How sensitive are epiphytic and epixylic cryptogams as indicators of forest naturalness? Testing bryophyte and lichen predictive power in stands under different management regimes in the Białowieża forest

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ABSTRACT

The aim of this study was to test the sensitivity of epiphytic and epixylic bryophytes and lichens as indicators of forest naturalness, by comparing their diversity patterns with forest structural, compositional and historical features associated with different management/protection regimes and protection time spans. The study was carried out in the Białowieża Forest (Poland). Out of 1370 pre-existing inventory plots established all across the Polish part of the Białowieża Forest, we randomly selected 10 plots for each of the 18 plot aggregation groups resulting from the combination of 3 management/protection regimes and 6 habitat types, for an overall number of 180 plots. At each of them, we carried out bryophyte and lichen sampling on four substrates (coarse woody debris – CWD, standing dead trees, stumps, living trees). The management/protection regimes exemplifying the gradient of forest naturalness were: the 100 years-old Białowieża National Park (BNP), a set of more recently established nature reserves and managed forests. We tested differences in mean species richness values among management/protection regimes, protection time spans, habitat types and stand age classes by analysis of variance and calculated coefficients of correlation with 45 selected structural and compositional features of forest stands. Differences in species composition of epiphytic and epixylic bryophytes and lichens among management/protection regimes were tested by ordination methods. Lastly, we compared frequency of red-listed species and primeval forest relics among management/protection regimes. Species richness of lichens was significantly correlated with the degree of forest naturalness assessed by structural and historical features along the naturalness gradient, with the highest number of species recorded in BNP and the lower in managed stands, while bryophyte number did not exhibit a clear dependence on the management regimes. Relic species of primeval forests and red-listed species occurred with significantly higher frequency in protected areas than in managed forests for both lichens and bryophytes, with the highest frequency observed in BNP for lichens and in nature reserves for bryophytes. Volume of deadwood, particularly of CWD in advanced decays stage, species richness of undergrowth vascular plants, tree layer diversity, shrub cover and herb layer cover exhibited the strongest correlation with cryptogam species richness and cover on the various substrates. Response to light availability strongly differentiated bryophyte and lichens optimal niches. The results of this study clearly show that cryptogams, and lichens in particular, are indeed reliable ecological indicators of forest status, since they sensibly intercepted the environmental changes observable along the tested naturalness gradient.

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1. Introduction

The concept of forest naturalness, although seemingly intuitive, is actually a tricky one, being an attribute which can be expressed at different degrees along a continuum or gradient, e.g. pristine/primeval (or virgin), near-natural, intact, semi-natural, conventionally managed, plantations (McRoberts et al., 2011), based on different criteria, expectations and aims and it is thus difficult to frame. It can be described on the base of such ecological features as stand structure, species composition, heterogeneity of niches for different groups of organisms (Christensen et al., 2005; Winter and Möller, 2008; Michel and Winter, 2009; Randius et al., 2009), as well as on “historical” data such as absence of direct management activity and human interference for a given length of time, spontaneity of stand regeneration and, last but not least, continuity of tree cover over time. Structural parameters, such as tree dimensions and distribution or stand age, can sometimes be misleading (Kubiak and Sucharzewska, 2012), since they can be also determined by specific environmental conditions and individual tree species physiological features (Kolstad et al., 2002). Not all specimens of very old trees necessarily reach imposing sizes and heights and in certain climatic regions we will never find much deadwood on the forest floor (e.g. in the equatorial belt), since it is quickly decomposed. Historical data, such as absence of management or continuity of forest cover are even trickier, since we need to arbitrarily establish a threshold beyond which we feel enough time has passed without human intervention for a forest to be defined as natural.

As in environmental chemistry, where the observation and analysis of biological organism reaction to variations in pollutant contents of air and water is recently gaining ground over the direct measurement of such contents, in forest ecology too specific sets of organisms are turning out to be reliable substitutes of forest structural, compositional, and historical features as indicators of different degrees of forest naturalness (Czyżewska and Cieśliński, 2003; Brunialti et al., 2010; Hofmeister et al., 2015; Mölder et al., 2015; Dymytrova et al., 2018). Biodiversity in forest ecology relies on those species sharing the following features: 1) they are local species; 2) they are typical forest species; 3) they exhibit a high degree of sensitivity to variation in forest conditions; 4) they are stenotopic species (Czyżewska and Cieśliński, 2003). Out of all forest species those best matching such requirements are cryptogams, i.e. bryophytes, lichens and fungi. The first two groups in particular are being increasingly used to assess the continuity and degree of forest naturalness (Czyżewska and Cieśliński, 2003; Frego, 2007; Brunialti et al., 2010; Hofmeister et al., 2015; Mölder et al., 2015; Dymytrova et al., 2018; Jaroszewicz et al., 2019). This is linked to their specific morphophysiological features, which make them “canaries in the coal mines” (Tuba et al., 2011), as well as their strict dependence on particular substrates and niches which are the first to disappear following human intervention (e.g. big, old living trees, lying and standing deadwood, bog habitats).

One of bryophyte features which makes them suitable bioindicators of forest naturalness is their high sensitivity to desiccation. As poikilo- hydric organisms, they cannot control water loss from their body surface, although the sensitivity of individual species is quite variable (Proctor et al., 2007). Very likely, primeval forest relics occurring in the stable conditions of natural forest lost or have very limited plasticity of response to changing air humidity. There is evidence that maintaining plasticity of response to unstable environmental conditions is an expensive process for plants, consequently in stable conditions they can loose such property (Pigliucci et al., 2006). Among bryophytes, liverworts are usually considered the more sensitive to micro-environmental changes, because of their strict dependence on water availability. Most liverwort species can be found only in particularly stable unmanaged forest areas. Increased exposure to desiccation, caused by changes in forest structure following management activities, can be the main reason for their disappearance in managed forests.

Lichens exhibit even greater sensitivity than bryophytes and are increasingly used in biomonitoring (e.g. Ciesiński et al., 1996; Kirschbaum et al., 2012; Stapper and John, 2015; Łubeck et al., 2018). It is stated that ca. 160 lichen species can be indicators of natural forests in Poland (Czyżewska and Cieśliński, 2003; Motiejunaite et al., 2004). All of them are threatened species reported in red lists at national and international level and most of them are under protection. In Latvia, Lithuania and Estonia for nature conservation targets they introduced a classification of forest ecosystems based on the occurrence of specialized species (fungi, bryophytes, lichens and invertebrates), whose existence would not be possible in managed forests (Brumelis et al., 2011).

Despite the growing number of studies highlighting the potential of cryptogams as ecological indicators of the state of forest ecosystems, very few attempts have been made so far to test the reliability of bryophyte and lichen diversity patterns as indicators of forest naturalness. Brunialti et al. (2010) and Hofmeister et al. (2015) addressed the issue of the correspondence between cryptogamic diversity and natural forest attributes, by correlating cryptogamic diversity and structural parameters at different forest sites in Italy and Czech Republic, respectively. However, they lacked the whole length of naturalness gradient, since there was no reference point at the edge of such gradient, namely a forest area which could exhibit primeval features, as well as a well-defined time threshold which could mark off the length of time without human intervention in the selected “unmanaged sites”. In this study we tried to fill this gap and tested the sensitivity of cryptogams to environmental variations along a “complete” gradient of forest naturalness in the Białowieża Forest (BF), the last lowland forest complex of Europe still retaining large patches with primeval features (Faliński, 1986; Jaroszewicz et al., 2019).

The main aim of this study was to test the sensitivity of epiphytic and epixylic bryophyte and lichen predictive power as indicators of forest naturalness, by comparing their diversity patterns with forest structural, compositional and historical features associated with different degrees of forest naturalness. We also tried to highlight the optimal habitat conditions for development of both groups in terms of habitat features, stand age and substrate species. To achieve these aims we sampled bryophyte and lichen species along a gradient of forest naturalness exemplified by three different management/protection regimes (hereinafter referred to simply as management regimes): 1) the Białowieża National Park (BNP), where half of the area undergoes strict protection since the second decade of the XX century; 2) a network of more recently established nature reserves, with highly natural and strictly protected stands; 3) managed forests, exhibiting different intensities of forest use.

Since the BNP includes areas set under protection at different time periods and the selected nature reserves have been established over the past 50 years, in order to assess not just the effect of extant protection regimes, but also the effective lengths of protection status, we also tested the response of bryophyte and lichens diversity patterns to different protection time spans. Within all management regimes we further distinguished 6 groups of forest types, which where tested for the effect of different micro-climatic, edaphic and vegetation features on epiphytic and epixylic bryophyte and lichen diversity.

2. Material and methods

2.1. Study site

The study was carried out in the BF (Poland), the last remnant of lowland mixed-deciduous forests which once covered the European continent, as well as a major hotspot for biological diversity in Europe, with a core area still retaining primeval forest features (Jaroszewicz et al., 2019). The most striking such features are the huge amount of deadwood (mean volume ~ 90 m³/ha in the Polish part of BF, but 146 m³/ha in the strictly protected area of BNP; Tabor, 2017), the exceptional diversity of vascular plants, bryophytes and lichens (1071, 254 and 334 species respectively) and the continuity of forest cover over the last 12,000 years (Latalowa et al., 2016). The vascular plants include 25
tree species, which build 26 forest plant communities (Faliński, 1986; Sokolowski, 2004). The BF stretches across the border between Poland and Belarus, extending over 55 km from east to west and 51 km from north to south. It covers a surface of about 1500 km², out of which 635 km² in Poland and 875 km² in Belarus, lying on a flat terrain with a mean altitude of 170 m above sea level (Sokolowski, 2004).

The local climate shows typically continental features, with cold, snowy winters and hot, dry summers. The mean annual temperature for the period 1955–2001 was 6.8 °C, with a minimum of −4.7 °C in January and a maximum of 17.7 °C in July. The mean annual precipitation totals over the period 1955–2001 were in turn of 633 mm. The growing season lasts for 205 days on average (Pierzgalski et al., 2002).

Around one third of the BF area on the Polish side is under different regimes of protection. The Białowieża National Park (BNP), established in 1921 and covering 10 502 ha, protects the best preserved patches of the BF. The area constituting the original core of the BNP, the Orłowska district, covering around 4 700 ha, has been for most part under strict protection since the second decade of the XX century, while the area known as the Hwoźna district, covering around 5 169 ha, has been added to the BNP in 1996 and is currently under strict and active protection. The 21 nature reserves (partly or strictly protected), mostly set in natural regenerated stands of BF, cover 12 012 ha and were established between 15 and 49 years ago (most of them in 1970 s). The remaining part is represented by managed forests, subject to different degrees of exploitation, depending on habitat and stand features. They too include several other sites excluded from use, e.g. the reference forests, swamp, riparian and bog habitats, buffer zones around the nests of protected bird species, and, from 2012, also old-growth stands with the age of dominant trees species above 100 years.

### 2.2. Sampling design

Sampling was carried out along a gradient of forest naturalness, encompassing areas undergoing three different management regimes: 1) the Białowieża National Park (BNP), including a core area undergoing strict protection mostly since 1920s (Orłowska district) and an additional area set under protection in 1996 (Hwoźna district); 2) nature reserves, mostly established since 1970; 3) managed forest.

In the frame of systematic phytosociological and stand structural surveys realized by Polish State Forests in 2016–2018 adjoining 650 × 650 m grids were set in the whole Polish part of the BF. Circular sample plots with 11.28 m radius and 400 m × 650 m grids were set in the whole Polish part of the BF. Circular sample plots with 11.28 m radius and 400 m × 650 m area were centred at each of the grid external nodes. Overall, 1370 such sample plots were set in the whole Polish part of the BF.

For the purposes of our study, we aggregated these plots according to the 3 above mentioned management regimes and, additionally, to 6 selected habitat types (Table 1). We then randomly picked up 10 plots per each of the resulting 18 groups out of the pre-existing 1370 plots, for an overall number of 180 plots. Because of total stand breakdown due to bark beetle outbreak in 3 sample plots set in bog and mixed forests, (out of which 2 in the managed forests and 1 in nature reserves, see Table 1), we had to leave such plots out of sampling which resulted in the final number of plots being 177, instead of the planned 180.

Protection time spans and number of sample plots per management regimes were as follows: 1) BNP: 25 plots protected for 86–97 years, 35 plots for 22–39 years; 2) nature reserves: 48 plots protected for 15–23 years and 11 plots for 39–49 years; 3) managed forests: 58 plots.

At each sample plot we compiled a list of bryophytes and lichens occurring on: 1) all living and standing dead trees older than 40 years and with a diameter at breast height (DBH) over 20 cm, up to an height of 2 m; 2) lying deadwood, as well as its fragments (with the thinnest end having a diameter above 10 cm and a length above 50 cm), hereinafter referred to as Coarse Woody Debris (CWD), and stumps (of height less than 1.30 m and a diameter of the thinnest end above 10 cm). Data on stand structure parameters, deadwood volume and decay classes, undergrowth species, soil properties and beetle species richness were taken from State Forests inventories performed on the same plots in 2016–2018 (Natural and cultural heritage portal of the State Forests, 2020). We included in the sample not just epiphytes and epixyls sensu stricto, but all the species of bryophytes and lichens occurring on the above-mentioned substrates, including occasional species.

For each bryophyte and lichen species cover relative to the substrate surface was recorded using the Braun-Blanquet scale (Braun-Blanquet, 1964): 5 ≥ 75% cover; 4 = 50–75% cover; 3 = 25–50% cover; 2 = 5–25% cover; 1 = numerous individuals, but less than 5% cover, or scattered individuals, with cover up to 5% + = few, with low cover; and r = rare, solitary, with low cover. Total percentage cover of bryophytes and lichens relative to the substrate type were also estimated. Such data were used to perform analyses of community similarity (see below) and species cover represented one of the features tested in the analyses of correlation with environmental variables. The quantitative assessment of bryophytes and lichens on living trees and deadwood was carried out in accordance with the general methodological assumptions employed in the frame of the monitoring protocol of ICP Forests plots in Poland (Solon and Wawrzoniak, 1999).

Most of the lichen species were recognized directly in the field. In the case critical taxa, specimens were collected for further anatomical or chemical analyses. The composition of secondary lichen metabolites was tested with thin layer chromatography (TLC) in B and/or C eluents (Solon and Wawrzoniak, 1999).

### Table 1

| Habitat types | Plot number in management regimes and their share (%) | Total |
|---------------|-------------------------------------------------------|-------|
|               | National Park (NP) | Nature reserves (NR) | Managed forests (MF) |
| Fresh and wet coniferous forests | 10 | 8.1 | 10 | 4.7 | 10 | 6.6 | 30 | 6.5 |
| Boggy coniferous and boggy mixed forests | 10 | 5.6 | 9 | 3.6 | 8 | 1.1 | 27 | 2.3 |
| Mixed coniferous forests | 10 | 15.0 | 10 | 8.7 | 10 | 20.7 | 30 | 17.3 |
| Deciduous and mixed deciduous forests | 10 | 51.3 | 10 | 55.1 | 10 | 59.5 | 30 | 57.2 |
| Alder carrs and mixed deciduous swamp forests | 10 | 9.8 | 10 | 8.3 | 10 | 3.7 | 30 | 5.7 |
| Deciduous riparian forests | 10 | 10.2 | 10 | 19.6 | 10 | 8.4 | 30 | 11.0 |

Total 60 100.0 59 100.0 58 100.0 177 100.0
cover (Braun-Blanquet, 1964).

The maps with plots showing the distribution of bryophytes and lichens species numbers are included in Appendices E-G.

2.3. Data analyses

We compared the mean values of species number across the selected categorical variables (management regimes, habitat types, substrate types, protection time spans and stand age classes) by using the ANOVA Kruskal-Wallis test with p < 0.05.

We also tested the correlation between cryptogamic species richness and 45 forest structural and compositional variables (see list in Appendix D) describing: 1) overall epiphytic and epixylic bryophyte and lichen species richness (total and red-listed), percentage cover of bryophytes and lichens on different type of substrate, 2) vegetation community structure according to phytosociological surveys, including percentage cover of forest community layers (tree, shrub, herb and bryophyte layer), number of species in individual layers and in total; 3) ecological indicator values for light, soil moisture, nutrient contents and soil reaction after Zarzycki et al. (2002); 4) forest stand structure parameters: age, volume of living trees and deadwood overall and in different types, decay classes, bark cover; 5) other additional variables related to the forest naturalness and condition: effective protection time span until 2018, number of saproxylic beetle species, MB – mean individual biomass of carabid beetles species number. The significance value of the R Spearman correlation was p < 0.05. Significance of differences between mean values (± standard error – SE) was calculated by using the package STATISTICA (StatSoft Inc., 2010). The ecological indicator values were calculated as weighted mean values after transformation from Braun-Blanquet scale in percent values (Braun-Blanquet, 1964).

The diversity patterns and similarity of bryophytes and lichens species composition across the different management regimes were assessed by Detrended Correspondence Analysis – DCA (Hill and Gauch, 1980). The mean ordination scores of DCA axes for the sample plots in the defined management regimes were compared by ANOVA using non-parametric Kruskal-Wallis test (K-W, with p < 0.05). Percentage species cover for the DCA analysis was transposed from the Braun-Blanquet scale (1964) to the numeric form proposed by Van der Maarel (1979). We calculated the regression coefficient R2 of individual environmental variables (ecological indicators, percentage cover of tree and shrub layer, wood volume of the living stand, basal area and age of dominant tree species), with DCA scores (envfit function) and defined its statistic significance by using the Monte Carlo permutation test (999 permutations) in the vegan package (Oksanen et al., 2019). DCA analyses as well as calculation of regression coefficients were performed by the vegan package (Oksanen et al., 2019) in R programme (R Core Team, 2017).

3. Results

3.1. General features of cryptogamic diversity in the different management regimes

Overall, 119 bryophyte and 173 lichen species were recorded from all sample plots. The highest number of bryophyte species occurred on CWD and stumps, especially in nature reserves (Table 2). On the contrary, the lowest bryophyte species richness was observed on standing dead trees. As for lichens, the highest number of species was recorded on living trees, in particular within the BNP, and, followingly on standing dead trees, while stumps exhibited the lowest number of species.

Seven species of bryophytes and 37 of lichens were recorded only in BNP, 8 species of both bryophytes and lichens only in the reserves and 9 species of both bryophytes and lichens were recorded only in the managed forests. Ten bryophyte and 18 lichen species were shared between BNP and nature reserves, 7 bryophyte and 13 lichen species among BNP and managed forests, 8 bryophyte and 3 lichen species among nature reserves and managed forests. The overall number of species shared among all the three management regimes amounted to 70 for bryophytes (60% of the total bryophyte species recorded) and 84 for lichens (50% of the total lichen species recorded).

Table 2

| Group     | Object | Substrate | NP  | NR  | MF  |
|-----------|--------|-----------|-----|-----|-----|
| Bryophytes| CWD    | 74        | 82  | 76  |
|           | S      | 51        | 67  | 66  |
|           | SDT    | 47        | 38  | 39  |
|           | LT     | 66        | 57  | 62  |
| Lichens   | CWD    | 66        | 54  | 49  |
|           | S      | 37        | 24  | 26  |
|           | SDT    | 69        | 53  | 38  |
|           | LT     | 124       | 94  | 89  |

3.2. Differences in the average species richness of bryophytes and lichens among management regimes

The mean number of bryophytes (both epiphytic and epixylic) varied between 16.9 in managed forests to 19.1 in the BNP (Fig. 1). No significant difference was observed in the mean number of bryophyte species among different management regimes.

In the case of lichens, the mean number of species was higher and varied between 15.4 in the managed forests and 24.3 in BNP. The mean species richness of epiphytic and epixylic lichens was significantly higher in BNP than in nature reserves (8 species more) and managed forests (9 species more) (Fig. 1).

3.3. Differences in the mean number of species per substrate among forest management regimes

The mean number of bryophyte species was the highest on living trees (10–11 species/plot) and CWD (9–11) and, slightly lower on stumps (8–9) and lowest on standing dead trees (5–6) (Fig. 2). In the case of CWD, standing dead trees and living trees, there was on average one bryophyte species more in BNP than in managed forests, while in the case of stumps it was the opposite. The mean number of bryophyte species for a single substrates did not significantly vary among the three different management regimes (Fig. 2).

The highest number of lichen species occurred on living trees in BNP

![Fig. 1](image-url)

**Fig. 1.** Mean variation (±SE) of the number of bryophyte and lichen species according to different management regimes on a sample plot of 400 m².

Management regimes: NP – Białowieża National Park (N = 60), NR – nature reserves (N = 59), MF – managed forests (N = 58). Significant difference among mean number of bryophyte and lichen species according to different management regimes were highlighted by different letters based on the Kruskal-Wallis test with significance p < 0.05.
20 species/plot – and was significantly higher than in nature reserves and managed forests (6 species/plots), which did not differ in terms of the mean number of species (Fig. 3). On the remaining types of substrates, for which 3 to 7 times less lichen species was recorded (on average 3–6 species/plot), a higher species number occurred again in BNP, but only in the case of CWD the difference was statistically significant (Fig. 3).

3.4. Differences in the average species richness of epiphytic and epixylic bryophytes and lichens among different protection time spans

As in the case of management regimes, the bryophyte species number did not exhibit significant differences depending on the protection time span. On the contrary, lichen species richness was the highest in stands with the longest history of protection (Fig. 4), but the stands with shorter protection time span (15–23 and 39–49 years) did not differ in total species number of lichen number of red-listed species.

3.5. Difference in the average species richness of epiphytic and epixylic bryophytes and lichens among age classes

The highest number of bryophyte species were recorded in stands with an age between 61 and 80 and 101–120 years (around 21 species/plot) and it was significantly higher than in forest stands of 41–60 years (Fig. 5). A similar pattern was found for red-listed bryophytes.

In the case of lichen the highest number of lichen species was recorded in stands with an age between 101 and 120 years (24 species/plot). The number was a significantly higher than in other age classes. The number of red-listed lichen species was significantly lower in the youngest stands (41–60 years).

3.6. Species richness depending on habitat type

The highest cryptogamic diversity was recorded in alder carrs and mixed deciduous swamp and deciduous riparian forests (20–23 species of bryophytes and lichens/plot), while among coniferous forest types the highest number of species was recorded in boggy coniferous and boggy mixed forests (17–19 species). Fresh and wet coniferous and mixed coniferous forests were generally the poorest in species among all the
Fig. 4. Mean variation (±SE) of the number of bryophyte and lichen species and red-listed (dotted bars) for protection time span. The rest symbols as in Fig. 1.

Fig. 5. Mean variation (±SE) of the number of bryophyte and lichen species and red-listed (dotted bars) for age classes. The rest symbols as in Fig. 1.

Fig. 6. Mean variance (±SE) of the number of bryophytes and lichens in different habitat types. Habitat types: C – fresh and wet coniferous forests, BC – boggy coniferous and boggy mixed forests, MC – mixed coniferous forests, D – deciduous and mixed deciduous forests, S – alder carrs and mixed deciduous swamp forests, R – deciduous riparian forests. Remaining symbols as in Fig. 1.
analysed habitat types (13–14 species of bryophytes and lichens) (Fig. 6).

For bryophytes, the strongest effect of habitat fertility gradient on species diversity was observed in the case of CWD and living trees, whereas no significant effect was emerged for standing dead trees (Fig. 7). The poorest habitats were fresh and wet coniferous and mixed coniferous forests while the richest ones were alder carrs/mixed deciduous swamp forests and deciduous riparian forests and, in the case of living trees, deciduous and mixed-deciduous forests. The bryophyte flora on the stumps was highly diverse and comparable to living trees as for number of species.

Lichens exhibited the highest variation in species richness on living trees in deciduous habitats (Fig. 8). The richest lichen species community was found in deciduous and mixed-deciduous forests, where we observed significantly higher species richness than in fresh and wet coniferous and mixed-coniferous. The remaining types of substrates, apart from stumps, did not show significant variations in lichen species richness among habitats. In the case of stumps, the lowest mean number of species occurred in mixed coniferous forests and was significantly lower than in boggy coniferous, alder carrs and swamp forests (Fig. 8).

3.7. Correlation analyses with structural and compositional features of forest stands and with ecological indicator values

Correlation analyses with selected structural and compositional features of the forest stands are not shown in the text and are reported in Appendix D.

Species richness of both bryophytes and lichens, as well as number of red-listed species, significantly increased together with the increase in deadwood volume, especially CWD and in the last decay class. The highest correlation values with volume of strongly decayed deadwood were exhibited by species richness and cover of bryophytes occurring on CWD. Deadwood volume overall had a positive correlation with bryophytes species number and cover on all deadwood types, but stumps. The mean bark cover of deadwood had negative influence on lichen species number.

Species number of both bryophytes and lichens, as well as of red-listed species, was also significantly and positively correlated with species richness of the phytocoenosis, and particularly of the herbaceous layer. The increase in the shrub layer cover exerted a positive effect on the number of red-listed and total bryophyte species, especially on CWD. Tree layer cover enhanced bryophyte species richness on living trees, but lowered species richness and cover of both bryophytes and lichens on standing dead trees.

Tree age positively affected lichen species richness, number of red-listed species, lichen species number and cover on living and standing dead trees and species number on CWD, while it did not exert any effect on bryophyte diversity.

The number of bryophyte and lichen species was positively correlated with the values of ecological indicators for vascular plant species of the herb layer recorded on the sample plots, like soil humidity, nutrient content and acidity. The indicator of light availability for ground vegetation was negatively correlated with bryophyte species number.

The number of saproxylic beetle species was not correlated with overall lichen and bryophyte species diversity, but only with number of lichens growing on standing deadwood and living trees. The mean individual biomass of carabid beetles was negatively correlated with epiphytic and epixylic species richness, but with red-listed species only in the case of lichens.

3.8. Red-listed species and primeval forest relics

Among red-listed species, we recorded 42 species of bryophytes and 73 species of lichens (Table 3). The highest number of red-listed bryophyte species occurred in nature reserves (77% of all species), slightly less in BNP (71%) and least in managed forests (62%). The highest number of red-listed lichen species was recorded in BNP (90% of all listed taxa), at a lesser extend in nature reserves (64%) and managed forests (50%).

Surprisingly, the same number of bryophyte species in the EN category occurred in managed forests and protected areas (1 species), while for lichens the highest number of species in this category was recorded in BNP (17 species) (Appendix A). The highest number of species in the VU category in case of bryophytes was recorded in nature reserves (5) and the the lowest in managed forests (2), while in the case of lichens the highest number was recorded in BNP (25 species), and the lower in nature reserves (14) (Table 3).

Bryophyte relic species were represented by 8 species recorded in BNP, 9 in nature reserves and 7 in managed forests (Appendix B). The only species which occurred only in BNP was Anomodon longifolius, while 3 species, Plagiothecium latebricola, Pseudobryum cincilioides, Cephalozi a catenulata, were recorded only in nature reserves. Out of 11 relic bryophyte species, 6 were recorded in all three management regimes. Apart from Plagiochila asplenoides, the highest frequency of shared species was observed in BNP. The mean frequency of occurrence of relic bryophyte species was up to 9% in BNP, 7% in nature reserves and 5% in managed forests (Appendix B).

Relic lichen species typical of primeval forests were recorded mainly...
Out of all the relic species recorded, 8 occurred exclusively in the BNP (Arthonia didyma, Bacidia arceutina, Cetrelia olivetorum, Cladonia norvegica, Lecanactis abietina, Micarea hedlundii, Pertusaria coronata, P. pupillaris), while 3 both in BNP and managed forests (Chaenotheca chlorella, Opegrapha vermicellifera, Pertusaria flavida) (Appendix C). Two relic species occurred just in the managed forests (Bacidia laurocerasi, Calicium adspersum), and one in the nature reserves (Cetrelia cetrarioides). Overall, in all the three management regimes we recorded 11 relic species, but 10 out of them were more than twice more frequent in BNP than in the remaining management regimes (Appendix C). The mean frequency of primeval forest relics reached up to 17% in BNP, 12% in nature reserves and 7% in managed forests.

### Table 3

Number of red-listed species of bryophytes and lichens according to forest management regimes. Categories of threat IUCN: CR – critically endangered, EN – endangered, VU – vulnerable, NT – near threatened; LC – least concern; DD – data deficient. The rest explanations as in Table 2.

| Group            | Category of threat | Management regimes | Total |
|------------------|--------------------|--------------------|-------|
|                  |                    | NP | NR | MF |       |
| Bryophytes       | EN                 | 1  | 1  | 1  | 2     |
|                  | VU                 | 3  | 5  | 2  | 5     |
|                  | NT                 | 3  | 3  | 1  | 3     |
|                  | LC                 | 22 | 24 | 22 | 31    |
|                  | DD                 | 1  |    |    | 1     |
| Total bryophytes |                    | 30 | 33 | 26 | 42    |
| Lichens          | CR                 | 5  | 2  | 4  | 6     |
|                  | EN                 | 17 | 12 | 9  | 31    |
|                  | VU                 | 25 | 14 | 16 | 27    |
|                  | NT                 | 15 | 12 | 10 | 15    |
|                  | LC                 | 1  | 1  | 1  | 1     |
|                  | DD                 | 3  |    |    | 3     |
| Total lichens    |                    | 66 | 41 | 40 | 73    |
| Total bryophytes and lichens | | 96 | 74 | 66 | 115 |

### 3.9. Similarity of epiphytic and epixylic communities among different management regimes

DCA analysis allowed to compare the three management regimes in terms of species composition patterns of bryophytes and lichens, both on living trees and on CWD. Epiphytic bryophyte species composition did not exhibit significantly different diversity patterns among the three considered management regimes (Fig. 9). The ordination pattern was in BNP. Out of all the relic species recorded, 8 occurred exclusively in the BNP (Arthonia didyma, Bacidia arceutina, Cetrelia olivetorum, Cladonia norvegica, Lecanactis abietina, Micarea hedlundii, Pertusaria coronata, P. pupillaris), while 3 both in BNP and managed forests (Chaenotheca chlorella, Opegrapha vermicellifera, Pertusaria flavida) (Appendix C). Two relic species occurred just in the managed forests (Bacidia laurocerasi, Calicium adspersum), and one in the nature reserves (Cetrelia cetrarioides). Overall, in all the three management regimes we recorded 11 relic species, but 10 out of them were more than twice more frequent in BNP than in the remaining management regimes (Appendix C). The mean frequency of primeval forest relics reached up to 17% in BPN, 12% in nature reserves and 7% in managed forests.

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Number of red-listed species of bryophytes and lichens according to forest management regimes. Categories of threat IUCN: CR – critically endangered, EN – endangered, VU – vulnerable, NT – near threatened; LC – least concern; DD – data deficient. The rest explanations as in Table 2.

| Group            | Category of threat | Management regimes | Total |
|------------------|--------------------|--------------------|-------|
|                  |                    | NP | NR | MF |       |
| Bryophytes       | EN                 | 1  | 1  | 1  | 2     |
|                  | VU                 | 3  | 5  | 2  | 5     |
|                  | NT                 | 3  | 3  | 1  | 3     |
|                  | LC                 | 22 | 24 | 22 | 31    |
|                  | DD                 | 1  |    |    | 1     |
| Total bryophytes |                    | 30 | 33 | 26 | 42    |
| Lichens          | CR                 | 5  | 2  | 4  | 6     |
|                  | EN                 | 17 | 12 | 9  | 31    |
|                  | VU                 | 25 | 14 | 16 | 27    |
|                  | NT                 | 15 | 12 | 10 | 15    |
|                  | LC                 | 1  | 1  | 1  | 1     |
|                  | DD                 | 3  |    |    | 3     |
| Total lichens    |                    | 66 | 41 | 40 | 73    |
| Total bryophytes and lichens | | 96 | 74 | 66 | 115 |

### 3.9. Similarity of epiphytic and epixylic communities among different management regimes

DCA analysis allowed to compare the three management regimes in terms of species composition patterns of bryophytes and lichens, both on living trees and on CWD. Epiphytic bryophyte species composition did not exhibit significantly different diversity patterns among the three considered management regimes (Fig. 9). The ordination pattern was
affected by wood volume and indicators of light intensity, substrate humidity and substrate pH.

Unlike with epiphytes, species composition patterns of epixylic bryophytes occurring on CWD (Fig. 10) showed significant difference between the tested management regimes according to the first ordination axis. This axis was correlated with the substrate pH on which epixylic bryophytes occurred as well as with the age of the dominant tree species, although the effect of this last variables in the ordination analysis was not significant. In addition ordination was affected by substrate humidity, pH, light availability, cover of the tree canopy layer and wood volume of the tree stand.

Epiphytic lichen species composition on living trees exhibited significant differences between BNP and the other two management regimes according to the second ordination axis (Fig. 11) and was significantly affected by age of dominant tree species, cover of tree canopy, light availability and nitrogen content in substrate. Diversity of epixylic lichens on coarse woody debris did not differ significantly among the three different management regimes (Fig. 12). However, significant factors correlating with the ordination space were: age of the dominant tree species, cover of the tree layer, nitrogen content and pH of substrate.

The analysed mean values of the ecological indicators for epiphytic and epixylic bryophytes (light, substrate humidity and pH) and epiphytic and epixylic lichens (light, substrate humidity, pH and nitrogen content) did not exhibit significant differences among the three different management regimes (test K-W, p < 0.05).

4. Discussion

Our results indicate that bryophytes and lichens possess a different predictive power as indicators of forest naturalness, at least when considering patterns of overall species richness. Lichens proved to be highly sensitive and reliable indicators of environmental conditions associated with different management regimes and protection time spans. Significantly higher lichen diversity was observed in BNP, where the forest has been excluded from use for the last 86–97 (ca. 50% of BNP), than in nature reserves (15–49 years of protection) and managed forests, even if no significant variations were emerged between the last two. The main differences regarded epiphytic species, which shows that lichen diversity is mainly driven by living trees structural features (volume, age), that clearly influence bark properties and micro-environmental conditions (e.g. light availability, occurrence of deep cracks in the bark), as well as by tree species composition of the forest stands.

These results are all the more significant when one considers that the total number of lichen species recorded in this study represent just 43% of the overall species number for the BF provided by Cieśliński (2003) and that, consequently, most rare species were not intercepted by the random sampling. The BNP can be thus expected to host a much higher number of species than we observed and most of those occurring in the BF.

As for red-listed and relic lichen species, most of them were invariably associated with the stands characterised by the highest degree of forest naturalness and the longest history of protection (BNP). Also the species shared with other management regimes exhibited a significantly higher frequency there than in reserves and managed forests. The sensitivity of numerous lichen species to management regimes had been already described by many authors (Cieśliński et al., 1995, 1996; Cieśliński and Czyżewska, 1998; Motiejunaite et al., 2004; Brumelis et al., 2011; Kubiak and Sucharzewska, 2012; Meżaka et al., 2012a, 2012b; Nascimbene et al., 2013; Perhans et al., 2014; Malíček et al., 2019). In this regard, it is worth mentioning the statement by Motyka (1934) that “a forest cut even once does not recover its lichen vegetation”. Several studies showed that some epiphytic lichens are restricted to old-growth forests because of their low dispersal range or specific substrate requirements (Cieśliński et al., 1996; Dymytrova et al., 2011; Nascimbene et al., 2013). Recently, Malíček et al. (2019) found that lichens with stalked apothecia, pigmented ascospores and large ascospores are more frequent in old-growth forests.

In the case of bryophytes, species richness did not exhibit a significant response to the gradient of forest naturalness expressed by the different management regimes and protection time spans. Similar results were obtained by Putna and Meżaka (2014), who found that anthropogenic disturbance did not cause immediate changes in epiphytic bryophyte species richness and community composition. The lower

Fig. 10. DCA diagram showing similarity in species composition of epixylic bryophytes occurring on CWD among sites under different management regimes. Values of the axes: DCA1 = 0.3658, DCA2 = 0.1957. Significant difference in the sample plot ordination scores of the first ax between BNP and managed forests, K-W test, p < 0.05. Remaining symbols as in Fig. 9.
sensitivity of rare bryophyte species compared to rare lichen species had already been highlighted by Brunialti et al. (2010), but the lack of response of overall bryophyte species richness to forest structural changes along the tested gradient of forest naturalness contrasts with the results of other studies showing that bryophytes diversity patterns promptly react to changes in forest structure determined by management activities (Hofmeister et al., 2015). Nonetheless, in our study, species such as Homalia trichomanoides, Neckera complanata, Anomodon viticulosus, A. longifolius, regarded as red-listed or primeval forest relics, showed a twice higher frequency in BNP and nature reserves than in the managed forests.

One possible explanation for the weak response of bryophytes to the forest naturalness gradient exemplified by the tested management regimes and protection time span, could be the considerable availability of deadwood in the BF. In 2017, the mean deadwood volume in BF managed forests reached 66 m³/ha (Tabor, 2017), which is 2 times less than in BNP, but up to 6 times higher than in average Polish forest and 4 time higher than in an average European forest (Puletti et al., 2019). Deadwood, and especially CWD, amount represents one of the most important factor influencing bryophyte diversity and occurrence of bryophyte red-listed and relic species, as highlighted in this study and in previous ones (e.g. Preikša et al., 2015; Fojcik et al., 2019). Besides, bryophytes exhibit a certain adaptability in terms of substrates. Among epiphytic bryophytes occurring in Europe there is just a few species which can be found exclusively on such a substrate (e.g. Ulota coarctata). Most of them can occur also on different types of rocks (Dierssen, 2001).
and some of them are able to colonize artificial substrates such as walls, concrete pillars, poles (Steibel, 2006). Exclusively epixylic species too are quite rare (e.g. Calypogea suecica). Although the optimal substrate for them is primarily represented by deadwood, most of them can occur also on humic soil or tree bark (especially at the trunk base). Such ability to colonize different substrates can account for the observed lack of clear differences in species richness among the tested management regimes. Anyway, it should be noticed that such results regard only species richness. Quantitative assessment, including frequency and abundance of typical forest species, especially primeval forest relics, clearly shows that their share in natural forests is significantly higher.

The occurrence of a certain number of relic and red-listed species in managed forest stands represents the legacy of the peculiar history of protection of this woodland complex and the resulting mosaic of protection regimes currently in force there, testifying the remarkably high level of naturalness and biological diversity which even managed stands in the BF can boast in comparison with other managed forests of Europe (Jarošzewicz et al., 2019; Blicharska et al., 2020). Specifically, persistence of such species may be due to the survival of patches of managed forests which have maintained continuity of forest cover over time, and consequently, these micro-habitats required for such species to survive, or, more likely, to the proximity of the close-to-primeval stands of BNP or nature reserves, which acting as refuges for such species, made it possible for them to recolonize some patches of exploited forests after having disappeared due to habitat disruption. Such scenario and its implication for forest management were highlighted by other authors, stressing out that heterogeneity of forest structure and availability of dead-wood substrates, such as that observed in unmanaged forests, is necessary for the maintenance of cryptogam diversity also in managed forests (Hofmeister et al., 2015). In this regard, the proposal of a shift in the conception of forestry practices towards what has been defined as “retention forestry” (Lindemayer et al., 2012) appears crucial.

Cryptogamic diversity overall exhibited a high degree of correlation with most of the stand structural and compositional parameters tested. Bryophyte species richness and number of red-listed taxa increased with increasing tree and shrub layer diversity, understory species richness, dead wood volume and quality (especially CWD in higher decay classes) and density of shrub layer, while decreased with stand volume. In the case of lichens, species richness and number of red-listed taxa increased with understory species richness, tree layer diversity, herb layer cover, stand age, protection time span and deadwood volume, especially in the highest decay class, while decreased with the increase in bryophyte layer cover, bark cover of deadwood and mean individual biomass of carabid beetles.

These results are in line with those from previous studies about the effect of environmental factors on cryptogams (Brunialti et al., 2010; Mezaka et al., 2012; Nascimbene et al., 2013; Hofmeister et al., 2015; Lubek et al., 2018). The positive effect of understory species richness, and particularly of number of undergrowth herbaceous species and epigymous bryophytes, indicates that this layers may be regarded as a good indicator of overall species diversity of forest ecosystems (Dittrich et al., 2014; Putna and Mezaka, 2014). The significant effect of the shrub layer cover for bryophytes, together with the contemporary lack of significant correlation with tree layer cover, indicates that shading provided by lower layers can be more effective in guaranteeing them protection against dessication. Tree and shrub layers diversity, on the other hand, increase both bryophyte and lichen diversity by providing substrates with different physico-chemical properties. The paramount importance of deadwood amount for bryophytes and lichens species richness, and particularly for sensitive species such as red-listed and relic ones, are confirmed by similar results from previous studies (Boch et al., 2013; Nascimbene et al., 2013; Fojcik et al., 2019). Deadwood appeared particularly crucial for bryophytes, among which a much higher number of species are strictly epixylic than among lichens. Another important factor which significantly affected species richness and composition of epiphytes was the age of the dominant tree species, which influenced also the number of red-listed species and the overall lichen species richness. This factor is strictly correlated with tree dimensions and bark properties, as described by Ulitzka and Angelstam (1999), Ranius et al. (2008), Mezaka et al. (2012).

Correlation analyses revealed that stand age significantly affect just lichen diversity and abundance, especially in the case of epiphytic species. At the same time, we also observed that, while the highest number of lichen species occurred in mature forest stands above 101–120 years old, which confirms the results of correlation analyses, in the case of bryophytes we observed two peaks in 61–80 and 101–120 years old stands. Such patterns highlight the paramount importance of old-growth stands for cryptogamic diversity. The double peak observed in the case of bryophytes further indicates that these, although generally preferring old-growth conditions (particularly in the case of epixylic species), are overall more plastic than lichens and can, in certain conditions, successfully adapt to sub-optimal niches.

Forest type also played a primary role in driving diversity patterns of both bryophytes and lichens, as already described by Putna and Mezaka (2014) and Lubek et al. (2018). In the case of bryophytes, the highest species richness was observed in alder carrs and mixed deciduous swamp and riparian forests, and followingly, in boggy coniferous and boggy mixed forests, while for lichens also in deciduous and mixed-deciduous forests, which is clearly related to the respective physiological requirements of these two groups. Bryophytes are indeed very strictly dependent on environmental moisture and their diversity is the highest in those habitats characterized by a constant supply of water, which enables them to sexually reproduce and colonize new sites (when conditions are unfavourable they mainly reproduce vegetatively and tend to expand their cover on already colonized sites). Lichens on the other hand, as mainly epiphytic species, seem to have higher requirements in terms of host tree species features, such as age, dimensions, pH of bark, which can explain why their species richness is highest in deciduous stands, where particularly old and large trees of different species, especially oaks, occur.

No relationship was observed between species richness and, the number of saproxylic beetle species, another acknowledged indicator of forest naturalness (e.g. Jarośzewicz et al., 2019), while a negative correlation was obtained between mean individual biomass (MIB) of carabid beetles, another indicator of the degree of forest naturalness (Jelaska et al., 2011), and species number of bryophyte, lichens and red-listed lichens.

Patterns of species richness of bryophytes and lichens clearly differed in their response to light availability. As expected, bryophyte species richness was negatively affected by light availability and positively correlated with increasing humidity level and nitrogen content. In the case of lichens, light availability had no significant effect on the species number. The different requirement of bryophytes and lichens in terms of light, humidity and nutrient content result from their intrinsic physiological features, which ultimately drive their species richness patterns.

As with species richness patterns, also the response of species composition patterns to the management regime differed between bryophytes and lichens, especially depending on the substrate. While epiphytic lichen community composition significantly differed among management regimes, no significant differences were observed in the case of bryophytes. On the contrary, epixylic bryophyte communities, especially those occurring on CWD, exhibited significant difference in their species composition depending on management regimes, whereas lichen epiphytic communities did not. This shows that the most obvious differences among bryophyte and lichen communities depending on management regime can be found on substrates characteristically hosting the majority of the species for that group (living trees for lichens and CWD for bryophytes).

5. Conclusions

The analysis of our data confirmed that lichen species diversity and
the number of relic and red-listed cryptogams overall are reliable indicators of forest naturalness, protection time span and forest continuity and can effectively substitute classical structural parameters and historical data used to evaluate forest status and value. In the case of the bryophytes the response was not so clear and regarded mainly red-listed and relic species.

Considering the high indicative power of epiphytic and epixylic species richness for specific degrees of forest naturalness, habitat properties and biological diversity, further development of biomonitoring by these groups of organisms is highly advisable, as it represents a powerful tool for assessing the impact of forest management activities and climate changes on forest ecosystems and their biodiversity. Sensitive bryophytes and lichen species in particular, given their diagnostic power, should thus represent one of the main objects of forest monitoring efforts.

Given the negative impact of management practices, especially clearcuts, on lichen species diversity and the number and frequency of red-listed and relic species of both lichens and bryophytes, it would be advisable to leave out of management those parts of forest characterized by the occurrence of old stands, as well as their surroundings. Such practice may give lichens and bryophyte species the chances to reestablish managed stands over time and to restore their natural life cycle. Maintenance or restoration of suitable conditions for establishment of sensitive bryophytes and lichen species, such as ensuring the presence of a sufficient amount of lying and standing deadwood and retaining big and old and big trees, should be envisioned in close to natural sylviculture or retention forestry and been systematically implemented during logging operations in managed forests.

Appendix A. Frequency (%) of red-listed bryophyte and lichen species among management regimes. The IUCN category of threat: CR – Critically endangered, EN – endangered, VU – vulnerable, NT – Near threatened, LC – Least concern, DD – Data deficient. NP – Białowieża National Park, NR – Nature reserves, MF – Managed forests. The dots indicate that the species were not present.

| Category of threat | Species                        | NP | NR | MF | Total |
|--------------------|--------------------------------|----|----|----|-------|
| Bryophytes         |                                |    |    |    |       |
| EN                 | Neckera pennata               | 3  | .  | 2  | 1     |
|                    | Pseudobryum cinclidioides     | .  | 3  | .  | 1     |
| VU                 | Ulota crispa                  | 10 | 10 | 16 | 12    |
|                    | Ulota brachi                  | 2  | 3  | 7  | 4     |
|                    | Dicranum bonjeani             | 2  | 2  | .  | 1     |
|                    | Cephalozia cernulata          | .  | 2  | .  | 1     |
|                    | Prullia tamarisci             | .  | 2  | .  | 1     |
| NT                 | Nowellia curvifolia           | 53 | 24 | 21 | 33    |
|                    | Odontoschisma demadenatum     | 10 | 8  | .  | 6     |
|                    | Geocalyx graveolens           | 3  | 2  | .  | 2     |
| LC                 | Lophocolea heterophylla       | 68 | 71 | 90 | 83    |
|                    | Plitidium pulcherrimum        | 67 | 58 | 59 | 61    |
|                    | Lepidonia reptans             | 58 | 61 | 47 | 55    |
|                    | Lophocolea bidensata          | .  | 37 | 36 | 24    |
|                    | Plagiochila asplenoides       | 22 | 29 | 21 | 24    |
|                    | Radula complanata             | 27 | 19 | 19 | 21    |
|                    | Metzgeria furcata             | 23 | 24 | 12 | 20    |
|                    | Bassania triloba              | 25 | 15 | 7  | 16    |
|                    | Prullia dilatata              | 13 | 8  | 21 | 14    |
|                    | Jamesoniella autumnalis       | 8  | 17 | 12 | 12    |
|                    | Cephalozia bicuspidata        | 15 | 8  | 9  | 11    |
|                    | Plagiochila percellidoides    | 12 | 10 | 3  | 8     |
|                    | Calypogeia integristratula    | 2  | 10 | 5  | 6     |
|                    | Riccardia laitrons            | 5  | .  | 9  | 5     |
|                    | Aneura pinguis                | 3  | 5  | 3  | 4     |
|                    | Pellia epiphylla              | 7  | 3  | 2  | 4     |
|                    | Riccardia palmata             | .  | 8  | 3  | 4     |
|                    | Blepharostoma trichophyllum   | 2  | 5  | 2  | 3     |
|                    | Dicranum viride               | 3  | 2  | 2  | 2     |
|                    | Calypogeia neesiana           | .  | 5  | .  | 2     |
|                    | Cephalozia communis           | 2  | 3  | .  | 2     |
|                    | Calypogeia musellariana       | 2  | 2  | .  | 1     |

(continued on next page)
| Category of threat | Species                      | NP | NR | MF | Total |
|-------------------|------------------------------|----|----|----|-------|
| DD                | Chiloscyphus pallescens      | .  | .  | 3  | 1     |
|                   | Lejeunea cariopila          | 3  | .  | .  | 1     |
|                   | Chiloscyphus polyanthos      | 2  | .  | .  | 1     |
|                   | Conocephalum conicum        | .  | 2  | .  | 1     |
|                   | Jungermannia leiantha       | .  | 2  | .  | 1     |
|                   | Lophozia ventricosa         | .  | 2  | .  | 1     |
|                   | Ptilidium ciliare            | .  | 2  | .  | 1     |
|                   | Orthothecium gymnocarpum    | .  | .  | 2  | 1     |
|                   | Orthothecium patens         | .  | .  | 2  | 1     |
|                   | Anomodon longifolius        | 5  | .  | .  | 2     |
| CR                | Menegazzia terebrata        | 10 | 15 | 9  | 11    |
|                   | Ochrolechia candelaris      | 17 | 3  | 3  | 8     |
|                   | Chaenotheca chloris         | 3  | .  | 2  | 2     |
|                   | Arthonia cinnabarina        | 2  | .  | .  | 1     |
|                   | Bacidia laurocerasi         | .  | .  | 2  | 1     |
|                   | Usnea westmuthii            | 2  | .  | .  | 1     |
| EN                | Loxospora elatina           | 43 | 29 | 16 | 29    |
|                   | Chaenotheca stemonea        | 22 | 3  | 3  | 10    |
|                   | Micarea elachista           | 20 | 7  | 2  | 10    |
|                   | Cladonia parasitica         | 15 | 7  | .  | 7     |
|                   | Thelotrema lepadinum        | 15 | 5  | 2  | 7     |
|                   | Opegrapha vermiculifera     | 8  | .  | 2  | 3     |
|                   | Pertusaria flavae           | 7  | .  | 3  | 3     |
|                   | Chaenotheca brunnea         | 3  | 2  | 2  | 2     |
|                   | Flavoparmelia caperata      | .  | 5  | 2  | 2     |
|                   | Inodermia byssaceae         | 7  | .  | .  | 2     |
|                   | Pyrenula nitidella          | 5  | 2  | .  | 2     |
|                   | Chaenotheca brachypoda      | 3  | 2  | .  | 2     |
|                   | Arthonia didyma             | 3  | .  | .  | 1     |
|                   | Bacidia arceae              | 3  | .  | .  | 1     |
|                   | Cetraria cetrarioides       | .  | 3  | .  | 1     |
|                   | Cetraria olivera            | 3  | .  | .  | 1     |
|                   | Hyperphysomya rotula        | 2  | 2  | .  | 1     |
|                   | Bacidia incompta            | .  | 2  | .  | 1     |
|                   | Calicium adspersum          | .  | .  | 2  | 1     |
|                   | Cladonia caespitica         | 2  | .  | .  | 1     |
|                   | Lecanacia abietina          | 2  | .  | .  | 1     |
| VU                | Ramalina farinacea          | 15 | 10 | 19 | 15    |
|                   | Opegrapha vulgaris          | 15 | 8  | 7  | 10    |
|                   | Arthonia leucopela          | 22 | 5  | 2  | 10    |
|                   | Zwackhia viridis            | 20 | 2  | 5  | 9     |
|                   | Pyrenula nitida             | 12 | 3  | 5  | 7     |
|                   | Peligera praestata          | 7  | .  | 5  | 4     |
|                   | Parmeliopsis hyperborea     | 5  | 2  | 3  | 3     |
|                   | Calicium abietinum          | 8  | .  | .  | 3     |
|                   | Calicium salicinum          | 5  | 2  | 2  | 3     |
|                   | Ramalina sellinaria         | 3  | 3  | 2  | 3     |
|                   | Acrocarpsia gemmata         | 2  | 2  | 3  | 2     |
|                   | Biatora asciliformis        | 3  | 2  | 2  | 2     |
|                   | Chaenotheca xyloxa          | 3  | 2  | 2  | 2     |
|                   | Pertusaria pertusa          | 2  | 2  | 3  | 2     |
|                   | Arthonia mediella           | 5  | .  | .  | 2     |
|                   | Ochrolechia androgyna       | 5  | .  | .  | 2     |
|                   | Pseudohypoloma rufescens    | 2  | .  | 3  | 2     |
|                   | Buellia discomiformis       | 3  | .  | .  | 1     |
|                   | Calicium glaucesum          | 2  | 2  | .  | 1     |
|                   | Micarea hedlundii           | 3  | .  | .  | 1     |
|                   | Usnea dasispina             | 2  | .  | 2  | 1     |
|                   | Bacidia rubella             | .  | .  | 2  | 1     |
|                   | Ochrolechia arborea         | .  | .  | 2  | 1     |
|                   | Opegrapha niveoatra         | 2  | .  | .  | 1     |
|                   | Pertusaria coronata         | 2  | .  | .  | 1     |
|                   | Thelocarpon intermediellum | 2  | .  | .  | 1     |
|                   | Varicella hispida           | 2  | .  | .  | 1     |
| NT                | Graphis scripta             | 43 | 39 | 31 | 38    |
|                   | Arthothecium ruanum         | 15 | 12 | 16 | 14    |
|                   | Chaenotheca trichialis      | 15 | 12 | 10 | 12    |
|                   | Pertusaria linosperma       | 10 | 12 | 10 | 11    |
|                   | Pertusaria cocodes          | 17 | 8  | 5  | 10    |
|                   | Evernia prunastri           | 7  | 8  | 9  | 8     |
|                   | Micarea melana              | 12 | 3  | 7  | 7     |
|                   | Arthonia vinosa             | 13 | 2  | 3  | 6     |
|                   | Chaenotheca furfuracea      | 10 | 5  | .  | 5     |
|                   | Alyxia varia                | 8  | .  | 2  | 3     |
|                   | Lichenomphalia umbilifera   | 5  | 5  | .  | 3     |

(continued on next page)
### Appendix B. Frequency (%) of relic bryophyte species of primeval forests among management regimes.

| Category of threat | Species                  | NP | NR | MF | Total |
|--------------------|--------------------------|----|----|----|-------|
|                    | Hypogymnia tubulosa       | 3  | 2  | 2  | 2     |
|                    | Pertusaria pupillaris     | 3  | .  | .  | 1     |
|                    | Vulpicida pinastri        | 3  | .  | .  | 1     |
| LC                 | Bacillia sulphurella      | 2  | 2  | .  | 1     |
|                    | Feltanera gigantopilosa   | 22 | 7  | .  | 11    |
|                    | Cladonia norvegica        | 5  | .  | .  | 2     |
|                    | Peltigera polydactylon    | 2  | .  | .  | 1     |
|                    | Trapelopsis glaucolepidea | 2  | .  | .  | 1     |

The dots indicate that the species were not present.

### Appendix C. Frequency (%) of relic lichen species of primeval forests among management regimes.

| Species                  | NP | NR | MF | Total |
|--------------------------|----|----|----|-------|
| Cladonia norvegica       | 8  | .  | .  | 3     |
| Arthonia disjuncta       | 6  | .  | .  | 2     |
| Bacidia arceutina        | 6  | .  | .  | 2     |
| Cetrula oliverorum       | 6  | .  | .  | 2     |
| Micarea hedlundii        | 6  | .  | .  | 2     |
| Pertussaria papillaris   | 6  | .  | .  | 2     |
| Lecanora obscura         | 3  | .  | .  | 1     |
| Pertussaria coronata     | 3  | .  | .  | 1     |
| Bacidia laurocerasi      | .  | .  | .  | 1     |
| Calicium adspersum       | .  | .  | .  | 1     |
| Cetrula carnosoides      | .  | 6  | .  | 6     |
| Pertussaria flavida      | 11 | .  | .  | 6     |
| Opegrapha verrucellifera | 14 | .  | 3  | 6     |
| Chaenotheca chloriella   | 6  | .  | .  | 3     |
| Loxospora elatina        | 72 | 49 | 27 | 50    |
| Menegazzia terebrata     | 17 | 26 | 15 | 19    |
| Fellhanera gyrothorica   | 36 | 11 | 9  | 19    |
| Micarea elachista        | 33 | 11 | 3  | 16    |
| Arthonia leucopolia      | 36 | 9  | 3  | 16    |
| Chrysothrix candelaris    | 28 | 6  | 6  | 13    |
| Micarea melana           | 19 | 6  | 12 | 12    |
| Thelotrema lapidum       | 25 | 9  | 3  | 12    |
| Arthonia vinosa          | 22 | 3  | 6  | 10    |
| Biatora ocelliformis     | 6  | 3  | 3  | 4     |
| Chaenotheca brunnea      | 6  | 3  | 3  | 4     |
Appendix D. Correlation matrix of variables (n = 177). Significant r Spearman was marked grey shadows and red fonts (p < 0.05).

| Variable | Description |
|----------|-------------|
| N Bryo | number of epiphytic and epixylic bryophytes |
| N Lich | number of epiphytic and epixylic lichens |
| Thre B | number of red-listed epiphytic and epixylic bryophytes |
| Thre L | number of red-listed epiphytic and epixylic bryophytes |
| CoB CWD | bryophyte cover of coarse woody debris |
| CoB S | bryophyte cover of stumps |
| CoB SDT | bryophyte cover of standing dead trees |
| CoB LT | bryophyte cover of living trees |
| CoL CWD | lichen cover of coarse woody debris |
| CoL S | lichen cover of stumps |
| CoL SDT | lichen cover of standing dead trees |
| CoL LT | lichen cover of living trees |
| NuB CWD | number of bryophyte species on coarse woody debris |
| NuB S | number of bryophyte species on stumps |
| NuB SDT | number of bryophyte species on standing dead trees |
| NuB LT | number of bryophyte species on living trees |
| NuL CWD | number of lichen species on coarse woody debris |
| NuL S | number of lichen species on stumps |
| NuL SDT | number of lichen species on standing dead trees |
| NuL LT | number of lichen species on living trees |
| Cov TL | cover of tree layer |
| Cov SL | cover of shrub layer |
| Cov HL | cover of herb layer |
| Cov BL | cover of bryophyte layer |
| Nu TL | number of species in tree layer |
| Nu SL | number of species in shrub layer |
| Nu HL | number of species in herb layer |
| Nu VL | number of species in phytosociological relevés |
| Nu Re | number of species in phytosociological relevés |
| L | ecological indicator values for light based on vascular plants in herb layer |
| W | ecological indicator values for soil moisture based on vascular plants in herb layer |
| Tr | ecological indicator values for nutrient contents based on vascular plants in herb layer |
| R | ecological indicator values for soil reaction based on vascular plants in herb layer |
| S Vol | stand volume |
| Tr Age | mean tree age in sample plot |

Explanation of variable abbreviations:
N Bryo – number of epiphytic and epixylic bryophytes
N Lich – number of epiphytic and epixylic lichens
Thre B – number of red-listed epiphytic and epixylic bryophytes
Thre L – number of red-listed epiphytic and epixylic bryophytes
CoB CWD – bryophyte cover of coarse woody debris
CoB S – bryophyte cover of stumps
CoB SDT – bryophyte cover of standing dead trees
CoB LT – bryophyte cover of living trees
CoL CWD – lichen cover of coarse woody debris
CoL S – lichen cover of stumps
CoL SDT – lichen cover of standing dead trees
CoL LT – lichen cover of living trees
NuB CWD – number of bryophyte species on coarse woody debris
NuB S – number of bryophyte species on stumps
NuB SDT – number of bryophyte species on standing dead trees
NuB LT – number of bryophyte species on living trees
NuL CWD – number of lichen species on coarse woody debris
NuL S – number of lichen species on stumps
NuL SDT – number of lichen species on standing dead trees
NuL LT – number of lichen species on living trees
Cov TL – cover of tree layer
Cov SL – cover of shrub layer
Cov HL – cover of herb layer
Cov BL – cover of bryophyte layer
Nu TL – number of species in tree layer
Nu SL – number of species in shrub layer
Nu HL – number of species in herb layer
Nu VL – number of species in phytosociological relevés
Nu Re – number of species in phytosociological relevés
L – ecological indicator values for light based on vascular plants in herb layer
W – ecological indicator values for soil moisture based on vascular plants in herb layer
Tr – ecological indicator values for nutrient contents based on vascular plants in herb layer
R – ecological indicator values for soil reaction based on vascular plants in herb layer
S Vol – stand volume
Tr Age – mean tree age in sample plot
DW Vol – total dead wood volume
CWD Vol – coarse woody debris volume
SDT Vol – standing dead trees volume
DW1 Vol – deadwood volume in first class of decay (non decompose)
DW2 Vol – deadwood volume in first class of decay (middle decompose)
DW3 Vol – deadwood volume in first class of decay (strongly decompose)
BCo DW – mean bark cover on deadwood
Prot P - Protection period (number of years till 2018) of area
N Sap – number of saproxylic beetle species
MIB – mean individual biomass of carabid beetles

Appendix E. Differentiation in the number of bryophyte species in the BF. The different shape of the plots reflects the age classes of the tree stands: circle 41–60, triangle 61–80, inverted triangle 81–100, square 101–120, diamond > 120 years.
Appendix F. Differentiation in the number of lichen species in the BF. The different shape of the plots reflects the age classes of the tree stands: Circle 41–60, triangle 61–80, inverted triangle 81–100, square 101–120, diamond > 120 years.
Appendix G. Differentiation in the number of red-listed bryophyte and lichen species in the BF. The different shape of the plots reflects the age classes of the tree stands: Circle 41–60, triangle 61–80, inverted triangle 81–100, square 101–120, diamond > 120 years.

References

Blicharska, M., Angelstam, P., Giessen, L., Hilszczaniski, J., Hermanowicz, E., Holeku, J., Jacobsen, J.B., Jaroszewicz, B., Konczal, A., Konieczny, A., Mikusinski, G., Mirek, Z., Mohren, G.M.J., Muys, B., Niedzialkowski, K., Soitrov, M., Stereńczak, K., Szogryn, J., Winder, G., Witkowski, Z., Zapata, R., Winkel, G., 2020. Between biodiversity conservation and sustainable forest use - a multidisciplinary assessment of the emblematic Białowieża Forest case. Biol. Conserv. 248, 108614 https://doi.org/10.1016/j.biocon.2020.108614.

Boch, S., Prati, D., Hessenmeller, D., Shulze, E.D., Fisher, M., 2013. Richness of lichen species, especially of threatened ones, is promoted by management methods furthering stand continuity. Plos One 6 (11). https://doi.org/10.1371/journal.pone.0055461.

Braun-Blanquet, J., 1964. Pflanzensoziologie, Grundzüge der Vegetationskunde, 3rd ed. Springer-Verlag, Berlin.

Brumelis, G., Jonsson, B.G., Kouki, J., Kuukuvainen, T., Shorobova, E., 2011. Forest naturalness in northern Europe: Perspectives on processes, structures and species diversity. Silva Fenn. 45 (5), 807–821.

Brunahl, G., Prati, L., Allefi, M., Martignani, M., Rosati, L., Buzzascano, S., Ravera, S., 2010. Lichens and bryophytes as indicators of old-growth features in Mediterranean forests. Plant Biosyst. 144 (1), 221–233. https://doi.org/10.1080/11263500903560959.

Christensen, M., Hahn, K., Mountford, E.P., Ödör, P., Standová, T., Rozenbergar, D., Diaci, J., Wijdeven, S., Meyer, P., Winter, S., Veska, T., 2005. Dead wood in European beech (Fagus sylvatica) forest reserves. Forest Ecol. Manag. 210 (1-3), 267–282. https://doi.org/10.1016/j.foreco.2005.02.032.

Cieślinski, S., 2003. Atlas rozmieszczenia porostów (Lichenes) w Polsce Północno- Wschodniej. Phytocoenosis (N.S.) 15. Suppl. Cart. Geobot. 15, 1–420.

Cieślinski, S., Czyżewska, K., 1998. Lichens as indicators of the synanthropization of plant cover and the environment. In: Falinński, J.B., Adamowski, W., Jackowiak, B.
Latałó, K., Klama, H., G. Kirschbaum, U., Cezanne, R., Eichler, M., Hanewald, K., Windisch, U., 2012. Long-term ecological Indicators 125 (2021) 107532 19 reliefs of the primeval (virgin) forest. Relict phenomena, in: Faliniski, J.B., Mulenko, W. (Eds.), Cryptogamous plants in the forest communities of Bialowieza National Park (Project CRYPTO 3). Phytoecology 84, 1-296. Cieczewska, K., Faliniski, J.B., Klama, H., Mulenko, W., Zarnowiec, J., 1996. Red list of the Lichenes in Poland. In: Mirek, Z., Zarzycki, K., Wojewoda, W., Staszek, Z. (Eds.), Red list of plants and fungi in Poland. W. Szafer Institute of Biology, Polish Academy of Sciences, Kraków, pp. 95-99. Cieczewska, K., Faliniski, J.B., Klama, H., Hanewald, K., Windisch, U., 2012. Long-term monitoring of environmental change in German towns through the use of lichens as bioindicators. Folia Cryptog. Estonica, Fasc. 51, 75–83. Pignucco, M., Murren, C.J., Schlüchting, C.D., 2006. Phenotypic plasticity and evolution by genetic assimilation. J. Exp. Biol. 209, 2362-2367. https://doi.org/10.1242/jeb.02070. Proctor, K.G. (Eds.), Synanthropization of plant cover in new Polish research. Phytocoenosis 10 182 . Zarnowiec, J., Stebel, A., Ochyra, R. (Eds.), Red list of plants and fungi in Poland. Archiv. Geobot. 4, 75-86. Ochyra, R. (Eds.), Bryological studies in the Western Carpathians. Sorus, Poznań, 2002. Ecological indicator values of vascular plants of Poland. W. Szafer Institute of Biology, Polish Academy of Sciences, Kraków, pp. 95-99. Ochyra, R. (Eds.), Cryptogams – a relic of the high naturalness of European forests. Forests 9, 276–285. Proctor, K.G., Oliver, M.J., Wood, A.J., Alpert, P., Stark, L.R., Clevitt, N.L., Mühlen, B., 2012. Darstellung von Indikatoren in bryophyten: a review. Biotropia 110, 595–621. Pulletti, N., Dallino, R., Mattioli, W., Gavrey, R., Corona, P., Czerpek, J., 2019. A dataset of forest volume deadwood estimates for Europe. Ann. For. Sci. 76, 68. https://doi.org/10.1007/s10316-019-0583-z. Putna, S., Metzka, A., 2014. Preferences of epiphytic bryophytes for forest stand and substrate in North-East Latvia. Folia Cryptog. Estonica, Fasc. 51, 75–83. R Core Team, 2017. R: A Language and Environment for Statistical Computing. https:// www.R-project.org/. StatSoft Inc., 2010. STATISTICA data analysis software system, version 10. www.statsoft.com. van der Meer, A., 2013. Microhabitats in lowland beech forests as monitoring tool for nature conservation. Forest Ecol. Manag. 255, 1251–1268. https://doi.org/10.1016/j.foreco.2013.05.015. Sarnecki-Tacik, H., Ruskowski, T., Niklasson, M., Berg, N., 2008. The influence of tree age and microhabitat quality on the occurrence of crustose lichens associated with old oaks. J. Veg. Sci. 19, 653–662. https://doi.org/10.1111/j.1654-1103.2008.00143.x. Sokołowski-Tacik, H., Ruskowski, T., Niklasson, M., Berg, N., 2009. Development of tree hollows in pedunculate oak (Quercus robur). Forest Ecol. Manag. 257, 303–310. Stapper, N.J., John, V., 2015. Monitoring climate change with lichens as bioindicators. Pollution Atmospheric 226. https://doi.org/10.1016/j.pollat.2015.08.030. Tubt, Z., Slack, N.G., Stark, L.R., 2011. In Bryophyte Ecology and Climate Change. Cambridge University Press. Ulicka, H., Angelstam, P., 1999. Occurrence of epiphytic macrolichens in relation to tree species and age in managed boreal forest. Ecography 22, 396–405. https://doi.org/10.1111/1600-0587.1999.tb00576.x. Van Der Meer, A., 1979. Transformation of cover-abundance values in phytosociology and its effect on community similarity. Vegetatio 39, 97–114. Winter, S., Möller, G., 2008. Microhabitats in lowland beech forests as monitoring tool for nature conservation. Forest Ecol. Manag. 255, 1251–1268. https://doi.org/10.1016/j.foreco.2007.07.029. Wirth, V., 2010. Ökologische Zeigerwerte von Flechten – Erweiterte und Aktualisierte Fassung. Herzogia 23 (2), 229–248. https://doi.org/10.13158/herz.23.2.2010.229. Zarzycki, K., Traczinska-Tacik, H., Ruskowski, T., Staszek, Z., Wójcik, J., Korzeniak, U., 2002. Ecological indicators of vascular plants of Poland. W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków. Zarnowiec, J., Stebel, A., Ochyra, R., 2004. Threatened moss species in the Polish Carpathian forests in the light of new list of mosses in Poland. In: Stebel, A., Ochyra, R. (Eds.), Bryological studies in the Western Carpathians. Sorus, Poznan, pp. 9–28.