, 2000; Panayotov et al., 2011; Maurer and Heinemann, 2020). Under the influence of cyclically recurring disturbances, mainly wind and spruce bark beetle degradation, *Picea abies* has developed a survival strategy that consists of a cohort generation shift in the so-called gaps (Stöcker, 2002). According to research conducted, among others, in the Bulgarian Rila Mountains (Panayotov et al., 2011) and the German Harz Mountains (Kathke and Bruehlheide, 2010), disturbances represent a natural element of the dynamics of these stands and do not lead to their

degradation. Natural disturbances with a regionally characteristic set of influencing factors form an integral part of the dynamics of forest ecosystems around the globe (Seidl et al., 2011; Kuuluvainen and Grenfell, 2012).

The post-hurricane gap is a space with completely different conditions compared to the surrounding, dense forest. The trunks of fallen trees are exposed to intense sunlight and wind, which causes rapid surface changes in humidity, light and temperature. Such change is often critical for epiphytic lichens that previously grew in the shadow zone (Solhaug and Gauslaa, 2012; Morillas et al., 2021). Yet, many individuals manage to survive, for example, on the side of the trunk protected from direct solar radiation. On the other hand, the light-demanding lichen species which show a greater resistance to drying settle periodically on the exposed parts of the fallen trees. With time, sites after bark fall off are colonized by facultative and obligatory wood-inhabiting communities, increasing species diversity in the ecotone zone, and thus doing so on a larger territorial scale (Ulanova, 2000; Czarnota, 2012; Haeleer et al., 2021; Langbehn et al., 2021).

Studies on the colonization of lying dead wood by lichens most often

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<https://doi.org/10.1016/j.funeco.2023.101228>

Received 16 July 2022; Received in revised form 30 January 2023; Accepted 6 February 2023

Available online 1 March 2023

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combine their diversity or species composition with age or the visually determined degree of decomposition of the studied substrate (Rudolphi, 2007; Bunnell et al., 2008; Botting and DeLong, 2009; Santaniello et al., 2017). Other emphasized predictors of lichen diversity include log diameter (Bunnell et al., 2008) as well as tree species composition and stand structure (Rheault et al., 2009). Sometimes, lying logs harbour similar lichen communities to that of stumps, in which a very important group are the epixylic and epigeic members of the genus *Cladonia* (Nascimbene et al., 2008b; Svensson et al., 2013). Also, logs generally represent habitats of less diverse lichen populations than snags (Holien, 1996; Humphrey et al., 2002; Svensson et al., 2016), but more or similarly diverse populations compared to those found on fine woody debris (FWD) (Kruys and Jonsson, 1999; Svensson et al., 2016; Moisejevs et al., 2019).

This paper aims to determine the course of lichen succession of windthrown spruce logs in the conditions of post-hurricane gaps and large-area windthrows in the Western Carpathian forests, as well as to assess the impact of these natural disturbances on the diversity and abundance of this lichen biota. Hypotheses included: (i) the spatial scale of the post-hurricane forest disturbance (small gaps with a few fallen spruces vs large-area windthrows) comprises the most important environmental predictor of species diversity and abundance of lichens that inhabit the wood of windthrown spruce logs in the Western Carpathians, (ii) the number of years since the fall of the tree (the age of dead wood) increases the diversity and abundance of lichen communities that inhabit the wood, and (iii) the degree of wood decay, expressed by the hardness of this substrate on the Shore scale, determines the individual stages of lichen succession in a manner more precise than the age of dead wood.

2. Study area

The study area encompassed the Gorce National Park established in 1981 (part of Gorce Mts; geographical coordinates: 49°37'18.802"–49°30'34.218"N and 20°01'20.867"–20°15'10.850" E; Fig. 1). The options for managing space in the Gorce National Park is limited by the landscape features and the needs of environmental protection, and thus saved the forests from intensive anthropogenic reconstructions, allowing for the preservation of vegetation dynamics based on natural cycles of disturbances.

Gorce is a small mountain range in the territory of southern Poland, which belongs to the chain of the Outer Western Carpathians. The highest peak, Turbacz, located at an altitude of 1310 m above sea level, does not reach the upper forest edge. In terms of species composition, the forests that cover the slopes of the Gorce Mountains are divided into

three main communities in which the Norway spruce participates. These are mixed beech-fir-spruce forests *Dentario glandulosae-Fagetum* and fir-spruce forests *Abieti-Piceetum* located in the lower mountain range, the upper mountain spruce forests *Plagiothecio-Piceetum* in a typical variant, as well as spruce forests with an admixture of beech *Plagiothecio-Piceetum fagetosum* in the transition zone.

3. Methods

3.1. Field data collection

The study was carried out at 43 sites selected in the strict protection zone of the Gorce National Park from a pool of permanent, circular monitoring plots arranged in a net of 400 × 400 m (36 plots) or compacted squares with sides of 200 m (3 plots), where at least one wind-thrown spruce was present. Every year since 2000, observations of Norway spruce population have been carried out in these areas for the survival of trees subjected to natural disturbances caused by the bark beetle outbreaks and hurricane winds. These data make it possible to understand the time and cause of death of each dead spruce in the study area, based on its azimuth position and distance from the center of the plot. To increase the pool of data, the analyses also included windthrows, examined on four sites, selected outside permanent plots, and affected by a large-scale disturbance in 2002.

The research was carried out in 2018 and 2019 and encompassed only the wood of uprooted spruces since only in their case was it possible to correctly establish the original trunk position prior to falling, and thus to identify it in the database from the stand inventory.

Each log, provided there were pieces of exposed wood present on it, was tested in three sections, each 1 m long, at the following distances from the trunk base: section I: 1.5–2.5 m; section II: 4.5–5.5 m; section III: 10.5–11.5 m. If a sufficiently large piece of exposed wood was missing in the designated section, i.e., at least 0.5 m², section offsets of up to 1 m up or down the trunk were accepted. Movements within two adjacent sections were always made in the same direction.

The coverage degree of a wood section by individual lichen species (lichen abundance) was determined by means of the modified Braun-Blanquet scale, the degrees of which corresponded to the percentage ranges of the coverage (Matuszkiewicz, 2005). The range means were then transformed to the coverage coefficients (Table 1).

The age of dead wood was determined on the basis of the spruce mortality monitoring data on the permanent study plots. The degree of wood decay was assessed by means of a handheld analog Shore durometer of the type A, with a scale of 1–100. This method is standardized and regulated by PN-ISO 868. Measurements were made in

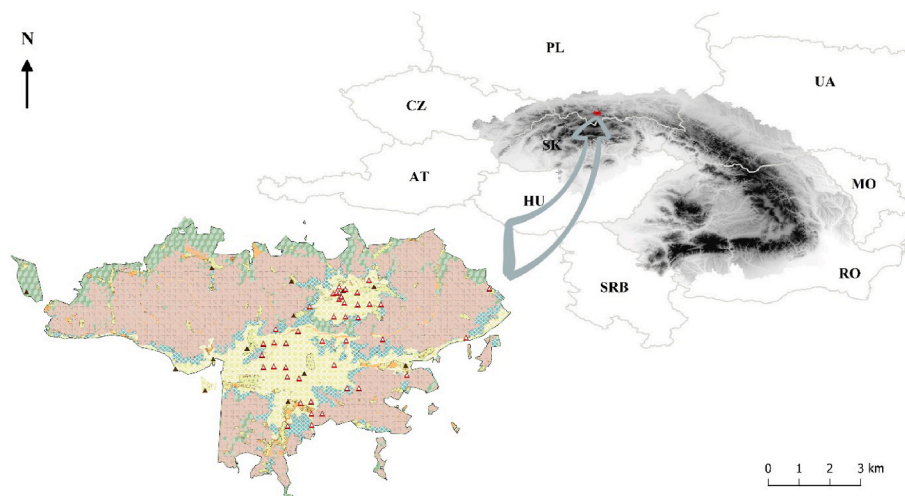


Fig. 1. Distribution of sites for the lichen survey (red triangles), selected from the grid of permanent plots for environmental monitoring in the area of Gorce National Park (39 plots), as well as the additional sites affected by large-area windthrows in 2002 (4 plots). These plots lie within the main plant communities: *Plagiothecio-Piceetum* (yellowish green), *Plagiothecio-Piceetum fagetosum* (blue), *Dentario glandulosae-Fagetum abietosum* (violet), *Abieti-Piceetum* (blue-green), as well as glades (bright green) and other forest communities (orange).

Table 1

The degrees of coverage scale of the examined wood sections designated to the lichen species in the field, and the corresponding percentage ranges and coverage coefficients (Tanona and Czarnota, 2022).

Degree of scale	Range [%]	Coverage coefficient
r	<0.1	0.01
+	0.1–1	0.05
1	2–5	0.35
2	6–25	1.6
3	26–50	3.8
4	51–75	6.3
5	76–100	8.8

triplicate under randomly selected thalli of each species found on a given section. For the most common species, the number of measurements was limited to 30–60 records (× 3 biological replicates).

The map of the distribution of study plots within the Gorce National Park border (Fig. 1) were prepared with Quantum Gis v. 3.4.9.

3.2. Species identification

Lichen specimens whose systematic affiliation was not obvious in the field, were assessed in the laboratory using the Zeiss STEMI DV4 stereomicroscope and the Zeiss Axiostar Plus light microscope. In addition to monitoring morphological and anatomical features, the thalli were subjected to simple tests for exhibiting color reactions with chemical reagents: aqueous solutions of sodium hydroxide (KOH) and calcium hypochlorite (CaOCl₂), iodine solution in potassium iodide (KI), and a solution of paraphenylenediamine in ethyl alcohol. Common species such as *Leprosia*, the differentiation of which requires more complex laboratory diagnostics, were identified down to the genus level as *Leprosia* spp. Similarly, species with a very high degree of morphological similarity were not distinguished in the groups *Cladonia pyxidatichlorophaea*, *Micarea prasina* s.l. (except *M. prasina* s.s., *M. soralifera* and *M. nowakii* s.l.) and *M. micrococca* s.l. (except *M. micrococca* s.s. and *M. byssacea*). Species names are based on the Index Fungorum database (<http://www.indexfungorum.org>) except *Frutidella furfuracea*, which is according to Svensson et al. (2017).

3.3. Statistical analysis

In total, the tests covered fallen logs of Norway spruce on 43 plots, in which 107 first, 125 second and 116 third sections on the logs were examined; providing 348 sections in total. The uneven number of sections stemmed from the coverage of this part of the log by bark, overgrowing of the log by plants, or damaging it during the fall of the tree (this concerned mainly section III).

The analyses were conducted at the level of a single section, and their subject was the lichen community expressed by the sum of the coverage coefficients and species diversity, described by the Shannon index (H) according to the following formula: $H = - \sum_{i=1}^S p_i \ln p_i$, where: S – number of lichen species, p_i – share of the i-th species in relation to the sum of the shares of all species occupying the study area.

3.3.1. Environmental factors vs lichen diversity and abundance

The tested environmental variables included: (i) the age of dead wood, counted in years from the treefall; (ii) the spatial scale of the forest disturbance with division into gaps <0.05 ha and large-area windthrows; (iii) position of the section on the log – as described in section 2.1; (iv) type of forest plant community (one of the three: *Dentario glandulosae-Fagetum*, *Plagiothecio-Piceetum fagetosum*, and *Plagiothecio-Piceetum*); (v) altitude, and (vi) slope exposure (as a cyclical factor occurring in eight categories, it has been converted using trigonometric functions (sine and cosine) into two continuous quantitative factors, i.e. the “northness” [cos (α rad)] and “eastness” aspects [sin (α rad)], according to the recommendation of Roberts et al. (1989). The number of

sections in each factor category is provided in Table 2.

The influence of environmental parameters on the dependent variables described above was determined, among others, by using nonlinear forms of generalized linear models (GLM) based on the Poisson distribution with a logarithmic link function. The best model fit was obtained on the basis of the backward elimination of factors which exhibited the weakest relationship with the dependent variable, determined on the basis of the Wald statistic, using the maximum likelihood estimate (sum of coverage indices) or quasi-likelihood (Shannon index) in relation to hyper-dispersion. Pearson’s chi-squared test and residual analysis were used as a measure of the model fit. The direction and strength of statistically significant relationships were additionally identified using Spearman’s rank correlation and the Mann-Whitney U test.

3.3.2. The age of dead wood vs lichen diversity and abundance

The values of the H index were correlated with the number of species in the community and the sum of the coverage coefficients in order to determine the influence of the index components on its diversity. The rarefaction analysis in individual age of dead wood was used to show the cumulative increase in the number of species, together with the number of individuals observed on examined logs.

Non-metric multidimensional scaling (NMDS) was used to distinguish lichen communities into larger groups on the ground of the average wood cover in particular years of wood decay (Table 2). The analysis was performed on the basis of the Bray-Curtis similarity after transforming the data with the square root. The boundary for dividing the age of dead wood into larger groups was set at 30% dissimilarity. Next, the age groups distinguished in NMDS were analyzed with one-way PERMANOVA based on 999 unrestricted permutations, and pairwise dissimilarities were calculated among all groups mentioned. A percentage similarity analysis (SIMPER) was performed to identify the species primarily responsible for the observed difference in wood coverage between successive age groups of logs.

3.3.3. The hardness of dead wood vs lichen succession

The measurements of wood hardness under the thalli of the observed lichen species were used to illustrate the potential succession sequence on fallen spruce logs along with the progress of wood decay. Box plots were prepared based on the hardness of wood inhabited by individual

Table 2

The number of examined, 1-m-long sections on windthrown spruce logs, in relation to tested variables; Altitude and the aspects of exposure (eastness and northness) are not included due to continuous nature of these factors; * – distance from the base of the trunk.

Environmental variable	Number of examined sections	Environmental variable	Number of examined sections
Age of dead wood (in years)		Position of the section	
2	3	1.5–2.5 m* - section I	107
3	1	5.5–6.5 m* - section II	125
4	33	10.5–11.5 m* - section III	116
5	15	Type of the forest plant community	
9	4	<i>Dentario glandulosae-Fagetum</i>	41
10	3	<i>Plagiothecio-Piceetum fagetosum</i>	29
11	5	<i>Plagiothecio-Piceetum</i>	278
12	4	Spatial scale of the forest disturbance	
13	16	Group	158
14	58	Large-scale	190
15	119		
16	31		
17	56		

species and arranged according to the decreasing median. The analysis took into account all species that occurred in at least 10 sections, which is the minimum for the basic assessment of their environmental preferences. Furthermore, the investigation encompassed all species that have so far been recorded only on wood in the Gorce Mountains or in the Polish part of the Carpathians (Czarnota, 2012; see Table 3), irrespective of the 10 occurrences criterion. These species play an important role in the context of this study; therefore, it was decided to indicate their hypothetical place in succession based on the measurements made. Finally, three groups of species characteristic for the subsequent stages of wood decay were selected: (1) species of undecomposed wood, early wood successors (Shore hardness of the order: $81 < x \leq 100$); (2) species of poorly decomposed wood ($51 < x \leq 80$); (3) species of decayed wood ($21 < x \leq 50$).

The statistical analyses were carried out using STATISTICA v. 13.1, CANOCO V. 5. and PAST 4.03 at the significance level of $\alpha = 0.05$.

4. Results

4.1. Species and their abundance

We identified 51 lichen species and three species of lichenicolous fungi, as well as *Mycocalicium subtile*, an early fungal wood colonizer, traditionally mentioned among wood-inhabiting lichen communities. Among these species, eight are considered to grow exclusively on wood in the Polish Carpathians (Czarnota, 2012), while as per the IUCN criteria, six species have been given a conservation status of various degrees in Poland (Cieślinski et al., 2006) (Table 3).

4.2. Environmental factors vs lichen diversity and abundance

The GLM models indicated that among the tested factors, only the age of dead wood and the aspect of “eastness” significantly justified the differences in the diversity of lichens inhabiting spruce logs, expressed by the Shannon H index (Table 4). The model fit based on the χ^2 Pearson test was $\chi^2/df = 0.26$. The effect of the age based on Spearman's rank

Table 4

The results of generalized linear models (GLMs) for the Shannon diversity index (H) and for the sum of trunk coverage coefficients against tested environmental variables, showing that age of dead wood was the most important predictor of both lichen diversity and abundance, while the scale of the forest disturbance only influenced abundance. Based on Wald's statistics, only the outcomes for factors of a significant ($p \leq 0.05$) effect on a tested parameter are mentioned. Abbreviations: b – regression coefficient, SE – standard error b, W – Wald's statistics, p (W) – Wald's statistics probability.

Effect	Effect level	b	SE	W	p (W)
Shannon H index					
(Intercept)		−2.42140	0.207184	136.59002	0.00000
Age of dead wood		0.14385	0.013762	109.25590	0.00000
Eastness		−0.15324	0.066896	5.24727	0.02198
Sum of cover coefficients					
(Intercept)		−2.34340	0.339114	47.75303	0.00000
Age of dead wood		0.15416	0.022573	46.64318	0.00000
Spatial scale of forest disturbance	Large-area scale	0.39747	0.110004	13.05557	0.00030
Northness		−0.1980	0.067103	8.70611	0.00317
Eastness		−0.28625	0.111373	6.60602	0.01016

correlation was significant and positive at $r_s = 0.37$, while the influence of “eastness” was negative and weaker, although still significant, with a score of $r_s = -0.18$.

Grouping of examined log sections in terms of the H index based on its variance according to the C & RT regression tree method illustrated the influence of the individual predictors analyzed (Fig. 2). The first breaking point for lichen diversity was the time since treefall at the level of 7 y, whereby lichens were nearly absent below this age (the pioneering species were *Absconditella lignicola* (3 occurrences), *Micarea misella* (2 occurrences), as well as *M. nowakii*, *Placynthiella dasaea* and *P. icmalea* (1 occurrence each). In the older age group, the first differentiating factor was the spatial scale of forest disturbance, where higher H

Table 3

The list of species including the number of occurrences and the sum of coverage coefficients per 348 studied spruce log sections with an area of at least 0.5 m²: PRLL – the category of threat according to the Polish Red List of Lichens (Cieślinski et al., 2006); SCC – the sum of coverage coefficients; ^/^ – a species found in the Gorce/the Carpathians only on deadwood (Czarnota, 2012); # – a lichenicolous/algicolous fungus.

Species name	PRLL	No. obs.	SCC	Species name	PRLL	No. obs.	SCC
<i>Absconditella celata</i> ^^		3	0.03	<i>Micarea nitschkeana</i>		5	0.43
<i>Absconditella lignicola</i> ^^		103	22.14	<i>Micarea nowakii</i> s.l. ^^		96	36.07
<i>Bachmanniomyces punctum</i> #		3	0.03	<i>Micarea prasina</i> s.s.		38	4.27
<i>Buellia griseovirens</i>		1	0.01	<i>Micarea prasina</i> s.l.		11	1.59
<i>Buellia arborea</i>		1	0.01	<i>Micarea soralifera</i>		3	0.07
<i>Epigloea soleiformis</i> #		2	0.02	<i>Mycocalicium subtile</i> ^^		17	5.63
<i>Epigloea urosperma</i> #		3	0.03	<i>Palicella filamentosa</i>		10	1.46
<i>Cladonia cenotea</i>		2	0.06	<i>Parmeliopsis ambigua</i>		4	0.12
<i>Cladonia coniocrea</i>		98	20.58	<i>Parmeliopsis hyperopta</i>	VU	1	0.01
<i>Cladonia digitata</i>		221	139.25	<i>Placynthiella dasaea</i>		188	93.88
<i>Coenogonium pineti</i>		1	0.01	<i>Placynthiella icmalea</i>		50	7.42
<i>Fellhanera subtilis</i>		1	0.35	<i>Placynthiella uliginosa</i>		25	11.24
<i>Frutidella furfuracea</i>		11	1.21	<i>Pseudevernia furfuracea</i>		1	0.01
<i>Fuscidea pusilla</i>		13	0.21	<i>Pycnora sorophora</i>		2	0.02
<i>Hypogymnia physodes</i>		31	14.14	<i>Scoliosporium chlorococcum</i>		1	0.01
<i>Lecanora conizaeoides</i>		4	0.38	<i>Strangospora moriformis</i>		1	0.05
<i>Lecanora expallens</i>		1	0.01	<i>Thelocarpon epibolum</i>	LC	8	0.12
<i>Lecanora pulicaris</i>		11	1.03	<i>Thelocarpon lichenicola</i>		2	0.02
<i>Lecanora subintricata</i> ^		4	1.67	<i>Trapelia corticola</i>		2	0.02
<i>Lecidea nylanderii</i>		1	0.01	<i>Trapeliopsis flexuosa</i>		63	8.3
<i>Lepraria</i> spp.		35	2.31	<i>Trapeliopsis glaucolepidea</i>	DD	3	0.07
<i>Lichenomphalia umbellifera</i> ^^	NT	8	1.9	<i>Trapeliopsis granulosa</i>		49	4.77
<i>Micarea botryoides</i>		1	0.01	<i>Trapeliopsis pseudogranulosa</i>		3	0.07
<i>Micarea byssacea</i>		2	0.02	<i>Violella fucata</i>		11	2.5
<i>Micarea denigrata</i>		2	0.06	<i>Xylographa paralella</i> ^^	EN	6	0.14
<i>Micarea micrococca</i> s.s.		18	1.66	<i>Xylographa vitiligo</i> ^^	DD	2	0.06
<i>Micarea micrococca</i> s.l.		10	0.64	sp. unknown		1	0.01
<i>Micarea misella</i> ^^		135	23.61				

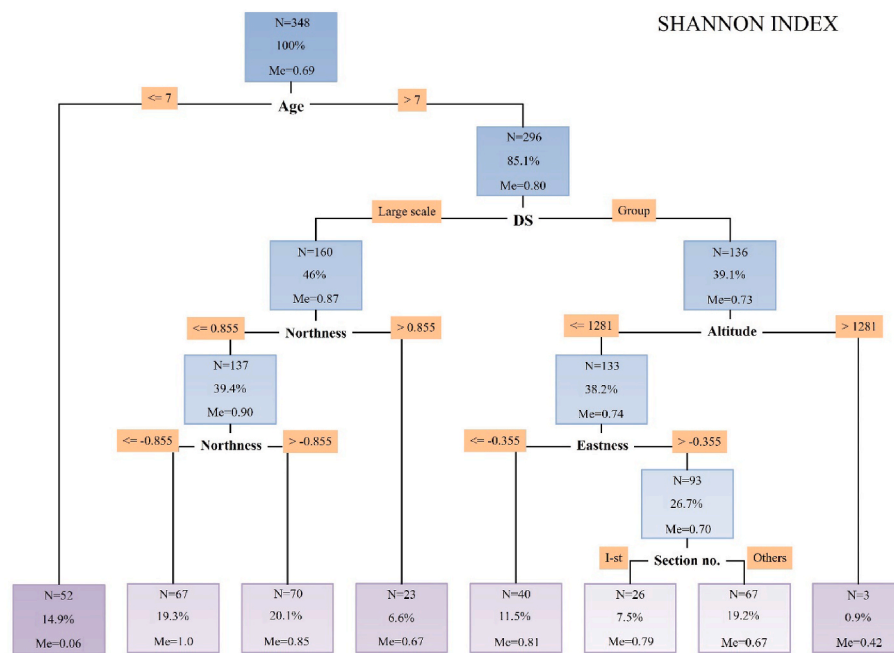


Fig. 2. The regression tree (C & RT) based on the Shannon diversity index (H) and the environmental variables tested, illustrating levels or categories of a given variable, that results in the separation of sets of samples with the most homogeneous variance, and also specifying the mean value of the index within the separated groups. The time since the fall of the tree and the spatial scale of forest disturbances were the most important ecological factors influencing wood-inhabiting lichen diversity on windthrown spruce logs. The second most influential factor affecting this diversity was when logs had been down for more than 7 y. Abbreviations: Age – age of dead wood (number of years since the fall of the tree); DS – spatial scale of the forest disturbance; Large scale – large-area disturbances; Group – small-scale disturbances (gaps); Altitude – elevation a.s.l.; Northness/Eastness – the aspects of slope exposure; Section no. – section number, the location of the section on the log.

values were favored by large-area windthrows. The third degree of classification involved a marked influence of terrain factors: the aspect of “northness” (>0.855 values of this factor denoting N exposure exhibit lower H values in their composition) and absolute altitude (higher H values occur below 1281 m above sea level, i.e., mainly in the lower mountain range). The fourth stage included both aspects of the exposure as the grouping aspects: “northness” (N exposure) had a slight negative effect on H values in its composition, while “eastness” (“≤−0.355” means NW exposure) had a weak positive effect. In the sixth stage, section I obtained higher H values).

The sum of the coverage coefficients of lichens inhabiting the wood of log sections was explained by four major factors: the time since treefall, the spatial scale of forest disturbance, and two aspects of exposure. The model fit based on Pearson’s χ^2 test was $\chi^2/\text{df} = 1.18$.

According to Spearman’s rank correlation, the age of the substrate positively influenced the total lichen coverage at the level of $r_s = 0.46$, while at the same time “northness” and “eastness” showed an opposite, though weaker relationship, at $r_s = -0.17$ and $r_s = -0.20$. The spatial scale of the forest disturbance was an important factor grouping the sum of patch coverage based on the Mann-Whitney U test at $p = 0.000007$, favoring a higher lichen coverage in stands, in which large-scale disturbances occurred.

The C & RT classification indicated the time since treefall as the most influential factor grouping the sums of the coverage factors in the examined plots (Fig. 3). The “younger” wood (<12.5 y) did not divide further and contained logs with a clearly lower total lichen coverage compared to the “older” wood (>12.5 y). In the second stage, older logs were divided according to the scale of the forest disturbance, where

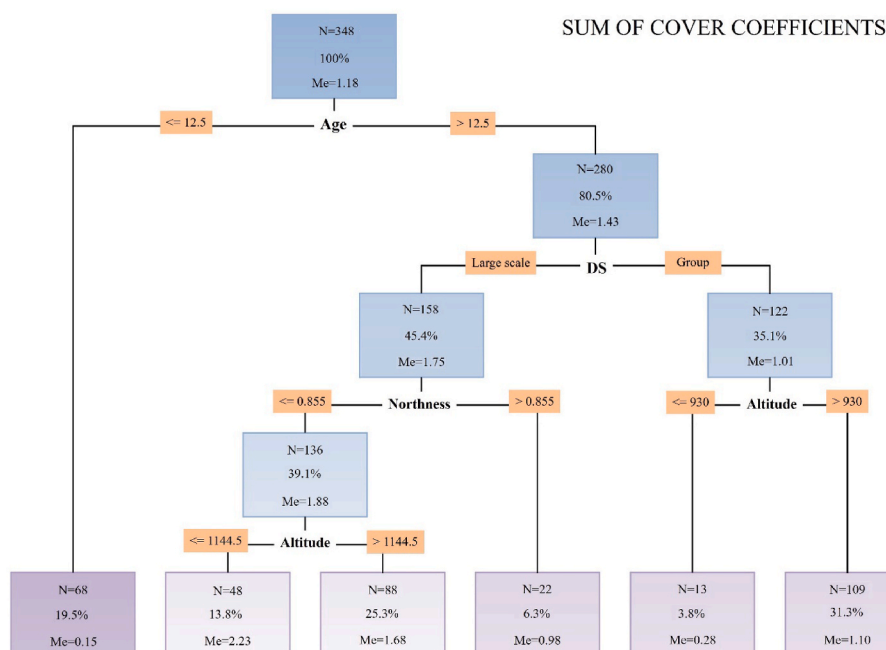


Fig. 3. The regression tree (C & RT) based on the sum of cover coefficients and the environmental variables tested, showing that the spatial scale of the forest disturbance affects lichen abundance only on older logs down for 13–17 y. Abbreviations used: Age – age of dead wood (number of years since tree death); DS – spatial scale of the forest disturbance; Large scale – large-area disturbance; Group – small-scale disturbance (gaps); Altitude – elevation a.s.l.; Northness – aspect of slope exposure.

areas affected by the large-area windthrows favored greater total lichen coverage. The grouping factors in the next two stages were: (i) “northness” (N exposure) and an altitude of 930 m above sea level, as well as (ii) altitude of 1144.5 m above sea level.

4.3. The age of dead wood vs lichen diversity and abundance

The Spearman's correlation between the H index values and the number of lichen species (species richness) and their coverage indicated that the first of the examined elements had greater weight in determining its value ($r_s = 0.72$), while the importance of the second was weaker ($r_s = 0.25$). The rarefaction plot (Fig. 4) allowed comparison of the species richness on the examined logs, based on the layout of curves created for individual log ages. No lichens were observed on the 2- and 3-y-old logs due to the recent loss of bark (most of 2- and 3-y-old logs were still covered with bark, hence they were excluded from the analysis). The species richness, as opposed to the number of individuals sampled, was the lowest on the youngest logs aged 4–10 y. Over the next 11–14 y after the fall of the tree, the number of wood-inhabiting species increased rapidly to the highest levels achieved, then diminished somewhat again on 15–17-y-old logs.

The lichen diversity described by the averaged Shannon index in subsequent years of wood decay (2–17 y) was characterized by a clear upward trend, which decreased at a later stage of this process (Fig. 5). An inverted trend in the studied period was characterized by the abundance of lichens on the basis of their average coverage factor: initially it grew slower, and then accelerated on older logs (Fig. 5).

The NMDS analysis distinguished four age groups of samples (logs), which were characterized by at least 60% similarity of the coverage data (Fig. 6; Table 5). The one-way PERMANOVA test and the post-hoc pair test confirmed the significance of differences between these groups. The PERMANOVA pseudo-F test result was 53.09 and it was significant at $p = 0.001$. Comparing individual groups showed significant differences between each formed pair at the level from 0.014 to 0.001.

The first age group, which includes 2- and 3-y-old logs, was not inhabited by lichens at all. In the second group, *Absoconditella lignicola*, which is an obligate epixylic lichen that prefers hardwood, was the dominant species responsible for most of the variability between the first and second age groups of dead wood. In the third group, the share of *A. lignicola* decreased, as it was displaced by *Placynthiella dasaea*, a species associated primarily with woody substrate and at the same time adapted to easily master new habitats (Fabiszewski and Szczepańska, 2010). In the oldest age group, the greatest change was related to a several-fold increase in the share of species that also commonly inhabited the bark of nearby live spruces, i.e., *Cladonia digitata* and *Hypogymnia physodes*, and the emergence of new obligately wood-inhabiting taxa: *Micarea nowakii* s.l. and *M. misella*, as well as the light-demanding *Placynthiella uliginosa* that inhabits mainly dry rot, humus, and strongly decomposed

wood.

4.4. The hardness of dead wood vs lichen succession

Measurements of the wood hardness under the thalli of the identified species of lichens enabled an objective assessment of their requirements in relation to the degree of the occupied substrate decay. Thus, these measurements allowed presentation of the succession sequence of lichens inhabiting the wood of windthrown spruces during its decaying (Fig. 7). At the initial stage of decay (wood hardness according to the Shore scale $81 < x \leq 100$), and after the falloff of the bark remnants, there were only a few species. These included the non-lichenized fungus *Mycocalicium subtile* and lichen species *Frutidella furfuracea* and *Fuscidea pusilla*. This group also included the microlichen *Absoconditella celata*, which is very rarely found in the Carpathians (Czarnota and Tanona, 2020). Wood in the second stage of decay ($51 < x \leq 80$) was more likely to be colonized by lichens; at least 16 taxa were found there, 6 of which should be considered exclusively wood-inhabiting, i.e.: *Absoconditella lignicola*, *Lecanora subintricata*, *Micarea misella*, *M. novakii* s.l., *Xylographa parallela*, and *X. vitiligo*. Logs in the third stage of decay ($21 < x \leq 50$) were occupied by seven taxa, including only one representing the ecological group of obligate epixyles, i.e., *Lichenomphalia umbellifera*. The group that grew on a very soft, rotten substrate ($1 < x \leq 20$) was not distinguished on the basis of the median hardness of the wood, although many species with a broad spectrum of occurrence inhabited wood with this degree of decay as well.

5. Discussion

5.1. The importance of lying dead wood for Western Carpathian lichens

The list of lichenized fungi found in these studies, which colonized the wood of fallen spruce logs, includes eurytopic and common Carpathian species, such as *Cladonia digitata*, *C. coniocraea*, and *Hypogymnia physodes*, which also grew on the bark of living trees in the same control plots. The more numerous groups consists of taxa for which decaying wood is the primary substrate and which can be considered as facultative epiphytic at best. These include, for example, taxa of *Micarea*, *Placynthiella*, and *Trapeliopsis* genera. The number of obligate wood-inhabiting species in the Polish Carpathians (according to Czarnota, 2012), including the non-lichenized fungus, *Mycocalicium subtile*, equaled nine, i.e., merely 16% of all identified taxa. In this context, the significance of natural disturbances in Western Carpathian forests, resulting in the supply of decaying spruce logs as a substrate for this specialized group of lichens, may appear minor. However, it has to be noted that in various geographic regions of the world, including the best-preserved fragments of old-growth forests, today the group that inhabits only wood is usually much less diverse compared to the group of epiphytic lichens (e.g., Cieśliński and Czyżewska, 1992; Juriado et al., 2003; Spribille et al., 2008; Vondrák et al., 2015; Urbanavichus et al., 2020). Our investigations did not include logs older than 17 y, since only 3 windthrown spruces were registered on the monitoring plots in 2000 and 2001, and no suitable and available wood sections were found on them during the research. This had its consequences in almost no representation of the lichen group that grows on well decayed wood, although it is known that the gradual overgrowing of the underlying logs with bryophytes and herbaceous vegetation significantly reduces the possibilities of lichen development on wood in the late stages of decomposition (Söderström, 1988a, 1988b). Given the dimensions of fallen trees and the observations of the decay rate of spruce wood in Gorce conditions, studies on the succession of logs older than 20 y seem impossible (Czarnota, unpubl. data). The amount of deposited dead-wood of windthrows in the Gorce National Park area, including specific habitats such as rootplates, undoubtedly provides lichens with far greater developmental opportunities than could be investigated since the methodology used was restricted to logs (compare Czarnota, 2012).

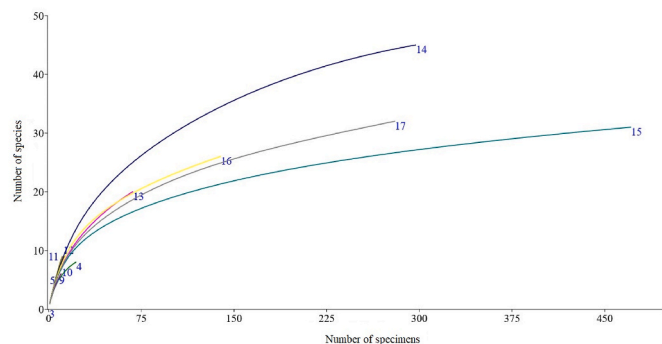


Fig. 4. Rarefaction plot showing the number of wood-inhabiting lichen species expected to be found depending on the number of specimens sampled in particular years of log decay.

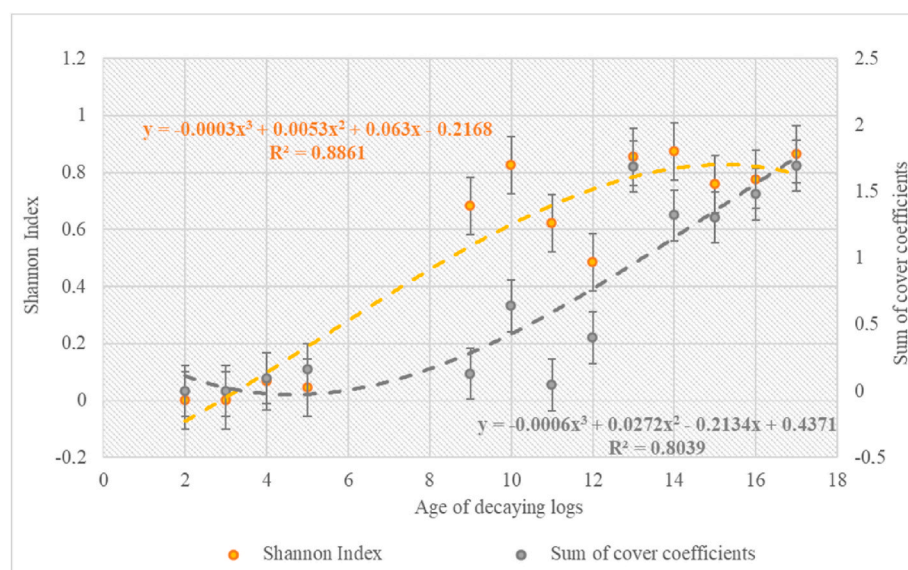


Fig. 5. Mean values of the Shannon H index and of the sum of coverage coefficients in subsequent years following fall of the spruce trees, including error bars and logarithmic trend lines (of the third degree). Lichen diversity increased rapidly, but subsequently decreased during the later stage of wood decay, while abundance increased more slowly, before accelerating on older logs.

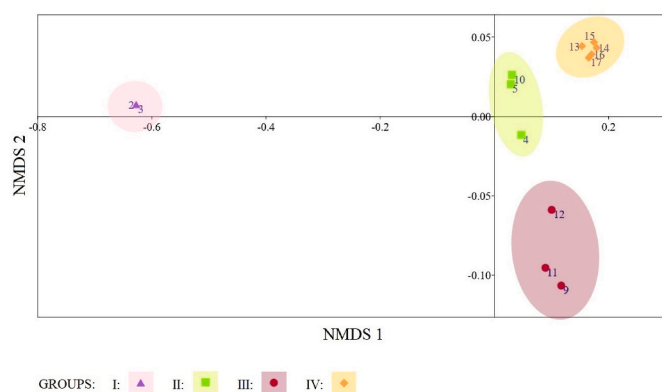


Fig. 6. Non-metric multidimensional scaling (NMDS) plot based on the mean wood-inhabiting lichen coverage in relation to years after the fall of the spruce tree, using the Bray-Curtis similarity measure, showing four different age groups of dead wood in terms of lichen coverage. Square root transformation was applied. Shaded area – age groups of wood decay with similarity values greater than 60%. Log sections at 9 and 10 y after fall arranged non-chronologically in groups II and III, probably due to the small sample size which do not sufficiently represent the variability of niches available to colonizing.

Parallel studies conducted in the same area on snags generated during bark beetle outbreaks (Tanona and Czarnota, 2022) demonstrated a greater number of lichen species and fungi compared to lying wood, i.e., 84, of which 15 occurred exclusively on wood. Key factors for this include: lack of microhabitat differentiation in the height gradient on the wood of fallen logs, longer rotten bark residence time, as well as faster shading of the lying wood with undergrowth vegetation, followed by saplings. Nevertheless, some of the rare species present on snags were very frequent on fallen logs, e.g., *Absoconditella lignicola*, *Micarea nowakii* s.l., *M. misella*, *Trapeliopsis granulosa*. This draws attention to the important role of various available coarse woody debris, the range and quantity of which is sufficiently wide due to natural disturbances in stands (Czarnota, 2012; Kulakowski et al., 2017; Langbehn et al., 2021).

As the decay of the bark of fallen trees progresses, the ground conditions for epiphytes begins to destabilize, and the last chance for their survival is to transfer their propagules to the exposed wood (Kushnevskaya and Shorohova, 2018). In our research, the decaying wood of fallen spruce trees represented an important substitute substrate for epiphytic lichens. The long-term effect of natural disturbances such as wind, fire and insect outbreaks which support species diversity in boreal forests has been well documented in numerous studies, including a wide meta-analysis performed by Thom and Seidl (2016), although in respect of lichenized fungi, when we consider a short time perspective, this effect can be considered negative (e.g., Johansson, 2008). The question remains open as to whether the conditional settlement of epiphytes on wood in the future will favor a faster or more effective colonization of

Table 5

Taxa contributing to the dissimilarity in the wood-inhabiting lichen species composition between successive age groups of decaying spruce logs (SIMPER analysis). 'AvAbu' – average abundance after square root transformation; 'AvDissim' – average dissimilarity of each taxon; 'Con' – taxon's contribution to the total dissimilarity; 'CuCon' – cumulative contribution of each taxon is set to a cut-off point of 30% dissimilarity; 'AvAbu 1'/'AvAbu 2' – average abundances of the species in the compared groups, the first and the second respectively.

Group (AvDissim)	Taxon	AvDissim	Con (%)	CuCon (%)	AvAbu 1	AvAbu 2
Group I vs II 100%	<i>Absoconditella lignicola</i>	37.88	37.88	37.88	0	0.686
Group II vs III 68.15%	<i>Absoconditella lignicola</i>	13.97	20.5	20.5	0.686	0.272
	<i>Placynthiella dasaea</i>	8.14	11.94	32.45	0.141	0.421
Group III vs IV 77.48%	<i>Cladonia digitata</i>	5.534	7.142	7.142	0.162	0.786
	<i>Micarea nowakii</i> s.l.	5.434	7.013	14.16	0	0.623
	<i>Hypogymnia physodes</i>	4.848	6.257	20.41	0.0667	0.611
	<i>Micarea misella</i>	4.236	5.467	25.88	0	0.468
	<i>Placynthiella uliginosa</i>	3.946	5.093	30.97	0	0.456

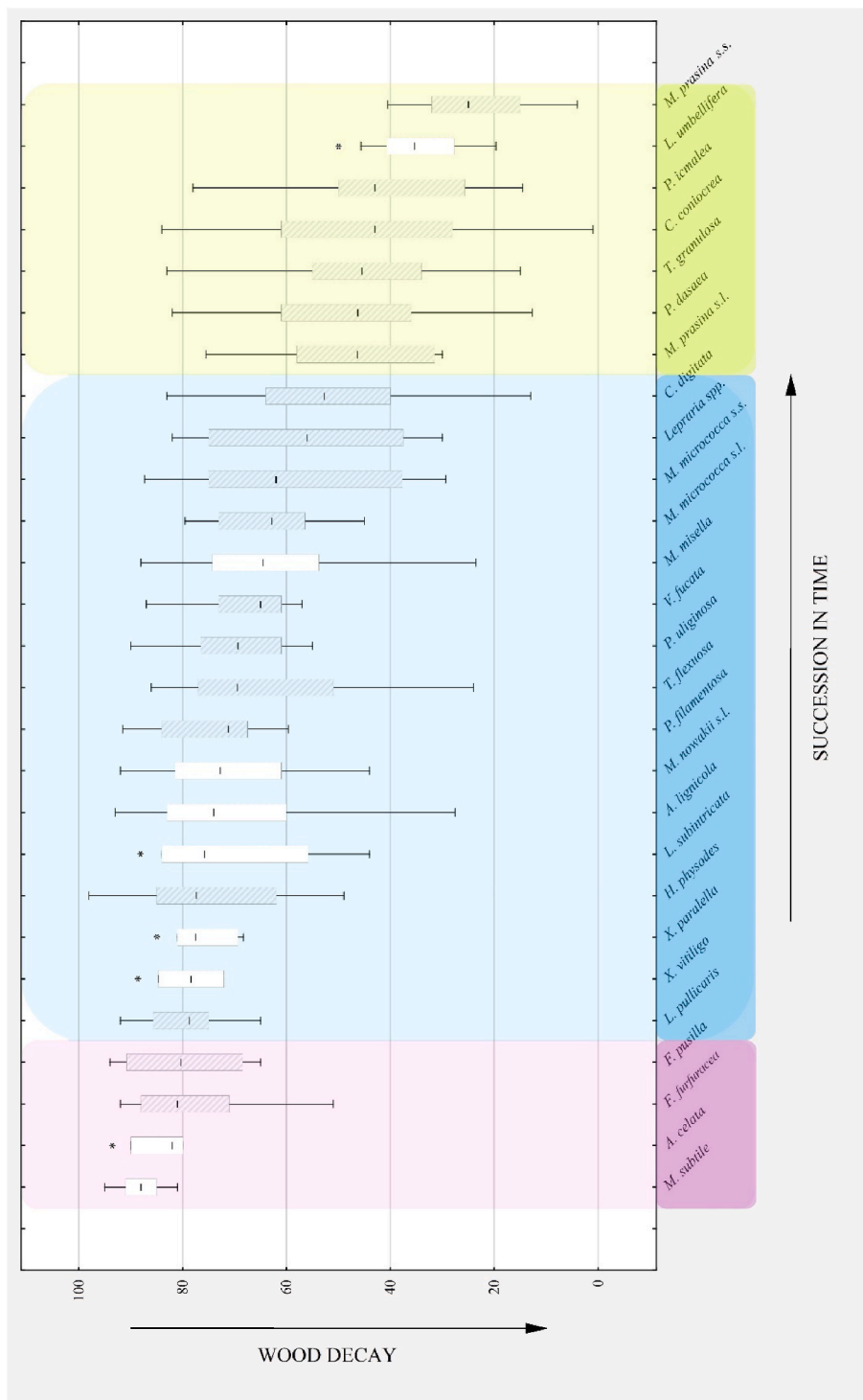


Fig. 7. Box graphs illustrating the relationship between wood hardness and lichen succession (box – three quartiles, whiskers – the non-outlier range). The white boxes refer to exclusively wood-inhabiting species. Species are ranked along with the progression of the wood decay (hardness in the Shore scale: 1–100). Species for which the number of records was less than 10 were denoted using an asterisk over a corresponding graph. Meaning of colors: violet: hardwood species, early wood successors (Shore hardness: 81 < x ≤ 100); blue: species of poorly decomposed wood (51 < x ≤ 80); green: soft wood species (21 < x ≤ 50). Full names of the species were listed in Table 3.

the regenerating stand. Taking into account the light requirements of the species found by us on rotting logs (Wirth, 1995, 2010; Fabiszewski and Szczepańska, 2010), when the gaps in the forest are covered by a dense undergrowth canopy, and the already decayed wood is covered with bryophytes, the vast majority of lichens will have to give way, and the re-colonization of the regenerating stand by lichens will take place primarily from the outside. However, the epiphytic biota inhabiting the wood of snags (e.g., Tanona and Czarnota, 2022) and the lobes of bark that remain on them are of no small importance for this process.

5.2. Environmental factors vs lichen diversity and abundance

The GLM and C & RT modeling results indicate that lichen diversity (Shannon H index), similarly to the lichen coverage of a wood section, depends mainly on the time that has passed since the fall of the log (the age of log). However, not very high values of the correlation coefficient suggest that this relationship is not linear. More likely, lichens have a narrower ecological optimum with regard to the degree of wood decay. The age of log is an indirect, albeit imperfect, measure of both: (i) the time that has passed since the bark detached from the wood surface, and thus the availability of the wood substrate, and (ii) the degree of wood

decay. As shown by the studies conducted by Caruso and Rudolphi (2009), Kharpukhaeva and Mukhortova (2016), Santaniello et al. (2017), and Staniaszek-Kik et al. (2019), the age and/or the extent of wood decay was one of the most important features of this substrate, influencing its colonization by lichens. More detailed studies of this factor demonstrated that the number of lichen species on lying wood was the highest within 11–14 y after the death of the tree, i.e., at a time similar to that previously reported by Caruso and Rudolphi (2009), who observed the peak of lichen diversity on 12–13-y-old spruce wood. On the other hand, no species were observed on the youngest, 2- and 3-y-old logs that had recently been stripped of their bark (only local occurrence was observed, which was most likely due to mechanical factors, rather than spontaneous falloff as a result of rot). This fact confirms the thesis of Kharpukhaeva and Mukhortova (2016), which states that epixylic succession begins only when the wood passes to the second decay phase. The lichen coverage of wood continued to increase until the last years of the study period over a time which was divided into four groups, characterized by a similar degree of coverage. Ultimately, the community was dominated by species of *Cladonia*, next to whom a still important place was occupied by, e.g., obligate epixylic species of the genus *Micarea* and mainly wood-inhabiting species of the genus *Placynthiella*.

A significant influence on the diversity and the sum of coverage coefficients in the models was also made by slope exposure; western exposures (NW, W, SW) were more favorable for both variables compared to the eastern ones (NE, E, SE), and the southern exposures (SW, S, SE) more than the northern ones (NW, N, NE). Lichenological studies taking into account the exposure of standing tree trunks, which were aimed at assessing the effect of light regime on the abundance and diversity of lichen biota, relatively consistently found that there are usually better conditions in northern exposures, which are sheltered from the damaging effects of direct sunlight (Svensson et al., 2005; Vondrák and Kubásek, 2019). However, there is much more shade on the surface of lying wood, therefore the presence of lichens on this substrate may be favored in more exposed locations on the northern mountain slopes which have limited insolation.

The spatial scale of stand disturbance showed no significant influence on the H index, although slightly higher averaged H values were related to the large-area windthrows. Recently, Langbehn et al. (2021) obtained opposite results. The authors demonstrated that the strength of the disturbance in the Carpathian spruce forests had a negative impact on the number of species of lichens observed. The abovementioned studies, in contrast to our investigation, used the total number of lichen species on the bark and on wood, indicating both live and dead spruce trees in the study plot. The spatial scale of the disturbance in our results was significant for the summed coverage of a wood section, resulting in a major increase of this parameter on the surfaces affected by a large-scale disturbance. It was not only light-demanding species that benefited from the improved light conditions, but above all, common species with a broad tolerance range, such as *Cladonia digitata* and *Placynthiella dasaea*.

The type of forest plant community was not a significant factor in our analyses, mainly due to the lack of appropriate representation in groups outside *Plagiothecio-Piceetum*. Nevertheless, absolute height was a major factor promoting the sum of the coverage factors in the studied sites. Higher values of patch coverage in higher mountainous locations may be partly related to the more frequent, large-area scale of disturbances in the upper mountain spruce forests, while the gap dynamics generally applies to mixed forests in the lower mountain range.

5.3. The hardness of dead wood vs lichen succession

The colonization of rotting logs by various lichen species, according to their preferences, took place over a period divided into 4 stages, based on the hardness of wood on the Shore scale. The durability of individual stages of wood decay varied across the entire log, since the decay rate depends mainly on the temperature and humidity of the microhabitat

(Käärik, 1983). When in direct contact with litter, the lower part of the log decomposes faster than when it remains suspended above the ground, and even faster compared to the upper part, which is exposed to sunlight and wind. Different decomposers (fungal species) also decompose at different rates/speeds (Boddy et al., 2008). Even the decay rate of the denser wood in sites with branch growth is different. Thus, the same log can be simultaneously inhabited by lichens that prefer extremely different stages of wood decay. At the initial stage of decomposition, this substrate is available for colonization only after the bark has fallen off. At the same time, a longer bark residence time on the log accelerates biological decomposition and, consequently, makes the already partially decayed substrate available for epixyles. Therefore, hard wood of windthrown logs is characterized by little diversity and an abundance of early colonizers (Fig. 7), which is also emphasized by the studies of Söderström (1988a), Kharpukhaeva and Mukhortova (2016) as well as Tanona and Czarnota (2022) with reference to a wider range of natural wood substrates. Lichens do not appear on “fresh” wood, even when it is devoid of bark from the very beginning, such as on various anthropogenic structures (Petersen et al., 2017). It is highly unlikely that the high density of the substrate represented a significant barrier for lichens (which grow on rocks), therefore it is possible that the development of lichens in the initial decay stage is delayed by inhibitors in the wood (e.g., phenolic compounds, resin) (Cowan, 1999; Phillips and Croteau, 1999; Nascimento et al., 2013), although this relationship has not yet been subject to extensive research for lichenized fungi. The second decay stage is characterized by a sudden leap in the representation of lichens, both in terms of diversity and abundance. According to the previously described hypothesis, this may be related not only to the time that has passed since the exposure of the bare wood surface, but also the breakdown of substances that inhibit lichen growth by some microorganisms (e.g., Bhat et al., 1998). The decreased concentration of these substances in wood is also uneven, i.e., it is faster in wet (but not saturated with water) parts of the trunk, which are more easily controlled by fungi and saprotrophic bacteria (e.g., Käärik, 1983; Piasczyk et al., 2022), which could account for the relationship between the degree of decay and colonization by lichens. The third stage is related to the repeated decline in the success of colonization, related to the gradual disintegration of the surface layers of the wood and thus the elimination of species that inhabited it earlier. At this stage, the succession is increasingly influenced by the non-woody ground vegetation and saplings, which gradually begin to shade the log and reduce evaporation. The fourth stage has not been identified due to the lack of representation of logs older than 17 y.

In addition to the abovementioned factors, the success of log colonization may be a result of the antagonistic interactions of lichens with saprotrophic fungi (Yamamoto et al., 2002) with bryophytes, or due to the ability of species to propagate quickly. Mechanical factors, such as woodpecker feeding or the movement of large animals through the undergrowth, may contribute to bark detachment and therefore to faster colonization of wood. Pakkala et al. (2017) described a case of preferential, seasonal feeding of Eurasian three-toed woodpecker *Picoides tridactylus* on the sap of pine trees damaged by fire, during early spring, i.e., the period of shortage of other sources of protein and at the same time the beginning of the breeding season. The likely reason was that environmental stress caused an increase in the level of amino acid nitrogen in the phloem (White, 1984; Eberhardt, 2000). In addition to drilling holes, woodpeckers also remove bark of trees infested with wood-boring beetles to select the larvae, which may be an important factor in exposing the wood during bark beetle outbreaks (Fayt et al., 2005).

In the sources available to date, the degree of CWD decay was determined in a uniform manner for the entire trunk (Söderström, 1988a; Staniaszek-Kik et al., 2019), the stump (Nascimbene et al., 2008a; Magnusson, 2010) or at least a large piece of wood (Kharpukhaeva and Mukhortova, 2016). This method failed to reflect the entire spectrum of habitat diversity offered by such large objects and did not allow determination of the ecological preferences of the organisms that

inhabit them. The applied method is more demanding, but also much more adequate in ecological research aimed at understanding the role of deadwood in the functioning of organisms that use it, including wood-inhabiting lichens.

6. Conclusions

1. Leaving the post-hurricane logs to decay naturally makes sense for preservation of the diversity and abundance of lichens in Western Carpathian forests. In national parks it should be a priority, regardless of the spatial scale of natural forest disturbance.
2. The time of wood decay (time since tree fall) is the major factor determining the diversity and abundance of lichens inhabiting exposed wood of spruce logs.
3. The composition of lichen communities on the exposed wood of windthrown spruce trees depends on the diversity of ecological niches on the log resulting from the different local rate of wood decay; the optimal stage of this habitat for lichens in the Polish Western Carpathians occurs a dozen or so years (11–17) after the fall of the trees.
4. Wood hardness measured in Shore degrees allows more objective assessment of the ecological preferences of lichens that inhabit this type of substrate, and can be successfully used for more precise research on the succession of lichens on wood; the wood inhabiting lichens colonize the wood of spruce logs mostly in its slightly decayed stage (51–80 Shore units).
5. Lichen diversity increases faster than the lichen abundance during the succession of exposed wood of windthrown spruce logs.
6. Many corticolous lichen species use wood of windthrows as an alternative habitat to grow.

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.

Acknowledgements

The work was financed from the resources of the Department of Ecology and Environmental Protection of the University of Rzeszów. The field studies were carried out with significant logistical support of the Gorce National Park. The study uses data from the scientific database of the Gorce National Park (Permission no. 530-17/2019).

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