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What determines the diversity and succession of lichens inhabiting post-bark beetle snags in the Western Carpathians?

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Abstract The life strategy of Norway spruce allows the recovery of European spruce forests in a scenario of catastrophic disturbances caused by the European spruce bark beetle. However, little is known about how the development of this insect infestation has influenced the preservation of the ecological balance in these forests over the last decades. Based on the upper montane spruce forests in the Polish Western Carpathians, we decided to check what species of lichens are using the decaying wood of post-bark beetle snags and how the progressive changes in wood hardness and stand decomposition affect the process of species exchange. In 2018–2019, we investigated spruce snags on permanent monitoring plots in Gorce National Park, whose cause and time of death have been recorded since 1999, and earlier in 1992 and 1997. The study covered 374 post-bark beetle spruce snags at 76 sites. We found 84 species, including 77 lichens, 6 lichenicolous fungi and one non-lichenised fungus, 15 of which were exclusively wood-inhabiting species in Gorce range. Using generalised linear models, the wood age (A) and the scale of the forest stand breakdown phenomenon (B) were compared with the altitude (C), the aspects of hillside exposure (D) and the forest plant community (E) in the assessment of their effect on lichen species diversity and abundance. "A” was the most important of the tested factors, significantly and positively influencing both parameters, while “B–D” only weakly influenced lichen abundance. Five groups of wood age, significantly different in the lichen abundance and the composition of species were distinguished, and a characteristic combination of dominant species was determined for each of them. Based on the measurements of the wood hardness under the thalli using Shore’s method, the succession of species during the colonisation of the post-bark beetle snags was determined and four groups of species were selected, most frequent in the successive stages of wood decay process. The wood of spruces killed by the bark beetle is both an important substrate enabling the survival of obligately wood-inhabiting lichen species, as well as providing a habitat supporting the maintenance of epiphytes in the Carpathian forests. This study extends the knowledge about the specific requirements of lichens inhabiting spruce snags, as well as the pace and course of lichen succession on this substrate.

Keywords: lichen ecology, lichen succession, lichen diversity, bark beetle outbreaks, deadwood, natural forest disturbances, forest ecology, permanent study plots, Norway spruce snags.

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Introduction

Over the last decades, due to the global increase in the Earth's temperature, the ecological significance of the spruce bark beetle *Ips typographus* (L.) infestations have increased in forests including Norway spruce Picea abies (L.) (Fahse & Heurich 2011, Marini et al. 2017, Jakoby et al. 2019, Netherer et al. 2021). Massive outbreaks of this cambiofagous beetle, indigenous in the spruce forests of Europe, constitute a natural phenomenon conditioning the dynamics of these forests (Čada et al. 2016, Langbehn et al. 2021). As a result, they contribute to the formation of gaps filled in by snags in the forest stand. The spatial development of forest stand decomposition, often boosted by storm winds, affects local and regional changes in forest ecosystem biodiversity (Kruys & Joonsson 1999, Müller et al. 2008, Pouska et al. 2010, Fukasawa et al. 2019, Przepióra et al. 2020), including modification of the biota of lichens (Czarnota 2012, Bässler et al. 2016, Thorn et al. 2018, Tanona & Czarnota 2020).

Natural disturbances, including spruce bark beetle outbreaks, shape the forest structure in Gorce National Park (GNP) in the Polish Western Carpathians (South Poland), among others, encompassing the remnants of a primeval Carpathian forest (Loch & Armatys 2014, Wężyk et al. 2018). The upper parts of the park are occupied by single-species spruce forests, while lower altitudes are covered with mixed beech-fir forests with an admixture of spruce and fir-spruce forests (Medwecka-Kornaś 2006). Since 1981, thanks to strict protection, subsequent fragments of the Gorce forests over much of this area have gradually taken on their natural character (Loch & Armatys 2008). Left in their original positions, post-bark beetle snags, apart from a series of other functions in the ecosystem, provide habitats for many organisms that depend on them to varying degrees (Radu 2007, Weaver et al. 2009). Both obligately wood-inhabiting and usually epiphytic lichens can be distinguished in this group (e.g., Lõhmus & Lõhmus 2001, Spribille et al. 2008, Czarnota 2012, Santaniello et al. 2017). Due to stand disturbance, both groups benefit from the possibility of spreading to surfaces free of competing organisms and from increased access to light (Spribille et al. 2008, Kharpukhaeva & Mukhortova 2016). For the epiphytes that slowly retreat from the bark remnants, the ability to inhabit the wood gives them a chance to survive (Kushnevskaya & Shorohova 2018, Langbehn et al. 2021).

Standing wood, due to its height and exposure gradient, is usually inhabited by more diverse communities of lichens, e.g., compared to lying wood (Holien 1996, Humphrey et al. 2002, Svensson et al. 2016). It is related to the different degree of insolation and humidity of the wood, which is dried from the top by wind and sun, and from the bottom it is shaded and moist from the adjacent vegetation. The above conditions also affect the speed of wood decay, which occurs faster in the wetter parts of the trunk (Staniaszek-Kik et al. 2019). The diversity of the available habitats favours the colonization of wood by lichens with different ecological requirements. More detailed study on the natural disturbances affecting Norway spruce forests, and the related consequences to forest lichens, the authors have previously included in a review article, devoted to this subject (Tanona & Czarnota 2019). Having data from GNP archives on the dynamics and the causes of spruce mortality in the area of the park over the last 25 years, we have investigated the succession of lichens on post-bark beetle snags, both with regard to the age of the wood, specified in years, and the stage of wood decay, based on the measurements of hardness under the observed thalli with the use of a Shore A durometer. This method used to assess the importance of wood hardness for lichens is innovative. Determining the relationship between the lichen species composition and the age of the wood is one of the most detailed ecological studies ever conducted. Moreover, in previous studies on the importance of this habitat for lichens, the wood decay at the level of the entire dead trunk (e.g., Söderström 1988, Staniaszek-Kik et al. 2019), stump (Nascimbene et al. 2008, Magnusson 2010) or its large fragment was assessed (Kharpukhaeva & Mukhortova 2016).

This study aimed to understand the species composition and the succession course of lichens inhabiting decaying wood in the Norway spruce snags, which have become abundant in the Carpathians as a result of naturally occurring phenomena of a destructive character, i.e., the infestation with the spruce bark beetle. The following hypotheses were assessed: i) the spatial scale of forest stand decomposition is the main environmental factor determining the diversity and abundance of lichens inhabiting post-bark beetle snags in the Carpathians, ii) the age of spruce snags (age of wood) affects on the composition of lichen communities and abundance of lichens inhabiting this substrate, iii) the subsequent stages of the wood decay (hardness of wood) better than the wood age determine particular stages of the lichen succession.

Study area

Gorce National Park (Figure 1; geographical coordinates: 49°37’18.802” – 49°30’34.218” N and 20°01’20.867” – 20°15’10.850” E), with an area of 7,030 ha, covers a part of the Gorce Mountain Range belonging to the External Western Carpathians in southern Poland. The hills of this range, spreading up to an altitude of 1,310 m, do not reach the upper borderline of the forest. In Gorce range, natural determinants have allowed for the formation of two climate-plant belts typical of the Western Carpathians, i.e., overgrown with a single species, the upper montane spruce forest *Plagiothecio-Piceetum* (Szaf., Pawł. et Kulcz. 1923; Br.-Bl., Vlieg. et Siss. 1939 em. J. Mat. 1977), and the beech-fir-spruce mixed forests *Dentario glandulosae-Fagetum* (Klika 1927 em. Mat. 1964) and spruce-fir forests *Abieti-Piceetum* (Szaf., Pawł. et Kulcz. 1923 em. J. Mat. 1978), which mainly occupy the lower montane belt. Moreover, a wide intermontane transitional zone formed by the beech-spruce forest *Plagiothecio-Piceetum fagetosum* can be distinguished in the Gorce range (Czarnota & Stefanik (eds) 2015).

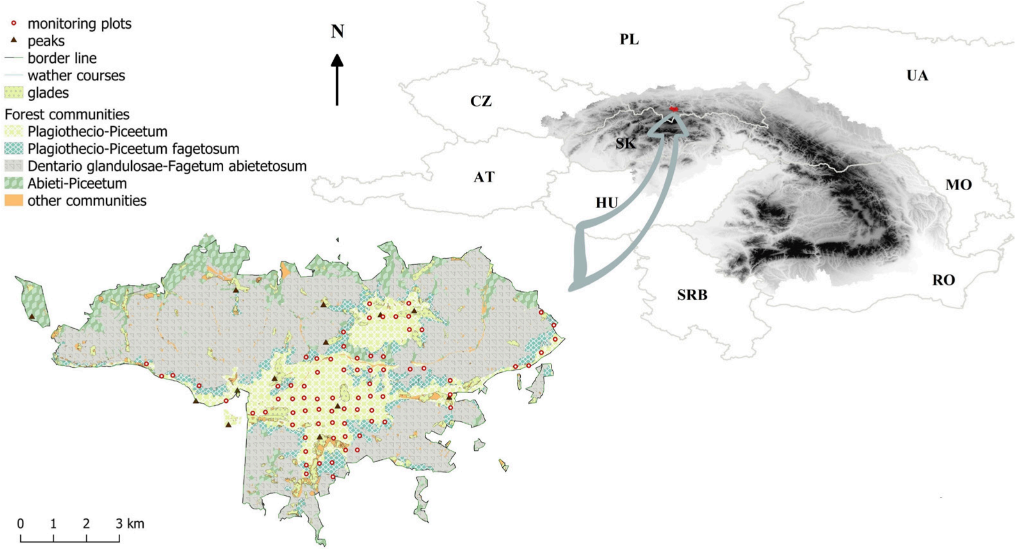

Figure 1 The distribution of research sites in the grid of permanent monitoring plots for forest dynamic study in the area of the Gorce National Park against the background of the main plant communities.

Methods

The selection of research sites and field data collection

Studies on wood-inhabiting lichens on spruce post-bark beetle snags were conducted during two seasons, 2018 and 2019, using sites selected from the regular network of circular permanent monitoring plots, 0.05 ha each (Figure 1). Since 1992, these plots have been subjected to repeated monitoring of the Norway spruce *Picea abies* (L.) H. Karst mortality. At the beginning, it was run irregularly, i.e., in 1992, 1997 and 1999; however, since 2000 it has been carried out annually. The identification of the respective dead trunks and the knowledge of their history, i.e., the time and cause of spruce dieback, were thanks to previous measurements of the azimuth and the distance from the fixed centre of the plot dating back to 1992, accompanied by the start of studies on the dynamics of forests in the area of GNP (Chwistek 2001). Due to the uneven intervals of data collection on the mortality of the spruces at the beginning, as well as two seasons of lichenological data collection, the age of the wood was grouped into classes, in accordance with Table 1.

Overall, the study covered 374 post-bark beetle spruce snags at 76 sites, located mainly within the *Plagiothecio-Piceetum* community (54 sites, 300 trunks) and in the *Plagiothecio-Piceetum fagetosum* transitional zone (15 sites, 51 trunks). A small share belonged to sites representing the *Dentario glandulosae-Fagetum* community (4 sites, 9 trunks) and the *Abieti-Piceetum montanum* community (3 sites, 14 trunks), where spruce was a co-dominant species in 1992.

An inventory of lichen species and the corresponding coverage degree was carried out on patches of unbarked wood of snags, with an area of at least 0.5 m2 from ground level up to a height of 2 m around the trunk. The degree of coverage was determined using an adapted Braun-Blanquet scale (Matuszkiewicz 2005). The degrees of the scale were transformed to coverage coefficients representing mean values for a class (Table 2).

Table 2 The degrees of coverage scale of the examined wood patches designated to the lichen species in the field, and the corresponding percentage ranges and coverage coefficients.

Degree of scale	Range of coverage classes [%]	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

To investigate the significance of the spatial scale of forest stand disturbance, for the diversity of wood-inhabiting lichens on post-bark beetle snags, the sites were divided to represent the following: the stand decomposition with single snags (<5 remote spruce snags in the plot; 16 sites, 78 trunks), the decomposition with grouping snags (covering an area <0.05 ha; 40 sites, 158 trunks) and the large-scale stand decomposition (area of snags >0.05 ha, 22 sites, 138 trunks). In the case of two plots, part of the trees was ranked as single, and the other part was ranked as the group type of stand decomposition.

The effect of the extent of the wood decay on the course of the succession process was defined based on the measurements of the wood hardness under individuals of the respective lichen species, taken in three technical repetitions using a manual Shore analogue

Table 1 The division of examined spruce snags into sixteen age classes and five groups of age classes (age groups) derived from NMDS, with their numbers within the classes.

Age class	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV	XVI
Age group	I′	II′	III′					IV′							V′	
Year interval	1–4	5–6	7–8	9	10	11	12	13	14	15	16	17	18	19–21	22–25	>25
No. of snags	17	21	25	28	42	38	28	18	14	13	9	16	27	20	21	37

durometer designated for average-density materials (type A). The device was equipped with a 1–100 scale (in accordance with Shore and complying with the PN-ISO 868 standard), for which lower-range values denoted soft timber, and the upper-range values represented hard timber. In the case of species occurring with a high frequency, the measurements were taken randomly to obtain a sufficient number of test samples (no less than 10, although the final number of measurements depended on the number of occurrences of the individual species; Table 3, compare with Table 8).

The identification and nomenclature of the species

Specimens that were questionable or indeterminable in the field studies were collected for identification based on their microscopic, anatomical and morphological features. Standard spot tests using aqueous solutions such as potassium hydroxide (KOH), calcium hypochlorite (a commercial whitener), iodine in potassium iodide (KJ) and an ethanol solution of p-phenylenediamine were carried out by applying a Zeiss STEMI DV4 stereoscope and a Zeiss Axiostar Plus optical microscope. The identification of common, poorly distinguishable in the field, often mixed species of the genus *Lepraria*, for which the chemistry of the thallus is the main taxonomic criterion, was abandoned. In ecological analyses, all representatives of this genus have been included in the taxon *Lepraria* spp. However, based on studies by Czarnota & Kukwa (2001), using thin-layer chromatography (TLC) as a research method, it is known that the most frequent species is *L. jackii* Tønsberg, while *L. elobata* Tønsberg, *L. lobificans* Nyl., *L. eburnea* J.R. Laundon and *L. incana* (L.) Ach. are less numerous on spruces in the area of the Gorce range. Species within the groups *Cladonia pyxidata-chlorophaea*, *Micarea novakii* s.l., *Micarea prasina* s.l. (excluding *M. prasina* Fr. s.s. and *M. soralifera* Guzow-Krzem., Czarnota, Łubek & Kukwa) and *M. micrococca* s.l. (excluding *M. byssacea* (Th. Fr.) Czarnota, Guzow-Krzem. & Coppins, *M. laeta* Launis & Myllys and *M. micrococca* (Körb.) Gams ex Coppins s.s.) have not been identified due to the high morphological similarity of species that were until recently considered cryptic and the resulting potential mistakes in distinguishing them in the field. Two, obviously different, taxa were not classified. They were listed in the analyses as “sp. unknown”. The taxa nomenclature according to the Index Fungorum database (Index Fungorum search page), except *Lecanora conizaeoides* Nyl. ex Cromb., follows Smith et al. (2009).

Statistical analysis

The analysis was performed at the level of a single snag with regard to parameters characterising the following: a) a research site including altitude, hillside exposure, plant community and the extent of forest stand decomposition; b) the studied snag, i.e., the classes of wood age; c) the respective species, i.e., the degree of wood decay manifested by its hardness under a particular specimen.

The field data were analysed in terms of the effect of environmental factors in the form of the sum of coefficients representing the coverage of a studied wood patch with species and the Shannon diversity index (H) (Shannon, 1948) expressed by the following formula: $H= -\sum_{1}^{S} p_i \ln p_i$, where S is the number of lichen species and p_i is the share of the species in relation to the sum of shares of all of the species occupying the studied patch. Shannon’s H, which is actually a measure of entropy, has been widely adopted in ecological researches to determine a diversity in species communities (Pallmann et al. 2012, Morris et al. 2014, Daly et al. 2018). This was justified by the fact that the diversity and entropy share many conceptual characteristics, such as symmetry and continuity of a function or the principal of evenness (according to Jost 2009).

The Spearman's correlation between H index values and the number of species in the community, as well as the sum of the coverage coefficients was carried out to specify the contribution of this indicator's components to its differentiation. Since the analysed diversity index was mainly related to the number of observed species on a snag, a rarefaction plot was constructed (Figure 2) to check whether the different number of individuals observed in each age class could have influenced the obtained results, assuming that a greater number of observations increases the probability of finding a greater number of species.

Because of the lack of distribution normality for the studied variables, both in total and within individual groups, they were tested using nonlinear forms of generalised linear models (GLM; Table 4) based on the Poisson distribution with a logarithmic linking function. The best-fitted models were obtained by means of a backward elimination of factors revealing the weakest impact, based on the Wald test, using the maximum likelihood (Shannon index) or quasi-likelihood approach (the coverage of a patch due to the over-dispersion phenomenon). The measure of model fit was χ^2 Pearson's test and residual analysis. The direction and strength of statistically significant relationships were additionally recognised based on the results of Spearman rank correlations and detailed comparison matrices for the levels of qualitative variables using the Kruskal–Wallis test and the multiple comparison test.

The grouping of tested parameter values under the influence of environmental predictors was used for the construction of regression trees (Figures 3&4) in the classification and regression trees (C&RT) algorithm (Breiman et al. 1984). In this case, this method's advantage was reflected in the lack of preliminary assumptions on the normality of distributions or the nature of the relationship among the analysed factors. This, in turn, allowed their usage in the assessment of nonparametric and nonlinear systems (StatSoft 2006).

Eight categories of exposure were analysed with Ward's method to separate groups of similar effects on the sum of snag coverage coefficients and the H index. Since this action failed to distinguish a satisfactory number of homogenous and, at the same time, relatively equal exposure groups, these data were transformed using trigonometric functions (sine and cosine) into two quantitative variables of a continuous nature, i.e., "northness" [cos (α rad)] and "eastness" [sin (α rad)], using a method recommended by Roberts et al. (1989).

Nonmetric multidimensional scaling (NMDS; Figure 5) was used to evaluate differences in a composition of the lichen community, based on the mean lichen coverage across sixteen classes of wood age. The boundary dividing age classes into larger groups was set at 60% similarity. The analysis was performed on the basis of the Bray-Curtis similarity after transforming the data with the square root. On the basis of NMDS, more extensive age groups were distinguished (Table 1).

One-way PERMANOVA (Table 5) was performed on the basis of 999 unrestricted permutations of data transformed with the square root, with five groups of age classes extracted in NMDS. Pairwise dissimilarities were calculated among all five abovementioned groups (Table 6).

The analysis of percentage similarity (SIMPER; Table 7) was carried out to determine the most abundant species in each of five age groups, responsible for the majority of intergroup similarity.

The succession of lichens on the wood of spruce snags was illustrated using box diagrams of wood hardness for the respective species (three quartiles), listed along with a descending median value and in line with the rotting progress. In this analysis, all of the species that appeared on a minimum of 10 examined snags were considered so that the number of hardness measurements (in each case, the average of three repetitions) could serve to determine the species preferences and allow for classification into one of the four succession stages. For the imaging of a species succession on the wood of post-bark beetle snags in the Carpathians, obligately wood-inhabiting species found in the Gorce range or in the Polish part of the Carpathians were also taken into account (Czarnota 2012; see Table 3), even though most often it did not meet the criterion of 10 occurrences. The purpose of the latter was exclusively to indicate their hypothetical rank in the succession based on the acquired measurements. Bearing in mind the preferred timber hardness (median), the species were allocated into one out of four groups featuring the stages of substrate decay in Shore's units, i.e., i) species characteristic of hard timber, early successors of the wood ($81<x\leq100$); ii) species of poorly rotten wood ($51<x\leq80$); iii) species of soft wood ($21<x\leq50$); iv) species inhabiting a very soft rotten wood ($1<x<20$).

The map of the study site distribution (Figure 1)

Table 3 The list of species including the number of occurrences and the sum of coverage coefficients per 374 studied spruce trunks.

Species name	PRLL	No. obs.	SCC	Species name	PRLL	No. obs.	SCC
Absconditella lignicola^^		4	0.42	*Micarea globulosella*		1	0.01
Amandinea punctata		1	0.01	*Micarea hedlundii*^^	VU	3	0.07
#*Arthonia digitatae*		1	0.01	*Micarea laeta*		1	0.01
#*Bachmanniomyces* punctum		3	1.96	*Micarea micrococca* s.s.		23	1.03
Calicium abietinum	VU	5	1.15	*Micarea micrococca* s.l.		6	0.18
Calicium glaucellum	VU	6	0.18	*Micarea misella*^		36	2.72
Calicium trabinellum^^	EN	11	3.44	*Micarea nigella*^^		3	0.07
Chaenotheca chrysocephala		4	0.42	*Micarea nitschkeana*		3	0.15
Chaenotheca ferruginea		22	21.78	*Micarea nowakii* s.l.^^		4	0.8
Chaenotheca stemonea	EN	4	1.71	*Micarea prasina* s.s.		60	13.38
Chaenotheca xyloxena^^	VU	27	5.89	*Micarea prasina* s.l.		7	2.46
#*Chaenothecopsis pusilla*^		3	0.03	*Micarea soralifera*		1	0.01
#*Chaenothecopsis pusiola*^		1	0.05	*Micarea* sp.		2	0.06
#*Chaenothecopsis* viridireagens		1	0.01	*Micarea* viridileprosa		1	0.01
Cladonia coniocraea		16	2.55	#*Monodyctis* epilepraria		1	0.01
Cladonia digitata		201	192.06	*Mycocalicium subtile*^		229	405.79
Cladonia pyxidata s.l.		1	0.35	*Ochrolechia microstictoides*		1	0.01
Coenogonium pineti		1	0.01	*Palicella filamentosa*		12	1.26
Elixia flexella^^	VU	3	0.41	*Parmeliopsis ambigua*		17	1.65
##*Epigloea bactrospora*		1	0.01	*Parmeliopsis hyperopta*	VU	2	0.02
##*Epigloea urosperma*		1	0.01	*Placynthiella dasaea*		139	63.23
Fellhanera subtilis		1	0.05	*Placynthiella icmalea*		44	8.75
Frutidella pullata		8	0.88	*Placynthiella uliginosa*		11	10.41
Fuscidea pusilla		9	0.47	*Platismatia glauca*		1	0.35
Hypocenomyce scalaris		45	16.28	*Pseudevernia furfuracea*		3	0.41
Hypogymnia physodes		207	199.02	*Pycnora sorophora*		1	0.01
Japewia subaurifera		1	0.01	*Pycnora xanthococca*		1	0.05
Lecanora conizaeoides		81	55.43	*Scoliciosporum chlorococcum*		8	5.01
Lecanora phaeostigma		11	1.59	*Scoliciosporum umbrinum*		1	0.01
Lecanora pulicaris		26	4.17	*Strangospora moriformis*		5	1.68
Lecanora saligna		1	0.35	*Trapelia corticola*		9	2.36
Lecanora sarcopidoides^^	NT	9	7.78	*Trapeliopsis flexuosa*		63	5.46
Lecanora subintricata^		16	1.76	*Trapeliopsis glaucolepidea*	DD	1	0.01
Lecidea leprarioides		13	7.98	*Trapeliopsis granulosa*		10	0.14
Lecidea nylanderi		18	1.78	*Trapeliopsis pseudogranulosa*		1	0.01
Lecidea turgidula^	VU	7	0.49	*Violella fucata*		20	1.24
Lepraria spp.		142	66.49	*Xylopsora caradocensis*		10	3.13
Lichenomphalia umbellifera	NT	1	1.6	cf. *Calicium* sp.		1	0.01
Melanelixia subaurifera		1	0.01	cf. *Japewia tornoensis*		1	0.01
Micarea anterior^^		2	0.02	cf. *Ochrolechia alboflavescens*		2	0.02
Micarea botryoides		1	0.01	sp. unknown 1		1	0.01
Micarea byssacea		8	0.46	sp. unknown 2		1	0.01

Note: PRLL – the category of threat according to the Polish Red List of Lichens (Cieśliński et al. 2006); SCC – the sum of coverage coefficients; ^/^^ – a species found in the Gorce/the Carpathians only on dead wood (Czarnota 2012); # – a lichenicolous fungus; ## – an algicolous fungus.

was prepared using Quantum Gis v. 3.4.9 software. The statistical analysis was carried out using STATISTICA v. 13.1, CANOCO v. 5 and PAST v. 4.03 application at the significance level of α=0.05.

Results

Species community

In this research, 77 taxa of lichenised fungi (lichens), 6 species of lichenicolous fungi, 2 species of algicolous fungi and a non-lichenised fungus *Mycocalicium subtile* (one of the first successors of dead wood commonly listed together with lichens) were identified. The list includes 15 taxa found exclusively on wood in the Gorce range and 10 in the Polish part of the Carpathians (Czarnota 2012). An algicolous fungus *Epigloea bactrospora* was recorded for the first time in the Carpathians (Czarnota & Tanona 2020). Twelve species were assigned various categories of threat on the Polish Lichen Red List in accordance with the IUCN criteria (Cieśliński et al. 2006) (Table 3).

The measure of diversity – Shannon index

As a result of the correlation between H index values and its two components, the species richness and coverage, the correlation coefficients have obtained values of r_s=0.83 and r_s=0.42, respectively, underlying the greater importance of the first of the examined elements in determining its value. The rarefaction plot in Figure 2 allows the comparison of the species richness on the examined snags based on the arrangement of the curves, created for individual age classes. It shows that the increase in species richness along with the number of individuals sampled, accelerated in a manner similar to the original order of age classes.

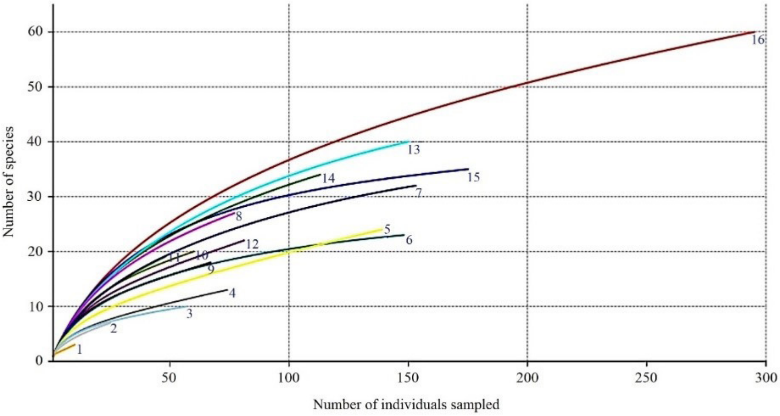

Figure 2 Rarefaction plot showing the number of species expected to be found for the number of individuals sampled for each of the sixteen age classes.

The effect of the environmental factors

The analysis performed with the use of generalized linear models (GLMs) showed that only the age of the wood, expressed in classes, had a significant influence on the Shannon diversity index (Table 4). The model adjustment, based on the Pearson χ^2 test, was χ^2/df=0.31. The Spearman rank correlation

Table 4 The results of generalised linear models (GLMs) for the Shannon diversity index (H) and for the sum of trunk coverage coefficients against tested environmental variables.

Effect	Eff. level	b	SE	W	p (W)
Shannon's H index Total					
(Intercept)		-1.31622	0.15627	70.94263	0.00000
Age class		0.09557	0.01361	49.28749	0.00000
Sum of cover coefficients					
(Intercept)		-1.60824	0.47592	11.41928	0.00073
Age class		0.05921	0.00654	82.09012	0.00000
Altitude		0.00185	0.00042	19.69030	0.00001
Northness		0.18365	0.03909	22.07021	0.00000
Forest d.s.	single	-0.26745	0.08751	9.33982	0.00937
Forest d.s.	large s.	0.16445	0.06632	6.15213	0.04614
Eastness		-0.16264	0.05698	8.14787	0.00431

Notes: Eff.level: Effect level; Forest d.s.: forest decomposition scale; large s.: large scale; b – a regression coefficient, SE – a standard error b, W – Wald's statistics, p (W) – Wald's statistics probability. Based on Wald's statistics, only the outcomes for factors of a significant (p≤0.05) effect on a tested parameter were mentioned.

between the H index values and the age classes demonstrated a significant relationship between these features at the level of r_s=0.60.

The grouping of the H index values, based on their variances, under the influence of the tested factors, was illustrated using a regression tree (Figure 3). The periods of faster growth (breakthrough points) in terms of the species diversity succeeded after the 3rd, 6th and 14th age classes, i.e., 8, 11 and 21 years after the tree's death, respectively. The classification presented indicates that the second most important factor grouping the values of the Shannon index was the spatial scale of the forest disturbances. However, both the results of the model and the test among three groups of the extent of stand decomposition, carried out by using the Kruskal–Wallis method, did not confirm the significance of the differences among the medians of the index in the respective groups (p=0.865).

Five out of the six factors studied, excluding the type of forest community, exerted a significant effect on wood patch coverage with species of lichens. A model for this variable equalled χ^2/df=2.03 in terms of Pearson's statistics. Again, the wood age turned out to be the paramount factor. It correlated positively with patch coverage at the level of r_s=0.34. Altitude constituted a less representative predictor exerting a positive effect on patch coverage (r_s=0.22). Exposure, presented in the form of "northness" and "eastness", revealed a very weak, although significant, relationship in the model formed with patch coverage at the levels of r_s=0.05 and r_s=–0.07, respectively.

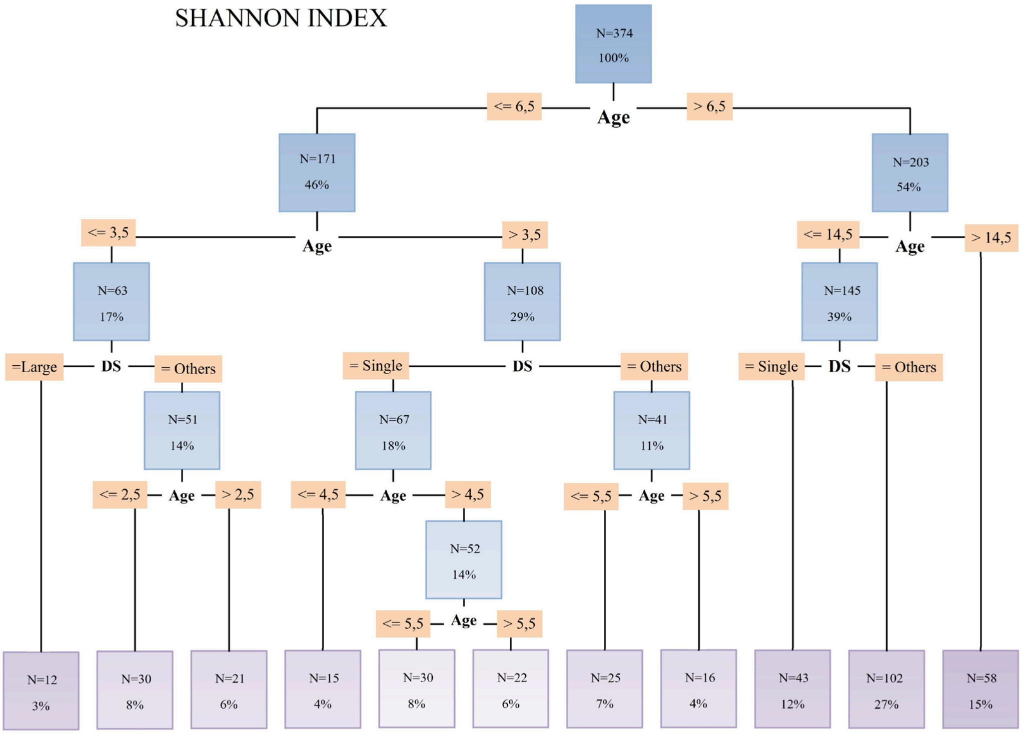

Figure 3 A regression tree (C&RT), based on the Shannon diversity index (H) and environmental variables significantly affecting it. Abbreviations used: Age – wood age classes; DS – the scale of the forest stand decomposition; Large – large-scale disturbances; Single – single standing snags.

This means that the “north” hillsides (NW-NE) were slightly more favourable for lichen growth on the snags compared to the “south” hillsides (SW-SE) and, similarly, the “west” (NW-SW) was more favourable than the “east” (NE-SE), although in the rank correlation, these did not demonstrate any statistically significant differences. The significance of differences among the three groups of forest stand decomposition in the scope of patch coverage was studied using the Kruskal–Wallis test, yielding a test probability of p=0.02. The multiple comparison test demonstrated a significantly greater coverage of the tested wood patches with lichens on the areas affected by the bark beetle outbreak on a large-area scale in contrast to the same phenomenon on a single disturbance scale. A regression tree built for the sum of the coverage coefficients (Figure 4) indicates that the largest increase in the cover of wood patches takes place on the spruce snags after 21 years (the 14th class of age). A distinct group is formed by dead trunks for up to 4 years (the 1st class of age), on which coverage with lichens is negligible or missing. In the highest age classes (>21 years), the only factor influencing patch coverage is altitude. In the middle classes of age (4–21 years), the main part for this parameter is played by the scale of stand decomposition followed by altitude and hillside exposure.

Further statistical analysis with regard to the coverage of wood with lichens required grouping the sixteen age classes based on the coverage data into larger groups using the NMDS analysis (Figure 5). The reason was that the differences in this factor were only noticeable on a larger scale. The analysis

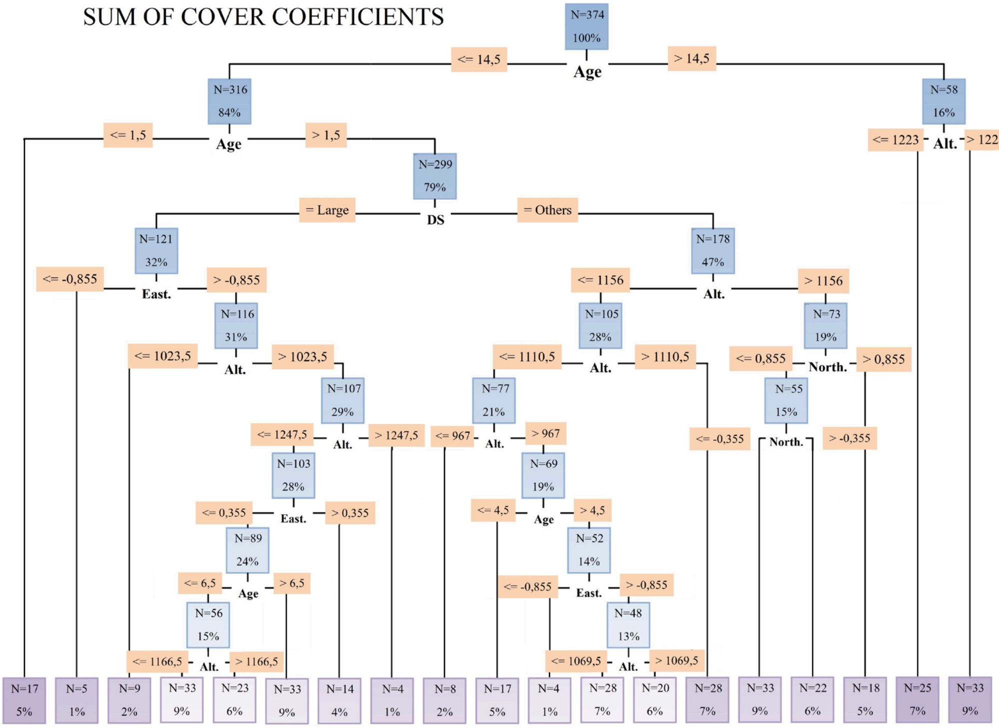

Figure 4 A regression tree (C&RT), based on the sum of coverage coefficients and environmental variables significantly affecting it. Abbreviations used: Age – wood age classes; DS – the scale of the forest stand decomposition; Large – large-scale disturbances; Alt. – altitude [metres above the sea level] North. – northness; East. – eastness.

resulted in separation of five groups of trunks with at least 60% similarity in terms of wood coverage, according to Table 1 (the same groups were created when using the C&RT algoritm with 'age classes' as the only one grouping factor). Permutational analysis of variance (one-way PERMANOVA) with the accompanying pair-wise test (Table 5 & 6) indicated significant differences of the wood coverage between all five age groups.

Table 5 One-way PERMANOVA results for lichen community composition based on Bray–Curtis distances of wood coverage data (means) in five groups of age.

Source of variation	df	SS	pseudo-F	*P*
Group	4	115320	24.35	0.001
Residual	369	436810		
Total	373	552120		

Notes: The pseudo-F value is based on 999 permutations in Monte Carlo test. Square root transformation was applied.

Table 6 Pair-wise tests results for PERMANOVA based on Bray–Curtis distances of wood coverage data (means) in five groups of age.

Groups	pseudo-F	P	Unique perms
1 vs 2	2.49	0.013	995
1 vs 3	4.22	0.001	998
1 vs 4	3.442	0.001	999
1 vs 5	5.592	0.001	999
2 vs 3	2.69	0.001	996
2 vs 4	3.34	0.001	999
2 vs 5	5.45	0.001	998
3 vs 4	5.13	0.001	999
3 vs 5	7.82	0.001	999
4 vs 5	4.14	0.001	998

Notes: The pseudo-F value is based on 999 permutations in Monte Carlo test. Square root transformation was applied.

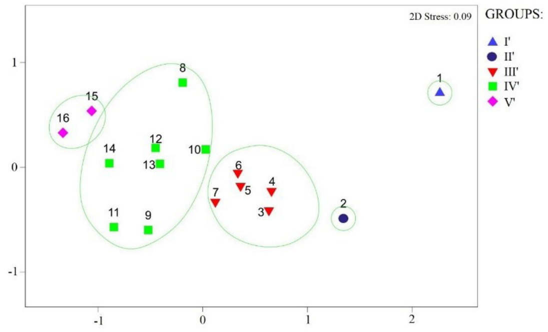

Figure 5 Nonmetric multidimensional scaling (NMDS) plot based on mean lichen coverage in sixteen age classes. Resemblance - Bray-Curtis similarity; Square root transformation was applied. Solid line - sites with similarity values greater than 60%.

The SIMPER analysis made it possible to distinguish the species most responsible for the intergroup similarity of the samples among five groups of wood age, i.e., the species that dominate the communities and keep a characteristic combination for the selected groups (see Table 7). In the arrangement of characteristic species, a gradual exchange was visible: *Mycocalicium subtile* dominated in the first, second and third groups, but its abundance increased over time. In the third group it was accompanied by *Hypogymnia physodes*. In the fourth group, its share decreased and was surpassed by *Cladonia digitata* and *H. physodes*, while *Placynthiella dasaea* also joined to the group of dominant species. In the fifth group, *M. subtile* ceases to be dominant. Its place is taken by species of the genus *Lepraria*.

Table 7 Taxa contributing to the similarity in the species composition within each of the five wood age groups (SIMPER analysis).

Group (AvSim)	Taxon	AvAbu	AvSim	AvSim / SD	Con (%)	CuCon (%)
Group 1 13.16%	*Mycocalicium subtile*	0.33	13.16	0.51	100.00	100.00
Group 2 28.66%	*Mycocalicium subtile*	1.00	27.74	0.78	96.79	96.79
Group 3 38.78%	*Mycocalicium subtile*	1.09	27.62	1.13	71.22	71.22
	Hypogymnia physodes	0.51	7.79	0.64	20.09	91.31
Group 4 21.40%	*Cladonia digitata*	0.47	5.99	0.61	27.98	27.98
	Hypogymnia physodes	0.39	4.58	0.47	21.40	49.38
	Mycocalicium subtile	0.36	4.02	0.40	18.77	68.15
	Placynthiella dasaea	0.30	3.44	0.47	16.09	84.24
Group 5 33.18%	*Cladonia digitata*	1.02	12.07	0.94	36.37	36.37
	Hypogymnia physodes	0.73	7.13	0.81	21.49	57.86
	Lepraria spp.	0.60	6.11	0.75	18.42	76.27
	Placynthiella dasaea	0.37	2.61	0.45	7.86	84.14

Notes: 'AvAbu' - average abundance after square root transformation; 'AvSim' - average similarity of each taxon; 'Con' - taxon's contribution to the total similarity; 'CuCon' - cumulative contribution of each taxon is set to a cut-off point of 80%.

The coverage with lichens demonstrated a fluctuational nature, with the fastest growth of the coefficient after the 14th class of age (21 years). On the other hand, the H index showed a more regular and increasing tendency, apart from a considerable increase in the value in the last two age classes, i.e., 21 years after the bark beetle killed the spruce trees (Figure 6).

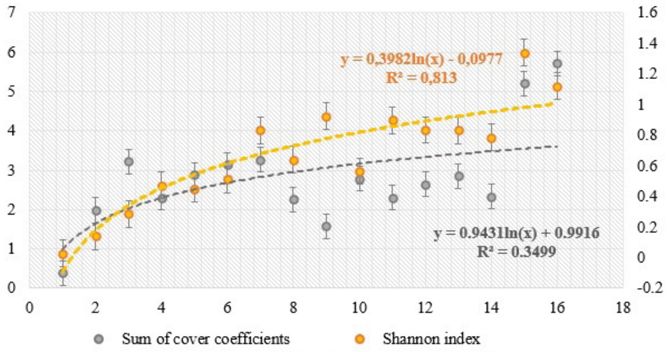

Figure 6 Mean values of the Shannon H index (the main axis) and of the sum of coverage coefficients (the auxiliary axis) within the classes of age, including error bars and logarithmic trend lines.

The primary succession on the rotting wood

Thanks to the measurement of wood hardness under particular thalli, it was possible to indicate the preferences of respective species as to the degree of the inhabited substrate decay, and at the same time to determine the most common succession sequence on the decaying spruce snags (Figure 7).

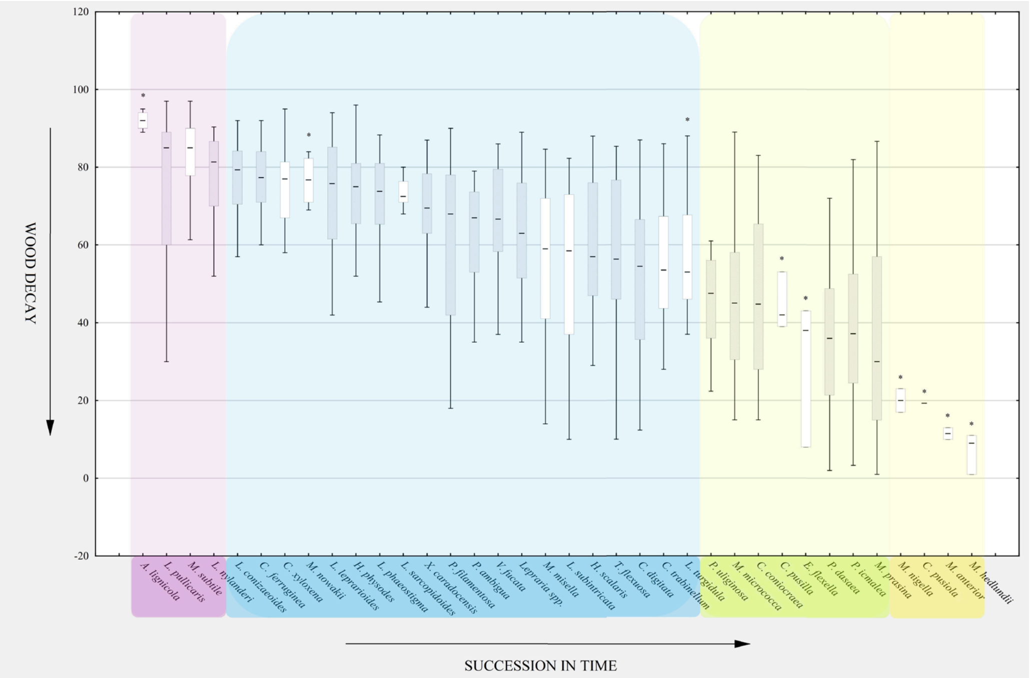

Figure 7 Box graphs (box – three quartiles, whiskers – the non-outlier range) illustrating the distribution of the wood hardness under the thalli of respective lichen species, the number of records for which exceeds 10 and the exclusively wood-inhabiting ones. Species are ranked along with the progression of the wood depreciation (hardness in the Shore scale: 1–100). White boxes belong to obligately wood-inhabiting species. Species in the case that the number of records did not exceed 10 were denoted using an asterisk over a corresponding graph. Full names of the species were listed in Table 3.

The first group of successors included only 4 species, the most common of which was *Mycocalicium subtile*, exclusively wood-inhabiting fungus. This species usually inhabits three-year-old snags but has been found on hard and poorly rotten wood up to the 15th age class of snags (22–25 years after death). The second stage of wood decay was favourable for the largest collection of 20 species. For seven of them, including *Calicium trabinellum*, *Chaenotheca xyloxena*, *Lecanora sarcopidoides*, *L. subintricata*, *Lecidea turgidula*, *Micarea misella* and *M. nowakii* s.l., deadwood is their only substrate for growth. The third group encompassed eight species, among which only the rare *Chaenothecopsis* pusilla and *Elixia flexella* can be classified as obligately wood-inhabiting lichens. The species *Micarea nigella*, *M. anterior* and *M. hedlundii*, as well as *Chaenothecopsis pusiola*, formed the fourth group confined to strongly decayed patches of snags. Both the abovementioned species from the *Chaenothecopsis genus*, with the status of facultative lichenicolous fungi (Diederich et al. 2018), coexisted with *Chaenotheca xyloxena*.

The correlation between the dead wood age and hardness demonstrated that the relationship was very differentiated (Table 8). In the case of some niches inhabited by, for example, *Chaenotheca xyloxena* and *Placynthiella icmalea*, a significantly negative relationship of the abovementioned features was found: the extent of the wood decay corresponded with its age at those sites. More often, a relationship between the age of the snag and the timber hardness was weak (niches inhabited by, i.e., *Cladonia digitata*) or even none (niches occupied by, i.e., *Hypocenomyce scalaris* and *Lecanora subintricata*). Biotopic niches, formed under the influence of strong insolation and inhabited by *Lecanora phaeostigma* and *Palicella filamentosa*, were characterised by a positive correlation between wood hardness and age. However, no statistical significance was found to confirm this observation.

Table 8 Spearman correlation between the wood age expressed in age classes (see Table 1) and wood hardness under the thalli of respective lichen species, including the number of compared samples (≥10).

Species name	rs	n	Species name	rs	n
C. trabinellum	-0.05	10	*Lepraria ssp.*	**-0.42**	40
C. ferruginea	0.12	21	*M. micrococca s.l.*	-0.40	20
C. xyloxena	**-0.54**	25	*M. misella*	-0.26	33
C. coniocrea	0.04	14	*M. prasina s.l.*	-0.13	27
C. digitata	-0.18	66	*M. subtile*	**-0.34**	76
H. scalaris	-0.02	31	*P. filamentosa*	0.26	11
H. physodes	0.05	71	*P. ambigua*	-0.15	11
L. conizaeoides	-0.04	40	*P. dasaea*	0.11	36
L. phaeostigma	0.43	10	*P. icmalea*	**-0.51**	32
L. pulicaris	**-0.56**	26	*P. uliginosa*	-0.57	10
L. sarcopidoides	-0.27	10	*T. flexuosa*	**-0.44**	34
L. subintricata	0.00	11	*V. fucata*	-0.39	18
L. leprarioides	0.13	12	*X. caradocensis*	-0.30	10
L. nylanderi	-0.21	13			

Note: Significant values of the correlation coefficient were highlighted in bold (rs). Full names of the species were listed in Table 3.

Discussion

When talking about the naturalness of forests, we mean that they meet certain criteria, such as the maintenance of ecological process continuity, the lack of considerable traces of human intrusion, the presence of large amounts of coarse woody debris (CWD) and the existence of the natural dynamics of plant communities (Larsson et al. 2001, MCPFE 2007, McRoberts et al. 2012). These criteria are dependent on each other in natural forests since the presence of natural vegetation dynamics, based on the regime of natural disturbances, favours a faster renewal of forest stand generations. Indeed, leaving decaying CWD at the site of a tree's death is crucial for the preservation of ecological processes in the forest by favouring the restoration of the habitat thanks to the recirculation of biogenic chemical elements, the stabilisation of microclimatic conditions and the provision of diaspore transfer (Merganičová et al. 2012, Marcot 2017, Thom et al. 2020). In light of the aforementioned assumptions, the forest, where natural disturbances work in a recurrent mode, from the point of supporting all of the ecosystem functions in it, should be considered a full-value asset.

The continuity of ecological processes in forests should not be interpreted in the sense of forest stand durability. Natural types of disturbances appear in ecosystems in a cyclic manner and usually encompass only fragments of biomes (Grebner et al. 2013). This leads to the development of adaptations in indigenous species and even allows the achievement of benefits in the face of an apparent disaster. Given that, the disturbances do not result in any imbalances, but they contribute to the diversification of the ecological conditions.

Spruce bark beetle outbreaks are the main source of the supply of CWD in the study area and within the whole range of Norway spruce, which is considered a necessary component conditioning the normal functions of forest ecosystems (Stanturf et al. 2014, De Grandpré et al. 2018). In relation to lichenised fungi, the role of decaying wood is contained in the fact that it forms the required habitats for the survival of species obligately associated with it, and it also serves in assisting the flow of epiphyte diasporas in the areas where disturbances took place. A study by Lõhmus & Lõhmus (2001) in Estonian forests showed that the species-richness of lichens (especially rare species) on decorticated spruce snags was much greater than on the bark of nearby living spruces. At the same time the lichen coverage showed exactly the opposite trend. The list of epiphytic lichens found on Norway spruce trees in 1993, 2013 and 2018 in the area of the Gorce National Park (Tanona & Czarnota, unpublished data), compared to data acquired in this paper, indicate that approximately 66% of them, after the onset of the disturbance and their phorophyte's death, were able to settle the wood as a replacement substrate. At the same time, the species diversity of all of the ecological groups of the wood-inhabiting lichens was greater than that found on the bark. Recently, similar results were reported by Langbehn et al. (2021), who showed that all the epiphytic species found on living trees around disturbed areas in Carpathian forests, expanded their niches on the decaying wood. More broadly, this substrate opportunism may facilitate more rapid and efficient regeneration of the epiphytic communities inside the mosaic of habitats.

For many species found during the presented studies, dead wood is the only substrate necessary for their survival. However, the frequency of these exclusively wood-inhabiting lichens, especially strongly decayed patches of snags, was low. This involves, among other things, a strict rigor in the selection of snags for surveys in evenly distributed small monitoring plots. For comparison, in similar studies by Czarnota (2012) conducted in the area of three Carpathian national parks in southern Poland (the Gorce NP, the Tatra NP and the Babia Góra NP), the species growing on the wood of dead spruces, such as *Calicium trabinellum*, *Chaenotheca xyloxena*, *Elixia flexella*, *Lecanora sarcopidoides* and *Lecidea turgidula*, were found to be common. The difference stemmed from methodological reasons manifested by a more unrestricted selection of snags for the studies in the best-preserved parts of old forests and from differences connected to the history of influencing ecological processes as well as the human activity within those protected areas.

The collected lichen data were analysed i.a., in terms of the Shannon diversity index. This factor was most strongly affected by the richness component of diversity, which was previously emphasised elsewhere in the literature (e.g., Tramer 1969, Kricher 1972, Nagendra 2002, Yeom & Kim 2011). The Shannon index has formerly been used to assess the diversity of epiphytic lichens in various parts of the world and in various environments, including e.g., nature reserves (Brodeková et al. 2006, Khastini et al. 2019), mountain forests (Vinayaka et al. 2011, Rashmi & Rajkumar 2019), as well as transformed areas with varying degrees of urbanization (Opdyke et al. 2011, Bacchus & Da Silva 2021). In the case of wood-inhabiting lichens, this index has been sparsely used so far (e.g., by Lõhmus & Lõhmus 2001), although it was applied on this substrate, for example, to assess the diversity of wood-inhabiting fungi and bryophytes (Ódor et al. 2006, D'Aguanno et al. 2016).

Among the appointed environmental factors, only wood age exerted a significant positive effect on the species diversity of lichens. Simultaneously, the same factor most favoured the increase in total snag coverage with thalli. The age of wood as a quantitative ecological factor has rarely been studied in the case of lichens, for example by Caruso & Rudolphi (2009), who found that higher species richness was associated with older wood. A similar positive effect on lichen biota development was observed in relation to the wood decay stages (e.g., Dittrich et al. 2014, Preikša et al. 2015, Santaniello et al. 2017), although some other studies also reported that more diverse communities were associated with the middle stages of wood decay (Nascimbene et al. 2008). The contribution of time elapsed to the increase in the diversity and abundance of lichens is understandable, at least due to an increase in the probability of their substrate's occupancy, bearing in mind that they are considered poor colonisers (Werth et al. 2006). However, in light of our further findings, it is equally important that a greater number of species prefer a more decomposed substrate. The analysis of the diversity and abundance of species occurring on soft wood (≤20 in the Shore scale) indicates that the final stages of this substrate decay lead to a decrease in lichen species and finally to a decline in facultative epiphytic lichens. This is associated with an increasing instability of the substrate where they grew previously, as well as the development of competing species of mosses and vascular plants (Caruso et al. 2010, Kharpukhaeva & Mukhortova 2016).

With regard to the management of the dead wood supply in the forest, how much time elapses before it starts being an accessible raw material for dependent organisms is an essential factor. In the area studied, which can be considered representative of a considerable part of the Western Carpathians, it seems that the crucial factor for the most prolific diversity and abundance of lichens inhabiting spruce post-bark beetle snags was a snag age between 22 and 25 years after the tree death.

The three-degree scale of forest stand decomposition used in our analyses did not significantly affect the diversity of lichen species on the snag, but it played a significant role in the sum of their coverage coefficients as an environmental factor in the GLMs. Lichens were more abundant in large-scale post-bark beetle outbreak areas than in areas representing a selective type of forest stand decomposition. It is related with much more serious changes in microclimatic conditions in the case of the first forest disturbance. First and foremost, it is manifested by an improvement in the light conditions but also a drop in the air humidity (Haughian & Frego 2017). Our results indicate that the more abundant lichen coverage of the spruce snag wood is mainly due to the former. Simultaneously, taking into account that the lichen species diversity index in each scale of the forest stand disturbance was similar, although the examined wood patches and research plots differed in the species composition of communities, the pressure of the spruce bark beetle in each scale of the spatial differentiation can be assumed to be valuable for the creation of habitats for wood-inhabiting lichens. The natural dynamics of mountain spruce forests favour the preservation of dependent epiphytic and epixylic lichen communities. However, the local balance can be disturbed in the future if the temperature on Earth continues to rise rapidly and Norway spruce will not be able to adapt to such changes as it does today (Hart-Meier et al. 2014). Currently observed global climate changes have resulted in an increase in the upper timberline elevations and at least regionally a reduction in natural mountain spruce forest zones (Gazda et al. 2018), entailing a decrease in the number of key habitats for spruce-dependent lichens (Neumann 2017).

Altitude and both the aspects of hillside exposure ("northness" and "eastness") influenced the lichen abundance on spruce snags but not the Shannon index (H). Study plots located in the upper mountain altitudes and on northern and western slopes favoured a larger lichen abundance. This corresponds to similar reports by Vondrák & Kubásek (2019) from the Czech Šumava that some lichen species exposed to direct insolation under mountainous conditions regress from the southern exposures of decaying trunks due to phototoxic damage to their thalli. According to the paper by Ardelean et al. (2015), altitude and "eastness" did not exert any effect on the species diversity; however, altitude affected the lichen species composition on snags.

Our analyses allowed us to have a better understanding of the preferences revealed by the respective lichen species in relation to the age of snags and the extent of their wood decay, as well as the interactions among these factors. We have not omitted rare wood-inhabiting lichens that are valuable in terms of the biodiversity of the studied area and with reference to the ecological requirements, which are important in the evaluation of the phenomena discussed in this paper. The greatest number of lichen species, including those exclusively inhabiting wood, were found on poorly decayed wood of snags, i.e., in the 2nd stage of its decay. This substrate hosts three times more species than at the 3rd stage, four and a half times more than at the 4th stage and six times more than at the 1st stage. The division of species into ecological groups in accordance with the stage of wood decay suggests that the relationship between the wood age and the extent of its decay cannot be linear (Figure 7). In fact, different parts of a snag are subjected to decay at various rates: decay of the lower part is usually faster due to the vicinity of humid litter and shading by plants, while decay in the upper part is slower since they are dried by wind and insolation. The period of bark remaining on the snag is also important for the rate of wood depreciation and colonization of this substrate by particular lichen communities. Additionally, the diversity of ecological niches depends on the spatial scale and rate of forest stand disturbances (Fahey & Puettmann 2007, Kern et al. 2013, Guo et al. 2019). For these reasons, the comparison of the list of wood-inhabiting lichen species with the degree of wood decay, determined for the entire snag (e.g., Bunnell et al. 2008, Nascimbene et al. 2008, Preikša et al. 2015) on the basis of its visual characteristics (Maser et al. 1979, Söderström 1988, Waddell 2002), may generate errors when interpreting substrate preferences of the examined species. During our hardness measurements, even closely neighbouring patches of wood were able to demonstrate totally different values. The composition and share of dominant species, as presented in this article with the use of SIMPER analysis, can be a more useful indicator in assessing the degree of wood decay, allowing the different stages of decomposition to be distinguished within the same piece of CWD. Nevertheless, we believe that quantitative analyses should better be supported by a more accurate durometer measurement.

Box graphs (Figure 7) illustrate that the scope of the ecological tolerance for each particular lichen species in relation to the degree of substrate decay is also differentiated. Some may occur in a broad spectrum of this factor, while others are bound to a narrow range of wood hardness (Bunnell et al. 2008, Caruso et al. 2010, Santaniello et al. 2017, Myllys & Launis 2018).

Conclusion

The lichen communities occupying decaying wood of the Norway spruce snags in the Carpathian forests are largely dependent on the supply of this substrate in the frameworks of the natural phenomena responsible for the dynamics of the spruce forests at various spatial and time scales. The wood of snags is an equally essential substrate enabling the survival of species exclusively confined to it, and it is a habitat supporting the maintenance of epiphytes in forests disturbed by spruce bark beetle outbreaks. Analyses carried out as part of this work allowed us to extend the current knowledge of the specific requirements of lichens inhabiting the post-bark beetle CWD and to learn about the rate and course of lichen succession on this substrate. Measurements of the wood hardness under the particular lichen thalli, taken with a Shore durometer, allowed for precise determination of ecological preferences of wood-inhabiting lichens in relation to their substrate. The largest group among analysed set of species were those, that preferred poorly rotten wood (51–80 in a Shore scale).

The scale of forest stand decomposition after spruce bark beetle attack influenced the abundance of lichens on snags but did not affect the Shannon diversity index (H) in lichen communities. Importantly, the species composition in the community was mainly determined by the degree of wood decay expressed as wood age and hardness. NMDS and PERMANOVA analyses separated five groups of wood age significantly different in terms of species abundance, while the SIMPER analysis revealed the dominant species in each group.

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