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Positive aspects of clear-cut logging? Ground bryophyte diversity along the age gradient of managed *Pinus sylvestris* stands

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Abstract – Bryophytes are important components of pine forests; however, the bryophyte layer is characterised by the dominance of a small number of taxa. Clear-cut logging changes microclimate conditions, while ploughing before planting young trees disrupts bryophyte patches. This promotes early successional species and can work in favour of species diversity provided that there are simultaneous regeneration of late successional species bryophytes. In the Tuchola Forest (north-western Poland), we investigated the occurrence and abundance of ground bryophytes using a chronosequence method. The study was carried out on plots that represented the following stand age classes: ≤ 10, 11-20, 21-40, 41-60, 61-80, > 80 years. Bryophyte richness was higher in the youngest stands than in the oldest ones. There are distinctive changes of species composition in the course of succession that range from colonists and stress-tolerant perennials to competitive perennials and from species growing in tufts to species growing in wefts. There are not "true" forest species even in the oldest stands. There is only a tendency for the exchange of species that prefer open habitats to species that prefer both forests and open habitats. However, clear cutting contributes to the increase of species richness of ground bryophytes and spatial diversity of plant patches in managed forests. The positive aspects of clear cutting can only be considered in relation to the species diversity in the oldest and managed stands but not with those in natural forests.

Scots pine forest / stand age classes / bryophytes of disturbed sites / mosses and liverworts richness/ ground species succession

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INTRODUCTION

Pinus sylvestris L. (Scots pine) stands are widespread and economically important in Central Europe (Kelly & Connolly, 2000). A crucial element of their physiognomy is an abundant bryophyte layer that is dominated by a small number of taxa (Walentowski *et al.,* 1994; Roo-Zielińska & Solon, 1997; Fenton *et al.*, 2003; Staniaszek-Kik & Woziwoda, 2011; Stefańska-Krzaczek, 2012). However, this is typical not only for temperate Scots pine forests but also for vast boreal forests (Esseen *et al.*, 1997; Hannerz & Hånell, 1997; Vellak & Paal, 1999; Mills & Macdonald, 2004). Moreover, even-aged coniferous stands both temperate and boreal ones that are poorest in nutrients are mostly managed by clear-cut logging. This is a prevalent form of a large-scale disturbance, which initiates ground layer succession (Caners *et al.,* 2013) and determines the vegetation dynamics (Tonteri, 1994; Karazija, 2003; Uotila & Kouki, 2005; Aavik *et al.*, 2009). The disturbance impacts especially bryophyte assemblages (Jonsson & Esseen, 1998). When a stand reaches the logging age, the bryophyte layer is almost completely destroyed as a result of clear cutting. Changes in the microclimate and habitat conditions and schematic practices for re-planting determine the succession of the bryophyte layer. Radically altered habitat conditions become unfavourable for shade-tolerant forest bryophytes and promote early successional species (Hannerz & Hånell, 1997; Fenton *et al.*, 2003; Åström *et al.*, 2005; Schmalholz & Hylander, 2009). Ploughing disrupts the compact bryophyte layer and mixes it with the mineral components of the soil. This favours the development of colonisers, which use the undergrowth-free surface for colonisation (Bergstedt *et al.*, 2008). Severe soil disturbance may be limiting for the sensitive species of the forest interior (Åström *et al.*, 2005; Nelson & Halpern, 2005). However, the recovery of late successional species has been observed mostly as a consequence of local survival or propagule rain (Hylander, 2009). The period of colonisation and the duration of the early successional bryophytes after logging are significantly limited by the dynamics of even-aged pine stands. Crowns of seven- and eight-year-old trees form a canopy (Puchniarski, 2008) and after that the conditions for light-demanding colonisers become unfavourable (Økland *et al.*, 2003; Stefańska-Krzaczek, 2012). In turn, shade plants have an opportunity to rebuild the population due to the better microclimate conditions than before the canopy closure (Nelson & Halpern, 2005). Moreover, their further recovery does not depend directly on the distance from mature forest patches (Hylander, 2009). However, a too dense canopy of young tree stands causes an excessive restriction of light intensity, which can also be a limiting factor for the forest species that have already recovered after reforestation (Økland *et al.*, 2003). However, no decline in the number of forest bryophytes was observed after canopy closure in *Picea abies* (L.) H. Karst. forests (Schmalholz & Hylander, 2009). In addition, the light conditions in dense stands improve in a short time because of the pre-commercial thinning that is carried out in the stands that are more than ten years old (Puchniarski, 2008). This silvicultural treatment can promote an increase in species diversity, especially in poor habitats in which the increase in the amount of light in the stand gaps lasts longer than in fertile habitats (Widenfalk & Weslien, 2009). In addition, the presence of fine decaying wood is important for the diversity of cryptogam species in managed forests (Kruys & Jonsson, 1999; Humphrey *et al.*, 2002) and lots of this type of wood is left on the forest floor after intensive thinning. This type of substratum can be settled by multi-substrate species, which can relocate to the soil layer after the decomposition of the primary substratum.

It can be assumed that the early successional bryophytes in monoculture pine stands on poor sandy soils that invade after logging will withdraw from the undergrowth after canopy closure and that their place will gradually be taken over by forest species. However, due to the pre-commercial thinnings, which improve light conditions, early successional species have an opportunity to still be present in young but closed-canopy stands. Moreover, enrichment of the species composition in maturing stands can be possible because of the small wood pieces that are left after pre-commercial and commercial thinnings. If we could confirm this course of succession, it would indicate that clear-cut logging in managed forests is an opportunity to increase the species and spatial (alpha and beta) diversity of the ground bryophyte layer. To investigate these hypotheses, the following specific questions were formulated for this study: 1) How long do the early successional species last in the plant community? 2) Can late successional species be identified among ground bryophytes? 3) When do the species that are typical for mature stands regain dominance in the bryophyte layer? 4) What are ecological attributes of the species that occur in the course of succession? 5) Do all of stand age classes have important input into the species diversity?

MATERIALS AND METHODS

The study was conducted within the Przymuszewo Forest District in the Tuchola Forest (north-western Poland). The coordinates of the outermost research plots are N: 53.98725, 17.676972; S: 53.87275, 17.61375; E: 53.976056, 17.680056; W: 53.919222, 17.505583. The forest complex is solid and has the same land-use history. There are large areas of poor soils that are formed on the sands of glacial origin. The loose glacial sands are optimal for pine forests and the community *Leucobryo-Pinetum* W. Mat. (1962) 1973 is the potential natural vegetation of the area that was studied (Matuszkiewicz, 2008). However, the actual vegetation is composed of managed *Pinus sylvestris* L. monocultures, which are mostly classified as *Leucobryo-Pinetum* (Stefańska-Krzaczek & Fałtynowicz, 2014). *Cladonia* species are distinctive for the communities that were studied, but their cover is minor (Stefańska-Krzaczek & Fałtynowicz, 2013). We chose pine plantations in the *Leucobryo-Pinetum* sites because this is a typical managed forest type for the sandy glacial sites in the temperate zone of middle Europe. Moreover, a uniform and predictable management scheme is applied to these stands across Polish lowlands, which directs the course of succession. The ground bryophyte diversity across the age gradient of stands was studied using the chronosequence method. This method is still applied when successional trajectories exceed the life span of investigators. However, we realise that this substitution of the study in a real time gradient can be criticised as it requires the assumption of biotic and abiotic constancy over the time span and sites that have not been disturbed. The same scheme of management practices works for the convergence of successional courses in managed forests despite the disturbances. Moreover, we carefully chose the stands for the study based on two criteria: 1) a homogeneous habitat, and 2) the age of the stand. Only poorly hydrated oligotrophic habitats with a similar topography were selected. Specifically, we chose plots that were located on a flat or slightly undulating terrain and that are classified as "fresh coniferous forest" according to Polish forest typology for the field study. This guaranteed the homogeneity of the soils, which were podzols that had formed from loose fluvioglacial sands. The stands represented six age classes:

I: ≤10 years (young stands before crown closure), II: 11–20 years (young stands with intensive height growth after recent crown closure), III: 21–40 years (young stands with intensive height growth), IV: 41–60 years (middle-aged, maturing stands), V: 61–80 years (pre-mature stands with an increasing biomass) and VI: > 80 years (mature stands before logging). The stands were selected from artificially reforested areas. Freshly ploughed sites were not studied; only re-forested areas were taken into account. Data were collected from 20 plots for each age class and a total of 120 plots were studied. Their spatial distribution was dependent on the distribution of the subdivisions that represented a particular stand age class. However, the set of data from one age class was intentionally not concentrated in one part of the forest complex. Research plots were in the shape of a rectangle measuring 10x15 m (150 m^2). We chose such a large plot in order to study the course of succession in a scale that reflects the changes of habitat conditions in schematically managed temperate *Pinus sylvestris* stands. The percentage of cover was estimated in the plots for the following layers: A (tree layer > 8 m in height), B (trees and shrubs 0.6-8 m in height), C (herb layer < 0.6 m in height), D (bryophyte-lichen layer). The species that occurred in them were recorded. All of the species of bryophytes and their cover in layer D were recorded using a slightly modified Braun-Blanquet (1951) scale: 5 (species cover 75.1-100% of the plot), 4 (50.1-75%), 3 (25.1-50%), 2 (10.1-25%), 1 (1.1-10%), + (up to 1%) and r (less than 1%, in practise only a few shoots or a small turf in the plot). We recorded the bryophytes that occurred on the forest floor on the soil, litter or fine woody debris that was in contact with the soil and formed a structural layer of the forest community. Epiphytes were not considered because there are different factors influencing the succession of this type of bryophytes in managed forests, in which old trees are removed and the substratum is absent in the youngest age classes. The course of succession is then dependent on the rate of tree growth and probably various factors not related to forest management. In the studied managed forests there is also a problem with the epixylic bryophytes, which can colonize stumps or branches remaining after thinning. The areas that were studied did not contain rocky outcrops, windthrows or any large objects of decaying wood. The data were included into the Polish Vegetation Database (Kącki & Śliwiński, 2012).

For a comparison of bryophyte patterns in the stand age classes, the average number of species and their average cover was calculated for each class. The significance of differences between means was tested using the Kruskal-Wallis test and multiple comparison tests. To demonstrate the relation between bryophyte richness and their cover, we examined the correlation between these two variables (Spearman rank order correlations at $p=0.05$). To show how the bryophyte richness and cover depend on the structure of a forest community and the tree stand age correlations of the number of bryophyte species and their cover with the average number of all species, the cover of the tree and herb layers and stand age we examined.

We used the Whittaker index to determine whether a variation in stand age impacts beta diversity (Van Dyke, 2008). This was calculated using the JUICE program (Tichý, 2002) with the formula p/a, where p is the total number of species that was recorded in the data set that was analysed and a is the average number of species in the data set that was analysed. To demonstrate the input of young and middle-aged stands in general species diversity, we applied the following procedure: the Whittaker index was calculated for the oldest age group (group 1: stands > 80 years) and then the calculations were carried out for the next five groups, which were created by adding plots that represented the successive age classes (group 2: stands >80 years and ≤10 years together; group 3: >80, ≤10 and 11-20 years; group 4: >80, ≤10, 11-20 and 21-40 years; group 5: >80, ≤10, 11-20, 21-40 and

41-60 years and group 6: all of the age classes). In each subsequent series, 30 calculations were performed for 80% of the plots in the series that was being analysed. To support the results, we carried out a DCA analysis to determine the length of the gradient along the first axis, which is also the measure of beta diversity (Šmilauer & Lepš, 2014).

To show the relationship of particular species with stand age classes, we compared the species composition of the bryophyte layer in successive age classes. The frequency in each class and the average percentage of cover were calculated for each bryophyte species. The following means were adopted for the degrees of the abundance scale (5, 4, 3, 2, 1, +, r) when calculating the average cover: 87.5; 62.5; 37.5; 17.5 and 5 (van der Maarel, 1979); 0.5 and 0.1 (Lepš & Šmilauer, 1999). To examine whether any species are associated with the stand age classes, we also assessed the fidelity of each species in the age classes. Fidelity shows the concentrations of species in vegetation units and it can be accessed via statistical measurements (Tichý *et al.*, 2010). We calculated the fidelity using the JUICE software (Tichý, 2002) and chose the phi coefficient as its measure (Tichý *et al.*, 2010). The phi coefficient only considers the presence/absence data. The values range from –1 to 1, but they are multiplied by 100 in the JUICE program and only positive values are presented. Moreover, the significance of the phi at a significance level of 0.05 was tested using the Fisher's exact test (Tichý *et al.*, 2010). We defined bryophytes for each of the age class groups based on their frequency, cover and fidelity: bryophytes that are characteristic for the class (minimum fidelity of 20), constant bryophytes (minimum frequency of 55%) and dominant bryophytes (at least 30% cover at a minimum frequency of 10%).

To show a character or tendency for ecological changes in the bryophyte composition as a result of clear cutting and across the age gradient, we analysed the life strategy (Dierβen, 2001) and growth form (Hill *et al.*, 2007) of species, the clear definition of forest species (Preussing *et al.*, 2011) and the light and moisture requirements of species based on the ecological indicator values (Düll, 1992). We calculated the cover and number of species that represented a particular life strategy, growth form and forest definition for each plot. Then, the average number and cover were calculated for each age class. We calculated the weighted ecological indices for the light and moisture requirements (L_{EIV}, F_{EIV}). The weight was the species cover transformed into the van der Maarel scale (van der Maarel, 1979). Then, the average indices were calculated for each age class. The significance of any differences between means was tested using the Kruskal-Wallis test and multiple comparison tests ($p=0.05$).

All statistical analyses were performed using STATISTICA software (StatSoft Inc., 2013). Species nomenclature is consistent with the study of Ochyra *et al.* (2003) and Klama (2006).

RESULTS

Species richness

Twenty-two species of bryophytes (18 moss species and 4 liverworts) were recorded in the area (Table 1). Moreover, 39 species of vascular plants and 32 lichen species were recorded in the undergrowth in the plots that were studied (species list not presented). The bryophyte flora constitutes 24% of all species. On average, the

Table 1. Bryophytes in stand age classes. FS: category of forest species according to Preussing *et al.* (2011): 1.1 = species of closed-canopy forests, 1.2 = species of forest edges and gaps, 2.1 = species that prefer both forests and open habitats, 2.2 = species that occur in forest communities, but that prefer open habitats. Life strategy according to Dierβen (2001): col. = colonists, com.per. = competitive perennials, l.l.sh. = long-lived shuttle, s.t.per. = stress-tolerant perennials. Growth form according to Hill *et al*. (2007). L: indicator value for light according to Düll (1992). F: indicator value for moisture according to Düll (1992). Percentage frequency (F%) and percentage of average cover (C%) in all the stand age classes considered. Species fidelity is given by the superscripts, its value is the phi coefficient multiplied by 100. Cover value 0 means value < 1%

Stand age class	*FS*	*Life strategy*	*Growth form*	*L*	*F*	*I: ≤ 10*		*II: 11-20*		*III: 21-40*		*IV: 41-60*		*V: 61-80*		*VI: >80*	
						F%	*C%*	*F%*	*C%*	*F%*	*C%*	*F%*	*C%*	*F%*	*C%*	*F%*	*C%*
Barbilophozia barbata (Schmidel ex Schreb.) Loeske	1.2	s.t.per.	mat, smooth	8	4											5	0
Brachythecium rutabulum (Hedw.) Schimp.	2.1	com.per.	mat, rough	5	4			5	0								
Campylopus introflexus (Hedw.) Brid.	2.2	per.	tuft	8	2	25^{33}	0	15	0								
Cephaloziella divaricata (Sm.) Schiffn.	2.2	col.	mat, smooth	9	2	5	0	5	0			10	0	5	0	5	0
Ceratodon purpureus (Hedw.) Brid.	2.2	col.	turf	8	2	90^{88}	1	5	0			5	0				
Dicranum polysetum Sw. ex anon.	2.1	com.per.	tuft	6	4	100	9	100	32	95	35	100	25	100	16	100	25
Dicranum scoparium Hedw.	2.1	com.per.	tuft	5	4	55	0	75	1	75	5	95^{18}	3	90	1	80	1
Dicranum spurium Hedw.	2.1	com.per.	tuft	7	2	20	0	20	0	40	1	40	0	10	0	35	0
Hylocomium splendens (Hedw.) Schimp.	2.1	com.per	weft	6	4			5	0	15	2	5	1	30	1	40^{30}	1
Hypnum jutlandicum Holmen & E. Warncke	2.1	per.	mat, smooth	7	2	40	0	40	1	50	0	55	1	40	1	50	2
Leucobryum glaucum (Hedw.) Ångstr.	2.1	per.	cushion	5	7					5	0	5	0	5	0		
Lophocolea heterophylla (Schrad.) Dumort.	1.1	com.per	mat, smooth	4	4					15^{36}	0						
Plagiothecium curvifolium Schlieph. ex Limpr.	2.1	com.per.	mat, smooth	5	4							5	0				
Pleurozium schreberi (Willd. ex Brid.) Mitt.	2.1	com.per.	weft	6	4	90	6	90	21	90	29	90	46	90	63	90	56
Pohlia nutans (Hedw.) Lindb.	2.1	com.per.	tuft	5	4	100^{36}	16	100^{36}	15	35	0	40	0	40	0	50	0
Polytrichastrum formosum (Hedw.) G.L. Sm.	2.1	com.per.	turf	4	6					5	0					5	0
Polytrichum juniperinum Hedw.	2.2	s.t.per.	turf	8	4	90^{48}	2	100^{57}	8	30	0			10	0		
Polytrichum piliferum Hedw.	2.2	s.t.per.	turf	9	2	100^{73}	11	65^{38}	2								
Pseudoscleropodium purum (Hedw.) M. Fleisch. ex Broth.	2.1	per.	weft	6	4					15^{36}	1						
Ptilidium ciliare (L.) Hampe	2.1	l.l.sh.	weft	8	4	30	0	55	0	55	0	75	1	60	0	85^{23}	1
Ptilium crista-castrensis (Hedw.) De Not.	1.1	p.col.	weft	4	6					5	0						
Sciuro-hypnum oedipodium (Mitt.) Ignatov & Huttunen	2.1	com.per.	mat, rough	3	6			5	0	5	0	5				5	0
Total species number						12		15		15		13		11		12	

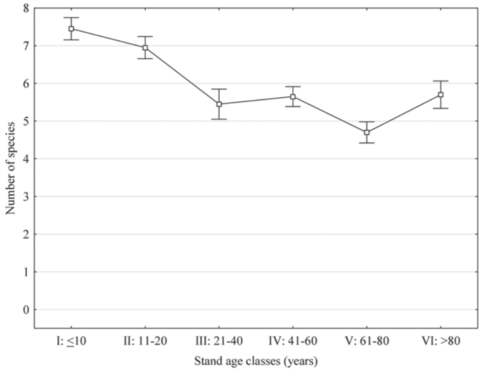

Fig. 1. Mean number (±standard error) of bryophyte species in stand age classes – Differences are statistically significant according to the Kruskal-Wallis test at p=0.05 between the stand age classes: I/III-VI, II/V.

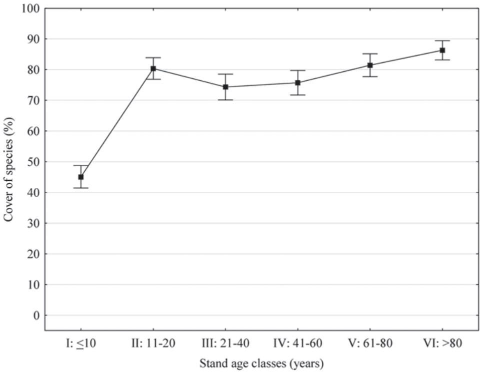

Fig. 2. Mean bryophyte cover (±standard error) in stand age classes – Differences are statistically significant according to the Kruskal-Wallis test at p=0.05 between the stand age classes: I/II-VI.

highest number of bryophyte species was recorded in the stands ≤ 10 years of age and only in comparison with young stands of 11-20 years the difference was not significant (Fig. 1). The number of species in the remaining age classes was significantly lower. Species cover showed the opposite tendency (Fig. 2). The bryophyte layer under the youngest stands was markedly least abundant (the difference was statistically significant). The value of this variable did not differ significantly among the older classes.

The number and cover of bryophyte species were weakly negatively correlated ($R = -0.297$, $p = 0.05$). The number of bryophyte species was clearly positively correlated with the number of all species that were recorded in the plots that were studied (list not presented). The correlation was also positive with the herb layer cover, but the value of the coefficient was lower. Bryophyte richness was negatively correlated with the stand age (Table 2). Bryophyte cover was positively correlated with the stand age, although it was negatively correlated with the number of all species.

Beta diversity

Beta diversity was lowest within the oldest stands and increased when the youngest stands were added to the analysis. It also increased when the consecutive stand age classes were included (Table 3).

Table 2. Correlation coefficients of bryophyte species number and cover with other variables (Spearman's coefficient). Coefficients statistically significant at p=0.05 are in bold. Number of all species = total number of vascular plants and lichens (neither is presented) and bryophytes

	Number of all species	*Cover of tree layer*	*Cover of herb layer*	*Stand age*
Number of bryophyte species	**0.767**	0.134	**0.244**	**0.376**
Cover of bryophytes	**0.45**	0.041	– 0.121	**0.96**

Table 3. Changes in the beta diversity of *Pinus sylvestris* forest when subsequent stand age classes are included. Stand series: Group 1: stands > 80 years; Group 2: > 80 years and ≤ 10 years together; Group 3: > 80, ≤ 10 and 11-20 years; Group 4: > 80, ≤ 10, 11-20 and 21-40 years; Group 5: > 80, ≤10, 11-20, 21-40 and 41-60 years and Group 6: all age classes, Whittaker index according to the formula: total number of species in the group/average number of species in the group

Stand series	*Group 1*	*Group 2*	*Group 3*	*Group 4*	*Group 5*	*Group 6*
Whittaker index	0.97	1.39	1.43	2.2	2.4	2.6
DCA lengh gradient	1.4	2.37	2.43	3.3	3.3	3.3

Species composition

The youngest stands were the only ones that were significantly qualitatively distinct due to the species that had a high fidelity and frequency: *Ceratodon purpureus* (Hedw.) Brid., *Pohlia nutans* (Hedw.) Lindb., *Polytrichum juniperinum* Hedw. and *P. piliferum* Hedw. (Table 1). At the same time, *Pohlia nutans* and *Polytrichum piliferum* belonged to the dominant species, which underlined the specificity of the bryophyte layer in the youngest stands. In the closed-canopy stands, regardless of the age, the dominant species were similar: *Pleurozium schreberi* (Willd. *ex* Brid.) Mitt. and *Dicranum polysetum* Sw. *ex* anon. In addition, the young stands of 11-20 years were qualitatively distinguished by the occurrence of *Pohlia nutans, Polytrichum juniperinum* and *P. piliferum*. Stands of 21-40 years were distinguished by two species but they were of a low fidelity and frequency: *Lophocolea heterophylla* (Schrad.) Dumort. and *Pseudoscleropodium purum* (Hedw.) M. Fleisch. *ex* Broth. Two species that had a low fidelity were also characteristic of the oldest stands: *Hylocomium splendens* (Hedw.) Schimp. and *Ptilidium ciliare* (L.) Hampe.

Species strategy, growth form and ecology

The number and cover of colonists and stress-tolerant perennials are significantly higher in the youngest stands than before clear cutting and re-forestation. Moreover, the cover of competitive perennials is significantly lower than before stand removal although their number does not differ significantly (Figs 3, 4). The number and cover of long-lived shuttles are significantly lower in the youngest stands than before clear cutting, however the values are generally very low. The number and cover of species growing in tufts is significantly higher in the youngest stands than before re-forestation while the opposite tendency was observed in terms of species growing in wefts (Figs 5, 6).

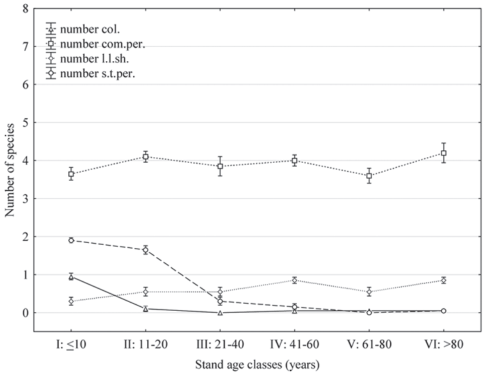

Fig. 3. Mean number (±standard error) of species that represent life strategy in stand age classes. See Table 1 for life strategy abbreviations. Differences are statistically significant according to the Kruskal-Wallis test at p=0.05 between the stand age classes for three life strategies: col. I/II-VI; l.l.sh. I/IV, I/VI; s.t.per. I-II/III-VI.

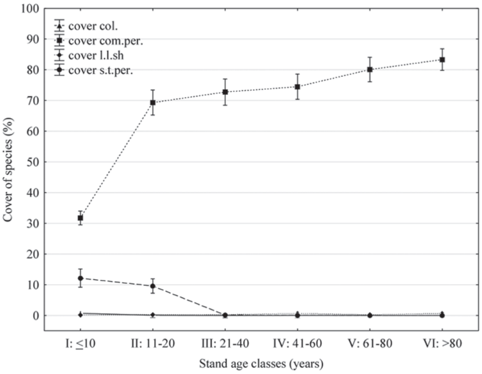

Fig. 4. Mean cover (±standard error) of species that represent life strategy in stand age classes See Table 1 for life strategy abbreviations. Differences are statistically significant according to the Kruskal-Wallis test at p=0.05 between the stand age classes for the four life strategies: col. I/II-VI; com.per. I/II-VI; l.l.sh. I/IV, I/VI; s.t.per. I-II/III-VI.

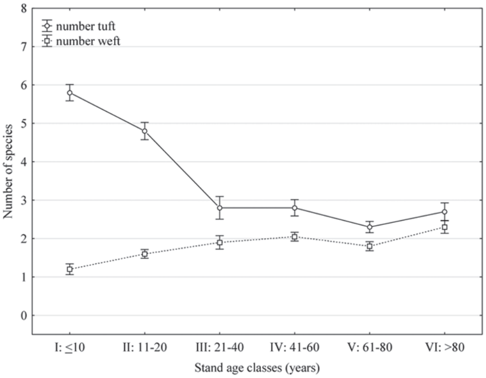

Fig. 5. Mean number (±standard error) of species representing the growth form in stand age classes. Growth forms according to Hill *et al.* (2007). Differences are statistically significant according to the Kruskal-Wallis test at p=0.05 between the stand age classes for the two growth forms: tuft I-II/III-VI; weft I/IV, I/VI.

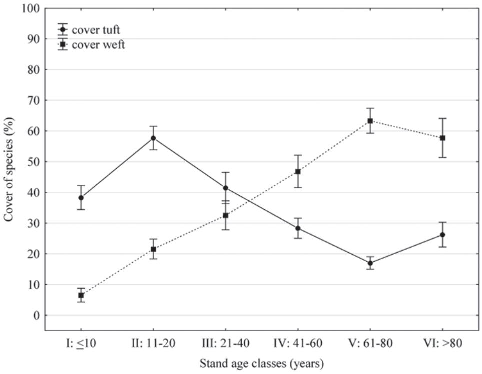

Fig. 6. Mean cover (±standard error) of species that represent the growth form in stand age classes. Growth forms according to Hill *et al.* (2007). Differences are statistically significant according to the Kruskal-Wallis test at p=0.05 between the stand age classes for the two growth forms: tuft I/V, II/IV-VI, III/V; weft I/III-VI, II/IV-VI, III/V.

Only two species of closed-canopy forest ("true" forest species) were recorded in the succession course: *Lophocolea heterophylla* and *Ptilium crista-castrensis*; however, they are not species that are specific to the oldest stands, but prefer middle-aged stands. The youngest (open-canopy) stands were characterised by high number and cover of species that occur in forest communities, but that prefer open habitats (Figs 7, 8). In closed-canopy stands, the number and cover of these species decreased in favour of a cover of species that prefer both forests and open habitats.

The light index (L_{EIV}) decreased along the age gradient, while the moisture index (F_{EIV}) increased (Table 4). The L_{EIV} correlated negatively with stand age ($R=-0.55$, $p=0.05$), while the F_{EIV} correlated positively ($R=0.64$, $p=0.05$).

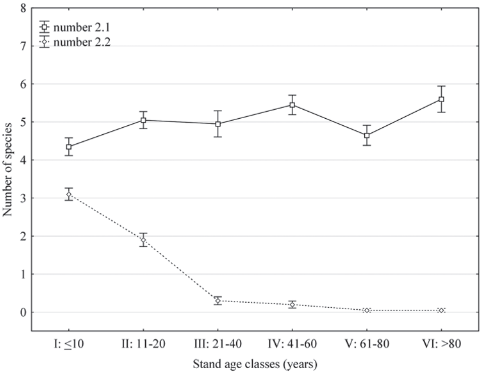

Fig. 7. Mean number (±standard error) of species that represent the category of forest species in stand age classes. See Table 1 for the category of forest species. Differences are statistically significant according to the Kruskal-Wallis test at $p=0.05$ between the stand age classes for one category of forest species: 2.2 I-II/III-VI.

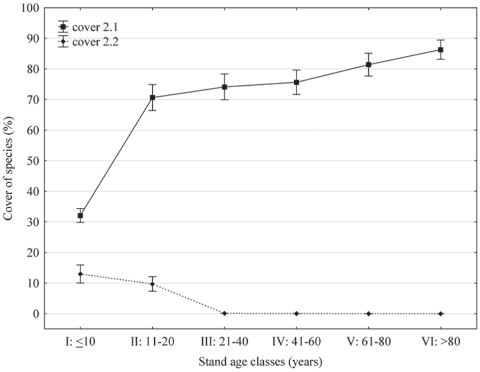

Fig. 8. Mean cover (±standard error) of species that represent the category of forest species in stand age classes. See Table 1 for the category of forest species. Differences are statistically significant according to the Kruskal-Wallis test at $p=0.05$ between the stand age classes for the two categories of forest species: 2.1 I/II-VI; 2.2 I-II/III-VI.

Table 4. Mean weighted ecological indicators for subsequent stand age classes. L_{EIV}: light index; F_{EIV}: moisture index; SD: standard deviation. Differences are statistically significant according to the Kruskal-Wallis test at $p=0.05$ between the stand age classes for light and moisture indices: L_{EIV} and F_{EIV} I-II/III-VI

	Stand age class (years)	*Mean*	*SD*
L_{EIV}	I: ≤10	6.5	0.19
	II: 11-20	6.1	0.30
	III: 21-40	5.7	0.18
	VI: 41-60	5.7	0.11
	V: 61-80	5.8	0.09
	VI: >80	5.7	0.12
F_{EIV}	I: ≤10	4.6	0.16
	II: 11-20	4.9	0.12
	III: 21-40	5.0	0.04
	VI: 41-60	5.0	0.03
	V: 61-80	5.0	0.03
	VI: >80	5.0	0.02

DISCUSSION

A high level of bryophyte species diversity is dependent on the availability of a variety of substrates and microhabitats (Rambo, 2001; Rambo & Muir, 1998; Mills & Macdonald, 2004, 2005; Evans *et al.*, 2012), which are abundant in natural forests (Vellak & Paal, 1999). In managed forests, "hot spots" of bryophyte diversity are located in specific habitats that occupy small areas (Vanderpoorten *et al.*, 2001). The forest type that was studied is situated on acid sandy soils with a few microhabitats, which is limiting for the species pool, and therefore the low species richness (22 species) should not be surprising. However, it was proved that numerous species of bryophytes have a chance of occurring on such sites during spontaneous succession, and that forest management is an additional constraint for the species diversity (Faliński *et al.*, 1993; Ross-Davis & Frego, 2002; Yan *et al.*, 2013). The plots that were studied were located in managed forests and the clear cuts were subject to succession, which was assisted by the silvicultural treatments, and therefore the total number of ground bryophyte species that were identified should be considered to be lower than in a spontaneous succession on poor and acid sites. However, there was a positive correlation between the number of bryophyte species and the number of all species in the community, which shows that these organisms make an important contribution to the species richness of managed Scots pine forests of acid sites.

The bryophyte layer in the old stands in the study area was dominated by competitive perennials that were growing in wefts. The dominant species that represented this life strategy and growth form in the area that was studied was *Pleurozium schreberi.* This species is characterised by efficient vegetative reproduction and rapid growth but only in favourable edaphic conditions and under a closed canopy (Uggla, 1959; Longton & Greene, 1979; During, 1990; Mäkipää & Heikkinen, 2003; Salemaa *et al.,* 2008; Frey & Kürschner, 2011), which makes it competitive in relation to species, particularly acrocarpous taxa (Jonsson & Esseen, 1990; Frego & Carleton, 1995; Palisaar & Poschlod, 2001). The other significant competitive perennial was *Dicranum polysetum*; however, because of its growth form (tuft), it was not as abundant as *Pleurozium schreberi*. Acrocarpous mosses are characterised by slow rates of length growth compared to pleurocarpous species (Glime, 2007), so that the latter are quantitatively dominant in the bryophyte layer (Heinken & Zippel, 2004). *Hylocomium splendens* is a qualitatively important competitive perennial. Its significant fidelity in the oldest stands could designate this species as an indicator of the late stages of succession in the habitats that were examined. In a broader gradient of temperate coniferous forests, it prefers more fertile and humid habitats (Caners *et al.* 2013; Stefańska-Krzaczek & Pech, 2014). In nutrient-poor forests, *Hylocomium splendens* finds favourable conditions only after the stabilisation of the forest microclimate and when soil moisture increases (Mäkipää & Heikkinen, 2003). In addition, this species does not regenerate from the diaspore bank as quickly as the other bryophytes that are present on the forest floor (Jonsson, 1993). Moreover, it does not have the ability to conduct photosynthesis in the difficult conditions of open area, like, e.g., *Pleurozium schreberi* (Mäkipää & Heikkinen, 2003). Apart from it, all of the species in the oldest stands were not "true" forest species, but were those that prefer both forests and open habitats (Preussing *et al.*, 2011). For example, *Ptilidium ciliare*, which occurred with the highest frequency and fidelity in the oldest stands, is a characteristic species of suboceanic heaths (Matuszkiewicz, 2001). The important role of such "not true" forest species on the forest floor of coniferous forests can be explained, firstly, by the specific conditions of Scots pine forests, where the transmittance of light is greater than in mixed or broadleaved forests (Lieffers *et al.*, 1999), especially in thinned stands (Widenfalk & Weslien, 2009). Secondly, the cyclical interruption of forest continuity by forest management results in the decline of specific moist and shadow forest microhabitats (Andersson & Hytteborn, 1991).

Clear cutting in managed forests counteracts the tendency of the reduction in species richness. The mechanical removal of dense moss patches in preparation of clear cuts for re-planting, combined with changes in the habitat conditions, provide an opportunity for other species to settle down (Åström *et al.,* 2005; Bergstedt *et al.*, 2008; Schmalholz & Hylander, 2009). The clearest evidence of this in the area that was studied was the increase in the number and cover of colonists and stress-tolerant perennials, which were mostly growing in turfs. Although this results in an increase in species richness, it is a short-term effect. The most characteristic species of the youngest stands were *Ceratodon purpureus, Pohlia nutans, Polytrichum juniperinum* and *P. piliferum.* These pioneer species tolerate strong sunlight, a high temperature of the substrate and very low humidity (Åström *et al.,* 2005; Stebel, 2006). They are species of the early successional stages in pine forests (Faliński *et al.*, 1993; Stefańska-Krzaczek, 2012, Staniaszek-Kik & Woziwoda, 2011), which act as soil stabilisers (Newmaster & Bell, 2002). However, in general, they are not "true" open area species. They are classified as species that may occur in forest communities despite their preference for open habitats (Preussing *et al.*, 2011). The immense number of spores that are produced by colonists favours the rapid occupation of re-exposed areas (During, 1979; Glime, 2013). In addition, the diaspores of early successional species are deposited in the soil bank (Jonsson, 1993; Caners *et al.*, 2009). A short time of population development is important, because the duration of the non-forest conditions on clear cuts is limited by the rates of pine growth and canopy closure.

Despite the drastic changes in microclimate conditions, the dominant species in the matured stands, i.e. *Pleurozium schreberi* and *Dicranum polysetum*, also occurred in the youngest stands, which is not surprising in the context of our result because these species are not "true" forest species. Nevertheless, the biological features of these species contribute to their occurrence. The fragmentation of moss patches during ploughing and mixing with the top layer of the soil creates a significant amount of diaspores in shoot fragments from which new individuals can develop (Longton & Greene, 1979, Heinken & Zippel, 2004). In addition, both species quickly regain the ability of photosynthesis after a dry period and retain it even under low soil moisture conditions (Mäkipää & Heikkinen, 2003). This allows the dominants of the oldest stands to already be present in open-canopy stands, although with a low cover.

As a result of the effective occupation by early successional species and the capability for rapid regeneration of species in the oldest stands, young stands have the highest bryophyte species richness before crown closure, but objectively it is not high (an average of eight species per plot). Clear-cut logging, however, on a relatively large area provides a chance for a species population with different life strategies than the bryophytes that are typical for the forest floor of the oldest stands to occur. It also increases the spatial diversity by generating the formation of different plant patches.

Most of the light-demanding species that are specific for open-canopy stands are still present in the young stands of 11-20 years, but their quantitative importance is significantly reduced in favour of competitive perennials with the growth of pines. Therefore, the period of increased species diversity is limited due to the short time of the exposure to a non-forest microclimate during the open-canopy stage. The study showed that species in the oldest stands that had already recovered were not adversely affected by canopy closure, which confirmed the results of a study on bryophyte succession in spruce stands (Schmalholz & Hylander, 2009). The cover of bryophytes in dense young stands is significantly higher than in open-canopy stands, thus the canopy closure is not the bottleneck for the bryophyte layer (Økland *et al.*, 2003). With the return of the forest microclimate, competitive perennials begin to extensively spread wefts on the forest floor and their ability to develop many new shoots allows them to quickly take control of the available areas (Frego, 1996; Longton & Greene, 1979). This limits the early successional species, because they are overgrown by perennials (Heinken & Zippel, 2004). As a result, young stands of 21-40 years resemble the oldest stands in terms of the bryophyte layer. Therefore, the assumption that early successional species will persist even after the formation of the stand canopy due to intensive thinnings proved to be wrong. This means that the forest floor vegetation, including the bryophyte layer, was formed relatively quickly in the stands that were examined (in about 20 years), which was also found for pine stands on former farmlands (Rūsiņa *et al.*, 2011).

Because of the improvement of light conditions after thinnings as well as the presence of fine wood pieces on the forest floor, we were expecting a higher species diversity in the middle-aged stands. However, no increase in diversity was observed. However, two species were identified in the 21-40 year stands, which may indicate the possibility of also increasing the species diversity of bryophytes in middle-aged stands. The species *Pseudoscleropodium purum* and *Lophocolea heterophylla* are indicators of more fertile coniferous forest habitats than those that were studied in this work (Stefańska-Krzaczek & Pech, 2014). *Pseudoscleropodium purum* is a species that is sensitive to the nutrient pulse (Bates, 1994), while *Lophocolea heterophylla* is an epixylic specialist with a wide substrate tolerance (Andersson & Hytteborn 1991; Ódor & van Hees, 2004). Moreover, *Lophocolea heterophylla* is classified as a species of closed forests ("true" forest species). Habitat enrichment in the organic matter that is derived from the decomposition of fine woody debris provides a chance for more nutrient-demanding species, which is important for the richness of managed forests (Kruys & Jonsson, 1999; Ódor & Standovár, 2001; Shields *et al.* 2007). Fine woody debris in middle-aged stands provides a substitution of the microhabitats that are typical of natural forests and that are crucial for biodiversity (Kruys & Jonsson, 1999; Vellak & Paal, 1999).

CONCLUSIONS

Clear-cut logging contributes to an increase in the species richness of the ground bryophyte layer. Early successional species (colonists and stress-tolerant perennials) which are in fact not "true" open-habitat species, survive in the community only during the open-canopy stage. Late successional species (competitive perennials) which are also not "true" forest species, mostly regenerate quickly and are dominant in the bryophyte layer after canopy closure. The increase of bryophyte richness can, however, be considered only in relation to the species diversity of the oldest managed forests and cannot be compared with natural forests. All of the stand age classes contribute to the alpha and beta diversity of managed Scots pine forests.

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