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Evaluation of Undergrowth under the Canopy of Deciduous Forests on Very Fertile Soils in the Lithuanian Hemiboreal Forest

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Abstract: In the hemiboreal forest zone, the first-generation natural forests of *Betula* spp., *Populus tremula* L., and *Alnus incana* (L.) Moench, which develop after clearcutting on very fertile forest sites, change to deciduous hardwood forests (*Quercus robur* L., and *Fraxinus excelsior* L.) due to successive processes. These processes also cause a specific response to the development of undergrowth species, which can have a decisive influence on forest regeneration. The undergrowth species in the mature *Betula* spp. (*Betula pendula* Roth. And *Betula pubescens* Ehrh.), *Populus tremula*, and *Alnus incana* forest stands were evaluated to provide knowledge on undergrowth species composition and development under different soil conditions, and to identify the forest stand age's impact on undergrowth species. The evaluation was based on the standwise forest inventory data and limited to the analysis of pioneer tree species forests usually developed as first-generation natural forests after clearcutting. The study results showed that deciduous forests have rich undergrowth species diversity with a dominance of the *Corylus avellana* L., *Padus avium* L., *Frangula alnus* Mill., *Sorbus aucuparia* L., and *Salix* spp., which are typical undergrowth species in the hemiboreal forest zone. The dense and medium density undergrowth with the predominant *Corylus avellana* was rather common in the *Betula* spp. and *Populus tremula* stands; and *Padus avium* was more abundant in the *Alnus incana* stands on very fertile sites. Larger areas with dense undergrowth were obtained in the low mixed and mixed *Alnus incana* stands than in the pure stands, while no clear relationship between the stand mixture and undergrowth density was obtained in the *Betula* spp. and *Populus tremula* stands. The area of *Corylus avellana* significantly increased, while the area of *Padus avium* decreased in all studied forests with increasing stand age. Other dominant undergrowth species–*Sorbus aucuparia*, *Frangula alnus*, and *Salix* spp.–decreased with increasing age of the *Betula* spp. and *Populus tremula* stands. In the context of biodiversity, a higher number of undergrowth species was obtained in the mixed *Betula* spp. stands than in the pure and low mixed stands. New insights about the undergrowth species and their development patterns under the canopy of pioneer deciduous forests on very fertile soils were provided. However, these findings do not strongly suggest that an unmanaged forest regime wins over conventional forest management in mature and older deciduous forests on fertile soils as regards the biodiversity and other ecological services provided by the undergrow species.

Keywords: pioneer tree stands; understory shrubs; forest succession; fertile sites; ecological forestry

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1. Introduction

Ecological forest management has developed a silvicultural approach to ensure a greater balance between the need for timber production and ensuring nature conservation requirements in the forest ecosystems [1,2]. Härdtle (2003) pointed out that, to formulate recommendations for conservation-based management in forestry practice, it is appropriate to conduct investigations that reveal the development of natural forests [3]. In addition to the stand-level forest management, it is appropriate to evaluate other components of the forest ecosystem, including the undergrowth species (bushes, shrubs, and small trees growing beneath the tree canopies), regardless of whether the main functions of these components are conservation or production [4].

The shrub layer is important in providing various services and functions in forest ecosystems. In these, shrubs are classified as auxiliary species, which primarily perform biocenotic and phytomelioration functions [4].

The undergrowth species grow beneath the main canopy layer and will never reach the canopy tree level. Undergrowth species contribute to supporting the cleaning of tree trunks, improving the climate conditions inside the forest, regulating the decomposition processes of the forest litter, enriching the forest floor with organic matter and essential nutrients, protecting the soil from drying out and performing other important functions [5].

The shrub vegetation is the most diverse component of the temporal and boreal forest plant community, contributing significantly to the forest biogeochemical cycles and the structure of plant communities. Together with other understory communities (lower tree layers, ground vegetation layer–dwarf shrubs and mosses), undergrowth communities are important for the succession of the canopy trees and influence their recovery success. Their species richness showed a variable response to biotic and abiotic drivers, and this response often depended on soil type [6]. In the context of climate change, a positive response of the shrub layer is observed. The undergrowth species, especially shrubs, are more drought-tolerant than tree species and can be one of the last barriers against soil erosion in regions with a normal soil moisture regime or in drier regions [7].

However, the undergrowth species, their abundance, and growth dynamics in both natural forests and forest plantations have not received as much attention as the main tree species [8]. Moreover, their role in forest ecosystem dynamics is not completely clear [4].

Shrub cover and species composition are the most important indicators for characterizing shrub communities [9]. Shrub cover reflects soil fertility and moisture conditions, distinguishing the availability of water and nutrients that vegetation uses to produce biomass. The formation of shrub cover is an important function in maintaining soil quality and increasing the contents of soil organic carbon and total nitrogen [10]. It positively influences water infiltration, reduces erosion processes, and is important for wildlife habitats and forage availability. Shrub cover positively affects the survival and initial growth of tree seedlings by contributing to water and temperature balances. Shrubs provide shade and protect seedlings from damage by domestic and wild ungulates. However, undergrowth species may negatively affect the growth of tree seedlings due to competition or other disturbances, such as the sharing of limited resources or the release of allelochemicals, etc. [9,11]. Due to the abovementioned conditions and effects, shrub clearance has long been recognized in many countries as a forestry practice to reduce the competition between shrubs and trees, facilitate silvicultural operations, and mitigate fire risk by reducing fuel load and breaking the vertical continuity of the fuel [12]. Moreover, it is reasonable to find out the effect of shrub cover on the growth dynamics of the main tree species. Therefore, it is important to assess how intensively the shrub cover or its change affects the regeneration and survival of tree species. This, in turn, can reveal whether the interactions between these forest ecosystem components and species-specific effects are balanced [13].

In many countries, national forest inventories and the obtained datasets are valuable sources of forest-related information, as they cover many field plots. In addition to tree information, shrubs are the vegetation component for which the most complete and detailed information can be obtained from national forest inventories. Specifically, species composition and cover of the undergrowth are the most appropriate indicators for characterizing this forest ecosystem component [14].

First-generation natural forests on very fertile forest sites, developing after clearcutting, are dominated by pioneer deciduous tree species. Due to the succession stage, specific processes also occur in other vegetation layers. Furthermore, in the later stages of succession, when *Betula* spp., *Populus tremula* L., and *Alnus incana* (L.) Moench change to deciduous hardwood forests (*Quercus robur* L., *Fraxinus excelsior* L., etc.) [15], it is unclear what effect the undergrowth layer may have on forest regeneration.

This study aimed to identify the species composition and distribution area of undergrowth in the stands of pioneer deciduous tree species: silver birch (*Betula pendula* Roth.) and downy birch (*Betula pubescens* Ehrh.), analyzed together as birch species (*Betula* spp.); European aspen *(Populus tremula*); and gray alder (*Alnus incana*). More specific objectives were to determine the undergrowth species development under different soil conditions and identify the forest stand age's impact on undergrowth species in the deciduous tree species forests, which represent the hemiboreal forest zone.

2. Materials and Methods

2.1. Study Sites

The study covered the entire territory of Lithuania with a total land area of 65,300 km^2. The country is located on the eastern coast of the Baltic Sea between 53°54′–56°27′ N latitude and 20°56′–26°51′ E longitude. The relief of the country is characterized by lowlands (up to 100 m a.s.l.), plains (100–150 m a.s.l.), plateaus (150–200 m a.s.l.), and hilly highlands (200–300 m a.s.l.) [16]. The territory of Lithuania lies in the northern part of the temperate climate zone. According to 1991–2020 climatic normal, the average annual temperature was 7.4 °C, and the average annual precipitation was 695 mm in Lithuania [17].

Lithuanian forests belong to the transitional hemiboreal forest zone of Europe with the prevalence of mixed deciduous and coniferous stands [18]. The total forest land covered 33.7% of the territory [19]. Coniferous stands covered 55.7%, softwood deciduous forests occupied 40.9%, and hardwood deciduous forests covered 3.4% of the forest area. The dominant tree species are *Pinus sylvestris* L. (34.5%), *Picea abies* (L.) Karst. (21.0%), and *Betula* spp. (22.0%).

Forest site types selected for this study were characterized as very fertile and highly fertile mineral soils of a normal moisture regime; very fertile and highly fertile mineral soils of a temporary overmoisture regime; and very fertile mineral soil on slopes (Table 1). In general, tree species such as *Picea abies, Betula* spp. (*Betula pendula* and *Betula pubescens*), *Fraxinus excelsior, Quercus robur*, *Populus tremula, Alnus incana*, and *Alnus glutinosa* (L.) Gaertn. are found in these forest sites [20]. The sites selected for this study were characterized as mature, overmature, and natural maturity deciduous forests of *Betula* spp., *Populus tremula*, and *Alnus incana* species growing on fertile soil.

2.2. Data Collection

For the evaluation of undergrowth species under the canopy of deciduous forests on very fertile soils, the standwise forest inventory data (updated in 2019) was analyzed. This study was limited to the analysis of forests of pioneer tree species, the stands of which usually develop as first-generation natural forests after clearcutting. These tree species have long been classified as secondary tree species; therefore, the scientific data have not been extensively analyzed. Distribution areas of the *Betula* spp. and *Populus tremula* L. forests in all of Lithuania are shown in Figure 1.

Table 1. Description of the forest site types according to the Lithuanian forest site type classification used for the selection of forest stands in this study. The given soil and vegetation characteristics describe typical very fertile forest site types in Lithuania.

Forest Site Type [1]: Code–Description	Soil Group [2]	Basic Soil Properties [3]	Dominant Ground Vegetation Species [3]	Undergrowth Species [3]
Šd—eutrophic/very fertile mineral soils on slopes (more than 15 degrees of slope)	Cambisols	Forest floor depth 2–5 cm; A horizon * depth 15–20 cm. Forest floor pH_{KCl} 5.5; mineral 0–20 cm topsoil pH_{KCl} 5.0–5.4, and humus amount 2.4–4.8%. Moisture drains through the soil surface.	*Hepatica nobilis* Mill., *Stellaria holostea* L., *Galeobdolon luteum Huds.*	*Corylus avellana* L., *Padus avium* L., *Euonymus verrucosus* Scop., *Sorbus aucuparia* L., *Lonicera xylosteum* L.
Nd—eutrophic/very fertile mineral soils (relatively high nutrient concentrations) of normal moisture.	Leptosols, Cambisols, Luvisols, Fluvisols	Forest floor with a depth of 2–6 cm gradually transitioning to the A horizon; Bw horizon ** more typical in deciduous forests. Forest floor pH_{KCl} 5.4; mineral 0–20 cm topsoil pH_{KCl} 4.8–5.2, mean C:N ratio 14 ± 1; humus amount 2.6–5.0%. Groundwater level below 2 m.	*Hepatica nobilis* Mill., *Oxalis acetosella* L., *Galeobdolon luteum Huds.*, *Stellaria holostea* L.	*Corylus avellana* L., *Sorbus aucuparia* L., *Lonicera xylosteum* L., *Frangula alnus* Mill., *Daphne mezereum* L., *Euonymus verrucosus* Scop., *Viburnum opulus* L., *Padus avium* L., *Rhamnus cathartica* L.
Ld—temporary over-moistened eutrophic/very fertile mineral soils.	Cambisols, Luvisols, Albeluvisols, Gleysols, Fluvisols	Forest floor depth 5–12 cm; A horizon depth 20–25 cm with high root density; Bt horizon *** in some places. Forest floor pH_{KCl} 5.2; mineral 0–20 cm topsoil pH_{KCl} 5.1–5.5, mean C:N ratio 11 ± 1; humus amount 3.1–6.4%. Groundwater level 1.5–2.0 m.	*Oxalis acetosella* L., *Anemone nemorosa* L., *Aegopodium podagraria* L., *Geum urbanum* L., *Galeobdolon luteum* Huds.	*Sorbus aucuparia* L., *Corylus avellana* L., *Frangula alnus* Mill., *Daphne mezereum* L., *Lonicera xylosteum* L., *Padus avium* L., *Euonymus europaeus* L., *Ribes nigrum* L., *Salix cinerea* L.
Nf—very eutrophic/highly fertile (very high nutrient concentrations) mineral soils of normal moisture.	Cambisols	Forest floor depth 1–3 cm; A horizon depth 20–30 cm; typical Bw horizon. Forest floor pH_{KCl} 5.6; mineral 0–20 cm topsoil pH_{KCl} 5.5–6.0; mean C:N ratio 9 ± 1; humus amount 4.3–7.1%. Groundwater level below 2 m.	*Aegopodium podagraria* L., *Anemone nemorosa* L., *Asarum europaeum* L., *Galeobdolon luteum* Huds., *Stellaria holostea* L., *Geum urbanum* L.	*Corylus avellana* L., *Sorbus aucuparia* L., *Lonicera xylosteum* L., *Frangula alnus* Mill., *Padus avium* L., *Daphne mezereum* L., *Euonymus verrucosus* Scop., *Viburnum opulus* L., *Ribes nigrum* L., *Euonymus europaeus* L., *Rhamnus cathartica* L.
Lf—temporary over-moistened very eutrophic/highly fertile mineral soils.	Cambisols, Luvisols	Forest floor depth 3–5(8) cm; A horizon depth 25–40 cm. Forest floor pH_{KCl} 5.4; mineral 0–20 cm topsoil pH_{KCl} 5.6–5.7; humus amount 4.6–8.7%. Groundwater level 1.5–2.0 m.	*Aegopodium podagraria* L., *Anemone nemorosa* L., *Asarum europaeum* L., *Galeobdolon luteum* Huds., *Stellaria holostea* L., *Geum urbanum* L.	*Frangula alnus* Mill., *Corylus avellana* L., *Sorbus aucuparia* L., *Padus avium* L., *Rhamnus cathartica* L., *Euonymus europaeus* L., *Salix cinerea* L., *Lonicera xylosteum* L., *Euonymus verrucosus* Scop., *Viburnum opulus* L., *Ribes nigrum* L., *Daphne mezereum* L.

[1] Information about Lithuanian forest site type classification given by ref. [20]; [2] Information about soil group according to the World Reference Base for Soil Resources [21] given by ref. [20]; [3] Information about basic soil properties and vegetation species given by refs. [20,22]. * A horizon—mineral surface horizon with maximum humus accumulation, typically dark-colored; ** Bw horizon—weakly developed mineral subsoil horizon; *** Bt horizon—illuvial mineral subsoil horizon with clay accumulation.

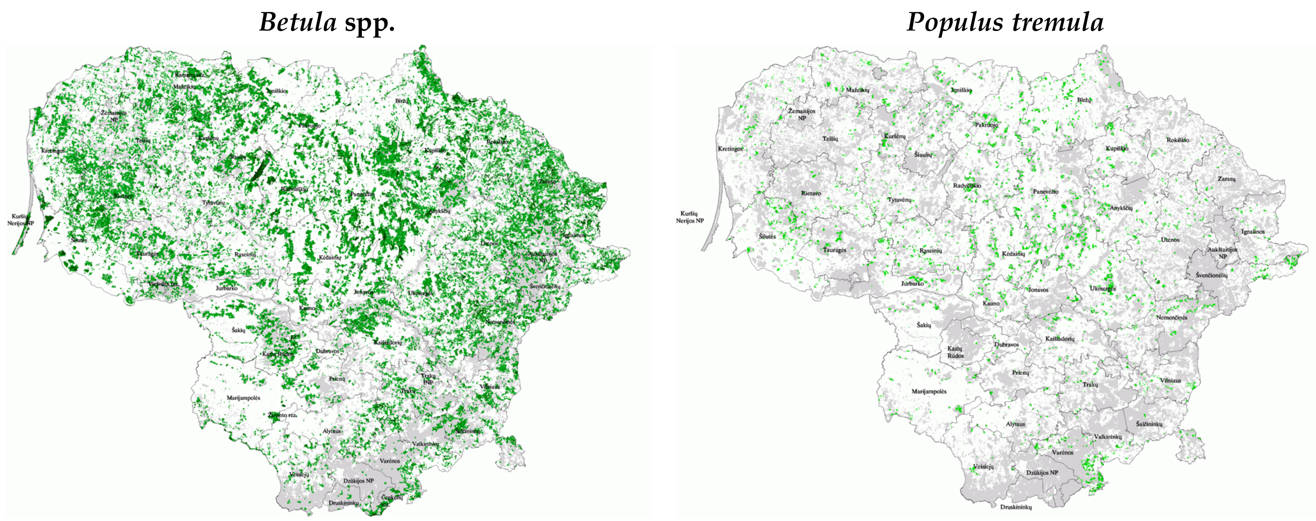

Figure 1. Distribution maps of *Betula* spp. and *Populus tremula* tree species in Lithuania. Distribution area of *Betula* and *Populus tremula* forests is shown in green color; distribution of other tree species is shown in gray color.

For this study, the selected birch species forests older than 60 years old covered 68,700 ha. Silver birch (*Betula pendula*) and downy birch (*Betula pubescens*) were evaluated together as *Betula* spp. The forests of European aspen (*Populus tremula*) older than 40 years old covered 36,406 ha, and gray alder (*Alnus incana*) forests older than 40 years old covered 48,065 ha. The detailed distribution of the stands growing on very fertile forest site types in Lithuania was given in ref. [23]. The forest stands where final felling without clearcutting, intermediate, sanitary, and other types of felling or afforestation was carried out in the last decade were not included in this analysis.

For the evaluation of the undergrowth species under the canopy of deciduous forests on very fertile soils, the following parameters were analyzed: (1) species composition, and plot area (ha) of the selected deciduous forest stands; and (2) species composition, plot area, and density of the bushes, shrubs, and small trees growing beneath the tree canopies and never reaching the canopy layer in a particular forest site type, described as undergrowth in this study.

The selected forest stands were grouped according to three indicators: (1) the predominant species of the main stand story (*Betula* spp., *Populus tremula*, and *Alnus incana*); (2) the species compositional structure of the main stand story: pure stands, where the dominant tree species occupy 86–100%; low mixed stands, where the dominant tree species occupy 66–85%; and mixed stands, where the dominant tree species occupy less than 65%; and (3) the stand age structure (age classes) of the main stand story: the age classes from class 7 (61–70 years old stands) to class 11 (101–110 years old stands) were analyzed for the Betula spp. Forests; the age classes 5–10 (from 41–50 to 91–100 years old stands) were analyzed for the *Populus tremula*; and the age classes 5–7 (from 41–50 to 61–70 years old stands) were analyzed for the *Alnus incana* forests. Moreover, forest stands were grouped according to the forest site types (see Table 1). Along with the deciduous tree species selected for this study (*Betula* spp., *Populus tremula*, and *Alnus incana*), other common tree species found in fertile forest sites are *Picea abies*, *Quercus robur*, *Fraxinus excelsior*, *Alnus glutinosa*, which together form mixed stands [24].

Additionally, the area covered by the undergrowth species, which was assessed visually, was assigned density categories: no undergrowth; low-density undergrowth, when the undergrowth species occupied an area lower than 30%; medium density undergrowth, when the undergrowth species occupied an area of 31–60%; and dense undergrowth, when the undergrowth species occupied an area higher than 60% [25]. Examples of undergrowth species under the canopy of deciduous forests are given in Figure 2.

A

B

C

Figure 2. Undergrowth cover under the canopy of deciduous forests: pure *Betula* spp. forest with *Picea abies* in the second story and a low-density *Corylus avellana* undergrowth (**A**); low mixed *Populus tremula* forest with *Picea abies* in the second story and medium density *Corylus avellana* undergrowth (**B**); and mixed *Populus tremula* forest with dense *Corylus avellana* undergrowth (**C**) (Photos: Marius Šilingas).

2.3. Statistical Analyses

The frequency tables of forest stand area distribution were created with the IBM SPSS Statistics 23 software package according to the selected indicators (in percent). A cross-tabulation was used to analyze the data. Additionally, chi-square tests (χ^2) and z-test with Bonferroni adjusted post hoc tests were used to identify the differences between the variables. We followed the assumption of the χ^2 criterion-identifying, which was that the expected frequencies/counts should be greater than 5 for 80% of the cells. Statistically significant differences between the selected variables at the significance level $\alpha = 0.05$ were identified with the different letters a, b, and c in the superscript in the tables. To calculate and draw a Venn diagram, we used an online program (http://bioinformatics.psb.ugent.be/webtools/Venn/ (accessed on 28 October 2022).

3. Results

The undergrowth species in mature stands of the studied pioneer tree species (*Betula* spp., *Populus tremula*, and *Alnus incana*), growing on very fertile soils, were unevenly distributed in the stands. Among other undergrowth species, *Corylus avellana* dominated in the *Betula* spp. and *Populus tremula* forest stands (Table 2). The area of *Corylus avellana* under the tree canopy increased significantly with the increase in stand mixture in both *Betula* and *Populus tremula* stands (Table 3).

Table 2. Percentage distribution of the predominant undergrowth species area in the *Betula* spp., *Populus tremula*, and *Alnus incana* stands. The values followed by different letters a, b, and c indicate statistically significant differences between the stands at $p < 0.05$.

Undergrowth Species	Predominant Tree Species of the Main Tree Story		
	***Betula* spp.**	***Populus tremula***	***Alnus incana***
	Distribution (%)		
No undergrowth	6.9 ^{a}	5.9 ^{b}	5.1 ^{c}
Corylus avellana	67.0 ^{a}	69.2 ^{b}	16.9 ^{c}
Padus avium	11.5 ^{a}	13.5 ^{b}	64.1 ^{c}
Sorbus aucuparia	3.8 ^{a}	2.6 ^{b}	1.8 ^{c}
Frangula alnus.	10.0 ^{a}	7.9 ^{b}	9.3 ^{c}
Salix spp.	0.4 ^{a}	0.5 ^{a}	2.3 ^{b}
Other species *	0.4 ^{a}	0.5 ^{b}	0.5 ^{b}
Total area (ha)	64,976	34,380	47,615

* The areas of other undergrowth species, such as *Lonicera* spp., *Cornus* spp., *Ribes* spp., *Sambucus* spp., *Ameliancier* spp., *Tilia* spp., *Euonymus* spp., *Crataegus* spp., *Physocarpus opulifolius* L., *Hippophae rhamnoides* L., *Cerasus avium* L., *Spiraea* spp., *Rhamnus cathartica* L., *Rosa* spp., *Juniperus communis* L., *Caragana* spp., *Syringa* spp., *Malus* spp., *Viburnum* spp., etc., were combined because of their relatively low areas (0.44%, 650 ha) obtained in the stands.

Table 3. Percentage distribution of the predominant undergrowth species area in pure (dominant tree species occupy 86–100%), low mixed (dominant tree species occupy 66–85%), and mixed (dominant tree species occupy less than 65%) *Betula* spp., *Populus tremula*, and *Alnus incana* stands. The values followed by different letters a, b, and c indicate statistically significant differences between pure, low-mixed, and mixed stands within each stand at $p < 0.05$.

Undergrowth Species	***Betula* spp.**			***Populus tremula***			***Alnus incana***		
	Pure	**Low Mixed**	**Mixed**	**Pure**	**Low Mixed**	**Mixed**	**Pure**	**Low Mixed**	**Mixed**
	Distribution (%)								
No undergrowth	9.9 ^{a}	6.9 ^{b}	6.1 ^{c}	7.3 ^{a}	5.9 ^{b}	5.6 ^{b}	5.4 ^{a}	5.2 ^{ab}	4.7 ^{b}
Corylus avellana	56.0 ^{a}	63.8 ^{b}	71.4 ^{c}	66.2 ^{a}	67.4 ^{a}	70.4 ^{b}	8.9 ^{a}	16.7 ^{b}	26.2 ^{c}
Padus avium	14.9 ^{a}	12.7 ^{b}	10.1 ^{c}	14.2 ^{ab}	14.3 ^{a}	13.0 ^{b}	72.5 ^{a}	63.4 ^{b}	55.1 ^{c}
Sorbus aucuparia	4.5 ^{a}	4.0 ^{a}	3.6 ^{b}	1.6 ^{a}	2.9 ^{b}	2.6 ^{b}	1.6 ^{a}	2.1 ^{b}	1.7 ^{a}
Frangula alnus	13.7 ^{a}	11.7 ^{b}	8.1 ^{c}	9.9 ^{a}	8.6 ^{a}	7.3 ^{b}	9.1 ^{a}	9.3 ^{a}	9.4 ^{a}
Salix spp.	0.6 ^{a}	0.5 ^{a}	0.4 ^{b}	0.4 ^{a}	0.4 ^{a}	0.5 ^{a}	1.9 ^{a}	2.6 ^{b}	2.5 ^{b}
Other species	0.4 ^{a}	0.4 ^{a}	0.3 ^{a}	0.5 ^{a}	0.4 ^{a}	0.6 ^{a}	0.5 ^{a}	0.6 ^{a}	0.4 ^{a}
Total area (ha)	9371	18,649	36,956	3599	9551	21,230	3599	9551	21,230

The predominant *Corylus avellana* undergrowth in the *Alnus incana* stands occurred less frequently than in the *Betula* and *Populus tremula* stands (Table 2). However, the increase in *Corylus avellana* area with increasing stand mixture was also statistically significant (Table 3). The predominant species of undergrowth in *Alnus incana* stands was *Padus avium* with the highest frequency in the pure *Alnus incana* stands. The frequency of dominant *Padus avium* undergrowth decreased significantly with increasing stand mixture. By increasing the *Betula* stand mixture, the prevailing *Padus avium* undergrowth frequency decreased significantly.

The *Frangula alnus* is the third most common undergrowth species in mature deciduous stands on highly fertile forest sites. The *Frangula alnus* mainly dominated in the *Betula* forests, while a lower frequency of this undergrowth species was obtained in the *Alnus incana*, and the lowest frequency in *Populus tremula* stands (Table 2). With the increase in stand mixture in the *Betula* forests, the frequency of predominant *Frangula alnus* undergrowth decreased significantly (Table 3). The prevalence of *Frangula alnus* in mixed *Populus tremula* was significantly less frequent than in low-mixed and pure stands. The frequency of *Frangula alnus* in *Alnus incana* stands did not depend on the stand mixture. The predominant *Sorbus aucuparia* undergrowth was the most common in the *Betula* forests, with smaller areas in the *Populus tremula* and *Alnus incana* forests. The frequency of the predominant *Sorbus aucuparia* did not depend on the stand mixture.

The prevalence of *Salix* spp. undergrowth was significantly higher in the *Alnus incana* than in the *Betula* and *Populus tremula* forests (Table 2). The *Salix* undergrowth was less common in the pure than in low-mixed and mixed *Alnus incana* stands (Table 3).

The highest proportion of the forests with no undergrowth was found in the *Betula* (6.9%) forests followed by *Populus tremula* (5.9%) and *Alnus incana* (5.1%) (Table 2). The stands with low-density undergrowth were arranged in the following order: *Betula* 9.7%^{A}, *Populus tremula* 8.0%^{C}, *A. incana* 5.7%^{B}. The stands with dense undergrowth were arranged in the following order: *Betula* 41.0%^{A}, *Populus tremula* 46.3%^{C}, *Alnus incana* 48.9%^{B}.

The Venn diagram revealed four undergrowth species specific to the mixed *Betula* forests (Figure 3). These species were *Hippophae rhamnoides, Cornus* spp., *Crataegus* spp., and *Cerasus avium.* No specific undergrowth species were found in the pure and low-mixed *Betula* forests. In the *Betula* stands of all compositional structures, the overlapped undergrowth species were *Corylus avellana, Sorbus aucuparia, Padus avium, Frangula alnus, Salix* spp., *Ribes* spp., *Malus* spp., *Lonicera* spp., and *Sambucus* spp. There were three specific species in the pure (*Spiraea* spp., *Cornus* spp., and *Syringa* spp.) and mixed (*Ribes* spp., *Rosa* spp., and *Cerasus avium*) *Populus tremula* stands (Figure 3). In all *Populus tremula* stands, six species overlapped, and those were *Sorbus aucuparia*, *Lonicera* spp., *Corylus avellana*, *Padus avium*, *Salix* spp., and *Frangula alnus.* In the *Alnus incana* forests, two specific undergrowth species were obtained in each pure (*Spiraea* spp. and *Tilia* spp.), low mixed (*Viburnum* spp. and *Rhamnus cathartica*), and mixed (*Juniperus communis* and *Cerasus avium*) stand. Irrespective of the species' compositional structure, nine undergrowth species overlapped in the *Alnus incana* forests, and those were *Corylus avellana*, *Padus avium, Sorbus aucuparia, Frangula alnus, Salix* spp., *Ribes* spp., *Lonicera* spp., *Cornus* spp., and *Sambucus* spp.

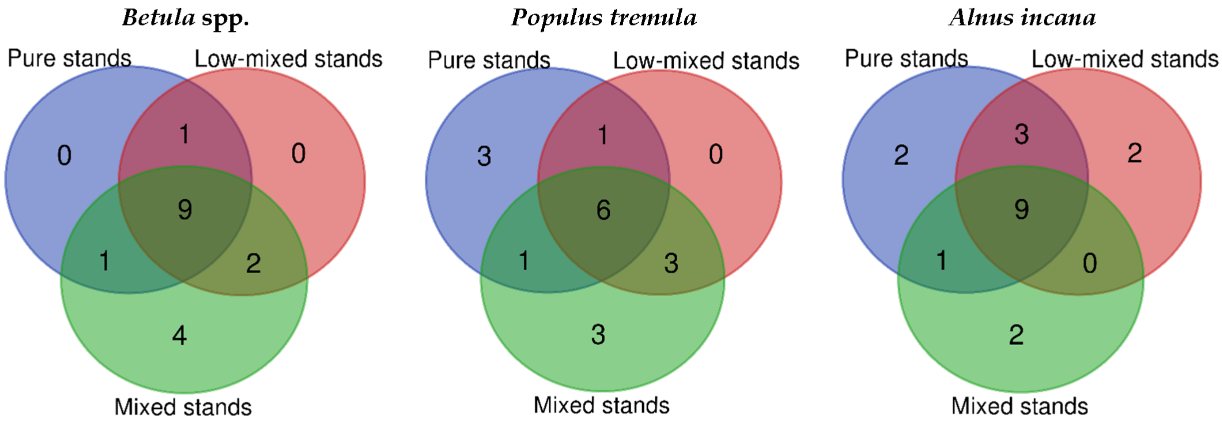

Figure 3. Venn diagram indicating the diversity of the selected predominant undergrowth species (*Corylus avellana*, *Padus avium*, *Sorbus aucuparia*, *Frangula alnus*, *Salix* spp., *Lonicera* spp., *Cornus* spp., *Ribes* spp., *Sambucus* spp., *Ameliancier* spp., *Tilia* spp., *Euonymus* spp., *Crataegus* spp., *Physocarpus opulifolius*, *Hippophae rhamnoides*, *Cerasus avium*, *Spiraea* spp., *Rhamnus cathartica*, *Rosa* spp., *Juniperus communis*, *Caragana* spp., *Syringa* spp., *Malus* spp., *Viburnum* spp.; non-identified species, assigned as 'other species' in the inventory database, were excluded) in the stands of different species compositional structures: pure, low mixed, and mixed stands, where dominant tree species occupy 86–100%, 66–85%, and less than 65%, respectively, represented by different colors.

The proportion of stands with no undergrowth was significantly higher in the pure *Betula* stands and this proportion decreased with increasing species admixture in the *Betula* stands (Figure 4). The proportion of the *Betula* forests with low-density undergrowth did not depend on stand species admixture, while the low-density undergrowth was less common in the mixed (8.9%) than in pure (10.7%) and low-mixed (10.9%) *Betula* stands. Medium density undergrowth was more common for the mixed *Betula* stands (44.4%), followed by low mixed stands (41.7%) and pure stands (36.0%). Dense underbrush was more common in pure *Betula* stands (43.5%) compared to the low mixed (40.5%) and mixed (40.6%) stands.

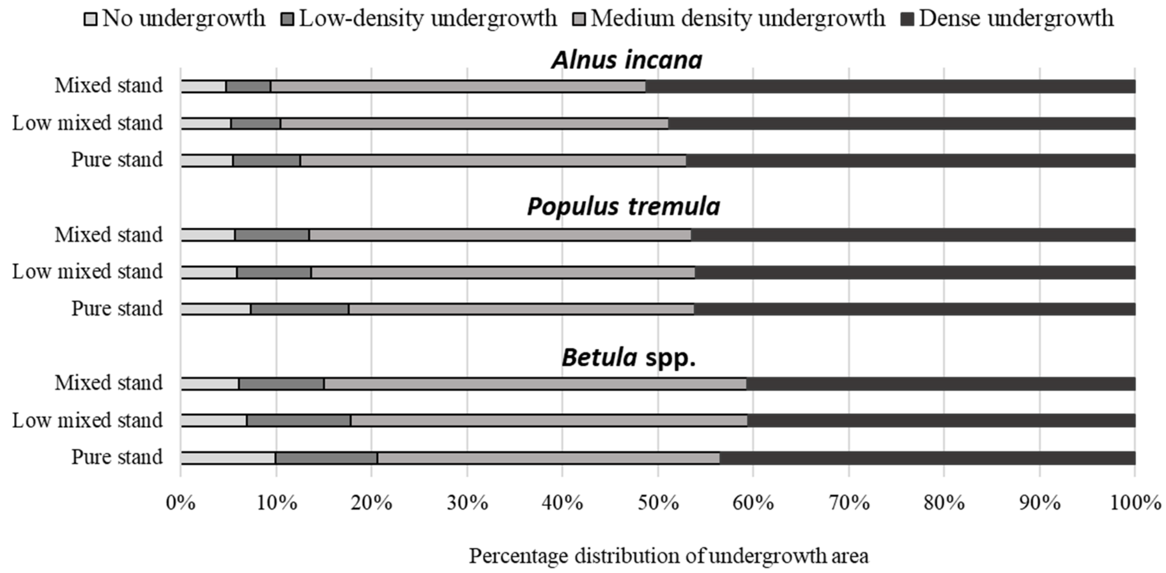

Figure 4. Percentage distribution of the undergrowth species areas, given for different undergrowth density categories (no undergrowth, low density—undergrowth species occupy less than 30%, medium density—31–60%, and dense undergrowth more than 60%) in the mixed (less than 65% of the dominant tree species), low mixed (66–85% of the dominant tree species), and pure (86–100% of the dominant tree species) stands.

There were no significant differences between the density of the undergrowth in the mixed and low mixed *Populus tremula* stands (Figure 4). However, the proportion of the pure *Populus tremula* stands with no undergrowth (7.3%) was higher than that of the mixed (5.9%) and low mixed (5.6%) stands. A higher proportion of low-density undergrowth was obtained in the pure (10.3%) than in the low mixed and mixed *Populus tremula* stands (7.7–7.8%). An admixture with other tree species did not change the proportion of the dense undergrowth in the *Populus tremula* stands. In the case of *Alnus incana* forests, the stands with no undergrowth were more common in the pure stands (5.4%) than in the mixed stands (4.7%) (Figure 4). The proportion of the *Alnus incana* stands with low-density undergrowth significantly decreased with increasing stand mixture (pure—7.1%^{C}, low mixed—5.2%^{B}, and mixed—4.6%^{A} stand). The proportion of the stands with medium density undergrowth did not depend on whether the *Alnus incana* stand was pure or mixed. The admixture with other tree species significantly increased the proportion of the dense undergrowth in the *Alnus incana* stand (47.0%^{C} pure, 48.8%^{B} low mixed, and 51.2%^{A} mixed stand).

The area of the predominant *Corylus avellana* undergrowth was significantly higher in the *Betula* and *Populus tremula* forests growing on highly fertile (Nf and Lf) than on very fertile (Šd, Nd, and Ld) forest site types (Table 4). However, the *Corylus avellana* area in the *Alnus incana* forests growing on highly fertile soil (Nf and Lf) was 2.5–2.6-times lower than in the *Betula* and *Populus tremula* forests representing similar forest site types. The lowest area of *Corylus avellana* was found in very fertile soils of a temporary over-moistured regime (forest site type Ld). The *Padus avium* undergrowth was less common in the *Betula* and *Populus tremula* forests on highly fertile (Nf and Lf) than on very fertile (Nd and Ld) forest site types. The area of *Padus avium* in the *Alnus incana* forests was similar in all forest site types. In all studied deciduous forests, the largest areas of the *Frangula alnus* undergrowth were obtained in the forest site type Ld, while the smaller areas were obtained in the forest site types Šd and Nd, and the smallest areas in the sites with the highest soil fertility (Nf and Lf). The *Sorbus aucuparia* undergrowth was the most common in the Nd, and less so in the Ld and Šd forest site types. The significantly lowest distribution areas of the *Sorbus aucuparia* undergrowth were obtained in the forest site types Nf (up to 1.0%) and Lf (up to 1.0%).

Table 4. Percentage distribution of the predominant undergrowth species area in *Betula* sp., *Populus tremula*, and *Alnus incana* stands growing in different forest site types. The values followed by different letters a, b, and c indicate statistically significant differences between different forest site types within each undergrowth species at $p < 0.05$.

Undergrowth Species	Forest Site Types				
	Šd*	**Nd**	**Ld**	**Nf**	**Lf**
	Distribution in *Betula* spp. forests (%)				
No undergrowth	5.6 ^{a}	9.2 ^{b}	7.0 ^{a}	7.9 ^{ab}	2.7 ^{c}
Corylus avellana	69.7 ^{a}	65.8 ^{ab}	64.4 ^{b}	82.4 ^{c}	82.5 ^{c}
Padus avium	12.0 ^{abc}	13.5 ^{c}	11.4 ^{b}	6.5 ^{d}	10.3 ^{a}
Sorbus aucuparia	5.3 ^{ab}	5.4 ^{b}	4.0 ^{a}	0.6 ^{c}	0.5 ^{c}
Frangula alnus.	4.1 ^{ab}	5.0 ^{b}	12.4 ^{c}	1.5 ^{d}	3.7 ^{a}
Salix spp.	0.4 ^{ab}	0.1 ^{bc}	0.6 ^{a}	0.0 ^{abc}	0.1 ^{c}
Other	3.0 ^{a}	0.9 ^{b}	0.2 ^{c}	1.1 ^{ab}	0.2 ^{c}
Total (ha)	1009	10,446	45,194	818	7509
	Distribution in *Populus tremula* forests (%)				
No undergrowth	8.3 ^{a}	6.7 ^{a}	6.1 ^{a}	1.3 ^{b}	2.8 ^{b}
Corylus avellana	66.9 ^{ab}	70.9 ^{b}	66.3 ^{a}	83.1 ^{c}	79.7 ^{c}
Padus avium	14.7 ^{ab}	14.4 ^{b}	13.1 ^{a}	13.1 ^{ab}	13.8 ^{ab}
Sorbus aucuparia	1.8 ^{a}	3.0 ^{a}	2.9 ^{a}	0.0 ^{b}	0.2 ^{b}
Frangula alnus.	3.3 ^{a}	3.6 ^{a}	10.8 ^{b}	2.1 ^{a}	3.0 ^{a}
Salix spp.	0.6 ^{ab}	0.3 ^{b}	0.6 ^{a}	0.0 ^{ab}	0.3 ^{ab}
Other	4.3 ^{a}	1.2 ^{b}	0.2 ^{c}	0.4 ^{bc}	0.2 ^{c}
Total (ha)	828	7869	21,163	467	4054

Table 4. *Cont.*

Undergrowth Species	Forest Site Types				
	Šd*	**Nd**	**Ld**	**Nf**	**Lf**
	Distribution in *Alnus incana* forests (%)				
No undergrowth	5.4 [a]	3.9 [b]	5.5 [a]	2.9 [ab]	4.0 [ab]
Corylus avellana	25.3 [a]	21.1 [b]	13.2 [c]	33.3 [ad]	31.6 [d]
Padus avium	57.1 [a]	64.6 [b]	65.7 [b]	56.9 [ab]	57.6 [a]
Sorbus aucuparia	0.9 [a]	3.7 [b]	1.5 [c]	1.0 [abc]	0.0 [d]
Frangula alnus.	7.7 [a]	4.8 [b]	11.0 [c]	5.9 [abc]	5.1 [b]
Salix spp.	2.4 [a]	1.1 [b]	2.7 [a]	0.0 [ab]	1.6 [ab]
Other	1.2 [a]	0.8 [ab]	0.3 [c]	0.0 [abc]	0.1 [bc]
Total (ha)	6916	8782	30,740	102	1076

* Šd—eutrophic/very fertile mineral soils on slopes (more than 15 degrees of slope); Nd—eutrophic/very fertile mineral soils (relatively high nutrient concentrations) of normal moisture; Ld—temporary over-moistened eutrophic/very fertile mineral soils; Nf—very eutrophic/highly fertile (very high nutrient concentrations) mineral soils of normal moisture, and Lf—temporary over-moistened very eutrophic/highly fertile mineral soils (more details are given in Table 1).

The percentage area of *Corylus avellana* increased significantly in all studied forests with increasing stand age: from 60.5%^{A} in the 7th age class to 86.1%^{E} in the 11th in the *Betula* stands; from 54.4%^{A} in the 5th age class to 79.7%^{E} in the 10th in the *Populus tremula* stands; and from 14.5%^{A} in the 5th age class to 24.8%^{C} in the 7th in the *Alnus incana* stand (Figure 5). On the contrary, the area of *Padus avium* decreased with increasing stand age: from 14.3%^{A} (7th age class) to 3.0%^{E} (11th age class) in the *Betula* forests; from 21.6%^{A} (5th age class) to 4.4%^{E} (10th age class) in the *Populus tremula* forests; and from 64.2%^{A} (5th age class) to 59.7%^{B} (7th age class) in the *Alnus incana* forests.

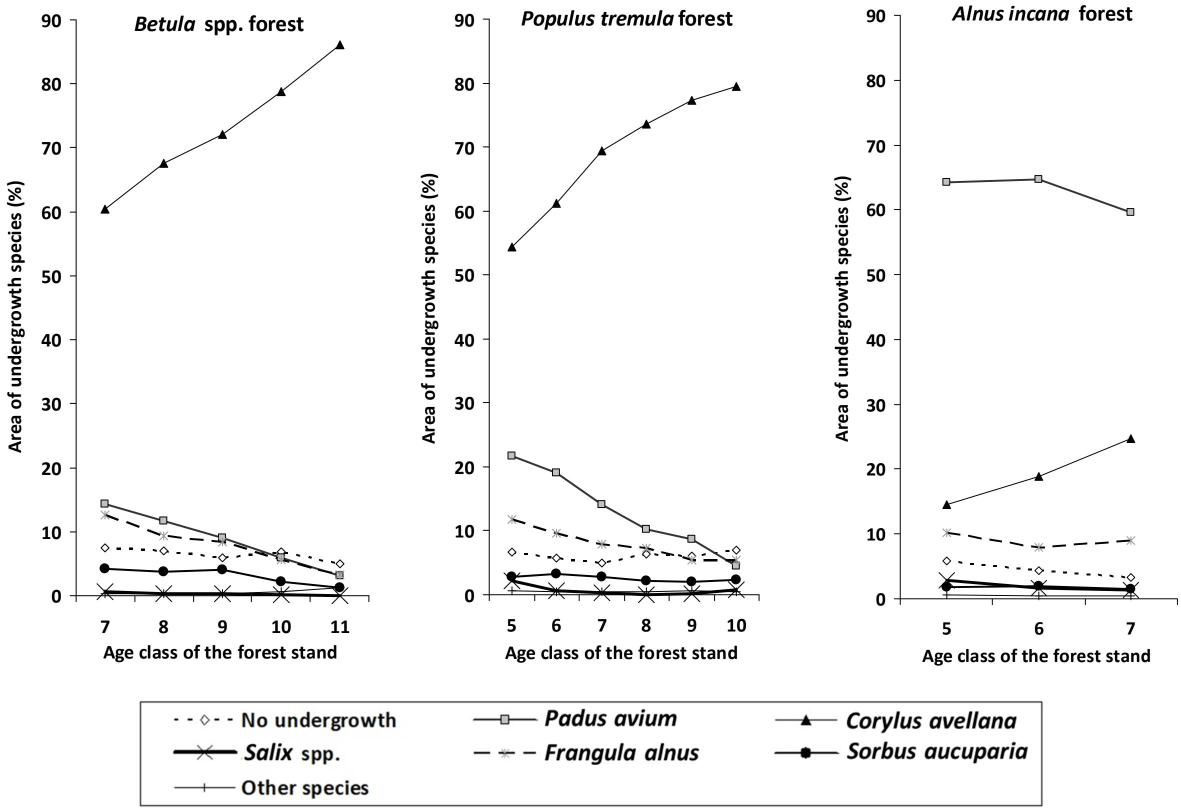

Figure 5. Changes in the undergrowth species areas in the *Betula* spp., *Populus tremula*, and *Alnus incana* forest stands, representing different tree age classes of the main stand story. The stand age structure shown on the *y*-axis means, for example, that age class 7 includes stands from 61 to 70 years old, age class 8 includes stands from 71 to 80 years old, etc.

In *Betula* forests, the area of *Sorbus aucuparia* undergrowth decreased significantly from 4.2%^{A} to 1.2%^{B}, but no similar trends were obtained for the *Populus tremula* and *Alnus incana* forests (Figure 5). The percentage area of *Frangula alnus* undergrowth decreased in the *Betula* (from 12.6%^{A} to 3.3%^{D}) and *Populus tremula* (from 11.7%^{A} to 5.3%$^{D, E}$) forests. The area of *Salix* spp. undergrowth decreased similarly in all studied stands of deciduous tree species: in the *Betula* forest from 0.7%^{A} to 0.0%^{B}; in the *Populus tremula* forest from 2.1%^{A} to 0.7%^{B}; and in the *Alnus incana* forest from 2.9%^{A} to 1.4%^{B}. The area of other predominant undergrowth species increased significantly from 0.3%$^{A, B}$ to 1.3%^{C} with the increasing age of *Betula* forests. The area with no undergrowth species decreased from 7.4%^{A} to 5.1%$^{B, C}$ with increasing *Betula* stand age, and from 5.9%^{A} to 3.3%^{C} with increasing *Alnus incana* stand age. However, no changes were obtained in the *Populus tremula* forests of different ages.

The study results showed an increase in the dense undergrowth area in the period from 61 to 100 years for the *Betula* stand, and from 41 to 70 years for the *Alnus incana* stand (Figure 6). Meanwhile, low and medium density undergrowth areas decreased with increasing *Betula* stands age. A similar decreasing trend of the medium density undergrowth was obtained for the *Populus tremula* (during the period from 41 to 100 years old) and for the *Alnus incana* forest stands (from 41 to 70 years old).

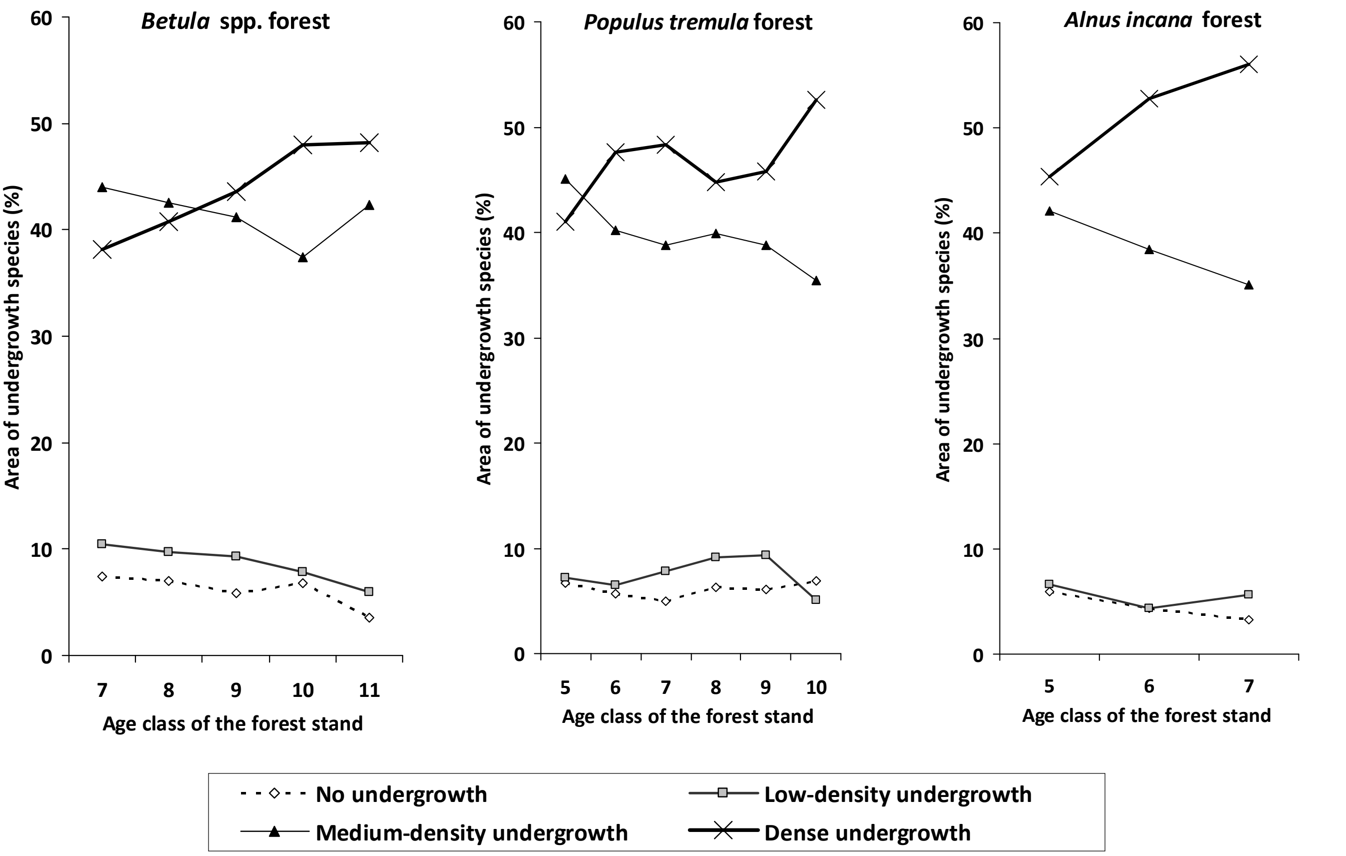

Figure 6. Changes in the undergrowth species areas in the *Betula* spp., *Populus tremula*, and *Alnus incana* forest stands, representing different tree age classes of the main stand story. The stand age structure shown on the *y*-axis means, for example, that class 7 includes stands from 61 to 70 years old, age class 8 includes stands from 71 to 80 years old, etc.

4. Discussion

Within managed forest ecosystems, a primary focus has been to enhance stand productivity by applying various silvicultural systems to the canopy trees of the dominant tree species. Very little data were found in the literature on how the undergrowth changes in naturally developing mature deciduous forests. An initial objective of this study was to identify the undergrowth species' composition and their distribution in the *Betula* spp. (*Betula pendula* and *Betula pubescens*), *Populus tremula*, and *Alnus incana* forest stands, which represent the pioneer deciduous tree species in the hemiboreal forest zone. The results of the present study indicated the most common undergrowth species, such as *Corylus avellana*, *Padus avium*, *Frangula alnus*, *Sorbus aucuparia*, and *Salix* spp. Among the undergrowth species, *Corylus avellana* and *Padus avium* were particularly abundant (see Table 2), and, potentially, the most important for the forest ecosystem's development. The predominant *Corylus avellana* undergrowth was identified in more than half of the *Betula* and *Populus tremula* stands. The *Corylus avellana* is an undergrowth species with a height of about 10 m, and generally grows as an understory species in mixed deciduous forests [24,26,27]. This undergrowth species is a highly adaptable pioneer species, relatively tolerant to seasonal drought or cool summers, cold winters, and even fire [28,29]. The importance of *Corylus avellana* undergrowth was also observed in the stands of other tree species [30]. The spread of both *Corylus avellana* and *Padus avium* is mainly determined by the internal biological properties, growth rate, height, and relatively high regeneration possibilities [26]. The *Corylus avellana* undergrowth, characterized by wide leaves and umbrella-shaped crowns, blocks the sunlight particularly well and creates unfavorable conditions for other species of trees, shrubs, and herbs [24]. Generally, *Corylus avellana* was a strong competitor in deciduous forests [31]. In the case of biodiversity, *Corylus* species is significantly associated with many other species in the forest ecosystem [32]. On the other hand, the *Padus avium* crown transmits more sunlight but is considered a strong competitor due to its ability to grow quickly in height, form curved stems, and grow stump sprouts [33].

The present study was designed to determine the effect of different forest site types (indicating levels of soil fertility and moisture, see Table 1) on the undergrowth species development. Overall, the dense and medium density undergrowth was very widespread in the deciduous stands on forest site types with nutrient-rich soils. The abundance of undergrowth in the deciduous forests clearly explains the relatively poor development of the understory and the second story trees [23]. The current study also found that *Corylus avellana* was more abundant on highly fertile forest soils, but no effect of soil moisture on this species' cover was obtained (see Table 4). These results reflect those of Ellenberg (1992), who indicated that the ecological behavior of *Corylus avellana* shows indifference concerning soil moisture [34]. Our study revealed that *Padus avium* was the most common undergrowth species in deciduous forests with very fertile mineral soils, regardless of soil moisture conditions (see Table 4). The previous studies indicated that *Padus avium* was commonly found on wet, and even flooded sites [33–35], or indicated that this species tolerates a wide variety of soil types [36]. Moreover, *Padus avium* was more demanding of nitrogen than *Corylus avellana* [34]. *Frangula alnus* was more common in the moist medium fertility sites (see Table 4). Due to their nutritional unattractiveness to deer, *Corylus avellana*, *Padus avium*, and *Frangula alnus* gain a competitive advantage in forests with large deer populations.

Another finding was that the distribution areas of *Sorbus aucuparia* undergrowth were rather common in the stands growing on very fertile soil with normal humidity, while rather uncommon in highly fertile sites, irrespective of whether they were of normal humidity or with temporary moisture excess (see Table 4). Generally, *Sorbus aucuparia* grows under a very wide range of growth conditions [34]. However, due to deer damage, intensive vertical growth, and sparse crown, this species is often considered a species that increases the vegetation diversity in forests, rather than a competing species [24,37]. The *Salix* spp. was more common in the undergrowth in sites with temporary moisture excess. In accordance with the present results, previous studies have shown that *Salix* spp. Is a light-demanding hygrophytic species that has a greater influence on the formation of stands in extremely wet soil conditions [34].

We found that the predominant *Padus avium* undergrowth was obtained in the *Alnus incana* stands (see Table 4), and this was also revealed by other authors [35]. The increased area of the predominant *Corylus avellana* undergrowth was obtained in the deciduous forest stands of *Betula* spp., *Populus tremula*, and *Alnus incana* with a higher admixture of other tree species (see Table 3). With the increase in the stand mixture, the frequency of *Padus avium* undergrowth decreased, and the proportion of *Corylus avellana* increased. This can be explained by the effect of *Betula* and *Populus tremula* admixture in *Alnus incana* stands. Previous studies have found that tree species admixture increased the richness and biomass of the understory species [38,39].

The analysis of the undergrowth species under the canopy in the stands of selected deciduous tree species showed that the area of *Corylus avellana* significantly increased, while the area of *Padus avium* decreased in all studied forests with increasing stand age (see Figure 5). These results corroborate the previous study's findings, which indicated that *Corylus avellana* could be present in mature natural forests, although often sporadically [40]. Other dominant undergrowth species such as *Sorbus aucuparia*, *Frangula alnus*, and *Salix* spp. showed a decreasing trend in the area with increasing age of the *Betula* spp. and *Populus tremula* stands up to approximately 100 years old, and *Alnus incana* stands up to 70 years old. These findings support previous observations, which showed that the density of *Frangula alnus* was higher in partial- and clearcut stands than in uncut stands [41]. Other authors indicated that competition for light limits the ability of *Frangula alnus* to persist in late successional stands [42].

Stands of *Populus tremula* and *Alnus incana*, and in some cases *Betula* spp., were characterized as forests of lower economic importance. However, there are various reasons for the preservation and expansion of these deciduous forests, including higher biodiversity and the occurrence of rare species compared to coniferous forests [31,43]. The non-management option of such forests can have several benefits, from increased forest biodiversity to an overall increase in the sustainability of the landscape of the area. Another option related to the forest management of the pioneer tree species could be an application of a forest management regime in the later development stages of the forest ecosystem, i.e., in mature and older stands. A previous study found weak to moderate negative correlations between the undergrowth and the density of the first and second tree layers of the canopy trees, and a very weak negative correlation between the undergrowth and the density of understory trees (small trees growing beneath the main canopy layer, which will reach the canopy level) and the stand age [23]. According to these relationships, optimal conditions should be created for forests to regenerate naturally. Based on the general trends in the forest development in Lithuanian hemiboreal forests, it can be assumed that these first-generation natural forests, growing on very fertile forest sites with dominant pioneer deciduous tree species, will be replaced by deciduous hardwood species such as *Quercus robur*, *Fraxinus excelsior*, etc. [15]. Therefore, further evaluation of shrub communities will also be very important. Sustainable forest regeneration depends on managing and optimizing the amount and density of competing vegetation, including undergrowth species. In this study, we identified that during the natural development of *Betula* spp. and *Populus tremula* stands, *Corylus avellana* undergrowth may dominate the forest. Similarly, the communities of *Padus avium* and *Corylus avellana* were common in the *Alnus incana* forests. The high dominance of these undergrowth species could interfere with the germination and growth of the desirable tree species. This may lead to the longer-term development of the *Corylus avellana* community without a forest stand cover. In addition to the forest ecological services, the stand productivity and biomass accumulation should be ensured by forming forest stands with a cover of the main tree species. Therefore, it is necessary to develop a silvicultural approach that would help the main tree species to compete successfully with the undergrowth layer and allow the desirable trees to replace the decaying first layer of the stand in time.

Overall, further research should be undertaken to explore the undergrowth development patterns under the current and projected warmer climates, as climatic conditions at the end of the century will become more suitable for almost all deciduous species, including *Betula pendula* and *Populus tremula* [44]. A reasonable approach would be to balance the management of older stands with their natural development.

5. Conclusions

The current study revealed that deciduous forests of *Betula* spp., *Populus tremula*, and *Alnus incana* have rich undergrowth species diversity with a dominance of the *Corylus avellana*, *Padus avium*, *Frangula alnus*, *Sorbus aucuparia*, and *Salix* spp. The obtained species were typical of hemiboreal forests under the northern part of the temperate climates. The stand compositional (pure, low mixed, and mixed stands) age structure in the pioneer deciduous forest stands and soil properties (soil fertility and moisture regimes) caused diverse changes in the undergrowth vegetation. The dense undergrowth with the predominant *Corylus avellana* was rather common in the *Betula* and *Populus tremula* stands on very fertile forest sites, while *Padus avium* was more abundant in the *Alnus incana* stands. Among all studied forest stands, significantly higher areas of dense undergrowth were obtained in the *Alnus incana* stands with a higher admixture of other tree species. However, the areas with no undergrowth or with low density undergrowth in the *Alnus incana* stands were significantly lower than in the *Betula* stands. The area of *Corylus avellana* significantly increased, while the area of *Padus avium* decreased in all studied forests with increasing stand age. Other dominant undergrowth species—*Sorbus aucuparia*, *Frangula alnus*, and *Salix* spp.—decreased with the increasing age of the *Betula* spp. and *Populus tremula* stands.

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Conflicts of Interest: The authors declare no conflict of interest.

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