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The lower storeys of main tree species in deciduous pioneer tree stands of fertile forest sites: case of Lithuania

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Abstract

Forest ecosystems face challenges of climate change and the pressure of economic activity on biodiversity. As European policies turn into Green Deal, ecological forestry systems, which aim to increase or at least not reduce biodiversity while maintaining high forest productivity, are becoming particularly relevant. This study examines distribution regularities of the lower storeys of main tree species in fertile not wet habitats of forest communities composed of pioneer deciduous tree species, the understanding of which will allow the development of forestry systems that exploit the natural forest regeneration potential. We used stand-wise forest inventory data on *Betula* spp., *Populus tremula*, *Alnus incana* mature and overmatured stands. We analysed how lower storeys are distributed in the stands of different tree species according to soil conditions, the age, stocking level and mixture. We found that most of stands are not in the second story and understory, from which new stands can be formed. *Betula* forests have the greatest potential for regeneration, and *Alnus incana* forests have the lowest one. The most important species of the second story and understory is *Picea abies*, rarer *Fraxinus excelsior* and *Tilia cordata*, other species are more random. With an increasing forest mixture, the second story and understory are found more often. To reduce clear-cutting in the fertile forests of pioneer tree species in forestry, we need to focus on measures to allow the development of lower storeys of the major climax tree species.

Keywords: ecological forestry, forest succession, fertile forest site type, pioneer tree stands, temperate hemiboreal forests

Introduction

Forest ecosystems are facing the challenges of climate change: rising average temperatures, changes in the humidity regime, more frequent and larger-scale extreme natural phenomena. The forest is also an important means of capturing and sequestering greenhouse gases. Another important challenge for forests is the loss of biodiversity. Intensive, clear-felling forestry systems put significant pressure on biodiversity (Kok et al. 2018). As European policies turn Green Deal way, sustainable, ecological forestry systems that increase or at least do not reduce/sustain biodiversity while maintaining high forest productivity, including carbon sequestration, become particularly relevant. Understanding the natural growth of forests is a prerequisite for the development of sustainable forestry (Bengtsson et al. 2012). The basis of ecological forestry (Pro Silva 2012) is partial simulation of natural processes in forests (Gamborg and Larsen 2003). The stand is forming by establishing conditions for the formation of lower storeys, their growth and gradual replacement of the main storey. Knowledge of the distribution of lower storeys and the patterns of development is required for the promotion of ecological forestry systems.

Regularities of natural development of Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* L.) infertile forests were studied in Lithuania in 2003–2007 (LMI 2008). Subsequently, the research on the development processes of fertile stands was extended: it was found that the naturally developing of woodsorrel-nemorose and wood sorrel *Picea abies* stands (Nc and Lc) have a first stand with slow decomposing, a second *Picea abies* storey in almost all stands and further *Picea abies* greening, which indicates the formation of *Picea abies* stands of various ages (Mikšys et al. 2013). As the uneven-aged of *Picea abies* stands increases, as well as the productivity and humidity of site types, the mixture of stands increases: mixed soft deciduous stands with a group arrangement of trees develop. Processes of self-recovery in most fertile soft deciduous stands, where the emergence of *Picea abies* understorey is weaker, have been insufficiently studied (Mikšys et al. 2013).

In traditional forestry systems focused on timber production, at the end of rotation period after clear-cutting, or after spontaneous catastrophic changes, the forest is regenerated artificially or left to selfregeneration. Such afforestation has long-term effects on biodiversity: apparent removal of woody vegetation, changes in herbaceous vegetation when light-demanding species spread, long-term effects on arthropod species composition and abundance (Siira-Pietikäinen and Haimi 2009, Sławski and Sławska 2019). Felling sites provide favourable conditions for the regeneration of pioneer tree species. Their rapid spread is associated with a large quantity of seeds and intensive growth of young trees (Fischer et al. 2002, Hynynen et al. 2010). European aspen (*Populus tremula* L.) and grey alder (*Alnus incana* L.) regenerate abundantly from stump shoots and root suckers (Navasaitis et al. 2003). These result in a high prevalence of stands of pioneer tree species in fertile habitats. Felling also provides favourable conditions to shrubs that are capable of growing stump shoots and root suckers, these shrubs can spread and compete with tree species (Deiller et al. 2003, Hamberg et al. 2015). Vegetatively recovering species in forest plantations bring about strong competition for planted tree species.

Forests of highly fertile habitats in the temperate mixed forest zone are characterized by frequent and complex changes (Karazija 2008). Many models of forest succession are described in the literature, the main ones being: parallel, cyclic, divergent, convergent, and individual (Frelich 2002). The course of change of forest communities is determined by biological and ecological properties of trees, primarily the need for light and soil conditions, growth rate, longevity and resistance to adverse effects (Karazija 2008). Tree species can be divided into 4 succession categories according to individual species characteristics and life history dynamics: gap colonizer (pioneer), gap competitors, forest colonizer, forest competitors (Petrokas et al. 2020). The development pattern of a particular forest is determined by the potential of the main tree species under specific climatic conditions and the regime of disturbances affecting the forest, such as human activities, extreme events and the prevalence of herbivores (Falinski 1988, Petrokas et al. 2020).

Under the stand cover, there are better conditions for the recovery of shade-tolerant tree species, but in the mixed broadleaved-coniferous forest zone there is a lack of tree species that could take advantage of fertile forest site types (Bush and Ievinj 1984). Adverse edaphic (forest litter and humus properties) conditions are unfavourable for the recovery of *Picea abies* (Karazija 2008). Oak (*Quercus robur* L.), European ash (*Fraxinus excelsior* L.), Norway maple (*Acer platanoides* L.) and European aspen (*Populus tremula*) recovery is negatively affected by a large (LRAM 2021) deer population (Belova et al. 2000, Navasaitis et al. 2003). *Fraxinus excelsior* is vulnerable to fungal diseases (Baral and Bemmann 2014). Small-leaved lime (*Tilia cordata* Mill.) is a shade-tolerant (Ellenberg et al. 1991) and drought-resistant species. *Tilia cordata* seed germination requires specific soil moisture conditions, but this species recovers well vegetatively and therefore it commonly grows in groups (De Jaegere et al. 2016). In Europe, there are 3 native species of elm (*Ulmus* spp.): the wych elm (*Ulmus glabra* Huds.) which is adapted to grow in drier, sloping sites, the European white elm (*Ulmus laevis* Pall.) is a tree of wetlands and river banks, and the field elm (*Ulmus minor* Mill.). However, all these species are undoubtedly associated with fertile and highly fertile site types (Napierał-Filipiak et al. 2021). *Ulmus* species are vulnerable to Dutch elm disease (*Ophiostoma novo-ulmi* Brasier.) and therefore their development is limited (Martin et al. 2019, Napierał-Filipiak et al. 2021). The borders of the ranges of the common hornbeam (*Carpinus betulus* L.) and the field elm cross the territory of Lithuania (Navasaitis et al. 2003). In the absence of the main tree species in the later stages of succession, pioneer species seeds such as silver birch (*Betula pendula* Roth.), downy birch (*Betula pubescens* Ehrh.) and *Populus tremula* can be restored due to the wide dispersion of seeds (Žemaitis et al. 2019). The storey of shrubs (underbrush) may play a decisive role in the formation of a stand, for example, common hazel (*Corylus avellana* L.) prevails in mature forest of *Quercus robur* (Karazija 2005), the bird cherry (*Padus avium* Mill.) grows often together with *Alnus incana* (Nestby 2020). Economic activity or natural disturbances make comfortable conditions for light demanding species of trees and shrubs in thinned stands or gaps (Kreyer and Zerbe 2006). The change of stands influences the species composition of herbaceous plant, but due to the different meteorological conditions of individual years, fluctuations in the species composition are strong (Karazija 2005).

Due to climate change, the migration of tree species from the south-west is likely, with more favourable conditions for deciduous tree species (except *Alnus incana*) and worse for conifers. It is most likely that suitable conditions in Lithuania will be deleloped primarily for European beech (*Fagus sylvatica* L.), as well as for field maple (*Acer campestre* L.), sycamore maple (*Acer pseudoplatanus* L.), black poplar (*Populus nigra* L.) and wild cherry (*Prunus avium* L.) (Ozolinčius et al. 2014). The main native tree species have a sufficiently high potential to adapt to the changing climatic conditions due to the existing genetic diversity (Verbylaitė et al. 2019).

The study represents forests in Lithuania. As there is not a sufficient number of highly fertile habitat research sites, a stand-wise forest inventory was used (VMT 2021).

The aim of the study is to find out how the middle storeys of stand pioneer tree species of highly fertile habitats develop in the context of local natural conditions and the

Table 1. Distribution of *Betula* spp., *Populus tremula* and *Alnus incana* stands in very fertile dry and humid site types in Lithuania in 2019

Forest site type	*Betula* spp.			*Populus tremula*			*Alnus incana*		
	Total, ha	Mature, ha	Mature, %	Total, ha	Mature, ha	Mature, %	Total, ha	Mature, ha	Mature, %
Šd	1,397	1,030	74	1,083	915	85	8,355	6,959	83
Nd	17,467	10,885	62	12,052	8,220	68	13,937	8,876	64
Ld	97,693	47,547	49	43,810	22,275	51	64,986	31,023	48
Nf	1,285	945	74	965	576	60	202	105	52
Lf	14,258	8,293	58	8,334	4,420	53	2,920	1,102	38
Total:	132,099	68,700	52	66,244	36,406	55	90,400	48,065	53

Note: the forest site type codes (Vaičys et al. 2006, VMT 2021): Š stands for slopes (> 15°), N stands for normal humidity, L stands for temporarily overmoisture (gleyic), d stands for very fertile, and f stands for the most fertile soils.

history of forest management. Two main objectives can be distinguished: 1) To determine a prevalence and a diversity of the second storey and understorey of stands; 2) To analyze interrelationships between indicators of the main and lower storeys of stands.

Materials and methods

Study area

The study covers forests within the territory of Lithuania, on the eastern shore of the Baltic Sea (53°54´–56°27´ N; 20°56´–26°51´ E), their elevations do not exceed 300 m a.s.l. BES. The average annual air temperature is 6.9°C (monthly: –3.2–17.9°C), annual precipitation is 695 mm (LHMT 2021).

The sample of the study: birch (silver birch, *Betula pendula* Roth., and downy birch, *Betula pubescens* Ehrh., were accounted together as *Betula* spp.), European aspen (*Populus tremula* L.) and grey alder (*Alnus incana* L.) stands of highly fertile forest stands (61, 41, 41 years old) and older ones, respectively (Table 1). Stand-wise forest inventory data (updated in 2019) was used (Kuliešis et al. 2010, VMT 2021). Since the native classification of forest sites was used in the stand-wise forest inventory data (Vaičys et al. 2006, VMT 2021), therefore we used it in the analysis.

Data collection

Taxation indicators were used for the analysis as follows: predominant tree species, plot area, site type, age class, species composition and stocking level of the first storey, species composition and stocking level of the second storey, species composition and density of understorey (trees up to 4 m high which could replace the main storey of stand), density of underbrush. Primary data processing was performed in MS Excel (2016) spreadsheet. Plots where performed economic measures were recorded during the decade (final felling without clear cutting, intermediate, sanitation and other fellings, partial afforestation) were rejected.

The stands were grouped:

1. According to the mixing of the first storey into: pure (predominant tree species is 9–10 tenths or 86–100%), low mixed (7–8 tenths or 66–85%) and mixed (≤ 6 tenths or ≤ 65%).
2. By species composition of the second storey: stands with the predominance (≥ 5 tenths or > 45%) of one tree species, by predominant tree species, stands with a mixed second storey and stands without the second storey.
3. According to the species composition of the understorey (similar to the second storey).

Data analysis

The graphic part was produced using MS Excel (2016). Frequency tables of stand area distribution according to tax indicators (their percentage) were created with IBM SPSS Statistics 23 software package (IBM 2015). A cross-tabulation was utilized to analyze the data obtained, χ^2 (chi-square test) and *z*-test (various letters indicate significant differences in superscript) were used for comparison (the significance level $\alpha = 0.05$ adjusted according to the Bonferroni method).

Assumptions of the chi-square criterion (expected frequencies for each cell are at least 1 and they should be at least 5 for 80% of the cells) determine data combination in some cases. Analysing the understorey by habitats, *Betula* spp., *Populus tremula*, *Alnus incana* and *Alnus glutinosa* were combined into a group of soft-leaved deciduous pioneer trees. Also, the understorey of broad-leaved tree species (except *Fraxinus excelsior*) was analysed by combining them into a group.

The nonparametric Kendall tau-b correlation ($\alpha = 0.05$) was used to check the relationship between the density and age of stand elements.

Results

We found significant linear relationships between indicators of individual stand elements and age (Table 2). Rank correlations of Kendall's tau-b show that as the age of the stand increases, the stocking level of the first storey decreases (weak association), but the stocking level of the second storey increases (moderate association). The density of the underbrush increases with decreasing the stocking level of the second storey (moderate association) and the stocking level of the first storey (weak asso-

Table 2. Linear relationships between main indicators of forest storeys. Kendall's tau-b correlations

	Stocking level of the 1st storey	Stocking level of the 2nd storey	Underbrush density	Understorey density	Age class
Stocking level of the 1st storey	1.0	0.008**	**–0.109****	0.027**	**–0.110****
Stocking level of the 2nd storey	0.008**	1.0	**–0.270****	0.086**	**0.278****
Underbrush density	**–0.109****	**–0.270****	1.0	–0.031**	–0.031**
Understorey	0.027**	0.086**	–0.031**	1.0	0.088**
Age class	**–0.110****	**0.278****	–0.031**	0.088**	1.0

Note: ** Correlation is significant at the level of 0.01 (2-tailed).

ciation). Other found significant linear relationships were very weak.

Composition of the understorey

The amount of understorey in the very fertile deciduous stands is very low (Figure 1).

The understorey of *Picea abies* is the most common (on average 8.1%), less of *Fraxinus excelsior* (on average 2.7%), the average frequency of understorey of other tree species reaches up to 0.5%, but the analysis of the stands according to individual indicators reveals regularities. The highest frequency of stands without understorey was in *Alnus incana* stands, 92.4%^{B}, in *Populus tremula* stands it was significantly less, 85.5%^{C}, the lowest frequency of stands without understorey was observed in the *Betula* spp. stands, 83.1%^{A} (^{1} $\chi^2 = 3200.9$; $df = 8$; $\alpha < 0.001$). We found that with the increase of stand mixture in the stands of all studied tree species, the frequency of stands without understorey decreases: 86.1%^{C} in the pure *Betula* spp. stands, 83.7%^{B} in the low mixed ones, and 82.0%^{A} in the mixed stands (^{2} $\chi^2 = 241.2$; $df = 18$; $\alpha < 0.001$); 93.4%^{B} in pure *Alnus incana* stands that is significantly more than in low mixed, 92.2%^{A}, and mixed ones, 91.5%^{A} (^{3} $\chi^2 = 174.2$; $df = 18$; $\alpha < 0.001$); 88.5%^{C} in pure *Populus tremula*, 86.6%^{B} in low mixed ones, 84.5%^{A} (^{4} $\chi^2 = 104.7$; $df = 18$; $\alpha < 0.001$) in mixed ones. Analyzing the distribution of understorey according to forest site types, we detected that the least common understorey is found in Šd site type: 90.4%^{A} of stands without understorey in *Betula* spp. stands, in *Alnus incana* – 97.2%^{B}, in *Populus tremula* – 94.3%^{C} ($\chi^2 = 219.4$; $df = 8$; $\alpha < 0.001$). We found least stands without understorey by site types: in the *Betula* spp. Ld stands is 83.0%^{C} and Lf is 83.2%^{C}, when Šd is 90.4%^{A}, Nd is 84,8%^{B}, and Nf is 86.7%^{A,B,C} (^{5} $\chi^2 = 1235.9$; $df = 16$; $\alpha < 0.001$); in the *Alnus incana* Nf stands is 85.1%^{C}, Lf is 89.6%^{C} and Ld is 91.7%^{C}, when Šd is 97.2%^{A}, and Nd is 92,7%^{B} (^{6} $\chi^2 = 825.9$; $df = 16$; $\alpha < 0.001$); in the *Populus tremula* Lf stands is 84.7%^{C} and Ld is 85.6%^{C,D} when Šd is 94.3%^{A}, Nd is 87,2%^{B}, and Nf is 90.1%^{A,B,D} ($\chi^2 = 499.3$; $df = 16$; $\alpha < 0.001$).

The highest frequency of *Picea abies* understorey was found in *Betula* spp. stands, 10.9%^{A}, on the average, significantly less in the *Populus tremula* stands, 8.7%^{C}, and the least in the *Alnus incana* stands, 3.7%^{B} (^{1}). Analyzing by stand mixture, the frequency of *Picea abies* understorey was found to be lower in pure stands than in mixed stands (^{2}). 8.5%^{B} in the pure *Betula* spp. stands, which is significantly less than in the low mixed, 10.9%^{A}, and mixed stands, 11.5%^{A}; in the pure *Alnus incana* stands is 2.9%^{B}, which is significantly less than in the low mixed, 4.1%^{A}, and mixed ones, 4.3%^{A} (^{3}); in the *Populus tremula* stands is 7.3%^{B} in pure and 8.1%^{B} in low mixed ones, which is significantly less than in the mixed ones, 9.2%^{A} (^{4}). Judging *Picea abies* understorey by site types, the most was found in Ld – 9.3%^{C}, the least in Šd, 1.8%^{A}. The Nf, 4.9%^{D}, Lf, 5.6%^{D}, and Nd, 7.3%^{B}, site types were in the intermediate position (^{7} $\chi^2 = 2633.9$; $df = 16$; $\alpha < 0.001$). In the stands of different predominant tree species, regularities of the distribution of the understorey of *Picea abies* by site types were similar.

The highest frequency of the understorey *of Fraxinus excelsior* (Figure 2) was found in the *Betula* spp. stands, on average 3.2%^{A}, significantly less in the *Populus tremula* stands, 2.8%^{C}, the least in the *Alnus incana* stands, 2.1%^{B} (^{1}). No significant differences in the frequency of

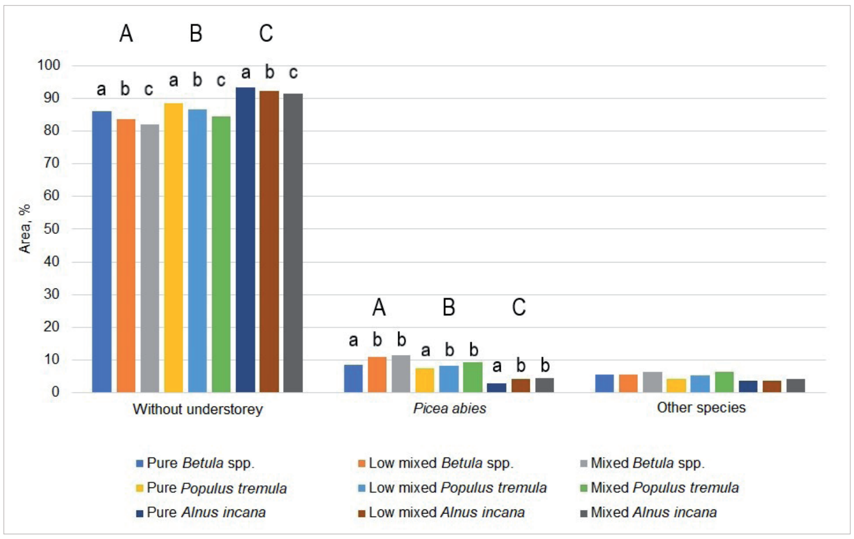

Figure 1. Distribution of understorey in the *Betula* spp., *Populus tremula* and *Alnus incana* stands of different composition

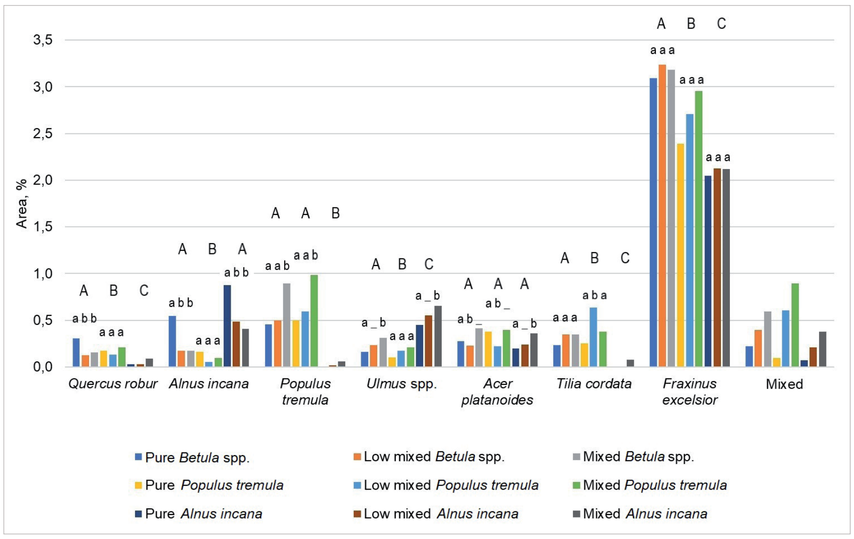

Figure 2. Distribution of predominant understorey tree species in the *Betula* spp., *Populus tremula* and *Alnus incana* stands of different composition

the *Fraxinus excelsior* understorey were found in the analysis of stand mixture. Judging by forest site types, the most *Fraxinus excelsior* understoreys was found in Lf forest site, 7.0%^{D}, significantly less in Nf, 3.2%^{C}, and Ld, 2.7%^{C}, even less in Nd, 1.8%^{B}, and the least in Šd, 0.4%^{A} ([7]). The distribution of the understorey of *Fraxinus excelsior* by habitats was similar in the stands of different tree species.

The understorey of *Populus tremula* in the mixed *Betula* spp. forests (0.9%^{A}) was found more often than in the low mixed and pure ones (0.5%^{B} and 0.5%^{B}; [2] respectively). In the *Populus tremula* stands the trend was the same: in the mixed (1.0%^{A}) more often than in low mixed and pure (0.6%^{B} and 0.5%^{B}; [4] respectively), the incidence of the *Populus tremula* understorey in the *Alnus incana* stands was less than 0.1%. The *Alnus incana* understorey was more frequent in the pure *Betula* spp. stands (0.6%^{B}) than in the low mixed and mixed ones (0.2%^{A} and 0.2%^{A}, respectively; [2]). The trend of the *Alnus incana* stands was the same in the pure (0.9%^{B}) than in low mixed and mixed (0.5%^{A} and 0.4%^{A}, respectively; [3]), the frequency of the understorey of *Alnus incana* in the *Populus tremula* stands was about 0.1%. Only isolated cases of the *Alnus glutinosa* understorey have been identified. It was found that soft deciduous understorey is mostly present in Nf, 2.7%^{D}, and Lf, 2.2%^{D} site types, the frequency decreases significantly with decreasing fertility and moisture (Ld is 0.8%^{C}, Nd is 0.5%^{B}, and Šd is 0.2%^{A} [7]).

Regardless of predominant tree species, more understoreys of *Acer platanoides* was found in the mixed (0.4%^{A}) than in low mixed and pure (0.2%^{B} and 0.2%^{B}, respectively) stands ([7]). The understorey of *Tilia cordata* is more common in the mixed and low mixed (0.3%^{A} and 0.3%^{A}, respectively) stands than in the pure (0.1%^{B}) stands ([7]), regardless of mixture in the *Betula* spp. stands, 0.3%^{A}, in the *Populus tremula* stands, 0.4%^{C}, and only isolated cases in the *Alnus incana* stands, less than 0.1%^{B} ([1]). The understorey of *Ulmus* was significantly higher in the mixed *Betula* stands (0.3%^{A}) than in the pure ones (0.2%^{B}; [2]). In the *Populus tremula* stands, there were 0.2% frequency of the understorey of *Ulmus,* on the average, and differences in stand mix did not affect the distribution of stands ([4]). The *Ulmus* understorey occurs mostly in the *Alnus incana* stands (0.5%, on the average): in the mixed stands, 0.7%^{A}, was more frequent than in the pure ones (0.4%^{B}; [3]). In the *Betula* spp. forests, broad-leaved understorey was found more often in the dry site type stands (Šd is 2.0%^{A}, and Nd is 2.7%^{A}) than in humid ones (Ld is 1.0%^{B}, and Lf is 0.9%^{B}); the frequency in Nf site type (1.7%$^{A, B}$) did not stand out significantly ([5]). In the *Alnus incana* stands, the broadleaf understorey was more frequent in the Nd (2,0%^{B}) than in humid forest sites (0.4%^{C} in Ld, and 0.6%^{A,C} in Lf ones), the Nf (6.9%^{D}) site type was markedly different due to the dominance of *Ulmus* species, 1,5%^{A,B} ([6]) in Šd ones. In the *Populus tremula* stands, broadleaf understorey was also more frequent in the Nd site type (1.9%^{B}) than in the humid one (1.2%^{A} in the Ld , and 1.0%^{A} in the Lf ones) and the Nf one (0.0%^{A}). It did not differ significantly at the slope site (0.8%$^{A, B}$ in the Šd site type; [6]).

Prevalence of the second storey

The 2nd storey was found more often in very fertile soft deciduous stands than the understorey, *Picea abies* also predominated here (24.1%, on the average) (Figure 3). The 2nd storey of *Tilia cordata* was found in 1.3% stands, the average frequency of other tree species was up to 0.6%.

The highest frequency of stands without the 2nd storey in the *Alnus incana* stands was 95.5%^{B}, less in the *Populus tremula* significantly, 71.0%^{C}, and the lowest frequency in *Betula* spp. Stands – 55.4%^{A} ([8] $\chi^2 = 22366.8$; $df = 10$; $\alpha < 0.001$). With the increase of stand mixture in the stands of all studied tree species, the frequency of stands without the 2nd storey decreased: 60.2%^{C} in the pure *Betula* spp. stands, 53.7%^{B} in the low mixed stands, and 55.1%^{A} in the mixed stands ([9] $\chi^2 = 372$; $df = 10$; $\alpha < 0.001$); 97.4%^{C} in the pure *Alnus incana*, 94.9%^{B} in the low mixed, and 94.1%^{A} in mixed stands ([10] $\chi^2 = 242.1$; $df = 10$; $\alpha < 0.001$); 76,0%^{C} in the pure *Populus tremula* stands, 71.8%^{B} in low mixed, and 69.8%^{A} in mixed ones ([11] $\chi^2 = 126.4$; $df = 10$; $\alpha < 0.001$). Analyzing the distribution of the 2nd storey according to forest site types, it was found that the 2nd storey is occured the least in the Šd site type (96.5%^{A} without the 2nd storey). Frequency of the 2nd storey increases with increasing moisture and fertility of site types (Table 3).

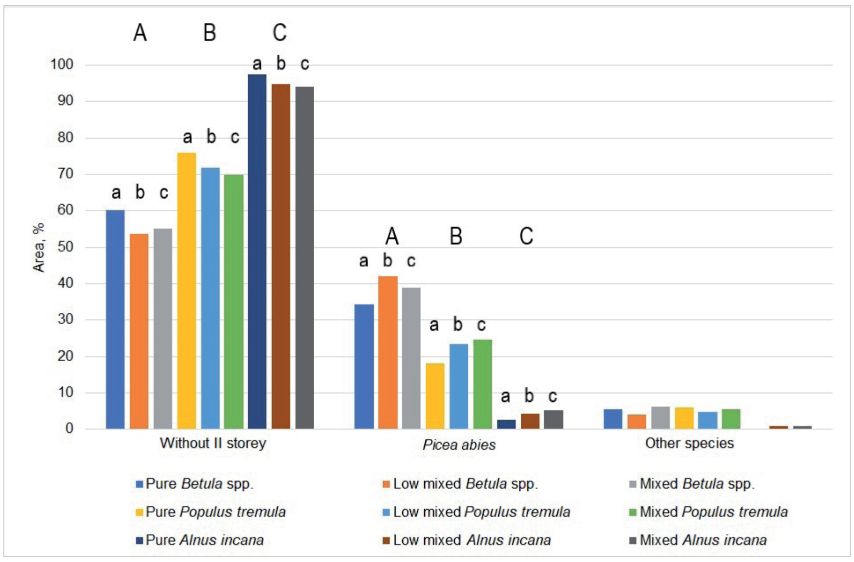

Figure 3. Prevalence of the 2nd storey in the *Betula* spp., *Populus tremula* and *Alnus incana* stands of different composition

Table 3. Distribution of predominant tree species of the 2nd storey in stands of different forest site types ($\chi^2 = 7429.6$; $df = 44$; $\alpha < 0.001$)

Tree species	Area (ha, %) by forest site type [12]					Total
	Šd	Nd	Ld	Nf	Lf	
Without 2nd storey	$8,445_{a}$	$21,517_{b}$	$66,359_{c}$	$1,014_{d}$	$8,575_{c}$	105,910
	96.5%	79.4%	68.3%	73.1%	67.9%	72.1%
Picea abies	181_{a}	$4,318_{b}$	$27,568_{c}$	278_{d}	$3,056_{e}$	35,401
	2.1%	15.9%	28.4%	20.0%	24.2%	24.1%
Populus tremula	2_{a}	$32_{a, b}$	254_{c}	$4_{b, c, d}$	89_{d}	381
	0.0%	0.1%	0.3%	0.3%	0.7%	0.3%
Alnus incana	4_{a}	35_{a}	393_{b}	15_{c}	60_{b}	507
	0.0%	0.1%	0.4%	1.1%	0.5%	0.3%
Quercus robur	1_{a}	76_{b}	55_{a}	$1_{a, b}$	17_{b}	150
	0.0%	0.3%	0.1%	0.1%	0.1%	0.1%
Acer platanoides	21_{a}	159_{b}	118_{c}	11_{b}	7_{c}	316
	0.2%	0.6%	0.1%	0.8%	0.1%	0.2%
Tilia cordata	29_{a}	219_{b}	$1,207_{c}$	35_{d}	475_{d}	1,965
	0.3%	0.8%	1.2%	2.5%	3.8%	1.3%
Ulmus spp.	$23_{a, b}$	114_{b}	47_{c}	$4_{a, b}$	$13_{a, c}$	201
	0.3%	0.4%	0.0%	0.3%	0.1%	0.1%
Carpinus betulus	33_{a}	515_{b}	345_{a}	9_{a}	21_{c}	923
	0.4%	1.9%	0.4%	0.6%	0.2%	0.6%

Note: [12] Explanation of forest site type codes (Vaičys et al. 2006, VMT 2021): Š – slopes (> 15°), N – normal humidity, L – temporarily excess moisture (gleyic), d – very fertile, f – the most fertile soils.

The highest frequency of the *Picea abies* 2nd storey was determined in the *Betula* stands, on average $39.1\%^{A}$, significantly less in *Populus tremula* stands, $23.6\%^{C}$, and the lowest in *Alnus incana* stands, $3.9\%^{B}$ ([8]). Analyzing according to stand mix, the frequency of the 2nd storey was found to be lower in the pure stands than in mixed ones: $34.3\%^{C}$ in pure *Betula* spp., $42.1\%^{B}$ in low mixed, and $38.8\%^{A}$ ([9]) in mixed stands. In the pure *Alnus incana* stands, it was found to be $2.5\%^{C}$, less in low mixed ones, $4.3\%^{B}$, and the least in mixed ones, $5.1\%^{A}$ ([10]). Analogous differences were also significant in *Populus tremula*: $18.1\%^{C}$ in the pure stands, $23.4\%^{B}$ in low mixed, and $24.7\%^{A}$ in mixed ones ([11]). The highest frequency of the *Tilia cordata* 2nd storey was found in the *Populus tremula* stands, $2.3\%^{C}$, less in *Betula* spp., $1.8\%^{A}$, and only sporadically, $<0.1\%^{B}$, were found in *Alnus incana* ([8]). Assessing the distribution of the *Tilia cordata* 2nd storey in the stands of different mixture, no clear trends were found.

Analyzing the distribution of the 2nd storey of all tree species (except *Picea abies*) according to the predominant tree species, stand mixture and site types due to low frequency, we found that the data did not fit the assumptions of the chi-square test, therefore they were assessed by mixture and site types but not according to the dominant tree species. Judging by forest site types, the highest frequency of stands without the 2nd storey was in slopes, and the lowest in "L" hygrotope (Table 3). The lowest frequency of spruce 2nd storey was determined in the Šd ($2.1\%^{A}$) site in all stands, the highest in the Ld ($28.4\%^{C}$) one. In the *Populus tremula* stands a more frequent 2nd storey of *Picea abies* was observed in the humid forest site types: $29.9\%^{C}$ (Ld) > $12.5\%^{B}$ (Nd), $18.1\%^{D}$ (Lf) > $11.3\%^{B}$ (Nf) ($\chi^2 = 1893.8$; $df = 20$; $\alpha < 0.001$).

The 2nd storey of *Tilia cordata* was more common in more humid and more fertile site types, the rarest on slopes (Table 3). The 2nd storey of *Populus tremula* was more often found in humid sites, *Alnus incana* in more fertile. The 2nd storey of *Acer platanoides* and *Ulmus* was more common in the normal irrigation site types, *Quercus robur* in the Nd site type, and *Betula* spp. in the drier and less fertile site types. The 2nd storey of *Fraxinus excelsior* was not found in slopes and was eliminated from analysis because did not fit assumptions of the chi-square criterion.

A trend was found when forest mixture increased, the frequency of the *Populus tremula*, *Alnus incana*, *Tilia cordata* and *Carpinus betulus* 2nd storey increased, and the frequency of the *Quercus robur* and *Acer platanoides* 2nd storey decreased (Table 4). We did not find any dependence of *Fraxinus excelsior* and the 2nd storey on forest mixture.

As the age of the stands increased, the frequency of the *Betula* spp. stands without the 2nd storey decreased from the 7th to the 8th age class and did not change significantly in the older stands ([13] $\chi^2 = 691.6$; $df = 20$; $\alpha < 0.001$). In *Populus tremula* stands a similar decrease was observed in the 6th–8th age classes ([14] $\chi^2 = 1026.2$; $df = 25$; $\alpha < 0.001$). In *Alnus incana* stands decrease in the frequency of stands without the 2nd storey was observed in the whole studied range – from 5th to 7th age classes ([15] $\chi^2 = 236.2$; $df = 10$;

Table 4. Distribution of predominant tree species of the 2nd storey according to stand mixture ($\chi^2 = 3136.1$; $df = 22$; $\alpha < 0.001$)

Tree species	Area (ha, %) by mixture of stands			Total
	Mixed	Low mixed	Pure	
Populus tremula	268_{a}	80_{b}	34_{b}	382
	0.4%	0.2%	0.1%	0.3%
Alnus incana	313_{a}	132_{b}	61_{c}	506
	0.4%	0.3%	0.2%	0.3%
Quercus robur	36_{a}	48_{b}	66_{c}	150
	0.0%	0,1%	0.2%	0.1%
Fraxinus excelsior	102_{a}	85_{a}	58_{a}	245
	0.1%	0.2%	0.2%	0.2%
Acer platanoides	125_{a}	112_{b}	79_{b}	316
	0.2%	0.3%	0.3%	0.2%
Tilia cordata	$1{,}258_{a}$	435_{b}	272_{b}	1,965
	1.7%	1.0%	0.9%	1.3%
Ulmus spp.	100_{a}	81_{a}	19_{b}	200
	0.1%	0.2%	0.1%	0.1%
Carpinus betulus	615_{a}	204_{b}	104_{c}	923
	0.8%	0.5%	0.3%	0.6%

$\alpha < 0.001$). The frequency of the *Picea abies* 2nd storey in the *Betula* spp. stands increased from the 7th to 8th age classes and decreased from the 9th to 11th ([13]) ones; in the *Populus tremula* stands it also increased from the 6th to 8th age classes, no change was observed in other age classes ([14]). Also, no significant change was observed in the *Alnus incana* stands ([15]). The frequency of the soft deciduous 2nd storey slightly increased with the age: in the *Betula* spp. stands, the 9th–11th age classes were more common than the 7th–8th ones ([13]), in the *Populus tremula* stands, the 9th–10th age classes were more common than the 5th–8th ones ([14]), in the *Alnus incana* groves frequency increases in the whole 5th–7th age class range ([15]). We found in the *Betula* spp. stands that the 2nd storey of *Tilia cordata* in the 10th–11th age classes was more frequent than in younger stands ([13]), as well as in the *Populus tremula* stands the 9th–10th age classes was more frequent than in younger ones ([14]). The 2nd storey of broad-leaved tree species was also more common with increasing stand age in stands of all tree species ([13, 14, 15]).

Discussion

Elements of stands, from which a replacement stand can be formed after the onset of stand decomposition of pioneer tree species in fertile habitats, the 2nd storey and understorey, are rare. They are the rarest in *Alnus incana* stands, and specific *Alnus incana* stands with *Padus avium* underbrush are most often formed (Nestby 2020). In the *Betula* spp. forests, due to the need of *Betula* spp. for light (Ellenberg et al. 1991), and therefore the higher amount of light transmitted to lower storeys, the understorey and the 2nd storey, are the most common. The most common species of the 2nd storey and understorey is *Picea abies*, its frequency is determined by the high distribution in fertile forest site types and shade tolerance (Ellenberg et al. 1991). The distribution of other tree species is more episodic.

The 2nd storey and understorey are more often found when the stand mixture increases. The same trend applies to the lower storeys of spruce, which can be explained by the higher prevalence of *Picea abies* in mixed stands, as well as the higher quantity of seed spread. Only *Betula* spp. stand out: in very mixed stands the frequency of the 2nd storey does not increase, probably due to the less favourable species, like *Populus tremula* and *Alnus incana* (Figure 3).

It would seem that the understorey made by *Populus tremula* and *Alnus incana* root suckers is common in our studied stands (Navasaitis et al. 2003), but trees up to 1 year of age are not counted during the stand-wise forest inventory (VMT 2021). Later their need for light increase and they die in consequence of lack of light. The 2nd storey and understorey of *Betula* spp. and *Quercus robur* are rare due to the high demand for light (Ellenberg et al. 1991), and their restoration requires gaps in the main storey of the stand (Petrokas 2020). *Quercus robur, Populus tremula*, *Ulmus* spp., *Acer platanoides* are vulnerable to abundant deer population (LRAM 2021). Although the frequency of *Fraxinus excelsior* understorey exceeds 2%, it develops the 2nd storey much less frequently, which can be explained by the deer damage (LRAM 2021), fungal diseases (Baral and Bemmann 2014) and the increased need for light in old age (Navasaitis et al. 2003). In the *Populus tremula* and *Betula* spp. stands, the second storey of *Tilia cordata* and *Carpinus betulus* is more abundant than other deciduous trees, but it should be noted that the natural range of *Carpinus betulus* occupies only a part of the territory of Lithuania (Navasaitis et al. 2003), therefore the *Carpinus betulus* recovery is more significant within the range.

As the age increases, the stands gradually become sparser, and the second storey of the stand becomes more frequent. Although the 2nd storey of deciduous tree species is rare, the share of their area increases with increasing stand age. The increase of the 2nd storey of spruce in the *Betula* spp. and *Populus tremula* stands up to the 8th age class and the stabilization of the frequency in older age can be explained by the fact that a part of the 2nd storey transforms into the 1st one.

The study involves a large amount of data, but their accuracy is limited, for example, understorey is recorded from 500 trees per ha (VMT 2021). Indicators of the stand-wise forest inventory show average characteristics of forest stands, the analysis of which is important for the assessment of general trends, but it is not possible to consider the group location of individual elements in the stand, which would require more detailed research. A one-time analysis of the stand-wise forest inventory data does not allow considering the different history of stand development and farming and may therefore show an incomplete picture of the relationship between individual stand elements. For example, similar deciduous stands with a second storey of *Picea abies* can be formed by natural growth of *Picea* *abies* understorey or when deciduous trees are outrivalling *Picea abies* stands.

A stand-wise forest inventory is carried out every 10 years by recording the actual situation of the stands (Kuliešis et al. 2010, VMT 2021), the boundaries and numbering of some plots change. Therefore, there is no visible the full history of thinning, sanitary and final non-clear felling. Forest management in private forests is also not reliably included in the data set. So results obtained must be assessed in the context of the historically established forest management regime. For more detailed long-term research on stand development, there is a serious lack of long-term naturally developing stands of highly fertile site types. That must be considered when expanding the network of protected areas.

Conclusions

The understorey and second storey of the mature *Betula* spp., *Populus tremula* and *Alnus incana* stands are weakly forming in most of the very fertile dry and humid forest site types. The second storey and understorey of *Picea abies* are most frequent, the second storey of *Tilia cordata* and *Carpinus betulus* and understorey of *Fraxinus excelsior* are less common. The lower storeys of other tree species develop rarely, episodically.

As the age and species mixture of stands increase, the understorey and second storey develop more often.

The density of the underbrush is related to the stocking level of the main and second storeys of stands, therefore it is necessary to continue analysing the data on underbrush distribution in fertile forests sites.

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