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Ground Cover Vegetation in Differently Managed Hemiboreal Norway Spruce Stands: Plantation vs. Natural Regeneration

Ilze Matisone *, Juris Katrevičs, Diāna Jansone, Ieva Jaunslaviete, Roberts Matisons, Agnese Anta Liepiņa and Āris Jansons

Latvian State Forest Research Institute Silava, Rigas Str. 111, LV2169 Salaspils, Latvia
* Correspondence: ilze.matisone@silava.lv; Tel.: +371-29351372

Abstract: Forest plantations, which have a simplified structure and composition, are becoming more frequent, raising concerns regarding their contribution to biological diversity in highly managed landscapes. The biological value of a stand has been related to stand age, although stand properties, which are often intercorrelated with it, yet are manageable, might be of primary importance. The relationships between stand properties (age, structure and composition) and ground cover vegetation, as a proxy for biological value, were assessed in Norway spruce stands with contrasting land use history (low-density plantations on former agricultural land, unmanaged and old-growth stands) in Latvia. The ground flora differed according to land use history of the stands. The principal gradients of ground cover vegetation were related to the degree of deciduous admixture in the tree stand, stand vertical heterogeneity (multi-layer; density and height of the understorey), light, age and site fertility. However, the plantations were more species-rich and diverse, appearing as promising in terms of biological diversity in intensively managed sites (especially periurban forests). The observed relationships between ground cover vegetation and stand characteristics suggest that diversification of the stand structures in plantations might reduce the recovery time of ground cover vegetation, contributing to the ecosystem services provided under intensifying management and disturbances.

Keywords: ground flora; management; land use; environmental indicators; stand structures; species richness

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1. Introduction

Over the past three decades, the increasing demand for timber has accelerated the expansion of forest plantations, thus contributing to the productive capacity of conventional forestry [1–4]. Hence, the share of plantation forestry in the world's roundwood productions has reached about 33% and continues to increase [5]. In northeastern Europe, both economically and ecologically important Norway spruce (*Picea abies* H. Karst.) is projected to decrease in abundance due to biotic and abiotic disturbances [6–9]. To mitigate such effects, shortening the rotation period is suggested [10], thus increasing the importance of plantation forestry [2,5]. The efficiency and intensity of plantation forest management can contribute to reductions in the cost of climate change mitigation efforts [11,12].

Due to intensive management, plantation forests can notably differ from natural forests in terms of species composition and ecosystem dynamics [13,14]. In Europe, forest plantations are mainly short-rotation monocultures, hence stands with a simplified composition and structure [5] contrasting with the structural diversity of old-growth forests [15]. This affects biodiversity and ecosystem services [16,17]; hence, mimicking the features associated with diversity via conventional management is essential in a highly managed forest landscape [18,19]. Due to productivity, intensive plantation forestry can compete for land with traditional forestry; however, productive plantations can also alleviate natural forests from the burden of timber production [2].

The biological value of a stand is largely determined by the composition and structure of the canopy/overstorey, hence the stand forming trees [20,21], deadwood of different decay stages [22,23] and veteran trees [24,25], which are essential for a set of taxa of trophic chains [19]. In this regard, the canopy composition and stand vertical structures, which are manageable stand properties [26], are considered the principal differences between intensively managed and conservancy old-growth forests [27–29]. The high biodiversity value of old-growth forests, however, has mostly been related to bryophytes and fungi [30,31], particularly the protected and rare ones [32]. In contrast, vascular ground cover vegetation favours disturbance; hence, it is richer and more diverse in younger stands, which are recovering from stand-replacing disturbance [18,29,33,34].

Ground cover vegetation is a vital habitat for invertebrates [35,36]; it also channels nutrient cycling [37], affecting stand productivity [38] and succession [39,40]. Ground cover is directly affected both by natural disturbance and management, acting as an indicator of ecosystem responses [19,41], although its succession carries the legacy effects of land use history [33,42,43]. Hence, the succession stages and ground cover vegetation of same-age stands with diverse land use history may differ [14]. Accordingly, ground cover vegetation can vary regionally and locally [44]; hence, local sampling is necessary.

Plantation forestry facilitates the advancement of vascular plants, especially weeds [45], similarly to severe wind disturbances [46,47]. The intensification of forest management suggests biologically rich sites, regardless of species composition, as essential in terms of both timber production and ecosystem services [48,49]. Hence, plantations providing rich and diverse ground cover vegetation can contribute to ecological networks, facilitating habitat connectivity in a fragmented landscape [50]. Furthermore, overgrown plantations (exceeding productivity optimum) can naturalise promptly and provide valuable habitats even for rare and endangered species [33,45].

The aim of the study was to assess the principal stand properties (age, structure and composition) affecting ground cover vegetation in Norway spruce stands with contrasting land use history (low-density plantations on former agricultural land, unmanaged and old-growth stands) in Latvia. Hence, the subordinate objective was to assess the potential of adaptive management in facilitating the biological diversity of intensively managed stands. We hypothesised that the composition and dimensions of the dominant (i.e., canopy/overstorey) trees were the principal drivers of ground cover vegetation, with land use having a secondary effect.

2. Materials and Methods

2.1. Study Area and Stand Selection

The relationships between the dimensions and structural diversity of the tree stand and ground cover vegetation in four plantations (PL), seven unmanaged (UM) and nine old-growth (OG) forest stands dominated by Norway spruce in Latvia (N 55°40′–58°05′, E 20°58′–28°14′) were studied (Figure 1). The study region is situated in a hemiboreal forest zone, where mixed stands of coniferous and broadleaved trees are typical [51,52]. Norway spruce is the second most economically important species after Scots pine (*Pinus sylvestris* L.), covering 19% of the total forest area (10.1% of the territory of Latvia).

The study region is situated in lowland conditions (less than 250 m above the mean sea level) with a flat topography. Forests are largely (40% of the total area) growing on post-glacial mesotrophic mineral podzolic soils (sandy and silty). The climatic conditions can be described as moist continental [53], though with explicit coastal features resulting from the proximity of the Baltic Sea. According to the National Weather Service (www.meteo.lv), the mean annual temperature was +6.5 °C (ranging from 5.7 °C in the more continental eastern part to 7.9 °C in the coastal areas), with February being the coldest (mean −3.1 °C) and July (mean 17.8 °C) the warmest month, respectively. The mean annual precipitation was 686 mm. The highest monthly precipitation fell during the vegetation period (May–September; ca. 75 mm/month); yet, April was the driest month (36 mm). The main climatic changes manifest as warming during the dormant period, which extends the vegetation period, with increasing variability in the moisture regime during the growing period [54].

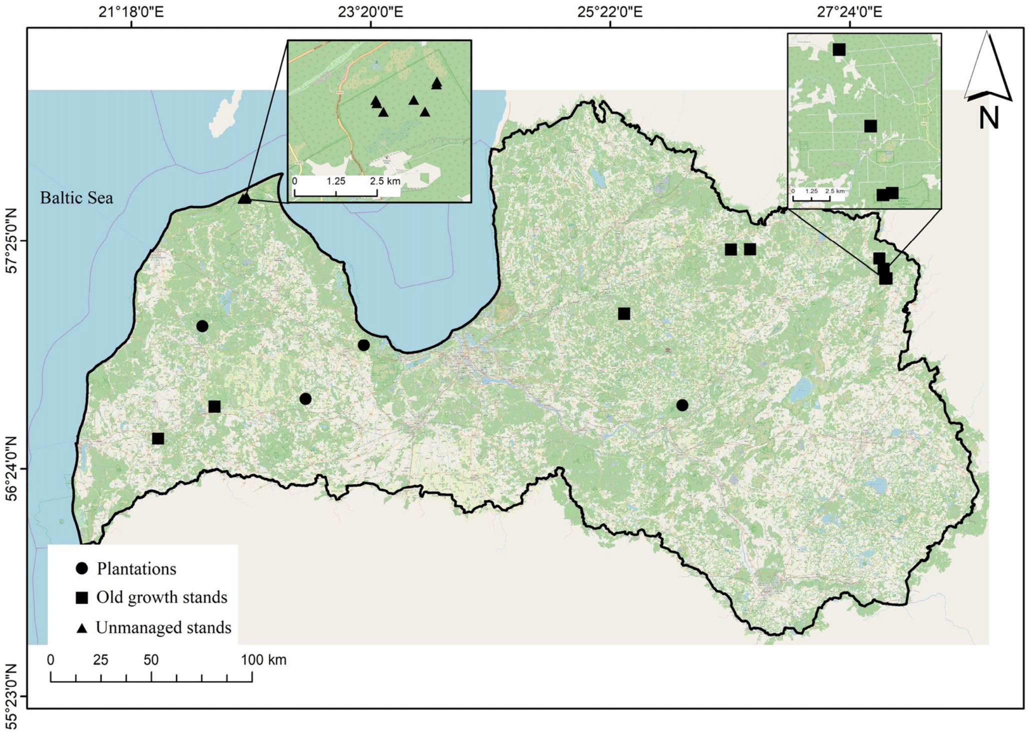

Figure 1. Location of the studied sampling plots of plantations, unmanaged and old-growth stands of Norway spruce in Latvia.

The studied PL were low-density Norway spruce monocultures established on former agricultural land with planting distances of 5 × 5 (400 trees ha^{-1}; two plantations), 5 × 7 (286 trees ha^{-1}) and 2 × 8 m (625 trees ha^{-1}). The age of the PL ranged from 26 to 62 years (mean 45 years), and the area of the PL ranged from 1.2 to 4.6 ha (Table 1). The studied UM stands were located in a protected area under coastal conditions in the northwestern part of Latvia (Slītere National Park; Figure 1). The stands were selected from the oldest reserve part of the national park, where no management has been performed since 1923, including the stand-replacing windthrow of 1969, which caused canopy loss of 90–95% [55]. Before the storm, Norway spruce, Scots pine and birch (*Betula pendula* Roth. and *Betula pubescens* Ehrh.) were the dominant tree species [55,56]. After the wind disturbance, the canopy/overstorey recovered with Norway spruce and birch, but the understorey and the advanced regeneration mostly consisted of spruce [55,56]. The criteria for selection were spruce as the dominating species in >50% of the stand basal area and an area of >0.5 ha. The canopy species composition was verified during direct surveys before sampling.

OG stands dominated by Norway spruce were selected from the forest inventory database according to the criteria of the age of the 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 (thinning). Spatially stratified (even) selection was implemented. Actual compliance with the pre-selected criteria was checked before sampling; the dominant cohort trees were cored to verify the age. In case of signs of recent (less than 40–50 years) management (stumps, sawn surfaces of logs, etc.), stands were omitted. The verified age of the surveyed OG stands ranged from 172 to 194 (mean 186) years. The studied OG stands were admixed with wych elm (*Ulmus glabra* Huds.) and small-leaved lime (*Tilia cordata* Mill.) (Table 1).

Table 1. Description and characteristics of plantations, unmanaged and old-growth stands of Norway spruce in Latvia. For stand characteristics, mean values ± standard error and differences by letters are shown; means with different letters are significantly ($p < 0.05$) different.

	Plantations	Unmanaged	Old-Growth	Total
No. of stands	4	7	9	20
No. of forest inventory and Vegetation plots (grids)	15	28	24	67
Stand age (mean, years)	26–62 (45)	(53)	172–194 (186)	
Total DBH (cm)	33.6 ± 1.5 a	15.6 ± 0.5 b	16.7 ± 0.8 b	
Canopy DBH (cm)	38.6 ± 1.3 a	21.1 ± 0.5 b	36.2 ± 1.4 a	
Total H (m)	20.8 ± 1.5 a	17.2 ± 0.3 b	14.9 ± 0.6 c	
Canopy H (m)	23.3 ± 0.9 a	22.9 ± 0.7 a	26.8 ± 0.7 b	
Total density (trees ha^{-1})	273.3 ± 19.6 a	1879.3 ± 116.1 b	970.0 ± 72.2 c	
Canopy density (trees ha^{-1})	222.7 ± 15.7 a	825.0 ± 35.9 b	232.5 ± 19.4 a	
Standing volume (m^3 ha^{-1})	264.8 ± 25.3 a	428.0 ± 18.1 b	371.8 ± 29.1 b	
Deadwood volume (m^3 ha^{-1})	5.9 ± 3.3 a	43.4 ± 9.0 b	62.1 ± 8.7 c	
Proportion of spruce (%)	98.7 ± 0.9 a	62.3 ± 3.49 b	52.8 ± 6.2 b	

2.2. Measurements

In each stand, depending on the size, two to four circular plots with an area of 500 m^2 were established (Figure 2); accordingly, 15, 28 and 24 plots in the PL, UM and OG stands were set up, respectively. Within each plot, the dimensions (height and diameter at breast height) and positions of all trees (living and dead) with the diameter at breast height (DBH) exceeding 6 cm were measured. The dimensions of undergrowth and advanced growth with DBH of 2.1–6.0 cm were measured in a 90° segment of a 100 m^2 subplot (with a common centre; Figure 2). For the lying deadwood thicker than 6 cm (thick end), the length and diameter at the thin and thick end within the margins of the sample plot (intersected by the plot) were measured. The surveys and sampling were conducted from 2020 to 2023.

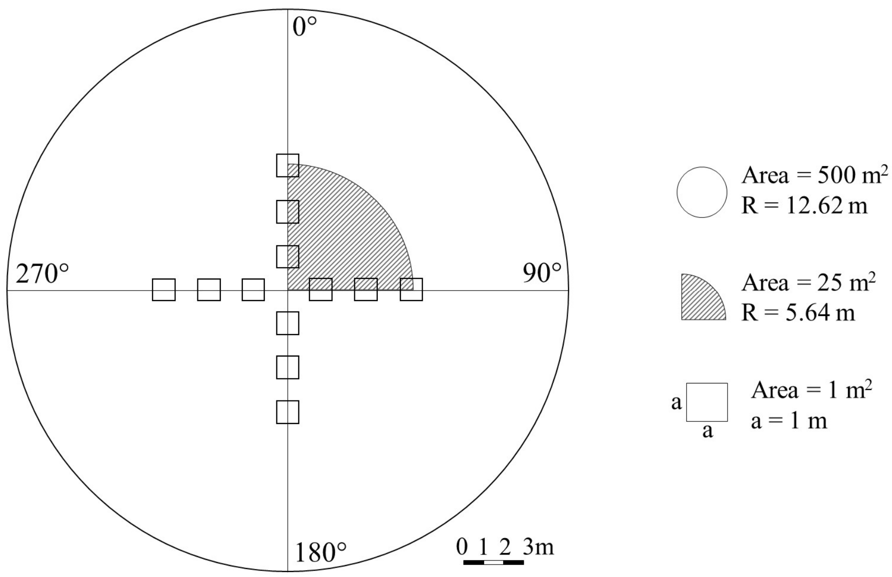

Figure 2. The scheme of the sample plot (tree stand), sector of the subplot (undergrowth) and grid plots used for vegetation sampling in the studied plantations, unmanaged and old-growth stands dominated by Norway spruce in Latvia.

For vegetation sampling, within each plot, a grid of 12 grid plots with dimensions of 1 × 1 m arranged regularly according to the four cardinal directions with a spacing of 1 m around the common centre was established (Figure 2). In each grid plot, the relative projective cover of ground cover vegetation, separately for vascular, woody plant (at herbaceous layer) and bryophyte layer, by species in each plot, was recorded. The projective cover was averaged for plots pooling the three layers; thus, the total projective cover was allowed to exceed 100%. Additionally, the projective cover of wood debris and forest litter was also recorded. Vegetation was surveyed in June–July 2022 for PL, 2019 for UM and 2021 for OG stands.

2.3. Data Analysis

Stand characteristics (density, basal area and standing stock) based on measurements of tree dimensions were calculated for each plot. Local volume equations [57] were used for the estimates. For the lying deadwood, volume was calculated as for the truncated cone. The structural diversity of tree dimensions was described by the interquartile difference between DBH and H (iqrD and iqrH, respectively). Compositional diversity was characterised by the share of deciduous trees, as well as the relative abundance of each species in the canopy and understorey in terms of the basal area and count, respectively.

For quantification of ground cover vegetation, species richness, occurrence, total cover, Ellenberg indicator values for vascular plants and Düll indicator values for bryophytes, as well as the Shannon–Wiener diversity index (H′), were calculated [58]. The overall similarity of ground cover vegetation among the PL, UM and OG stands was assessed using the Analysis of Similarity (ANOSIM; [59]). Jaccard dissimilarity over 5000 permutations was evaluated. To assess the main environmental gradients affecting ground cover vegetation in the studied stands, detrended correspondence analysis (DCA, detrending with 26 segments and downweighing rare species; [60]), which is an indirect assessment of ecological gradient, was based on sample plot data. The DCA was supplemented with a matrix of site properties (73 variables in total, among which 55 reflected the tree stand) to test for correlation with the principal two gradients in ground cover vegetation. The site properties tested were the derivatives of the measurements of tree stand and the composition of ground cover vegetation of the plots. Linear multiple mixed regression was used to estimate the principal environmental drivers related to the first two estimated ground cover vegetation gradients from those showing significant correlations. To account for dependencies in the data arising from sampling design, the stand was used as the random effect. An arbitrary selection principle was implemented for the selection of fixed effects. Collinearity of the predictors was evaluated using the variance inflation factor; the compliance of the models with statistical assumptions was evaluated using diagnostic plots. Data analysis was conducted in R v. 4.2.3 [61] using the packages “lme4” [62] and “vegan” [63].

3. Results

The studied stands differed in structure, with the UM and OG stands having stratified diverse canopy as opposed to PL, which had a more simplistic structure with single-layer canopy. Accordingly, the differences in the mean values of the canopy and overall DBH and H were higher in UM, and particularly OG stands. Nevertheless, the dimensions of canopy trees were similar among the PL, UM and OG stands (Table 1). The standing volume of UM and OG stands (mean $\pm$ standard error of 428.0 $\pm$ 18.1 and 371.8 $\pm$ 29.1 m^3 ha^{-1}, respectively) was twice as high as in PL (264.8 $\pm$ 25.3 m^3 ha^{-1}), although in OG, it ranged more widely (82.8–608.4 m^3 ha^{-1}). The density of UM stands was seven times denser than that of PL (1879.3 $\pm$ 116.1 and 273.3 $\pm$ 19.6 trees ha^{-1}) and two times denser than that of OG (970.0 $\pm$ 72.2 trees ha^{-1}). The PL had little deadwood, while UM and OG stands were quite rich in deadwood (5.9, 43.4 $\pm$ 9.0 and 62.1 $\pm$ 8.7 m^3 ha^{-1}, respectively); however, in OG stands, most of the deadwood was lying (42.9 $\pm$ 5.7 m^3 ha^{-1}) (Table 1).

The canopy of PL stands was formed by a single species (222.7$\pm$ 15.7 trees ha^{-1}; Table 1); nevertheless, a slight silver birch and goat willow (*Salix caprea* L.) admixture (single trees per plot) recruited the canopy between planted spruces. Considering natural regeneration, the UM stands (canopy and undergrowth trees) were composed of nine species; their canopy was mixed and mostly dominated by spruce (ca. 331 trees ha^{-1}), co-dominated by common aspen (*Populus tremula* L.) (ca. 315 trees ha^{-1}), silver birch (ca. 247 trees ha^{-1}) and with an admixture of Norway maple (*Acer platanoides* L.) (ca. 50 trees ha^{-1}). The composition of OG stands was even more diverse, with 18 species; yet, their canopy was formed by spruce (ca. 170 trees ha^{-1}) and pine (ca. 84 trees ha^{-1}), with an admixture of common aspen (ca. 30 trees ha^{-1}) and silver birch (ca. 28 trees ha^{-1}). Accordingly, the admixture of deciduous species in the canopy in PL was only 1%, while in UM and OG stands, it was more than one-third (38 and 43%, respectively, Table 1).

The second canopy storey in the PL stands was scarce, formed by the slower growing spruce trees (16 trees ha^{-1}) and a few naturally recruiting birch and goat willows. In the UM and OG stands, the second canopy storey was explicit. In the UM stands, it consisted mostly of spruce (61%), but in the OG, the second canopy storey was diverse, formed by spruce (27%) and deciduous species, among which small-leaved lime, wych elm (both 16%) and black alder (*Alnus glutinosa* (L.) Gaertn.) were the most common. In the PL stands, the undergrowth was formed only by scarce spruces (29 trees ha^{-1}); in the UM, the undergrowth had a density of 184 axes ha^{-1}, dominated by rowan (*Sorbus aucuparia* L.) (48%), hazel (*Corylus avellana* L.) (32%) and spruce (18%), but a relatively denser and richer understorey was found in OG stands (487 axes ha^{-1}, 14 species, particularly hazel and spruce).

The total projective cover of ground cover vegetation exceeded 100% only in PL, indicating an overlap of the layers, while in UM and OG, it was smaller by almost half, while ranging widely in UM stands (Table 2). The lowest cover of litter was found in PL (16.8 ± 6.3%, p-value < 0.001), while UM and OG stands were rich in litter, which covered approximately half of the sample plot area (47.6 ± 6.2%). In general, bryophytes were the most abundant; vascular plants were slightly less frequent; and woody plants were scarce. The overall richness of ground cover vegetation of the studied stands was generally intermediate, with 152 ground cover species counted in total. Among these, 107, 22 and 23 were vascular plants, woody plants and bryophytes, respectively. Nevertheless, total species richness, as well as that of vascular plants, was higher in PL and OG compared to UM (Table 2). The richness of bryophytes was similar, irrespectively of management type. The distribution of ground cover species, as indicated by H′, was intermediate. Nevertheless, the H′ was higher for vascular plants in the PL stands; yet, in UM and OG stands, the lower values implied that vascular vegetation had an explicit dominance structure.

Table 2. General description of ground cover vegetation in the studied spruce plantations (PL), unmanaged (UM) and old-growth (OG) stands in the hemiboreal forest zone, Latvia. Mean value ±95% confidence interval (CI) are shown. Different letters (a b c) indicate significance between management types; means with different letters are significantly (p < 0.05) different.

	Management Type	Ground Flora	Vascular	Woody	Bryophyte
		Mean ± CI	Mean ± CI	Mean ± CI	Mean ± CI
Number of species	PL	31.3 ± 1.1 a	21.3 ± 1.2 a	2.2 ± 1.4 a	7.7 ± 1.2 a
	UM	17.8 ± 1.2 b	8.2 ± 1.3 b	2.4 ± 1.3 a	7.2 ± 1.1 a
	OG	23.5 ± 1.1 c	12.9 ± 1.2 c	3.6 ± 1.2 b	6.9 ± 1.2 a
Relative projective cover (%)	PL	134.7 ± 14.1 a	54.8 ± 10.2 a	1.6 ± 1.8 a	78.4 ± 16.9 a
	UM	40.4 ± 51.2 ab	12.8 ± 23.9 b	0.8 ± 4.1 a	26.8 ± 41.3 a
	OG	87.9 ± 13.9 b	34.6 ± 9.3 b	2.1 ± 1.7 a	52.30 ± 15.5 a
Shannon–Wiener index	PL	2.8 ± 0.2 a	2.6 ± 0.2 a	1.1 ± 0.2 a	0.9 ± 0.2 a
	UM	2.5 ± 0.1 b	1.7 ± 0.2 b	1.4 ± 0.1 b	0.8 ± 0.2 a
	OG	2.6 ± 0.1 ab	2.0 ± 0.2 c	1.2 ± 0.2 ab	0.8 ± 0.2 a

The composition of ground cover vegetation in the studied stands differed, as evidenced by the dissimilarity estimate R = 0.64 (p = 0.001). Separate dissimilarity estimates for bryophytes and vascular plants were somewhat lower (R = 0.58 and R = 0.52, respectively). The main dissimilarities were related to the occurrence of species characteristic of meadows, scrublands and open forests, dominated by, e.g., *Anthoxanthum odoratum*, *Veronica chamaedrys* and *Dactylis glomerata* (Table 3), which were abundant in PL stands. The generalist forest species, e.g., *Oxalis acetosella*, *Vaccinium myrtillus*, *Calamagrostis arundinacea*, *Hylocomium splendens* and *Pleurozium schreberi*, were more common in the ground cover vegetation of UM and OG stands (Table 3).

Table 3. Occurrence and mean projective cover of most common species in the Norway spruce plantations, unmanaged and old-growth stands (plots).

Plantation			Unmanaged			Old-Growth		
Species	Cover	Occurrence	Species	Cover	Occurrence	Species	Cover	Occurrence
				Vascular				
Anthoxanthum odoratum	10.91	66.67	*Vaccinium myrtillus*	6.56	82.14	*Oxalis acetosella*	10.64	91.67
Veronica chamaedrys	8.74	93.33	*Oxalis acetosella*	5.02	89.29	*Vaccinium myrtillus*	6.84	58.33
Oxalis acetosella	7.63	60.00	*Calamagrostis arundinacea*	3.57	64.29	*Calamagrostis arundinacea*	5.21	75.00
Melampyrum pratense	7.54	93.33	*Maianthemum bifolium*	2.16	89.29	*Anemone nemorosa*	4.26	45.83
Equisetum pratense	6.58	53.33	*Deschampsia flexuosa*	1.55	25.00	*Mercurialis perennis*	2.90	29.17
Poa nemoralis	6.31	60.00	*Carex digitata*	0.97	35.71	*Galeobdolon luteum*	2.80	58.33
Dactylis glomerata	4.92	73.33	*Dryopteris carthusiana*	0.89	46.43	*Dryopteris carthusiana*	2.69	70.83
Mycelis muralis	2.32	66.67	*Luzula pilosa*	0.83	32.14	*Luzula pilosa*	2.39	83.33
Hypericum perforatum	2.07	66.67	*Equisetum sylvaticum*	0.65	39.29	*Vaccinium vitis-idaea*	2.03	33.33
Galium mollugo	1.99	73.33	*Trientalis europaea*	0.56	35.71	*Carex digitata*	1.98	54.17
Solidago virgaurea	1.99	80.00	*Gymnocarpium dryopteris*	0.53	25.00	*Maianthemum bifolium*	1.84	70.83
				Woody				
Picea abies	3.43	60.00	*Picea abies*	1.21	75.00	*Corylus avellana*	5.54	37.50
Sorbus aucuparia	0.57	26.67	*Populus tremula*	0.84	60.71	*Sorbus aucuparia*	1.95	79.17
Frangula alnus	0.47	33.33	*Sorbus aucuparia*	0.84	46.43	*Picea abies*	1.18	29.17
Acer platanoides	0.40	40.00	*Acer platanoides*	0.18	14.29	*Ribes rubrum*	1.10	37.50
Corylus avellana	0.37	26.67	*Fraxinus excelsior*	0.11	7.14	*Populus tremula*	0.67	29.17
				Bryophytes				
Rhytidiadelphus squarrosus	43.49	100.00	*Hylocomium splendens*	12.07	96.43	*Hylocomium splendens*	19.00	79.17
Pleurozium schreberi	27.58	86.67	*Cirriphyllum piliferum*	9.47	100.00	*Eurhynchium angustirete*	15.45	75.00
Hylocomium splendens	23.20	86.67	*Rhytidiadelphus triquetrus*	8.29	82.14	*Pleurozium schreberi*	8.89	58.33
Cirriphyllum piliferum	22.62	80.00	*Pleurozium schreberi*	8.05	78.57	*Rhytidiadelphus triquetrus*	8.13	58.33
Rhytidiadelphus triquetrus	10.50	46.67	*Dicranum polysetum*	4.25	100.00	*Plagiochila asplenioides*	7.11	70.83
Plagiomnium undulatum	5.12	53.33	*Plagiochila asplenioides*	3.56	60.71	*Sphagnum angustifolium*	5.98	25.00
Polytrichum commune	4.48	20.00	*Polytrichum commune*	3.13	57.14	*Sphagnum girgensohnii*	4.46	12.50
Plagiomnium affine	3.38	73.33	*Aulacomnium androgynum*	1.58	35.71	*Dicranum polysetum*	2.77	45.83
Plagiomnium ellipticum	2.49	46.67	*Dicranum majus*	1.44	28.57	*Polytrichum commune*	2.45	37.50
Dicranum polysetum	2.40	60.00	*Plagiomnium undulatum*	0.82	28.57	*Plagiomnium ellipticum*	2.40	45.83

Based on the projective cover of ground cover vegetation, two continuous principal gradients were estimated using the DCA (Figure 3a,b). According to these gradients, the UM and OG stands largely overlapped, while OG stands showed a wider range of scores, indicating a higher diversity of site conditions. The PL stands formed a distinct group with a slightly wider range than UM, especially regarding the primary gradient.

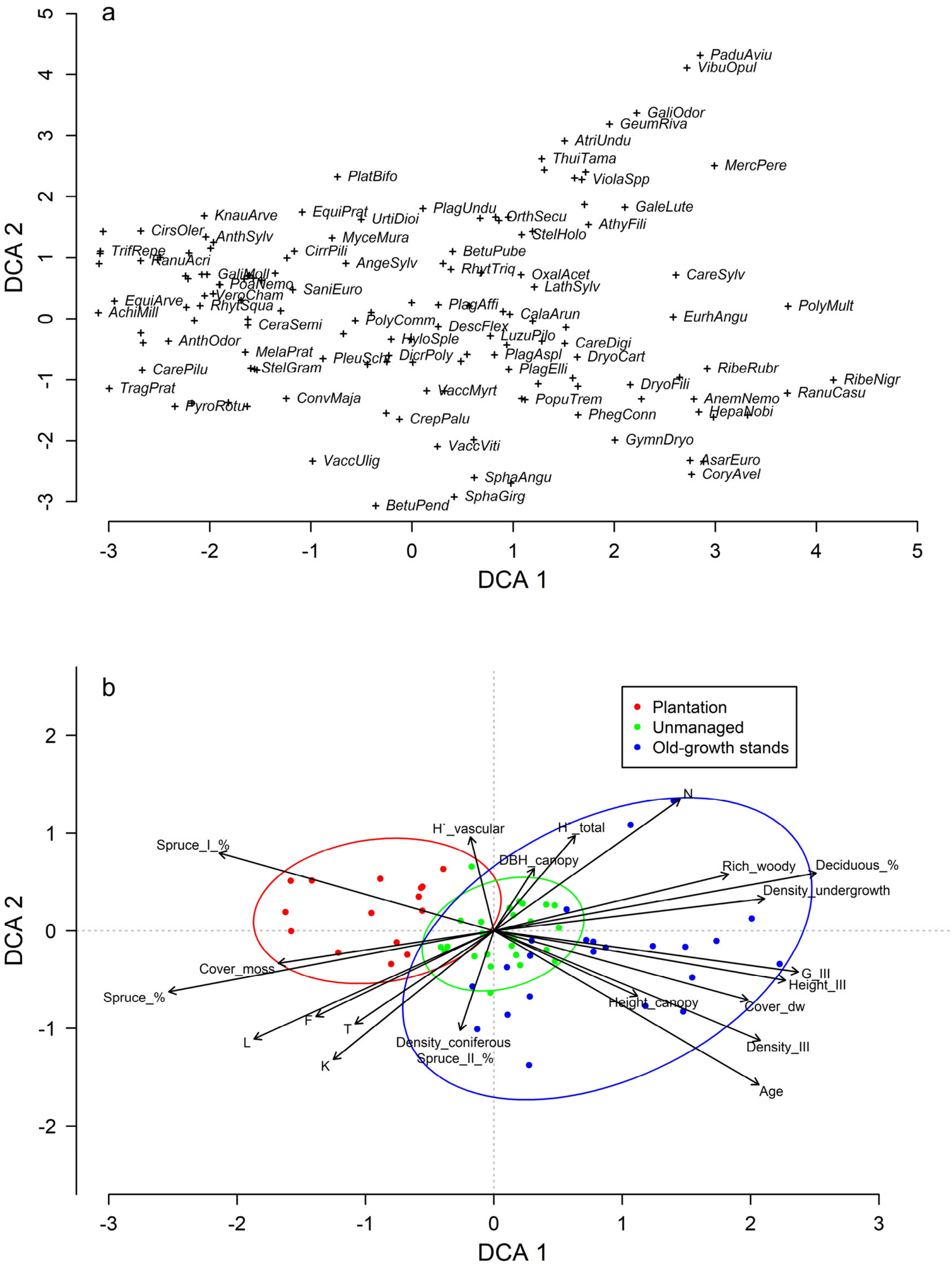

Figure 3. DCA ordination of ground cover vegetation species (**a**) and sample plots (**b**) according to their projective (relative) cover in plantations, unmanaged and old-growth stands of Norway spruce in Latvia. Species' acronyms (eight letters) are used according to [64]. Vectors show the correlation between the principal two gradients represented by the scores of DCA and site properties.

Abbreviations of vector names: L—light, K—continentality, F—moisture, T—temperature, N—nitrogen, H′_total—Shannon–Wiener diversity index of all species, H′_vascular—Shannon–Wiener diversity index of vascular species, Rich_woody—richness of woody species, Cover_moss—cover of bryophyte layer, Cover_dw—cover of deadwood on ground, DBH_canopy—diameter at breast height of canopy tree, Height_canopy—canopy height, Height_III—understorey height, Density_III—understorey density, Density_coniferous—density of coniferous trees, Density_undergrowth—density of undergrowth, G_III—basal area of undergrowth, Deciduous_%—proportion of deciduous trees, Spruce_%—proportion of spruce, Spruce_I_%—proportion of spruce in canopy, Spruce_II_%—proportion of spruce in second canopy layer, Age—stand age. Note that scales differ between the panels.

The primary gradient represented by DCA1 was related to tree stand composition (the proportion of spruce and deciduous species) and light conditions, as indicated by the strongest correlations with the proportion of spruce (also separate spruce in the canopy) and the Ellenberg light indicator values. These factors (Figure 3b) were also positively intercorrelated with continentality, humidity, temperature and cover of bryophytes. The multiple regression indicated that the first gradient was complex, yet explicitly (high R^2) represented the light, temperature, height of the understorey and deadwood cover (on the ground) (Table 4), as well as the proportion of spruce in the canopy, which were not collinear. The analysis showed that the dimensions of canopy trees' DBH, H and density were not decisive for ground cover vegetation in this study. Species' ordinations supported the diversity and complexity of environmental variables related to the first gradient (Figure 3a). Light-demanding species, such as *Melampyrum pratense*, *Stellaria graminea* and *Tragopogon pratensis*, represented the high light part of the gradient, which corresponded to sites with a lower proportion of deciduous trees (Figure 3a,b). Species typical for semi-open coniferous forests, e.g., *Vaccinium myrtillus*, *Pleurozium schreberi* and *Hylocomium splendens*, represented the mid-part, but full-shade species, such as *Oxalis acetosella* and *Mercurialis perennis*, represented the low light part of the gradient. Most of the accounted ground cover species were associated with medium light conditions (Figure 3b), while the high light conditions were related to a smaller set of ground cover species—hence, a higher cover of bryophytes. The low light part of the gradient consisted of sites with a higher admixture of deciduous trees, favouring shade-tolerant species (*Mercurialis perennis*, *Athyrium filix-femina*, *Galeobdolon luteum*) and higher evenness of ground flora (higher H′).

Table 4. The relationships between the first two gradients of ground cover vegetation in the studied plantations, unmanaged and old-growth stands and stand properties.

DCA1		
Fixed effects		
	χ^2	*p*-value
Proportion of spruce in stand	7.4	0.007
Light	19.7	<0.001
Temperature	14.2	<0.001
Height of understorey	7.8	0.005
Cover of deadwood (on the ground)	17.5	<0.001
Model performance		
R^2, marginal	0.78	
R^2, conditional	0.92	
DCA2		
Fixed effects		
	χ^2	*p*-value
Nitrogen	10.5	0.001
Stand age	9.6	0.001
Model performance		
R^2, marginal	0.23	
R^2, conditional	0.64	

The second gradient of ground cover vegetation of the studied stands was shorter and related to the age and fertility of stands, as indicated by the correlations with stand properties (age, N; Figure 3a,b), while showing a marginal correlation with DBH of canopy trees and the proportion of spruce in the second canopy layer (Figure 3a,b). The gradient showed a correlation with richness (ground flora, vascular plants, bryophytes), evenness (ground flora, vascular plants, bryophytes) and the cover of vascular and woody species (Figure 3b), which were related to the fertile parts of the gradient and the larger diameter canopy trees. Stand age, which was considered the main factor of biodiversity, was intercorrelated with the height of the canopy, density, height and standing volume of the understorey, as well as the cover of deadwood, all of which are stand structure elements typical for older forests. Nevertheless, the multiple regression indicated the nitrogen estimate and stand age as the principal drivers of the secondary gradient, the effects of which were considerably weaker, indicating a subordinate role in ground cover vegetation (Table 4). The strongest correlation with the second gradient was observed for *Mycelis muralis*, *Cirsium oleraceum*, understorey shrub species, e.g., *Padus avium*, *Viburnum opulus*, and bryophytes, such as *Thuidium tamariscinum* and *Atrichum undulatum*.

4. Discussion

The studied PL of Norway spruce appeared promising for the provision of ground cover of similar richness compared to OG and UM stands, despite the differences in age and stand history. Although the ground flora species' composition differed between the management types, their composition was still typical for mesotrophic hemiboreal forests on mineral soils within the Baltic region [65,66]. The compositional differences between the PL and UM/OG stands obviously highlighted the land use and diverse stages of forest succession, which led to differences in the stand structure and composition. PL stands contained species characteristic for meadow-edge, scrublands and open forests, e.g., *Anthoxanthum odoratum*, *Poa nemoralis*, *Veronica chamaedrys*, *Dactylis glomerata* and *Rhytidiadelphus squarrosus* (Table 3), indicating recent disturbance, corresponding to forests on former agricultural land and forests at early stages of succession [67–70]. Although UM stands experienced a large-scale (stand-replacing) wind disturbance half a century ago, the estimated continuous gradients of ground cover vegetation (Figure 3a,b) indicated that the conditions in UM and OG stands have reached equilibrium [33] while continuing to diversify locally [52].

In the OG and UM stands, ground cover species characteristic for the stable successional stage of development, e.g., *Vaccinium myrtillus*, *Hylocomium splendens* and *Pleurozium schreberi* (Table 3), were the most common [67,71–73]. This suggested a rapid recovery of ground cover vegetation after wind disturbance in unmanaged forests due to sufficient propagules sheltered by residues of a previous stand [68,72], which was not the focus of this study but gives us an opportunity to discuss the development of stands of similar age in forest and non-forest lands. Consequently, in the PL, weeds and meadow-edge species characteristic for former agricultural land were widely represented, but typical forest species were absent. Therefore, a succession of ground cover vegetation is specific to the site and stand history [14]. Hence, the efforts to mimic and/or accelerate the natural regeneration of climax species have been considered from challenging to impossible, as the principal gradients might be altered [74,75]. Accordingly, a similar study in PL on agricultural and forest land must be highlighted in future research.

The ordination of sample plots (Figure 3b) showed that management type was significant for ground cover vegetation, as grouping was visible. The close grouping of the UM plots may also be due to the close location of stands (Figures 1 and 3b), hence the similar site conditions, while the estimated dissimilarities within OG stands could likely be attributed to differences in microsite conditions and fertility gradient (N, Figure 3b), which favoured ferns and forbs, such as *Anemone nemorosa*, *Hepatica nobilis* and *Asarum europeaum* (Figure 3a; [76,77]). The separate and relatively close group of PL plots could be related to the homogeneous stand age, composition, structure and land use history characteristic for the PL [29].

Ground cover vegetation was related to stand properties, suggesting linkage with management and stand history [18,21,78], as indicated by the correlations of the main identified gradients (Figure 3a,b). The proportion of deciduous/broadleaved canopy trees, light conditions, fertility and structural diversity of the understorey, which determines the microclimate [79], appeared to be the main drivers of ground cover vegetation (Figure 3a,b; Table 4). However, light was intercorrelated with continentality, temperature, humidity and the proportion of spruce (as opposed to the proportion of broadleaved trees; Figure 3b), indicating the complex effects of stand structure [21]. In this case, the admixture of broadleaved trees and the multi-layer structure (Table 4) apparently had a positive effect on habitat quality (specific species characteristic for the habitat), rather than the richness of ground cover vegetation alone [80].

The stand density of coniferous trees (the layer and understorey; Figure 3b; Table 1), which affects light availability, has been positively related to ground cover species' richness in low-density PL stands, likely favouring herbs [20,67,81], especially on former agricultural land [68]. This supports the crucial role of light climate in ground cover flora, which interacts with decreased litter under conifers (~17%), thus facilitating the establishment of herbs [29]. In UM and OG stands, a high occurrence of feather mosses and dwarf shrubs was observed, which could outcompete other ground cover vegetation lifeforms [33,82]. However, higher ground cover and its richness in monospecies PL (Table 2) contradicted the correlation between canopy and ground cover richness [20,83], suggesting the persistent biological value of low-density stands [84,85]. Nevertheless, the studied PL were still too young for the formation of peaty forest floor and coarse humus with an acidic reaction [33], which inhibits vascular plants [86–88]. The cover of lying deadwood, which is related to the diversity of invertebrate and epiphyte communities [89,90], had a significant effect on ground cover vegetation, particularly in OG and UM stands (Table 4). All of the stand variables mentioned above, which improve the conditions for growth of ground cover species, are manageable [91], suggesting explicit positive effects of broadleaved admixture and slower growing understorey regarding the biological value of PL.

The second estimated gradient for ground cover vegetation (DCA2 in Figure 3a,b) was related to stand age and fertility (Table 4). However, stand age, which is mostly considered to be the key indicator for the biodiversity of forest ground vegetation [19,92], was subordinate to stand structures (canopy composition, species' proportion, understorey density and height, etc.). This suggests the potential for intensive adaptive forest management to facilitate biodiversity of commercial stands by reducing the time necessary for recovery of vegetation, and hence, related communities. This is also promising for shortening the rotation periods, allowing the mitigation of climatic risks [93]. The most fertile conditions were observed under closed canopies of more mixed tree stands, where light is limited (which can be correlated with N concentrations; [20,81]). The relatively high fertility in UM stands was expected as nitrate leaching that is characteristic after wind disturbance reached pre-storm levels during the fifth/sixth years in spruce stands [94]. Furthermore, the highest richness, cover and evenness (H′) of ground cover vegetation was observed in the younger PL stands, indicating the potential of management-facilitated biological diversity and ecological connectivity of habitats in managed stands [95]. On the other hand, these relationships might be an artefact of disturbances [80], which were explicit in UM and PL stands, but in most cases, they were not an indicator of the quality and functioning of the ecosystem [92].

This study confirms that PL are more species-rich (especially of vascular plants) than UM and OG stands (Table 2; [80]), but this is mostly based on the high diversity of vascular plants, which is not the case for bryophytes (Table 2; [28]). The establishment of PL was comparable to large-scale and high-intensity disturbance of recultivation favoured by light-demanding vascular plants (Table 3; [33,34]), while the DCA analysis (Figure 3a,b) indicated that the dominant species of UM and OG stands favoured semi-open conditions (mid-part of the light gradient in Figure 3a,b; [96–98]) formed as a result of forest self-thinning. Some older sites with clearer vertical structures contained more shade-tolerant late successional species, such as *Oxalis acetosella* [99] and *Mercurialis perennis* (Figure 3a,b). Accordingly, the PL were more species-rich until some quality aspect of the species was introduced. However, with the gradual introduction of forest species, the PL become naturalised, and hence similar to UM and OG forests in terms of structure, composition and even habitat [33,45,100]. Under the conditions of increasing forestry intensity, PL, as species-rich sites, provide habitats for a wide range of native forest plants, animals and fungi [45]), promote connectivity and provide buffering edge effects, being useful components in urban forestry, open (rides) and degraded habitats, such as sanitary landfills, wind farms, etc. [48,101,102].

5. Conclusions

The comparable effect of stand structural characteristics and stand age on ground cover vegetation indicated that specific management might be an effective way to sustain the biodiversity of middle-aged low-density commercial stands. This would contribute to connectivity. Considering higher floristic indicators (richness, cover, evenness) in plantation stands, they can be used as a promoter of biological diversity in intensively managed/disturbed sites (especially periurban forests), but in forest landscapes, more attention should be paid to species' composition and their quality. Moreover, the origin of plantations on former agricultural land absent of the origin material for forest-specific species should be considered.

The unmanaged stands were able to maintain and restore their floristic condition relatively quickly (the same age as plantations) after a strong wind storm, becoming conditionally stable, thus performing the functions required by other taxonomic groups. Accordingly, promoting stand composition (mixed with deciduous species) and structural (height, diameter) and vertical (multi-layer) diversity in low-density plantations, which mimics natural forest dynamics, can be effective in areas, which are essential for connectivity under intensive management, sustaining forest multi-functionality.

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References

1. Carle, J.; Vuorinen, P.; Del Lungo, A. Status and trends in global forest plantation development. *For. Prod. J.* **2002**, *52*, 12–23.
2. Heilmayr, R. Conservation through intensification? The effects of plantations on natural forests. *Ecol. Econ.* **2014**, *105*, 204–210. [CrossRef]
3. Routa, J.; Kilpeläinen, A.; Ikonen, V.P.; Asikainen, A.; Venäläinen, A.; Peltola, H. Effects of intensified silviculture on timber production and its economic profitability in boreal Norway spruce and Scots pine stands under changing climatic conditions. *Int. J. For. Res.* **2019**, *92*, 648–658. [CrossRef]
4. Temperli, C.; Stadelmann, G.; Thürig, E.; Brang, P. Silvicultural strategies for increased timber harvesting in a Central European mountain landscape. *Eur. J. For. Res.* **2017**, *136*, 493–509. [CrossRef]

5. Freer-Smith, P.; Muys, B.; Bozzano, M.; Drössler, L.; Farrelly, N.; Jactel, H.; Korhonen, J.; Minotta, G.; Nijnik, M.; Orazio, C. *Plantation Forests in Europe: Challenges and Opportunities*; European Forest Institute: Joensu, Finland, 2019; Volume 9, pp. 1–52.
6. Albert, M.; Nagel, R.V.; Nuske, R.; Sutmöller, J.; Spellmann, H. Tree species selection in the face of drought risk—Uncertainty in forest planning. *Forests* **2017**, *8*, 363. [CrossRef]
7. Jactel, H.; Petit, J.; Desprez-Loustau, M.L.; Delzon, S.; Piou, D.; Battisti, A.; Koricheva, J. Drought effects on damage by forest insects and pathogens: A meta-analysis. *Glob. Chang. Biol.* **2012**, *18*, 267–276. [CrossRef]
8. Krisans, O.; Saleniece, R.; Rust, S.; Elferts, D.; Kapostins, R.; Jansons, A.; Matisons, R. Effect of bark-stripping on mechanical stability of Norway spruce. *Forests* **2020**, *11*, 357. [CrossRef]
9. Seidl, R.; Thom, D.; Kautz, M.; Martin-Benito, D.; Peltoniemi, M.; Vacchiano, G.; Wild, J.; Ascoli, D.; Petr, M.; Honkaniemi, J.; et al. Forest disturbances under climate change. *Nat. Clim. Chang.* **2017**, *7*, 395–402. [CrossRef] [PubMed]
10. Hanewinkel, M.; Cullmann, D.A.; Schelhaas, M.J.; Nabuurs, G.J.; Zimmermann, N.E. Climate change may cause severe loss in the economic value of European forest land. *Nat. Clim. Chang.* **2013**, *3*, 203–207. [CrossRef]
11. Fayet, C.M.; Reilly, K.H.; Van Ham, C.; Verburg, P.H. The potential of European abandoned agricultural lands to contribute to the Green Deal objectives: Policy perspectives. *Environ. Sci. Policy* **2022**, *133*, 44–53. [CrossRef]
12. Strengers, B.J.; Minnen, J.G.; Eickhout, B. The Role of Carbon Plantations in Mitigating Climate Change: Potentials and Costs. *Clim. Chang.* **2007**, *88*, 343–366. [CrossRef]
13. Barlow, J.; Gardner, T.A.; Araujo, I.S.; Ávila-Pires, T.C.; Bonaldo, A.B.; Costa, J.E.; Esposito, M.C.; Ferreira, L.V.; Hawes, J.; Hernandez, M.I.M.; et al. Quantifying the Biodiversity Value of Tropical Primary, Secondary, and Plantation Forests. *Proc. Natl. Acad. Sci. USA* **2007**, *104*, 18555–18560. [CrossRef] [PubMed]
14. Stephens, S.S.; Wagner, M.R. Forest Plantations and Biodiversity: A Fresh Perspective. *J. For.* **2007**, *105*, 307–313. [CrossRef]
15. Burrascano, S.; Keeton, W.S.; Sabatini, F.M.; Blasi, C. Commonality and variability in the structural attributes of moist temperate old-growth forests: A global review. *For. Ecol. Manag.* **2013**, *291*, 458–479. [CrossRef]
16. Roberge, J.-M.; Laudon, H.; Björkman, C.; Ranius, T.; Sandström, C.; Felton, A.; Sténs, A.; Nordin, A.; Granström, A.; Widemo, F.; et al. Socio-ecological implications of modifying rotation lengths in forestry. *Ambio* **2016**, *45*, 109–123. [CrossRef] [PubMed]
17. Zimová, S.; Dobor, L.; Hlásny, T.; Rammer, W.; Seidl, R. Reducing rotation age to address increasing disturbances in Central Europe: Potential and limitations. *For. Ecol. Manag.* **2020**, *475*, 118408. [CrossRef] [PubMed]
18. Ferris, R.; Peace, A.J.; Humphrey, J.W.; Broome, A.C. Relationships between vegetation, site type and stand structure in coniferous plantations in Britain. *For. Ecol. Manag.* **2000**, *136*, 35–51. [CrossRef]
19. Oettel, J.; Lapin, K. Linking forest management and biodiversity indicators to strengthen sustainable forest management in Europe. *Ecol. Indic.* **2021**, *122*, 107275. [CrossRef]
20. Barbier, S.; Gosselin, F.; Balandier, P. Influence of tree species on understory vegetation diversity and mechanisms involved: A critical review for temperate and boreal forests. *For. Ecol. Manag.* **2008**, *254*, 1–15. [CrossRef]
21. Coote, L.; Dietzsch, A.C.; Wilson, M.W.; Graham, C.T.; Fuller, L.; Walsh, A.T.; Irwin, S.; Kelly, D.L.; Mitchell, F.J.G.; Kelly, T.C.; et al. Testing indicators of biodiversity for plantation forests. *Ecol. Indic.* **2013**, *32*, 107–115. [CrossRef]
22. Lassauce, A.; Paillet, Y.; Jactel, H.; Bouget, C. Deadwood as a surrogate for forest biodiversity: Meta-analysis of correlations between deadwood volume and species richness of saproxylic organisms. *Ecol. Indic.* **2011**, *11*, 1027–1039. [CrossRef]
23. Parisi, F.; Lombardi, F.; Sciarretta, A.; Tognetti, R.; Campanaro, A.; Marchetti, M.; Trematerra, P. Spatial patterns of saproxylic beetles in a relic silver fir forest (Central Italy), relationships with forest structure and biodiversity indicators. *For. Ecol. Manag.* **2016**, *381*, 217–234. [CrossRef]
24. Larrieu, L.; Paillet, Y.; Winter, S.; Bütler, R.; Kraus, D.; Krumm, F.; Latchat, T.; Michel, A.K.; Regnery, B.; Vandekerkhove, K. Tree related microhabitats in temperate and Mediterranean European forests: A hierarchical typology for inventory standardization. *Ecol. Indic.* **2018**, *84*, 194–207. [CrossRef]
25. Sever, K.; Nagel, T.A. Patterns of tree microhabitats across a gradient of managed to old-growth conditions: A case study from beech dominated forests of South-Eastern Slovenia. *Acta Silvae Ligni* **2019**, *118*, 29–40. [CrossRef]
26. Bauhus, J.; Puettmann, K.; Messier, C. Silviculture for old-growth attributes. *For. Ecol. Manag.* **2009**, *258*, 525–537. [CrossRef]
27. Commarmot, B.; Bachofen, H.; Bundziak, Y.; Bürgi, A.; Ramp, B.; Shparyk, Y.; Sukhariuk, D.; Viter, R.; Zingg, A. Structures of virgin and managed beech forests in Uholka (Ukraine) and Sihlwald (Switzerland): A comparative study. *For. Snow Landsc. Res.* **2005**, *79*, 45–56.
28. Humphrey, J.W.; Davey, S.; Peace, A.J.; Ferris, R.; Harding, K. Lichens and bryophyte communities of planted and semi-natural forests in Britain: The influence of site type, stand structure and deadwood. *Biol. Conserv.* **2002**, *107*, 165–180. [CrossRef]
29. Paillet, Y.; Bergès, L.; Hjältén, J.; Ódor, P.; Avon, C.; Bernhardt-Römermann, M.; Bijlsma, R.; De Bruyn, L.; Fuhr, M.; Grandin, U.; et al. Biodiversity differences between managed and unmanaged forests: Meta-analysis of species richness in Europe. *Conserv. Biol.* **2010**, *24*, 101–112. [CrossRef] [PubMed]
30. Crites, S.; Dale, M.R. Diversity and abundance of bryophytes, lichens, and fungi in relation to woody substrate and successional stage in aspen mixedwood boreal forests. *Can. J. Bot.* **1998**, *76*, 641–651. [CrossRef]
31. Viljur, M.L.; Abella, S.R.; Adámek, M.; Alencar, J.B.R.; Barber, N.A.; Beudert, B.; Burkle, L.A.; Cagnolo, L.; Campos, B.R.; Chao, A.; et al. The effect of natural disturbances on forest biodiversity: An ecological synthesis. *Biol. Rev.* **2022**, *97*, 1930–1947. [CrossRef]

32. Elofsson, M.; Gustafsson, L. Uncommon vascular plant species in an East-Central Swedish forest area—A comparison between young and old stands. *Nord. J. Bot.* **2000**, *20*, 51–60. [CrossRef]
33. Chernenkova, T.; Kotlov, I.; Belyaeva, N.; Suslova, E.; Morozova, O.; Pesterova, O.; Arkhipova, M. Role of silviculture in the formation of Norway spruce forests along the southern edge of their range in the Central Russian Plain. *Forests* **2020**, *11*, 778. [CrossRef]
34. Mayor, S.J.; Cahill, J.F., Jr.; He, F.; Sólymos, P.; Boutin, S. Regional boreal biodiversity peaks at intermediate human disturbance. *Nat. Commun.* **2012**, *3*, 1142. [CrossRef] [PubMed]
35. Felton, A.; Knight, E.; Wood, J.; Zammit, C.; Lindenmayer, D. A meta-analysis of fauna and flora species richness and abundance in plantations and pasture lands. *Biol. Conserv.* **2010**, *143*, 545–554. [CrossRef]
36. Felton, A.M.; Wam, H.K.; Stolter, C.; Mathisen, K.M.; Wallgren, M. The complexity of interacting nutritional drivers behind food selection, a review of northern cervids. *Ecosphere* **2018**, *9*, e02230. [CrossRef]
37. Hart, S.A.; Chen, H.Y.H. Understory vegetation dynamics of North American boreal forests. *Crit. Rev. Plant Sci.* **2006**, *25*, 381–397. [CrossRef]
38. Chavez, V.; Macdonald, S.E. Partitioning vascular understory diversity in mixedwood boreal forests: The importance of mixed canopies for diversity conservation. *For. Ecol. Manag.* **2012**, *271*, 19–26. [CrossRef]
39. Nilsson, M.C.; Wardle, D.A. Understory vegetation as a forest ecosystem driver: Evidence from the northern Swedish boreal forest. *Front. Ecol. Environ.* **2005**, *3*, 421–428. [CrossRef]
40. O'Brien, M.J.; O'Hara, K.L.; Erbilgin, N.; Wood, D.L. Overstory and shrub effects on natural regeneration processes in native Pinus radiata stands. *For. Ecol. Manag.* **2007**, *240*, 178–185. [CrossRef]
41. Kuuluvainen, T.; Angelstam, P.; Frelich, L.; Jõgiste, K.; Koivula, M.; Kubota, Y.; Lafleur, B.; Macdonald, E. Natural disturbance-based forest management: Moving beyond retention and continuous-cover forestry. *Front. For. Glob. Chang.* **2021**, *4*, 629020. [CrossRef]
42. Kutnar, L.; Nagel, T.A.; Kermavnar, J. Effects of disturbance on understory vegetation across Slovenian forest ecosystems. *Forests* **2019**, *10*, 1048. [CrossRef]
43. Mausolf, K.; Härdtle, W.; Jansen, K.; Delory, B.M.; Hertel, D.; Leuschner, C.; Temperton, V.M.; von Oheimb, G.; Fichtner, A. Legacy effects of land-use modulate tree growth responses to climate extremes. *Oecologia* **2018**, *187*, 825–837. [CrossRef]
44. Biber, P.; Borges, J.G.; Moshammer, R.; Barreiro, S.; Botequim, B.; Brodrechtová, Y.; Brukas, V.; Chirici, G.; Cordero-Debets, R.; Corrigan, E.; et al. How sensitive are ecosystem services in European forest landscapes to silvicultural treatment? *Forests* **2015**, *6*, 1666–1695. [CrossRef]
45. Brockerhoff, E.G.; Jactel, H.; Parrotta, J.A.; Quine, C.P.; Sayer, J. Plantation forests and biodiversity: Oxymoron or opportunity? *Biodivers. Conserv.* **2008**, *17*, 925–951. [CrossRef]
46. Castelli, J.P.; Casper, B.B.; Sullivan, J.J.; Latham, R.E. Early understory succession following catastrophic wind damage in a deciduous forest. *Can. J. For. Res.* **1999**, *29*, 1997–2002. [CrossRef]
47. Lain, E.J.; Haney, A.; Burris, J.M.; Burton, J. Response of vegetation and birds to severe wind disturbance and salvage logging in a southern boreal forest. *For. Ecol. Manag.* **2008**, *256*, 863–871. [CrossRef]
48. Alvey, A.A. Promoting and preserving biodiversity in the urban forest. *Urban For. Urban Green.* **2006**, *5*, 195–201. [CrossRef]
49. Pesola, L.; Cheng, X.; Sanesi, G.; Colangelo, G.; Elia, M.; Lafortezza, R. Linking above-ground biomass and biodiversity to stand development in urban forest areas: A case study in Northern Italy. *Landsc. Urban Plan.* **2017**, *157*, 90–97. [CrossRef]
50. Jaeger, J.A.; Soukup, T.; Schwick, C.; Madriñán, L.F.; Kienast, F. Landscape fragmentation in Europe. In *European Landscape Dynamics*, 1st ed.; Feranec, J., Soukup, T., Hazeu, G., Jaffrain, G., Eds.; CRC Press: Boca Raton, FL, USA, 2016; pp. 157–198.
51. Ahti, T.; Hämet-Ahti, L.; Jalas, J. Vegetation zones and their sections in northwestern Europe. *Ann. Bot. Fenn.* **1968**, *5*, 169–211.
52. Petrokas, R.; Baliuckas, V.; Manton, M. Successional categorization of European hemi-boreal forest tree species. *Plants* **2020**, *9*, 1381. [CrossRef]
53. Kottek, M.; Grieser, J.; Beck, C.; Rudolf, B.; Rubel, F. World map of the Köppen-Geiger climate classification updated. *Meteorol. Z.* **2006**, *15*, 259–263. [CrossRef]
54. Avotniece, Z.; Rodinov, V.; Lizuma, L.; Briede, A.; Kļaviņš, M. Trends in frequency of extreme climate events in Latvia. *Baltica* **2010**, *23*, 135–148.
55. Bāders, E.; Silamiķele, I.; Polyachenko, O.; Kiviste, A.; Jõgiste, K.; Jansons, Ā. Long-term effects of salvage logging on stand composition in seminatural spruce forests. *Eur. J. For. Res.* **2020**, *139*, 17–27. [CrossRef]
56. Bāders, E.; Senhofa, S.; Purina, L.; Jansons, A. Natural Succession of Norway Spruce Stands in Hemiboreal Forests: Case Study in Slitere National Park, Latvia. *Balt. For.* **2017**, *23*, 522–528.
57. Liepa, I. *Tree Growth Study*; LUA: Jelgava, Latvia, 1996; 123p.
58. Ellenberg, H.; Weber, H.E.; Düll, R.; Wirth, V.; Werner, W.; Paulissen, D. *Zeigerwerte von Pflanzen in Mitteleuropa*, 2nd ed.; Scripta Geobotanica: Göttingen, Germany, 1992; pp. 1–248.
59. Clarck, K.R. Non-parametric multivariate analyses of changes in community structure. *Aust. J. Ecol.* **1993**, *18*, 117–143. [CrossRef]
60. Correa-Metrio, A.; Dechnik, Y.; Lozano-García, S.; Caballero, M. Detrended correspondence analysis: A useful tool to quantify ecological changes from fossil data sets. *Bol. Soc. Geol. Mex.* **2014**, *66*, 135–143. [CrossRef]
61. R Core Team. *R: A Language and Environment for Statistical Computing*; R Foundation for Statistical Computing: Vienna, Austria, 2022; Available online: https://www.R-project.org/ (accessed on 16 January 2024).

62. Bates, D.; Maechler, M.; Bolker, B.; Walker, S. Fitting Linear Mixed-Effects Models Using lme4. *J. Stat. Softw.* **2015**, *67*, 18637. [CrossRef]
63. Oksanen, J.; Simpson, G.; Blanchet, F.; Kindt, R.; Legendre, P.; Minchi, P.R.; O'Hara, R.B.; Solymos, P.; Stevens, M.H.H.; Szoecs, E.; et al. _vegan: Community Ecology Package_. R Package Version 2.6-4. 2022. Available online: https://CRAN.R-project.org/package=vegan (accessed on 15 January 2024).
64. Heinken, T.; Diekmann, M.; Liira, J.; Orczewska, A.; Schmidt, M.; Brunet, J.; Chytrý, M.; Chabrerie, O.; Decocq, G.; De Frenne, P.; et al. The European forest plant species list (EuForPlant): Concept and applications. *J. Veg. Sci.* **2022**, *33*, e13132. [CrossRef]
65. Bušs, K. *Forest Ecology and Typology*; Silava: Rīga, Latvia, 1981; 68p.
66. Marozas, V.; Racinskas, J.; Bartkevicius, E. Dynamics of ground vegetation after surface fires in hemiboreal *Pinus sylvestris* forests. *For. Ecol. Manag.* **2007**, *250*, 47–55. [CrossRef]
67. Aubin, I.; Messier, C.; Bouchard, A. Can plantations develop understory biological and physical attributes of naturally regenerated forests? *Biol. Conserv.* **2008**, *141*, 2461–2476. [CrossRef]
68. Hermy, M.; Verheyen, K. Legacies of the past in the present-day forest biodiversity: A review of past land-use effects on forest plant species composition and diversity. *Ecol. Res.* **2007**, *22*, 361–371. [CrossRef]
69. Petrokas, R. Forest climax phenomenon: An invariance of scale. *Forests* **2020**, *11*, 56. [CrossRef]
70. Taylor, A.R. Concepts, Theories and Models of Succession in the Boreal Forest of Central Canada. Ph.D. Thesis, Lakehead University, Thunder Bay, ON, Canada, 2009.
71. Busby, J.R.; Bliss, L.C.; Hamilton, C.D. Microclimate control of growth rates and habitats of the boreal forest mosses, *Tomenthypnum nitens* and *Hylocomium splendens*. *Ecol. Monogr.* **1978**, *48*, 95–110. [CrossRef]
72. Lõhmus, A.; Remm, L. Disentangling the effects of seminatural forestry on an ecosystem good: Bilberry (*Vaccinium myrtillus*) in Estonia. *For. Ecol. Manag.* **2017**, *404*, 75–83. [CrossRef]
73. Timoshok, E.E. The ecology of bilberry (*Vaccinium myrtillus* L.) and cowberry (*Vaccinium vitis-idaea* L.) in Western Siberia. *Russ. J. Ecol.* **2000**, *31*, 8–13. [CrossRef]
74. Gravel, D.; Canham, C.D.; Beaudet, M.; Messier, C. Shade tolerance, canopy gaps and mechanisms of coexistence of forest trees. *Oikos* **2010**, *119*, 475–484. [CrossRef]
75. Lienard, J.; Florescu, I.; Strigul, N. An appraisal of the classic forest succession paradigm with the shade tolerance index. *PLoS ONE* **2015**, *10*, e0117138. [CrossRef]
76. Diekmann, M. Deciduous forest vegetation in boreo-nemoral Scandinavia. *Acta Phytogeogr. Suec.* **1994**, *80*, 1–116.
77. Hitchcock, C.L.; Cronquist, A.; Ownbey, M.; Thompson, J.W. *Vascular Plants of the Pacific Northwest. Vascular Plants of the Pacific Northwest*; University of Washington Press: Seattle, WA, USA, 1969; 914p.
78. Ćosović, M.; Bugalho, M.N.; Thom, D.; Borges, J.G. Stand structural characteristics are the most practical biodiversity indicators for forest management planning in Europe. *Forests* **2020**, *11*, 343. [CrossRef]
79. Kovács, B.; Tinya, F.; Ódor, P. Stand structural drivers of microclimate in mature temperate mixed forests. *Agric. For. Meteorol.* **2017**, *234*, 11–21. [CrossRef]
80. Boch, S.; Prati, D.; Müller, J.; Socher, S.; Baumbach, H.; Buscot, F.; Gockel, S.; Hemp, A.; Hessenmöller, D.; Kalko, E.K.; et al. High plant species richness indicates management-related disturbances rather than the conservation status of forests. *Basic Appl. Ecol.* **2013**, *14*, 496–505. [CrossRef]
81. French, L.J.; Smith, G.F.; Kelly, D.L.; Mitchell, F.J.; O'Donoghue, S.; Iremonger, S.F.; McKee, A.M. Ground flora communities in temperate oceanic plantation forests and the influence of silvicultural, geographic and edaphic factors. *For. Ecol. Manag.* **2008**, *255*, 476–494. [CrossRef]
82. Petersson, L.; Holmström, E.; Lindbladh, M.; Felton, A. Tree species impact on understory vegetation: Vascular plant communities of Scots pine and Norway spruce managed stands in northern Europe. *For. Ecol. Manag.* **2019**, *448*, 330–345. [CrossRef]
83. Coroi, M.; Skeffington, M.S.; Giller, P.; Smith, C.; Gormally, M.; O'Donovan, G. Vegetation diversity and stand structure in streamside forests in the south of Ireland. *For. Ecol. Manag.* **2004**, *202*, 39–57. [CrossRef]
84. Fang, Z.; Bao, W.; Yan, X.; Liu, X. Understory structure and vascular plant diversity in naturally regenerated deciduous forests and spruce plantations on similar clear-cuts: Implications for forest regeneration strategy selection. *Forests* **2014**, *5*, 715–743. [CrossRef]
85. Hedwall, P.O.; Holmström, E.; Lindbladh, M.; Felton, A. Concealed by darkness: How stand density can override the biodiversity benefits of mixed forests. *Ecosphere* **2019**, *10*, e02835. [CrossRef]
86. Esteso-Martínez, J.; Gil-Pelegrín, E. Frost resistance of seeds in Mediterranean oaks and the role of litter in the thermal protection of acorns. *Ann. For. Sci.* **2004**, *61*, 481–486. [CrossRef]
87. Graae, B.J.; Heskjær, V.S. A comparison of understorey vegetation between untouched and managed deciduous forest in Denmark. *For. Ecol. Manag.* **1997**, *96*, 111–123. [CrossRef]
88. Saetre, P.; Saetre, L.S.; Brandtberg, P.O.; Lundkvist, H.; Bengtsson, J. Ground vegetation composition and heterogene-ity in pure Norway spruce and mixed Norway spruce–birch stands. *Can. J. For. Res.* **1997**, *27*, 2034–2042. [CrossRef]
89. Andringa, J.I.; Zuo, J.; Berg, M.P.; Klein, R.; van't Veer, J.; de Geus, R.; de Beaumont, M.; Goudzwaard, L.; van Hal, J.; Broekman, R.; et al. Combining tree species and decay stages to increase invertebrate diversity in dead wood. *For. Ecol. Manag.* **2019**, *441*, 80–88. [CrossRef]

90. Dittrich, S.; Jacob, M.; Bade, C.; Leuschner, C.; Hauck, M. The significance of deadwood for total bryophyte, lichen, and vascular plant diversity in an old-growth spruce forest. *Plant Ecol.* **2014**, *215*, 1123–1137. [CrossRef]
91. Fries, C.; Johansson, O.; Pettersson, B.; Simonsson, P. Silvicultural models to maintain and restore natural stand structures in Swedish boreal forests. *For. Ecol. Manag.* **1997**, *94*, 89–103. [CrossRef]
92. Smith, G.F.; Gittings, T.; Wilson, M.; French, L.; Oxbrough, A. Identifying practical indicators of biodiversity for stand-level management of plantation forests. In *Plantation Forests and Biodiversity: Oxymoron or Opportunity?* Biodiversity and Conservation; Springer: Dordrecht, The Netherlands, 2007; Volume 9, pp. 67–91. [CrossRef]
93. Matisone, I.; Jansone, D.; Jaunslaviete, I.; Matisons, R.; Liepiņa, A.A.; Jansons, Ā. Stand Structure Beats Age for Ground Cover Vegetation in Ageing Hemiboreal Scots Pine and Norway Spruce Stands. *Sustainability* **2023**, *15*, 7594. [CrossRef]
94. Olsson, B.A.; Bergholm, J.; Alavi, G.; Persson, T. Effects of long-term N fertilization on nitrate leaching and vegetation responses in a spruce stand after severe wind damage. *For. Ecol. Manag.* **2022**, *520*, 120422. [CrossRef]
95. Royer-Tardif, S.; Bauhus, J.; Doyon, F.; Nolet, P.; Thiffault, N.; Aubin, I. Revisiting the functional zoning concept un-der climate change to expand the portfolio of adaptation options. *Forests* **2021**, *12*, 273. [CrossRef]
96. Johnson, E.A. Vegetation organization and dynamics of lichen woodland communities in the Northwest Territories, Canada. *Ecology* **1981**, *62*, 200–215. [CrossRef]
97. Klinka, K.; Krajina, V.J.; Ceska, A.; Scagel, A.M. *Indicator Plants of Coastal British Columbia*; University of British Columbia Press: Vancouver, BC, Canada, 1989; 288p.
98. Porley, R.; Hodgetts, N. *Mosses and Liverworts*; HarperCollins: London, UK, 2005; 495p.
99. Packham, J.R. Biological Flora of the British Isles. No. 141. *Oxalis acetosella* L. *J. Ecol.* **1978**, *66*, 669–693. [CrossRef]
100. Flinn, K.M.; Marks, P.L. Agricultural legacies in forest environments: Tree communities, soil properties, and light availability. *Ecol. Appl.* **2007**, *17*, 452–463. [CrossRef] [PubMed]
101. Buchholz, S.; Kelm, V.; Ghanem, S.J. Mono-specific forest plantations are valuable bat habitats: Implications for wind energy development. *Eur. J. Wildl. Res.* **2021**, *67*, 1. [CrossRef]
102. Nixon, D.J.; Stephens, W.; Tyrrel, S.F.; Brierley, E.D.R. The potential for short rotation energy forestry on restored landfill caps. *Bioresour. Technol.* **2001**, *77*, 237–245. [CrossRef]