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Stand Structure Beats Age for Ground Cover Vegetation in Ageing Hemiboreal Scots Pine and Norway Spruce Stands

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Abstract: Intensifying forest management and a reduction in the rotation period necessitates the development of intensive biodiversity conservation strategies, such as the triad concept, which aims at ensuring habitat connectivity. Such an approach depends on the relationships between biodiversity components and manageable stand characteristics. Mostly, the biological value of stands has been associated with age, although stand structures, which are often intercorrelated with age, might be of primary importance. The relationships between ground cover vegetation, which is a principal component and indicator of the biological value of temperate conifer forests, and stand characteristics were assessed in pre-harvesting/harvesting age and old-growth coniferous stands in the eastern Baltic region (Latvia). The old-growth stands were nearly two times older than the pre-harvesting/harvesting age stands. Both stand groups showed generally similar ground cover flora, though ground cover vegetation showed higher variability in the old-growth stands. The principal gradients of ground cover vegetation were related to light, site fertility, and structural diversity, as well as the degree of deciduous (particularly *Betula* spp.) admixture in a tree stand. Considering the explicit contrasts, stand age did not affect ground cover vegetation, implying the principal effects of stand structure, which are manageable characteristics. This implies the potential for specific management to aid the ecological connectivity of stands in commercial forest landscapes.

Keywords: ground flora; stand age; indicators; stand structures; species richness

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1. Introduction

The increasing demand for timber necessitates the intensification of forest management [1,2]. In Northern Europe and the Eastern Baltic region, the application of intensive forest management is increasing the productivity of stands [3], thus allowing a reduction of rotation period, which is crucial for meeting the demand and economic performance [4,5]. The strong relationship between forest age and the vulnerability to disturbances [6], particularly for the non-climatic climax species [7], supports the shortening of the rotation period to reduce economic risk [8]. This also agrees with the green course and climate goals, as the maximum biomass production (and hence carbon sequestration) appears to be reached at substantially earlier stages than the OG stage and is independent of the degree of management [9].

The shortening of the rotation period could affect forest ecosystem services with effects on biodiversity, and hence ecosystem stability is mostly considered negative or neutral [6,10]. Such effects have been related to the dynamics, composition, and structure of the stands, the persistence of which has been related to the abundance and diversity of forest-dwelling species [11]. Under such conditions, practices actively stimulating biological diversity and connectivity appear necessary to maintain a wider spectrum of ecosystem services and the stability of the intensively managed forest landscape [12,13]. The triad zoning, incorporating a network of reserves and areas, which are managed extensively according to the sharing-sparing and near-natural principles, into the intensively managed forest landscape has been suggested [14,15]. Still, due to complexity, there is still uncertainty about the optimal solutions for such an approach [16,17]. Hence, local information on the efficiency of the extensively managed stands/areas for maintaining ecological networks and biodiversity is crucial for sustaining the multifunctionality of intensively managed forests under the triad concept [15,18,19].

In the highly managed European landscape, the old-growth (OG) forests are considered among the ecosystems most valuable for biodiversity, which contrast with the simplified composition and structure of commercial stands [20]. Regarding the OG forests, it has been presumed that their biodiversity value is a primary result of age and, hence, is a specific (late) stage of succession, as hinted by bryophytes and mycorrhizae [21–23]. However, the richness of vascular ground cover vegetation and, subsequently, the species related to it favours (increases after) disturbances, implying a relation to specific stand structures/openings and the local rejuvenation of the tree stand [24,25]. After a clear-cut in coniferous stands in the hemiboreal zone, vegetation can become similar to that in OG stands by the age of 70 years (corresponding to harvesting or pre-harvesting age and mid-successional stage) as the tree stand diversifies and canopy openings appear [11,14,26,27]. Thus, stand age alone cannot not be considered the sole predictor of the biodiversity value of a stand, and a complex assessment of composition and structures, as well as history, which have primary effects, is needed [26,28,29]. However, age is often correlated with the crucial structural characteristics and composition of stands, implying their sufficiency for screening [30].

The composition and structural diversity of canopy trees, hence the vertical structure and openings of the canopy [31,32] along with the deadwood of different decay stages [33,34] and veteran trees bearing various microhabitats [35,36] have been identified as the principal determinants of the biological value of a stand. The explicit positive effect of such structures has been observed on ground cover, bird, and ground-dwelling communities [28]. The main differences between the intensively managed and the conservancy OG forests can be largely attributed to the characteristics of canopy trees [25,37,38], which are manageable by close-to-natural regeneration and selective cutting [14]. Regarding the triad approach, this highlights the high potential to increase the functionality of extensively managed areas, even at a relatively young (maturing) age [15,28]. The local disentanglement of the effects of stand characteristics is necessary [17]. The ground cover vegetation is closely related to the forest development stages [26], playing a vital role as a habitat and food for faunal communities [39,40], nutrient cycling [41], stand productivity [42], and in forest regeneration and succession [43,44]. Furthermore, ground cover vegetation is directly affected both by natural disturbances and management; therefore, its inventory is widely used for the assessment of biodiversity [28,45].

In the Eastern Baltic region and Latvia in particular, the projected changes in tree distribution largely concern the economically important Scots pine *Pinus sylvestris* and Norway spruce *Picea abies* [46,47]. These species are anticipated to decrease in abundance [48] due to intensifying disturbances [49–52]. Nevertheless, a network of OG pine and spruce forests still persists in Latvia, aiding the multifunctionality of the forest [53,54], yet its connectivity might be affected by the decreasing age of managed commercial stands, and hence specific management appears necessary to sustain it.

The aim of this study was to compare ground cover vegetation between OG and the pre-harvesting/harvesting age (PHH) stands of Scots pine and Norway spruce stands in Latvia and to assess the main stand characteristics affecting the diversity of ground cover vegetation. We hypothesised that the canopy tree dimension and stand density were the primary determinants of ground cover vegetation, with the stand age having a secondary effect.

2. Materials and Methods

2.1. Study Area and Stand Selection

The relationships between dimensions and the structure of tree stands and ground cover vegetation were studied in 27 OG and 47 PHH forest patches dominated by Scots pine and Norway spruce dispersed across the territory of Latvia (55°40′–58°05′ N, 20°58′–28°14′ E; Figure 1). This study region represented the hemiboreal forest zone, where coniferous and broadleaved trees are mixed both at the stand as well as the landscape level [55]. According to the national forest inventory, forests cover 53% of the territory of Latvia, among which 26 and 19% of stands are dominated by Scots pine and Norway spruce, respectively. The study region represents lowland conditions (<250 m a.s.l.) with a generally flat topography. Postglacial mesotrophic mineral podzolic soils (sandy and silty) are the most common edaphic conditions of the forest lands (40% of the area). The climatic conditions can be described as moist continental [56], though with explicit coastal features due to the dominant westerlies bringing air masses from the Baltic Sea and Northern Atlantic. The mean annual temperature was +6.5 °C, with February being the coldest and July the warmest month, respectively (with the mean monthly temperature of −3.1 and 17.8 °C, respectively). The mean annual precipitation was 686 mm, and the highest monthly precipitation fell during the vegetation period (May–September; ca. 75 mm/month). Climatic changes were expressed as warming, particularly during the dormant period, which has been extending the vegetation period, as well as increasing the variability of the thermal and precipitation regime in summer, with warmer dry periods tending to extend [57].

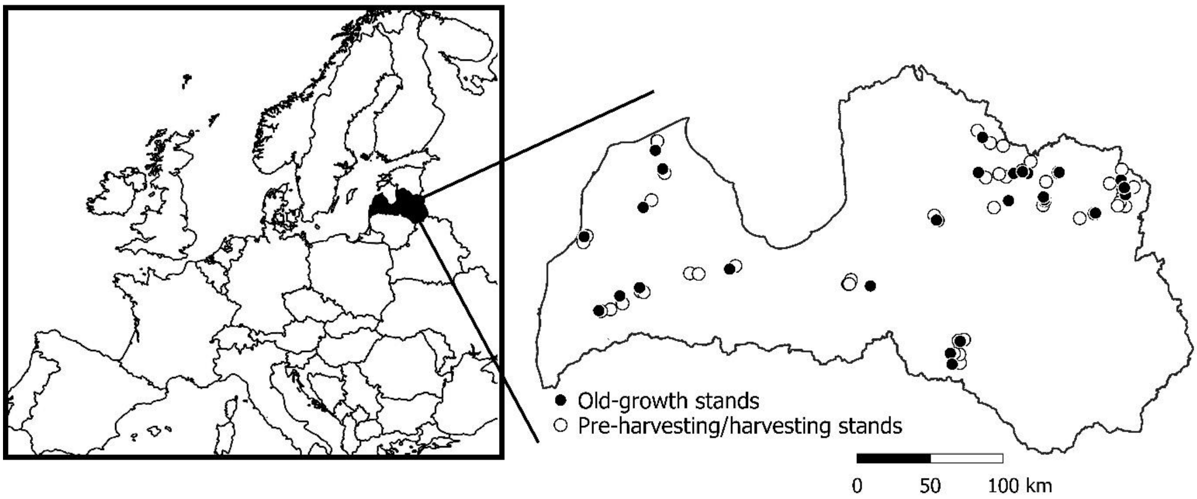

Figure 1. Location of the studied sample plots.

A stratified selection of the OG stands was based on the national forest inventory database. Stands dominated by conifers were selected according to the criteria of the age of dominant cohort >160 years, area of >0.5 ha, distance from villages (or larger settlements) and roads of >5 and 1 km, respectively, and no recent record of management (e.g., thinning). The selection was also made to represent the regional distribution of the forest. The pre-selected stands were visited to check their actual compliance with the criteria, and increment cores were taken to verify age. In case of signs of recent (younger than 40–50 years) management (stumps, sawn surfaces of logs, etc.), stands were not investigated. For comparison, one or two adjacent conventionally managed (undergone thinning) PHH stands (80–110 years for pine and 60–90 years for spruce according to the regional specifics of commercial management) with similar composition and edaphic conditions were selected from the inventory. The verified age of the selected OG and PHH stands ranged 164–219 and 69–96 years, with a mean value of 184 and 79 years, respectively. Hence, the stands explicitly differed by age.

2.2. Measurements and Census

In each stand, depending on size, four to eight circular plots with an area of 500 m^2 were established (Figure 2); in total, 109 and 188 plots were set in the OG and PHH age stands, respectively (Figure 3). Within each plot, the dimensions and positions of all trees (living and dead) with a diameter at breast height (DBH) exceeding 6 cm were recorded. To account undergrowth and advanced growth, in a 90° segment of a 100 m^2 subplot (with a common centre), the dimensions of all trees with DBH of 2.1–6.0 cm were measured. The measurements were performed in February and March 2020. For the lying deadwood thicker than 6 cm, the length and diameter at the thin and thick ends within the sample plot were measured, as well as the decay stage, which was recorded according to [58].

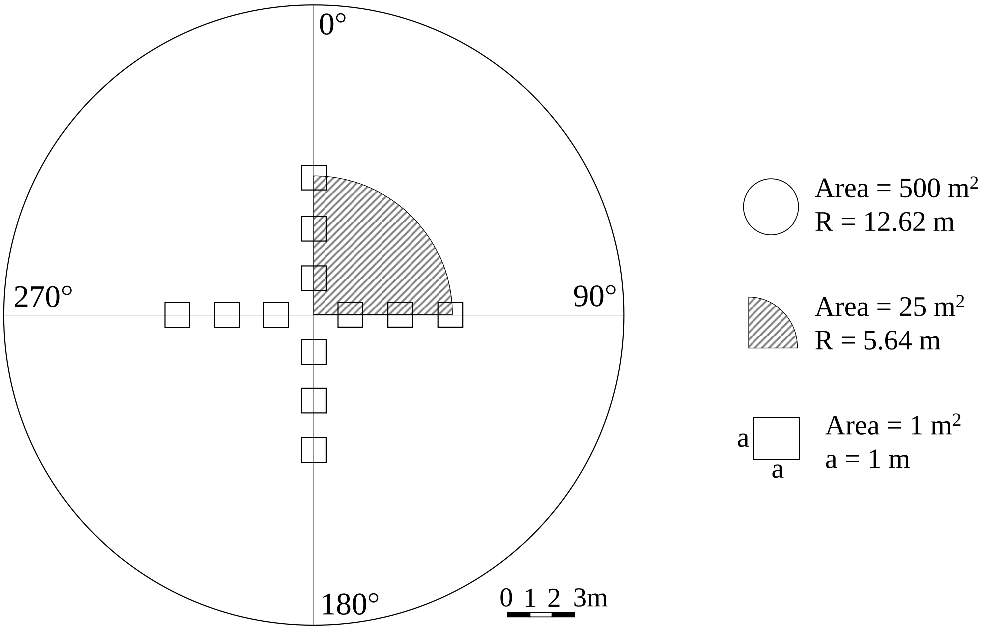

Figure 2. The scheme of a sample plot, sector of subplot and grid plots used for census of the vegetation in the studied OG and PHH stands dominated by Scots pine and Norway spruce.

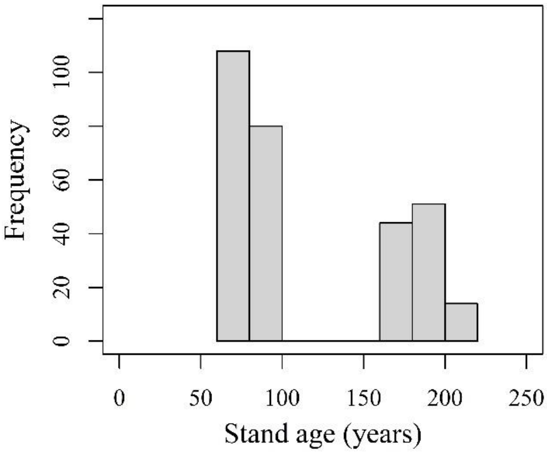

Figure 3. Frequency of the established sample plots according to stand age.

Vegetation was surveyed in June and July 2021. The relative projective cover of ground cover vegetation in each plot was recorded according to a grid of 12 grid plots of 1 × 1 m arranged regularly according to the four cardinal directions with the spacing of one m around the common centre (Figure 2). The cover of individual species was recorded for the herbaceous vascular plant, the woody plant (at the herbaceous layer) and the bryophyte layers. Thus, the total projective cover of plots was allowed to exceed 100%, yet such a restriction was applied to each of the ground cover vegetation layers. The projective cover of wood debris and bare soil was also recorded.

2.3. Statistical Analysis

For the description of the tree stand in each plot, density, basal area, and standing stock (according to a local equation [59]) of the canopy, as well as the undergrowth trees, was calculated. The volume of standing deadwood was calculated according to the national equation [59], yet the volume of lying deadwood was calculated as for a truncated cone. The diversity of DBH and tree height (H) in each plot was characterised by the interquartile difference (iqrD and iqrH, respectively). For the description of stand composition, the proportion of coniferous and deciduous species in the canopy, the proportions of each canopy species (according to their number), mean DBH, H, the basal area of the canopy and understory trees (canopy strata) by species and taxonomic groups were also calculated.

The mean projective cover of species of the 12 grid plots was calculated to describe the ground cover vegetation of the plots. Species richness, occurrence (% of plots with a species), total cover, and Shannon–Wiener index (H′) were calculated to describe the diversity of ground cover vegetation in each plot. A simple t-test was used to compare these metrics between the age groups. Ellenberg's indirect environmental indicator values/indices (ordinal scale) for vascular plants and Düll's values for bryophytes (i.e., nutrients/nitrogen, light, reaction, temperature, continentality, and moisture) [60] were reciprocally estimated as the proxies of the site conditions of the plots. Such estimates are sufficient to substitute the resource-demanding direct environmental measurements [60]. The nonparametric ANOSIM (analysis of similarity), which is a randomization method used for the evaluation of similarity of multidimensional vegetation data within and among groups of observation, was used to compare the ground cover vegetation (and its components) of the plots between the OG and PHH stands using the "anosim" function and Bray's distance [61]; 5000 permutations were performed. The ground cover vegetation matrix of the plots was used as the response, and the age group was used for contrast (grouping variable).

The detrended correspondence analysis (DCA, detrending with 26 segments and downweighing rare species) based on the relative cover of species in the plots [62] was used to assess the main ecological gradients and communities of ground cover vegetation in the studied stands. To assess the relationships of the two main ecological gradients of ground cover vegetation with the tree stand and site conditions (represented by Ellenberg's indicator values), correlations between DCA axes and the matrix of the stand characteristics (containing 70 variables in total, among which 50 were differential characteristics of a tree stand, e.g., iqrD, iqrH, mean DBH, H, basal area of trees of different canopy strata and species, etc.) were estimated.

The sets of the environmental and stand characteristics showing the strongest relationships with the DCA scores of the first two gradients of the plots were distinguished using a linear mixed multiple regression analysis. Stand and site characteristics showing correlations with DCA axes were tested as the sets of predictors, and an arbitrary selection principle (considering ecological meaning) was used to select the best-fitting set of the effects. As multiple plots per stand were established, the stand was included in the models as a random intercept term. Predictors were checked for collinearity using the variance inflation factor, and model residuals were checked for compliance with the assumptions using diagnostic plots. Data analysis was conducted in R v. 4.2.2 [63] using the packages "lme4" [64] and "vegan" [61].

3. Results

The studied PHH and OG stands had a similar standing volume (mean ± standard error of 413.1 ± 8.7 and 429.1 ± 17.9 m^3 ha^{-1}, respectively), though they had a wider range in the second (91.1–932.1 and 82.8–1233.9, respectively). However, the PHH stands were two times denser than the OG stands, with a mean density of canopy trees of 502.9 ± 11.8 and 261.1 ± 9.7 trees ha^{-1}, ranging 120–1040 and 60 to 820 trees ha^{-1}, respectively. The amount of deadwood was two times higher in the OG than in the PHH age stands (43.9 ± 4.2 and 24.9 ± 2.1 m^3 ha^{-1}, respectively), and approximately half of it was lying.

The PHH stands (canopy and undergrowth) were composed of 14 trees species; their canopies were dominated by spruce (ca. 369 trees ha^{-1}) and pine (ca. 146 trees ha^{-1}) with an admixture of silver birch *Betula pendula* Roth. (ca. 73 trees ha^{-1}) and common aspen *Populus tremula* L. (ca. 35 trees ha^{-1}). The OG stands were more diverse with 20 tree species; their canopies were co-dominated by spruce (ca. 167 trees ha^{-1}) and pine (ca. 96 trees ha^{-1}) with an admixture of silver birch (ca. 29 trees ha^{-1}), wych Elm *Ulmus glabra* Huds. (ca. 23 trees ha^{-1}), common aspen (ca. 17 trees ha^{-1}) and black alder *Alnus glutinosa* (L.) Gaertn. (ca. 12 trees ha^{-1}). Accordingly, the admixture of deciduous canopy trees was higher in the OG compared to the PHH stands (24 vs. 12%, respectively). The stands of both age groups had an explicit understory (secondary canopy layer), which was formed by conifers and deciduous species, among which Norway spruce was the most common (21.4% and 24.9% of understory trees in the PHH and OG stands, respectively). The undergrowth in the PHH stands was dominated by hazel (46%, ca. 125 axes ha^{-1}), but in the OG stands by hazel (34%, ca. 350 axes ha^{-1}) and spruce (17%, ca. 176 trees ha^{-1}).

The ground cover vegetation richness of the studied stands was generally intermediate. In total, 175 ground cover species were surveyed, among which 118, 28, and 29 were vascular herbaceous plants, woody plants, and bryophytes, respectively. The age of the stand had an effect on ground cover species richness. The total ground cover vegetation species richness, as well as the richness of vascular plants and bryophytes, was higher in the PHH age than in the OG stands (total richness 21.1 ± 2.4 and 19.1 ± 2.7 species per plot, p-value = 0.03; Table 1). Irrespectively of the age group, the evenness of ground cover species distribution was similar, as indicated by the lack of differences in the Shannon diversity index (p-value > 0.13), which was intermediate (H′ = 2.40), and hence, indicated a lack of dominance.

Table 1. General description of ground cover vegetation in the studied coniferous stands of pre-harvesting/harvesting (PHH) and old-growth (OG) age in the hemiboreal forest zone, Latvia. SE—standard error.

		Ground Flora		Vascular		Woody		Bryophyte	
		Mean	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**
Number of species	PHH	21.13	2.35	11.63	1.63	3.07	0.47	6.42	0.66
	OG	19.08	2.68	10.67	1.78	2.71	0.67	5.71	0.96
Relative projective cover (%)	PHH	112.03	4.34	43.48	5.53	3.77	1.19	64.78	6.28
	OG	103.19	6.06	42.57	7.08	2.61	1.19	58.01	9.90
Shannon-Wiener index	PHH	2.45	0.14	1.89	0.17	1.25	0.11	0.48	0.13
	OG	2.37	0.16	1.83	0.19	1.1	0.16	0.44	0.17

The studied stands were rich in litter, which covered approximately one-third of the sample plot area (30.2 ± 1.2%). Bare soil was estimated with a mean relative cover of 7.9 ± 0.7% of the grid plots, irrespective of the age group, indicating a similar level of disturbance. The total projective cover of ground cover vegetation exceeded 100% in both age groups indicating an overlap of the layers, among which bryophytes were the most abundant, particularly in the PHH stands. Herbaceous vascular plants were slightly less abundant, while woody plants (including seedlings of trees) were scarce.

The composition of ground cover vegetation in the studied stands was significantly similar, as the differences between the age groups estimated by ANOSIM were negligible (R = 0.08; p-value < 0.001). The composition of bryophytes and vascular plants showed an even higher similarity (for both, R = 0.007, p-value < 0.001), indicating that the stable equilibrium of ground cover vegetation had been reached. Generalist species, e.g., *Vaccinium myrtillus*, *Oxalis acetosella*, *Luzula pilosa*, *Calamagrostis arundinacea*, *Hylocomium splendens*, *Pleurozium schreberi* were the most common in the ground cover vegetation of the studied stands (Table 2). Nevertheless, there was a higher richness of the rare vascular species (e.g., *Campanula persicifolia*, *Lathraea squamaria*) in the PHH age stands.

Table 2. Occurrence (% of plots) and mean projective cover (% of area) of most common species in the pre-harvesting/harvesting age and old-growth stands (plots).

Pre-Harvesting/Harvesting Age Stands			Old-Growth Stands		
Species	**Cover**	**Occurrence**	**Species**	**Cover**	**Occurrence**
Vaccinium myrtillus	18.27	89.36	*Vaccinium myrtillus*	14.30	79.82
Oxalis acetosella	9.55	78.19	*Oxalis acetosella*	12.63	80.73
Calamagrostis arundinacea	9.54	76.60	*Calamagrostis arundinacea*	4.38	54.13
Maianthemum bifolium	2.42	79.26	*Maianthemum bifolium*	3.36	81.65
Pteridium aquilinum	2.35	28.19	*Luzula pilosa*	2.77	77.98
Luzula pilosa	2.03	70.21	*Vaccinium vitis-idaea*	2.58	50.46
Vaccinium vitis-idaea	2.02	41.49	*Pteridium aquilinum*	2.07	20.18
Carex digitata	1.79	46.81	*Athyrium filix-femina*	1.83	21.10
Melampyrum pratense	1.75	37.23	*Trientalis europaea*	1.66	57.80
Trientalis europaea	1.68	67.02	*Melampyrum pratense*	1.61	31.19
Rubus saxatilis	1.59	32.45	*Rubus saxatilis*	1.70	26.61
Dryopteris carthusiana	1.45	43.09	*Dryopteris carthusiana*	1.57	37.61
Festuca ovina	1.25	13.30	*Carex digitata*	1.56	42.20

Based on the projective cover of ground cover vegetation, two continuous principal gradients were estimated by the DCA (Figure 3A,B). The ordination of the stands (plots) showed that the age groups completely overlapped, though the OG stands showed a somewhat wider range of scores of the first two gradients, indicating higher diversity of local conditions. The primary gradient represented by the first axis of DCA was apparently related to light conditions, as indicated by its correlation with Ellenberg's indicator values. Light (L, Figure 3B) was also positively intercorrelated with continentality, temperature, humidity, and reaction (acidity) while being negatively related to the diversity of vascular ground cover vegetation, indicating collinear effects of environmental factors. Among the tested characteristics of the tree stand, the proportion of conifers correlated with the first gradient, relating conifers with increased light transmission. Among the correlated variables, light, reaction, moisture, the proportion of conifers, and *Betula* sp. in the canopy were estimated by multiple regression to have consistent non-collinear relationships with the primary gradient (Table 3). The effects of the share of the main conifer species in the canopy (Scots pine and Norway spruce), however, differed, as indicated by contrasting correlations with the gradients (Figure 3B).

Table 3. The relationships between the first two gradients of ground cover vegetation in the studied coniferous stands of pre-harvesting/harvesting and old-growth age and stand/site characteristics.

	DCA1	
	Fixed effects	
	χ^2	*p*-value
Light	357.7	<0.001
Reaction	120.0	<0.001
Moisture	15.6	<0.001
Canopy coniferous, %	74.6	<0.001
Understory stock	5.0	0.02
Density of *Betula* in canopy	13.0	<0.001
	Model performance	
R^2, marginal	0.77	
R^2, conditional	0.88	

Table 3. *Cont.*

DCA2		
	Fixed effects	
	χ^2	*p*-value
Nitrogen	36.4	<0.001
Total standing stock	6.8	0.009
	Model performance	
R^2, marginal	0.13	
R^2, conditional	0.70	

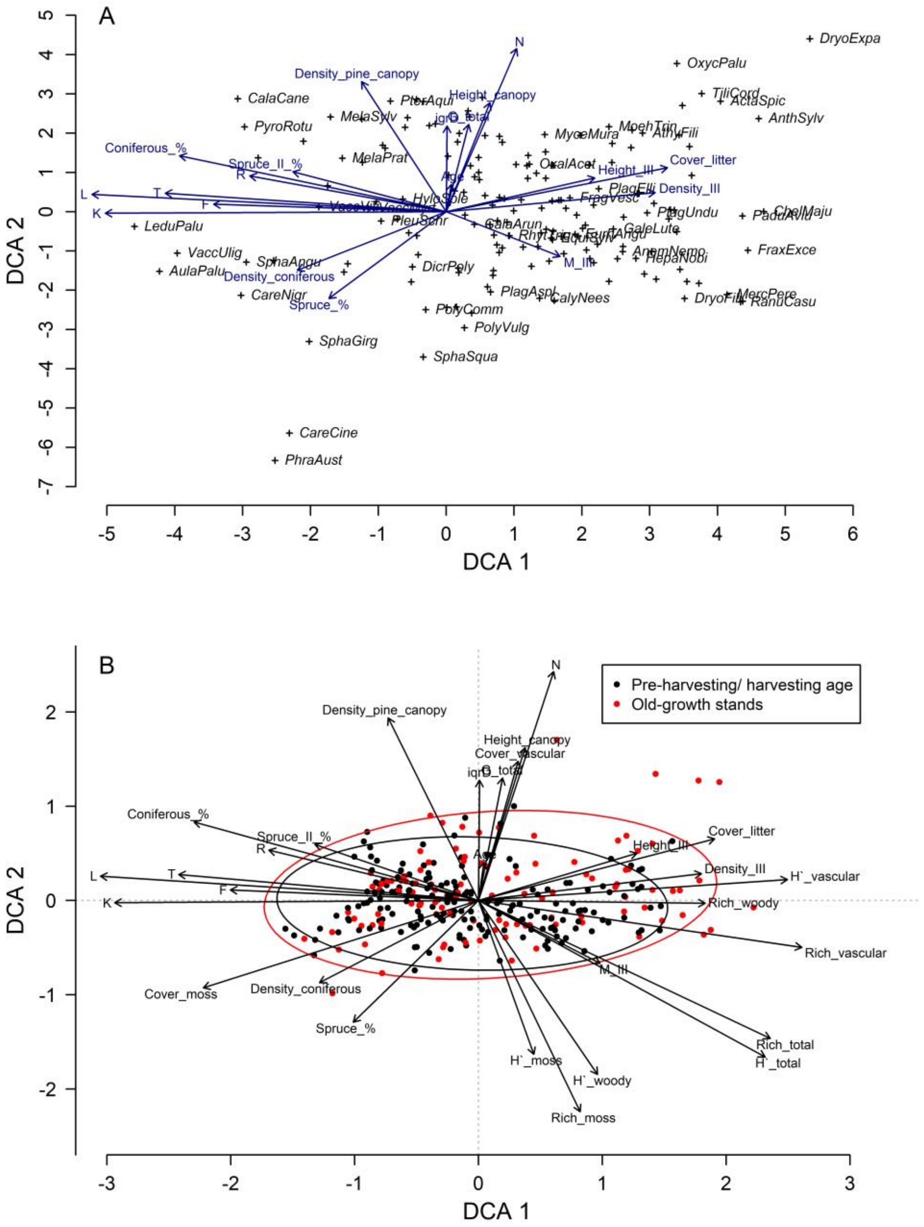

Figure 4. DCA ordination of ground cover vegetation species (**A**) and sample plots (**B**) according to their projective (relative) cover in the coniferous stands of pre-harvesting/harvesting and old-growth age. Species acronyms (eight letters) were used according to [65]. Abbreviations of vector names: L—light, T—temperature, K—continentality, F—moisture, R—reaction, N—nitrogen, H′_total—Shannon–Wiener diversity index of all species, H′_vascular—Shannon–Wiener diversity index of

vascular species, H′_woody—Shannon–Wiener diversity index of woody species, H′_moss—Shannon–Wiener diversity index of bryophytes, Rich_total—richness of all species, Rich_vascular—richness of vascular species, Rich_woody—richness of woody species, Rich_moss—richness of bryophytes, Cover_litter—cover of litter layer, Cover_vascular—cover of vascular layer, Cover_moss—cover of bryophyte layer, Height_canopy—canopy height, Height_III—understory height, Density_coniferous—density of coniferous in canopy, Density_III—understory density, M_III—understory stock, G_total—total basal area, iqrD—interquartile range of canopy tree diameter, Coniferous_%—proportion of coniferous in canopy, Spruce_%—proportion of spruce in canopy, Spruce_II_%—proportion of spruce in second canopy layer, Density_pine_canopy—density of canopy pine, Age—stand age. Note that scales differ between the panels.

The complexity of the effects of the environmental variables related to the first gradient was also supported by species ordinations (Figure 3A). Species favouring open conditions, such as *Ledum palustre*, *Vaccinium uliginosum*, and *Aulacomnium palustris,* were associated with the high light part of the gradient, while the species favouring oligotrophic/mesotrophic semi-open conditions, e.g., *Vaccinium myrtillus*, *Vaccinium vitis-idaea*, *Pleurozium schreberi*, and *Hylocomium splendens* were related to the mid-part of the first gradient. However, the high light conditions were generally related to a narrow and specific set of ground cover species, as indicated by the correlation with vascular species richness and evenness (Figure 3B). In contrast, the low light part of the gradient, which coincided with sites that had a higher admixture of deciduous trees, was associated with shade-tolerant forest species, e.g., *Athyrium* sp., *Oxalis acetosella*, *Hepatica nobilis*, and *Actea spicata*, as well as the presence of seedlings of *Tilia cordata* and *Fraxinus excelsior* (Figure 3A). This part of the gradient was associated with most of the accounted ground cover species; hence, vegetation was more diverse (higher richness and H′), even though the share of litter was the highest.

The second gradient of the ground cover vegetation of the studied stands was continuous, yet shorter than the first (Figure 3B). Still, a small group of three plots with increased score values representing fern-rich sites was distinguished (Figure 3A,B). The gradient was apparently related to fertility, as implied by its correlations with nitrogen value (N, Figure 3A), tree height, and standing volume, as well as the variability in tree dimensions (interquartile range, qD, Figure 3A,B). Accordingly, the gradient correlated with the abundance of vascular (positively) and bryophyte (negatively) ground cover species and richness (Figure 3B) were associated with the fertile and nutrient-poor parts of the gradient, respectively (Figure 3A). The strongest correlation with the second gradient was estimated for *Mycelis muralis*, *Athyrium filix-femina* and *Oxalis acetosella*. Among the stand characteristics, nitrogen value and the total standing stock had non-colinear relationships with the second gradient; however, these effects were affected by the stand (random effect), as indicated by the explicit differences between the conditional and marginal R^2 values (Table 3). Additionally, species associated with low scores of the second gradient were hygrophytes, e.g., *Phragmites australis*, *Carex cinerea*, as well as *Sphagnum* sp., thus suggesting relationships to moisture, particularly soil waterlogging. Stand age, which was considered as a principal driver, had a negligible relation with the main estimated gradients despite the explicit differences among the stand groups, thus indicating the stand structure to have a primary effect on ground cover vegetation.

4. Discussion

The ground flora in stands of both age groups was generally typical for a mesotrophic hemiboreal forest on freely draining mineral soils within the region [66,67]. The estimated continuous gradients (Figure 3A) indicated that conditions essential for ground cover vegetation have equalized in stands older than 70 years [26], though the diversification of local conditions occurred. The most common vascular and bryophyte ground cover species were *Vaccinium myrtillus, Hylocomium splendens,* and *Pleurozium schreberi* (Table 2), indicating the late successional stage of development while implying stand history without intensive disturbances [68–70]. The abundance of these species could be explained by explicit competitiveness [71], particularly under the oligotrophic and acidic conditions caused by conifer litter decomposition [72,73]. Under more shaded conditions under spruce and caused by deciduous trees, *Oxalis acetosella*, which is also an indicator of the late successional stage [74], was common (Table 2), supporting the stable equilibrium of ground cover vegetation. The estimated minor dissimilarities in the composition of the ground cover vegetation of the age groups could likely be attributed to the outlying OG plots (Figure 3A), which was likely due to micro-site conditions (e.g., more fertile depression with discharge) favouring ferns *Athyrium* sp. [75]. However, the highest species richness (especially of vascular plants) in the PHH stands could be explained by the specific stand development stage, when species (particularly herbaceous) favouring large-scale disturbance still remained [24,26]. Furthermore, similar ground cover diversity (H′) supported the fact that the equilibrium of ground cover vegetation [71] had already been reached by the PHH.

Despite the differences in age of the studied stands, the light conditions, fertility and structural diversity of tree stand, which determine the microclimate [76], were the main drivers of ground cover vegetation, as explicitly indicated by the sample plot and species ordination (Figure 3A,B). Light, though, was intercorrelated with temperature, humidity, and continentality indices (Figure 3B), stressing the role of the canopy layer structure on microclimate [32]. Although light availability has been positively related to ground cover species richness in deciduous forests [31,77], the opposite was observed (Figure 3B), suggesting contrasting relationships in coniferous stands. Such differences might be partially related to the higher occurrence of feather mosses and dwarf shrubs, which outcompete other ground cover vegetation lifeforms when conditions stabilize in oligotrophic/mesotrophic stands [71]. Hence, lower light conditions in the stands with a higher admixture of deciduous trees in the canopy were related to higher ground cover richness (Figure 3B), linking the diversity of the tree stand and ground cover vegetation [31,78].

The litter of deciduous trees is less acidic compared to that of conifers [79], thus providing more favourable (fertile) conditions for a higher number of vascular ground cover species due to nutrient availability [80]. Deciduous litter also affects the humidity and thermal regime of the top-soil layers, thus facilitating the development of vascular species [81,82]. This highlights the positive effects of deciduous admixture (Figure 3B), particularly birch (Table 3), in coniferous stands [79,83]. Alternatively, the relationships between light conditions and ground cover vegetation might be related to the occurrence of the stands in the hemiboreal zone, where interactions between boreal and nemoral species can be specific [27].

The second estimated gradient for ground cover vegetation (DCA2; Figure 3A,B) was related to fertility, as indicated by the relationships with the nitrogen value and total standing volume (Table 3). This showed edaphic conditions to have a secondary role under the canopies of the tree stand, where the light was strictly limiting [31,77]. The second gradient was also clearly correlated with the characteristics of the tree stand, such as the H and DBH distribution of trees (Figure 3B), prioritizing the effects of the stand structure, which are manageable, over the stand age [84], even though these characteristics are usually intercorrelated [30]. However, standing and laying deadwood, which is considered as one of the main factors promoting biodiversity [33,34], did not show relationships with ground cover vegetation (Figure 3A,B), albeit OG stands showing comparable amounts to nature reserves (mean 32.9 m^3 ha^{-1}, [85]). This also suggested comparable effects of deadwood in PHH and OG stands. Still, deadwood is of primary importance for the invertebrate and epixylic communities [86,87], which were not surveyed.

The main stand characteristic of interest in this study, stand age, appeared secondary to the composition and structure of PHH and OG coniferous stands in the hemiboreal zone, contradicting the assumption of stand age as the key characteristic for the most researched part of the biodiversity—forest ground vegetation [28,29]. Hence, stand structures (canopy composition, cover and species proportion, standing volume of the canopy, understory density and height), which are generally manageable [88], were estimated as the primary drivers of ground cover vegetation. This indicates the potential for specific management to facilitate biological diversity and the ecological connectivity of habitats under a reduction in the rotation period in intensively managed forest landscapes [18], thus supporting the implementation of the triad conservation concept [15]. For this, closeness to natural management appears promising, as it would increase stand structural diversity [14].

5. Conclusions

The prevalence of relationships between ground cover vegetation and structural characteristics rather than stand age in hemiboreal coniferous PHH and OG stands confirmed the study hypothesis. Such relationships imply that specific management could be implemented to sustain the biodiversity of commercial stands by the pre-harvesting age, thus aiding ecological connectivity under an intensively managed landscape. Considering a similar floristic composition in PHH and OG stands, their main differences were related to the structural and compositional diversity of the tree stand, which favoured the ground cover species with a lower occurrence. This also implies that the currently applied rotation period of ca. 70–110 appears efficient for ground cover vegetation, which is host for large proportion of other taxonomic groups, to reach a stable state. Accordingly, a conservative management strategy regarding the rotation period while facilitating the compositional and structural diversity of stands appears efficient for areas crucial for connectivity under the triad conservation concept, aiding the sustainability and multifunctionality of forests.

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