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Semicentennial dynamics of old silver birch (*Betula pendula* Roth) forests in the Belavezhskaya Pushcha National Park

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Abstract

In this study, we present the results of an investigation of the long-term dynamics of natural silver birch (*Betula pendula* Roth) forests within the Belavezhskaya Pushcha National Park, Belarus. Six sample plots represent two primary forest associations: *Tilio-Carpinetum* and *Querco roboris-Pinetum sylvestris*. All stands originated from clear-cuttings in the early 20th century, and their age varies from 84 to 111 years as of 2023. The study spans from 1972 to 2023, encompassing the observation of various forest parameters, including diameter at breast height (DBH), tree height, canopy positioning, living ground cover, and the shrub layer, conducted multiple times (from 2 to 4).

Successional patterns were observed to develop in three main directions, contingent upon the initial composition of the forest stand. In most cases, *Betula pendula* forests transition directly to spruce (*Picea abies*) forests or through the short (around 20 years) European aspen (*Populus tremula*) phase. The emergence of broadleaved forests in their place typically occurs no earlier than 200 years after logging, coinciding with the period of decline of *Picea abies* due to droughts and bark beetle attacks. Exceptions are observed in forest phytocenoses thriving on more fertile soils, where *Quercus robur* and/or *Acer platanoides* can swiftly replace mixed *Populus tremula-Betula pendula* stands after a century of development. Consequently, a considerable reduction in *Betula pendula* forests within Belavezhskaya Pushcha is anticipated in the forthcoming decades, gradually replaced by *Picea abies* and mixed broadleaved forests. These findings are significant for predicting the stand structure, biodiversity, and carbon sequestration potential of unmanaged forests.

Keywords: long-term study; permanent plots; *Betula pendula*; DBH structure; regeneration; succession

Introduction

Silver birch, *Betula pendula* Roth, is naturally distributed throughout most of Europe (Beck et al. 2016). It is a light-demanding pioneer species that can grow rapidly even in poor soils. Its seeds are efficiently dispersed by wind, and its roots readily form associations with many ectomycorrhizal fungi (Atkinson 1992). These characteristics enable *Betula pendula* to quickly colonise areas affected by clear-cutting, windfall, forest fires, and abandoned agricultural land. The widespread presence of *Betula pendula* forests in northern and eastern Europe has led to their extensive use in forestry practices (Hynynen et al. 2010). Consequently, outside of strictly protected areas, forestry activities often result in the almost complete absence of old-age *Betula pendula* forests, which are typically harvested when they reach 60–70 years of age. However, *Betula pendula* forests, along with other pioneer deciduous forests in general, play a crucial role in the natural regeneration process of primary broadleaved forests (Popadyuk et al. 1994).

In Belarus, birch forests cover 23.4% of the forested area, totalling 1.9 million hectares (Klimchik and Belchina 2022). They are equally dominated by either silver birch (*Betula pendula*) or downy birch (*Betula pubescens*). *Betula pendula* exhibits a wide ecological range, capable of replacing almost all types of *Pinus sylvestris*, *Picea abies*, and *Quercus robur* forests (Yurkevich et al. 1992). However, most studies on birch forests in Belarus and neighbouring countries have focused on their typology, logging practices, structural changes, and growth patterns up to the age of final felling (Chubanov 1969, Geltman 1982, Yurkevich et al. 1992, Fedorovich et al. 2013, Labokha and Borko 2015, Maleki and Kiviste 2016, Ķēniņa et al. 2022). Studies on the successional processes of old *Betula pendula* forests unaffected by human activities are exceedingly rare (Starikova et al. 2022).

According to some studies (Yurkevich et al. 1992, Labokha and Borko 2015) on *Betula pendula* forests in Belarus, trees typically reach heights of 20–25 meters by the age of 40–50 years and then undergo a growth slowdown. Natural thinning of the stands commences, with *Picea abies* emerging beneath the *Betula pendula* canopy, eventually replacing it as the dominant species in the upper layer by 80–100 years of age (Yurkevich et al. 1992). However, our research in the Berezinsky Biosphere Reserve revealed that in the northern part of Belarus, *Betula pendula* often maintains dominance in stands for up to 120–130 years, gradually yielding to *Picea abies* with the involvement of *Acer platanoides*, *Quercus robur*, and *Tilia cordata* in the lower layers (Starikova et al. 2022). The transition of *Betula pendula* forests to *Quercus robur* forests likely follows a similar pattern; however, the process of natural forest regeneration in Belarus is poorly understood, because it typically requires more than one generation of secondary forest.

The structure and dynamics of old-age *Betula pendula* at the boundaries of *Picea abies* distribution in southern Belarus remain unclear yet. At the same time, understanding the direction of successional processes is particularly crucial for protected areas, as it enables the prediction of future forest structures. Hence, our research aimed to address two main questions: 1) At what age do *Betula pendula* forests transform into other types of forest in the southern regions of Belarus? *and* 2) What are the primary successional pathways in *Betula pendula* forests as they transition out of existence?

Materials and methods

The research was conducted in Belavezhskaya Pushcha National Park, situated near the southern periphery of the *Picea abies* distribution range, where the competitive dynamics between *Picea abies*, *Carpinus betulus* and *Quercus robur* are particularly pronounced. This, in turn, can lead to the emergence of various pathways of succession observed within mature secondary forests.

Historical context

Belavezhskaya Pushcha is a vast forest on the border between Poland and Belarus (52°43′N, 23°59′E) (Figure 1). This is one of the most famous intact forests in Europe, which forms the Białowieża Forest UNESCO World Heritage Site (82.3 thousand hectares in Belarus and 59.6 thousand hectares in Poland). Since the 15th century, this territory has held a special protected status, serving as the hunting grounds for ruling families such as the Grand Duchy of Lithuania, the Polish-Lithuanian Commonwealth, and the Russian Empire (Semakov and Cherkas 2007). Although it was not subject to strict protection measures, only certain types of economic activities were allowed (Bobiec 2012). The entire forest maintained a special protective status until World War I, when it fell

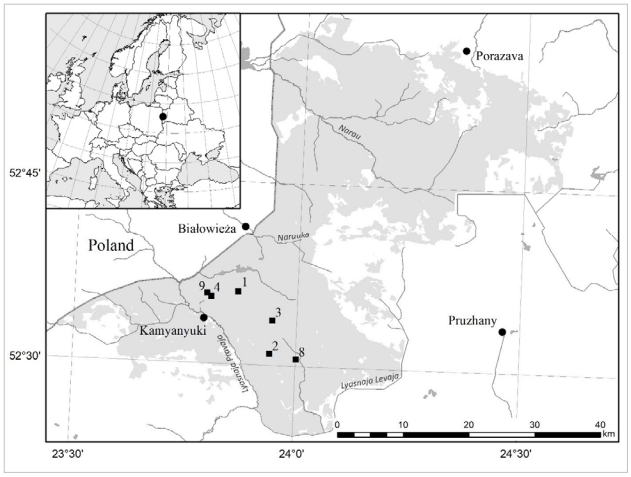

Figure 1. Location of the sample plots in the Belavezhskaya Pushcha National Park

under German occupation. During this period, several sawmills were erected, and approximately 300 kilometres of railways were laid for timber exportation. Exploitation of the forests persisted post-war, with up to 20% of the Belavezhskaya Pushcha forest being felled by the 1930s (Semakov and Cherkas 2007). These fellings followed a period of exceptionally high game populations at the beginning of the 20th century, as well as other natural and human-induced disturbances throughout the 19th century (Bernadzki et al. 2009). Pioneer forests of *Betula pendula* and *Populus tremula* arose in places of broadleaved and broadleaved-coniferous forests. Presently, many stands of *Betula pendula* and *Populus tremula* stands, originating in the early 20th century, have reached an age of 80–100 years. Natural regeneration under the forest canopy throughout the 20th century developed under very high ungulate density, leading to the elimination of saplings of broadleaved species and the dominance of *Picea abies* and *Carpinus betulus* in the lower stand layers.

The forests of *Betula pendula* in Belavezhskaya Pushcha today cover 9.2 thousand hectares. Of this area, 43% is part of the *Tilio-Carpinetum* association, while 27% belongs to the *Querco roboris-Pinetum sylvestris* association.

Geomorphology

The territory of the Belavezhskaya Pushcha is a plain situated on the watershed of the Neman, the Bug, and the Pripyat rivers. The terrain was formed by fluvioglacial sand and sand-pebble deposits during the final phase of the Penultimate Glacial Period, approximately 194,000 to 135,000 years ago (Voznyachuk et al. 1969). The lowest point is 141 meters a.s.l. BS, located at the southern border of the National Park, where the Lyasnaja Levaja and Lyasnaja Pravaja rivers meet, while the highest point reaches 243 meters a.s.l., near the northern border, close to Porazava. The area is intersected by several rivers and streams. The main watercourses are the Narau, the Narauka, the Lyasnaja Levaja, and the Lyasnaja Pravaja rivers.

Climate

The climate is temperate continental with no dry season and warm summer; it corresponds to the Dfb region according to the Köppen-Geiger climate classification (Beck et al. 2018). The average January temperature is –5.4°C, and July +17.8°C; the absolute minimum was –40.1°C (1950), the absolute maximum was +37.7°C (2019). The growing season is about 200 days (according to the meteorological station in Kamyanyuki). The average annual sum of precipitation is 648 mm, and 65% of it falls during the growing season. Prevailing winds are west and south-west (Loginov et al. 2020).

Study plots

The research was conducted on six permanent trial plots (Figure 1), which were established in the most common *Betula pendula* forest types between 1972 and 1979 by the Scientific Department of the Belavezhskaya Pushcha National Park as part of the network for long-term study of forest dynamics. Five stands (BPBP01, BPBP02, BPBP03, BPBP04, BPBP09) are located on fresh sod-podzolic loamy sandy soil, while one stand (BPBP08) grows on dry sod-podzolic sandy soil. The first soil type has slightly higher fertility, which contributes to greater forest stand productivity and increased floristic diversity.

Each rectangular plot covers an area of 0.3–0.4 hectares, depending on the age of the forest stands at the time of the initial inventory, ranging from 35 to 60 years (Table 1). This indicates that *Betula pendula* appeared between 1911 and 1941. Typically, the emergence of this type of forests is closely associated with various forest disturbances such as windfalls, logging, and fires. Unfortunately, there is limited reliable information available regarding the forests preceding the *Betula pendula* stands and the disturbances accompanying their formation. However, they probably originated following the clearance of mixed *Quercus robur-Pinus sylvestris* forest stands. This inference is supported by several factors: 1) the rectangular shape of the forest stands; 2) the presence of *Quercus robur-Pinus sylvestris* forests 190–210 years old on the periphery of the *Betula pendula* forests; *and* 3) the Forest Plan of Belavezhskaya Pushcha in 1858, compiled from materials of the second forest inventory (a copy is held in the Brest Regional Library), which indicates the existence of forests dominated by *Pinus sylvestris*. Furthermore, the vast area of secondary *Pinus sylvestris* forests that formed after extensive fires in the early 19th century occupied sites with unusually fertile soils (Bobiec 2012).

Stand and vegetation surveys

During the initial inventory, the diameters of all living trees with a DBH exceeding 6 cm were measured with a tree calliper in two perpendicular directions with an accuracy of 1 cm. Tree heights were selectively measured with a hypsometer (three trees from each 4-cm DBH class). The trees were visually classified into two layers. The second layer consisted of trees that were more than 20% lower in height than those in the main layer. The number of saplings and shrubs was assessed in smaller plots, evenly distributed throughout the main plot. The area of these smaller plots exceeded 100 m^2 within each main plot. A description of the living ground cover was conducted on at least 20 small plots (1 × 1 m) per every main plot, recording the species composition and projective cover as a percentage.

The permanent plots were revisited and updated between 2020 and 2023, with the same research protocols applied. However, tree heights were measured for all trees. The trees were classified into layers based on a minimum height difference of 20% between the layers. Although DBH measurements were conducted multiple times between the 1980s and 2010s, for brevity, we have included data only from years with the most comprehensive studies.

Forest type identification was conducted in accordance with the syntaxonomy of forest vegetation of Belavezhskaya Pushcha, as developed by Belarusian phytocenologists (Tsvirko and Grummo 2020). Changes in the ecological characteristics of phytocenoses were determined using Ellenberg-type indicator values (Ellenberg 1992, Tichý et al. 2023), which reflect plant species' preferences for specific environmental factors. The indicator value for a plant community along a given ecological gradient (soil moisture or fertility) was calculated as the weighted average of the indicator values of individual plant species, using their projective cover as weights.

Results

Forest typology

The phytocenosis structure in the 2020s reveals that five out of six phytocenoses belong to the *Tilio-Carpinetum* association Traczyk 1962, class *Carpino-Fagetea sylvaticae* Jakucs ex Passarge 1968, while only phytocenosis BPBP08 belongs to the *Querco roboris-Pinetum sylvestris* association J. Matuszkiewicz 1988, class *Vaccinio-Piceetea* Br.-Bl. 1939 (Tsvirko and Grummo 2020). The distribution of phytocenoses across the Ellenberg ecological scales (soil moisture and fertility) reflects age-related changes during the observation period (Figure 2). Relatively young phytocenoses (35–40 years old) shifted towards higher soil nitrogen richness by 0.7–1.6 points over 40–50 years. Older stands experienced slight changes on this scale (–0.5 to +0.3 points). The variation in humidity fell within the range of –0.3 to +0.1 points, except for BPBP09, where humidity increased by 0.7 points. As the stands age, the differences in soil moisture and nitrogen richness between the two associations diminish. At ages exceeding 80 years, all *Tilio-Carpinetum* phytocenoses exhibit a moisture range of 5.1–5.7 and a soil nitrogen richness scale of 4.6–5.7. For the *Querco roboris-Pinetum sylvestris* association, moisture levels reach 5.3, with soil nitrogen richness at 4.3.

Table 1. Changes in the forest stands characteristics

Calendar year (Stand age)	Layer	Composition *	DBH, cm	H, m	Tree density, trees ha^{-1}	Basal area, m^2 ha^{-1}	Volume, m^3 ha^{-1}
		BPBP01 – 0.4 ha					
1972 (60)	1	9Bp1Ps, s. Pt	22.7	24.1	663	27.6	316
	2	9Pa1Bp, s. Qr, Cb, Pt	12.6	11.7	770	9.0	60
		Total	-	-	1,433	36.6	376
1982 (70)	1	9Bp1Ps, s. Pa, Pt	25.2	25.2	553	27.8	331
	2	10Pa, s. Bp, Cb, Qr, Pt	15.9	13.3	630	11.9	87
		Total	-	-	1,183	39.7	418
2022 (110)	1	6Bp3Pa1Ps, s. Pt	36.9	30.5	238	26.6	367
	2	9Pa1Bp+Cb, s. Qr	25.8	21.8	183	9.8	105
	3	7Pa2Qr1Cb	20.5	17.4	78	2.7	21
	4	7Pa2Pt1Cb	14.5	10.8	38	0.5	3
		Total	-	-	537	39.6	496
		BPBP02 – 0.3 ha					
1976 (50)	1	7Bp3Pt, s. Qr, Cb	19.9	22.8	777	27.0	300
	2	4Cb3Bp1Ap1Qr1Pa, s. Pt	9.6	12.8	694	5.4	33
		Total	-	-	1,471	32.3	333
2021 (95)	1	8Pt2Bp, s. Qr	35.2	33.6	137	26.8	471
	2	4Ap4Cb1Bp1Qr, s. Pa	21.6	26.0	70	3.0	36
	3	9Cb1Ap+Bp	17.6	20.7	160	4.1	37
	4	9Cb1Ap, s. Pa	12	12.6	167	1.8	9
		Total	-	-	534	35.7	553
		BPBP03 – 0.4 ha					
1976 (65)	1	5Bp4Pt1Ps+Qr, Pa, s. Cb	25.8	25.7	373	26.3	322
	2	6Pa2Qr2Cb+Bp, s. Ap, Tc, Ps	12.2	10.0	495	5.3	44
		Total	-	-	868	31.6	366
1993 (82)	1	5Pt2Bp1Pa1Qr1Ps+Cb	54.6	30.6	225	19.8	239
	2	7Pa2Cb1Qr, s. Ap, Tc, Ps	15.9	13.9	295	4.8	54
		Total	-	-	520	24.7	293
2022 (109)	1	6Pa1Bp1Pt1Qr1Ps	43.0	29.7	63	10.4	154
	2	6Pa3Cb1Qr+Bp, s. Ap, Ps	29.5	21.0	160	10.7	110
	3	7Pa2Cb1Qr	16	10.1	58	1.3	7
		Total	-	-	281	22.4	271
		BPBP04 – 0.3 ha					
1976 (35)	1	9Bp1Ps, s. Pa, Ag, Pt	23.6	21.3	434	18.9	192
	2	5Pa3Bp2Qr+Cb,Ps, s. Tc, Ag, Sc, Fe, Pt	11.9	10.6	880	7.9	49
		Total	-	-	1,314	26.8	241
2022 (81)	1	9Bp1Pa+Ps, Ag, Pt, s. Cb	41.4	31.9	157	19.4	269
	2	5Pa4Bp1Qr+Cb,Ps, s. Tc	29.7	24.1	360	20.4	232
	3	4Pa3Qr3Cb, s. Bp	13.4	10.9	284	5.3	41
		Total	-	-	801	45.1	542
		BPBP08 – 0.3 ha					
1976 (35)	1	10Bp+Pt, s. Ps, Qr	15.1	18.3	907	18.1	161
	2	7Bp1Ps1Pa1Qr, s. Pt	8.8	14.1	153	1.1	7
		Total	-	-	1,060	19.2	168
2023 (82)	1	9Bp1Pt +Pa, Ps	32.0	31.1	317	26.1	357
	2	7Pa2Cb1Qr+Bp	17.7	17.9	187	4.4	37
	3	8Pa2Cb+Bp	10.2	8.9	210	1.5	6
		Total	-	-	714	32.0	400
		BPBP09 – 0.4 ha					
1979 (40)	1	7Bp3Pt, s. Pa, Ps, Qr	16.6	19.0	855	20.0	190
	2	8Pa1Qr1Cb, s. Bp, Ps, Pt	12.0	13.8	695	7.0	40
		Total	-	-	1,550	27.0	230
2022 (83)	1	6Bp3Pt1Pa, s. Qr, Cb, Ps	28.4	30.7	348	25.3	364
	2	8Pa1Bp1Cb+Qr, s. Pt	24.5	22.7	263	11.2	117
	3	7Pa2Cb1Qr, s. Bp	16.5	14.6	263	4.4	31
		Total	-	-	874	40.9	512

* Ag – *Alnus glutinosa*, Ap – *Acer platanoides*, Bp – *Betula pendula*, Cb – *Carpinus betulus*, Fe – *Fraxinus excelsior*, Pa – *Picea abies*, Ps – *Pinus sylvestris*, Pt – *Populus tremula*, Qr – *Quercus robur*, Tc – *Tilia cordata*, Sc – *Salix caprea*, s. – *single trees*, "+" – less than 5%.

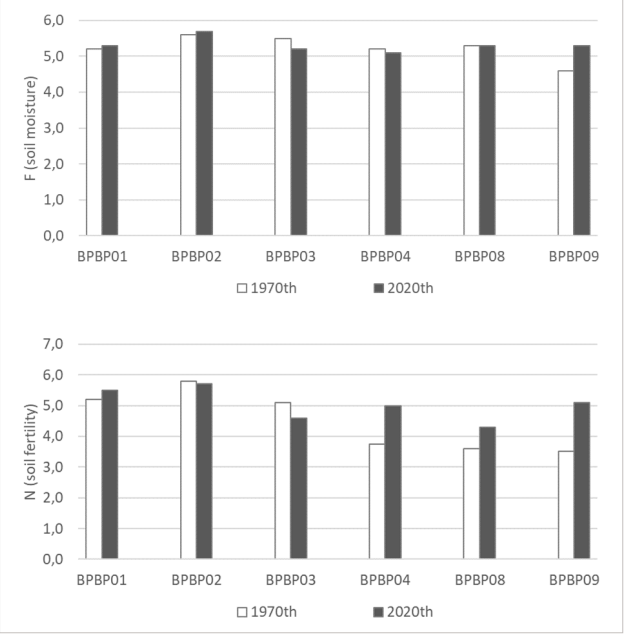

Figure 2. Distribution of the study plots according to the Ellenberg-type indicator values for soil moisture and fertility in the 1970s and 2020s

Forest stands dynamics

BPBP01

In 1972, it was one of the oldest studied stands, reaching an age of 60 years. The tree canopy exhibited two distinct layers: *Betula pendula* dominated the upper layer, alongside occasional *Pinus sylvestris*, and solitary *Populus tremula* trees were present. In the lower layer, *Picea abies* prevailed, accompanied by *Betula pendula*, as well as a few *Carpinus betulus*, *Quercus robur*, and *Populus tremula* trees (Table 1). In the undergrowth, *Picea abies* and *Populus tremula* were the dominant species, with a density of 5,200 pcs ha^{-1}.The proportion of *Betula pendula* in the upper layer gradually declined from 90% to 60% by the age of 110 years, while the share of *Picea abies* increased from 0% to 30%. Over the past 40 years, the wood volume of *Betula pendula* has decreased by 27%, now equalling the volume of *Picea abies*. The proportions of *Pinus sylvestris* and broad-leaved species remained unchanged. Changes in the DBH distributions (Figure 3) indicate a continued strengthening of *Picea abies'* position, with a shift of large number of trees towards the right side of the distributions.

Despite its advanced age and a significant decrease in tree numbers, *Betula pendula* still dominated the upper layer. Individual *Picea abies* trees began appearing in the upper layer when the *Betula pendula* reached 70 years old. Big individual *Pinus sylvestris* and *Populus tremula* trees were also retained in the upper layer. The gradual decline of *Populus tremula* and *Betula pendula*, coupled with the vigorous growth of *Picea abies*, *Quercus robur*, and *Carpinus betulus*, has led to a differentiated vertical profile of the stand. In 1972, only two layers were clearly discernible, whereas by 2022, the forest stand had become vertically closed, now comprising four layers (Table 1, Figure 4).

Betula pendula dominated the first layer, accompanied by *Picea abies*, *Pinus sylvestris*, and a few *Populus tremula* trees. Furthermore, *Pinus sylvestris* and *Populus tremula* initially appeared alongside *Betula pendula* 110 years ago, while *Picea abies*, being younger trees, emerged beneath the *Betula pendula* canopy and have now caught up with it in height. In the second layer, *Picea abies* and *Betula pendula* (suppressed trees aged 110 years) were present, along with *Carpinus betulus* and *Quercus robur*. The third and fourth layers were comprised of *Picea abies*, *Quercus robur*, *Carpinus betulus*, and *Populus tremula*. The emergence of the *Populus tremula* trees was associated with gaps in the canopy.

The structure of the understory has changed significantly (Table 2). *Picea abies* has nearly disappeared, replaced by *Carpinus betulus*, while the total number of saplings has increased almost threefold (up to 15,100 pcs ha^{-1}).

BPBP02

In 1976, the stand was a 50-year-old mixed *Populus tremula-Betula pendula* forest, with occasional *Carpinus betulus* and *Quercus robur* trees in the upper layer. *Carpinus betulus* dominated the clearly defined second layer,

Table 2. Changes in the understory

Num PP	Calendar year (Stand age)	Composition *	Nr ha^{-1}	Height, m
BPBP01	1972 (60)	5Pa3Pt1Cb1Qr	5,200	1.4
	2022 (110)	8Cb2Qr+Pt, Ap, s. Tc	15,100	0.9
BPBP02	1976 (50)	7Cb1Qr1Pa1Ap	1,500	1.5
	2023 (97)	9Pt1Cb	9,700	0.6
BPBP03	1976 (65)	6Pa2Qr1Cb1Pt	2,250	1.1
	2022 (109)	10Cb, s. Pa, Qr, Pt	36,300	0.8
BPBP04	1976 (35)	5Pa4Cb1Bp	2,333	5.9
	2022 (81)	8Cb1Pt1Qr+Pa	3,900	0.9
BPBP08	1976 (35)	10Qr	167	0.4
	2023 (82)	8Cb2Pt+Bp, Pa	3,800	0.9
BPBP09	1979 (40)	6Cb2Pa1Pt1Qr+Bp	5,800	0.8
	2022 (83)	6Pt3Cb1Ap+Qr, Pa	14,600	0.5

* Ap – *Acer platanoides*, Bp – *Betula pendula*, Cb – *Carpinus betulus*, Pa – *Picea abies*, Pt – *Populus tremula*, Qr – *Quercus robur*, Tc – *Tilia cordata*, s. – *single trees*, "+" – less than 5%.

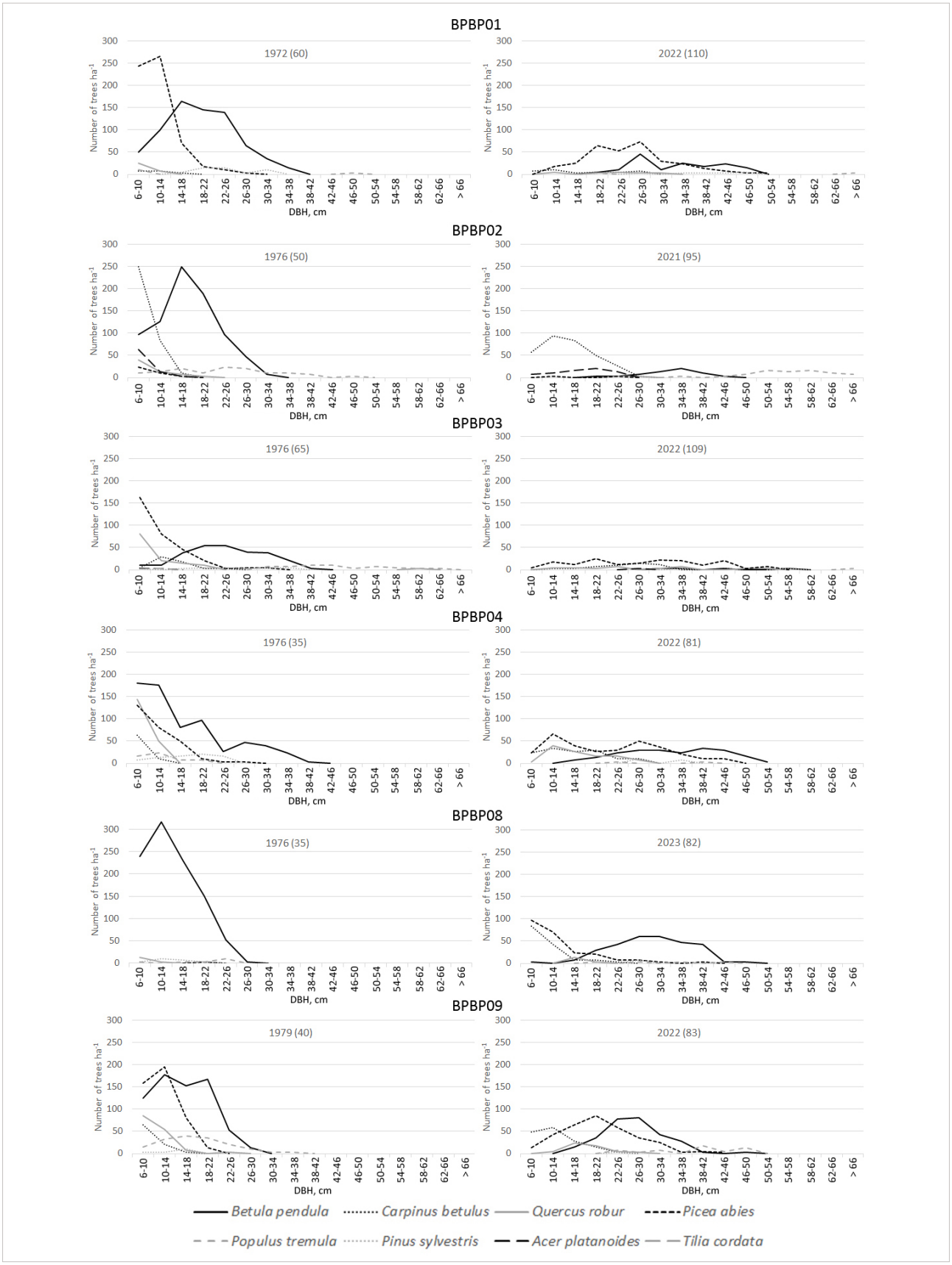

Figure 3. Changes in DBH distribution over the period 1970s–2020s

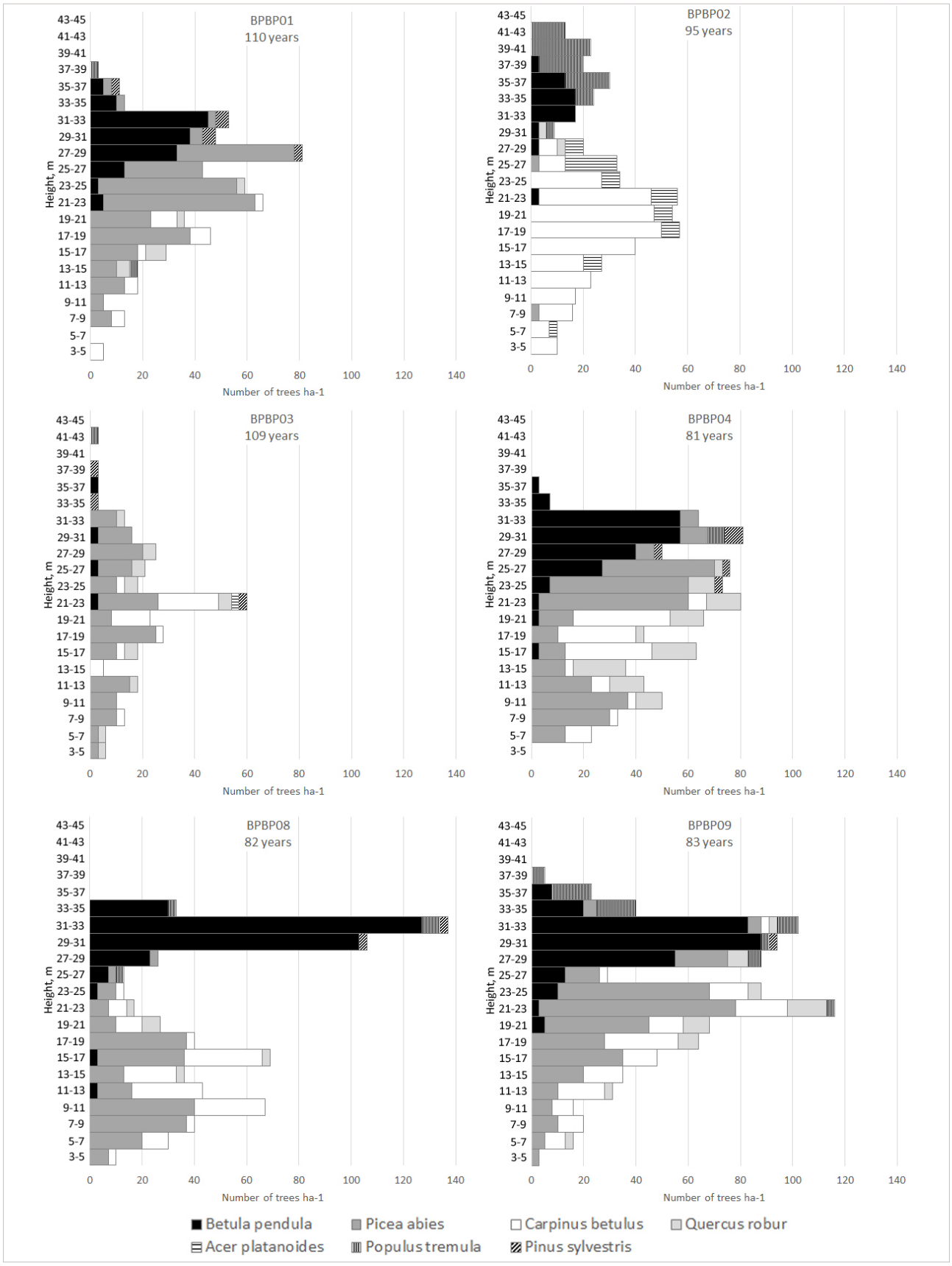

Figure 4. Tree height distribution in the 2020s

while *Betula pendula*, *Acer platanoides*, *Quercus robur*, and *Picea abies* were also present (Table 1). *Carpinus betulus* also dominated the understory (Table 2).

The proportion of *Betula pendula* gradually declined (from 70% to 20%) between ages 55 and 95, with *Populus tremula* assuming dominance in the upper layer. Aspen's share increased from 30% to 80%. The volume of *Betula pendula* decreased by 2.5 times, while that of *Populus tremula* increased by four times. The transformation from a *Betula pendula* forest to a *Populus tremula* forest occurred around 70–80 years of age. Despite the sparse tree count in the upper layer (137 trees ha^{-1}), its volume reached 471 m^3 ha^{-1}, primarily due to exceedingly large *Populus tremula* trees.

The vigorous growth of *Populus tremula*, the decline of *Betula pendula*, and the differentiation of trees in the lower layers led to the formation of a vertically closed forest stand. By 2022, four stand layers were identified (Table 1, Figure 4). *Populus tremula* dominated the upper layer (with heights ranging from 29 to 42 meters), with occasional *Betula pendula* and *Quercus robur* trees in the lower part. All *Populus tremula* trees were affected by extensive stem rot. *Acer platanoides* and *Carpinus betulus* dominated the second layer (with heights ranging from 24 to 29 meters), alongside *Betula pendula*, *Quercus robur*, and *Picea abies*. *Carpinus betulus* also dominated the third (with heights ranging from 18 to 24 meters) and fourth layers (below 18 meters), accompanied by *Acer platanoides*.

The total number of saplings increased from 1,500 to 9,700 pcs ha^{-1} due to the appearance of *Populus tremula* in gaps, while the number of *Carpinus betulus* remained nearly unchanged.

BPBP03

In 1976, the forest stand consisted of a mix of *Betula pendula* (50%), *Populus tremula* (40%), and *Pinus sylvestris*, with occasional *Picea abies*, *Carpinus betulus*, and *Quercus robur* trees, all at the age of 65 years (Table 1). *Picea abies* dominated the second layer, accompanied by *Quercus robur*, *Carpinus betulus*, and solitary *Acer platanoides*, *Tilia cordata*, and *Pinus sylvestris* trees (Table 1). In the undergrowth, *Picea abies* dominated (2,250 pcs ha^{-1}), accompanied by *Quercus robur*, *Carpinus betulus*, and *Populus tremula* (Table 2). By the age of 70 (10 years into the observation period), the number of *Betula pendula* trees and their volume began to decline sharply under the dense canopy of *Populus tremula* on one side and the rapid growth of *Picea abies* from the second layer.

After 110 years, both *Betula pendula* and *Populus tremula* had nearly vanished from the forest stand, leaving *Picea abies* as the dominant species in the upper layer. The wood volume of *Betula pendula* decreased from 159 m^3 ha^{-1} in 1976 to 20 m^3 ha^{-1} in 2022. Only four *Betula pendula* and one *Populus tremula* tree from the original stand remained in the permanent plot. The proportion of *Picea abies* in the total wood volume increased from 8% to 57%. Similar to the BPBP02 stand, the disappearance of the *Betula pendula* forest was preceded by its transformation into a *Populus tremula* forest at around 80 years of age. However, succession aimed at forming a mixed *Carpinus betulus*-*Picea abies* stand with broadleaved species.

In 2022, three stand layers were identified. In the upper layers (29.7 meters), *Picea abies* accounted for 60% of the volume, with the remaining volume evenly distributed among *Betula pendula*, *Populus tremula*, and *Pinus sylvestris* trees. Solitary *Quercus robur* trees were also present. In the second layer (21 meters), *Picea abies* dominated (70%), with significant amounts of *Carpinus betulus* (30%) and solitary trees of *Quercus robur*, *Betula pendula*, *Acer platanoides*, and *Pinus sylvestris*. The third layer (10.1 meters) was also dominated by *Picea abies* (70%), *Carpinus betulus* (20%), and *Quercus robur*. Although *Picea abies* currently dominates the stand, *Quercus robur* is represented almost throughout its entire height range (from 8 to 34 meters), as well as *Carpinus betulus* (from 3 to 23 meters) (Figure 4).

The undergrowth was abundant (36,300 pcs ha^{-1}), mainly consisting of *Carpinus betulus*, with minor contributions from *Picea abies*, *Quercus robur*, and *Populus tremula*.

BPBP04

In 1976, the forest stand consisted solely of *Betula pendula*, with occasional *Pinus sylvestris*, *Picea abies*, and *Alnus glutinosa* trees, all of them aged 35 years (Table 1). Despite the young age of the stand, a second layer (10.6 meters) was identified, comprising ten tree species: *Picea abies* (50%), *Betula pendula* (30%), *Quercus robur* (20%), *Carpinus betulus*, *Pinus sylvestris*, *Fraxinus excelsior*, *Tilia cordata*, *Alnus glutinosa*, *Populus tremula*, and *Salix caprea* (Table 1). Eight of these species (excluding *Fraxinus excelsior* and *Salix caprea*) survived in different layers until 2022. *Picea abies* and *Carpinus betulus* dominated the undergrowth (Table 2).

At age 81, the total wood volume of both *Betula pendula* and *Picea abies* continued to increase (Table 1). Over 45 years, the volume of *Betula pendula* increased by only 30% (reaching 277.3 m^3 ha^{-1}), while the volume of *Picea abies* increased eightfold (to 181.6 m^3 ha^{-1}). The volume of other deciduous species also increased, but their proportion in the forest stand remained almost unchanged (Table 1, Figure 3).

By 2022, a vertically closed forest stand had formed, with three clearly visible layers (Table 1, Figure 4). *Betula pendula* still dominated (90%) the first layer (31.9 meters), accompanied by *Picea abies*, *Pinus sylvestris*, *Alnus glutinosa*, *Populus tremula*, and *Carpinus betulus*. The second layer (24.1 meters) was comprised of *Picea abies* (50%), suppressed *Betula pendula* (40%) trees, and solitary *Quercus robur*, *Carpinus betulus*, *Pinus sylvestris*, and *Tilia cordata* trees. In the third layer, *Picea abies* (40%),

Quercus robur (30%), *Carpinus betulus* (30%), and occasional *Betula pendula* trees, which appeared in gaps, were present. Despite *Picea abies*' dominance in the lower layers of the stand, it was almost completely absent from the undergrowth (Table 2).

BPBP08

In 1976, the stand was predominantly comprised of *Betula pendula*, with a few *Pinus sylvestris*, *Populus tremula*, and *Quercus robur* trees, all of them aged 35 years (Table 1). The sparse second layer included weakened *Betula pendula*, *Pinus sylvestris*, *Picea abies*, *Quercus robur*, and solitary *Populus tremula* trees. Undergrowth was mostly absent, with only a few individuals of *Quercus robur* found (Table 2). The stand BPBP08 is the youngest of all the studied stands; by 2023, it had reached 82 years old. In 2023, the proportion of *Betula pendula* remained unchanged at 90%, but its wood volume increased from 157 to 256 m^3 ha^{-1} (Table 1). The share of *Picea abies* rose from 7 to 11%.

Significant changes occurred in the structure of the lower layers over the 44-year study period.

The DBH distribution clearly indicated that *Picea abies* appeared under the *Betula pendula* canopy, forming a closed second layer only by 2020 (Figure 3). *Carpinus betulus* was not noted in the stand in 1976 and 1981, but appeared in the tree stand in 2023, dominating the undergrowth (Table 2).

By 2023, the forest stand was clearly revealed in three layers (Table 1, Figure 4). The first layer (with an average height of 31.1 meters) was still dominated by *Betula pendula* (90%), with a small percentage of *Populus tremula* (10%) and solitary *Pinus sylvestris* and *Quercus robur* trees. In the second layer, which is almost two times lower (17.9 meters), *Picea abies* (70%), *Quercus robur*, and *Carpinus betulus* predominate, and also in the second layer, there are single weakened trees of *Betula pendula*. In the third layer, *Picea abies* (80%) and *Carpinus betulus* (20%) predominated; in the gaps, individual small trees of *Betula pendula* were found.

BPBP09

The initial phase of the research took place in 1979. At that time, it was a 40-year-old mixed stand of 70% *Betula pendula* and 30% *Populus tremula*, with a amounts of *Pinus sylvestris*, *Quercus robur*, and *Picea abies* (see Table 1). The next measurements had occurred only in 2022, by which time *Betula pendula* had reached 83 years of age.

Over the span of 43 years, the wood volume of *Betula pendula* increased from 136 to 234 m^3 ha^{-1} (a 72% increase), while the volume of *Picea abies* surged from 34 to 144 m^3 ha^{-1} (a 320% increase). Concurrently, the structure of the upper layer remained largely unchanged, with a slight increase in the share of *Picea abies* and the appearance of individual *Carpinus betulus* trees.

The DBH (Figure 3) and height (Figure 4) distributions show that differentiation into layers has begun in the lower part of the forest stand. In 1979, the forest stand consisted of two layers, but by 2022, it had morphed to a three-layered stand. The first layer was characterised by *Betula pendula* (60%) and *Populus tremula* (30%), although aspen dominated its upper portion, as evidenced by the height distribution of trees (Figure 4). The second layer was predominantly occupied by *Picea abies*, with the presence of *Carpinus betulus*, *Quercus robur*, and *Betula pendula* trees. The third layer, with an average height of 14.6 meters, was comprised of *Picea abies*, *Carpinus betulus*, and *Quercus robur*.

The understory was notably dense (14,600 pcs ha^{-1}), with *Populus tremula* and *Carpinus betulus* dominating (Table 2). The prevalence of aspen saplings in the understory is attributed to gaps in the tree stand canopy. However, most of these saplings were young individuals measuring up to 0.5 meters in height, and they are expected to perish in the near future.

Discussion

Succession in *Betula pendula* stands in Belavezhskaya Pushcha takes various pathways, even under similar soil conditions. These divergences are contingent upon the initial composition of the forest stand, which, in turn, hinges on the presence of seeds from different tree species in the surrounding forest and the periodicity of seed mass production. Another factor influencing the structure of forest stands during the early phases is the pressure from ungulates. According to research (Bernadzki et al. 2009, Yermokhin et al. 2019), the high number of ungulates in Belavezhskaya Pushcha contributed to the replacement of broad-leaved species by *Picea abies*. In some cases, their activities have even completely stopped forest regeneration. This issue was particularly acute between the 1960s and 1990s. As a result, the current composition of undergrowth and young trees in the studied forests may be linked to this factor. However, the impact on the structure of the first and second layers of the forest stand canopy was less significant, since the period of their formation in the 1920s–1940s, the ungulate populations were lower, which was associated with the consequences of the First and Second World Wars (Bernadzki et al. 2009). According to our research, the forest stands can be classified into several main types of successions (Figure 5).

In the forest stands, BPBP02, BPBP03, and BPBP09, succession exhibits a similar direction. A significant proportion of *Populus tremula* (30–40%), which emerges concurrently with *Betula pendula*, persists in stands 50–70 years post-felling. *Populus tremula* outpaces *Betula pendula* in growth, assuming a dominant position in the first layer. This leads to the suppression and premature demise (around 100 years) of the light-demanding *Betula pendula*. These forests swiftly transition into *Populus tremula* forests at 80–90 years, and both *Betula pendula* and *Populus tremula* disappear by 110 years. BPBP09 is presently at the

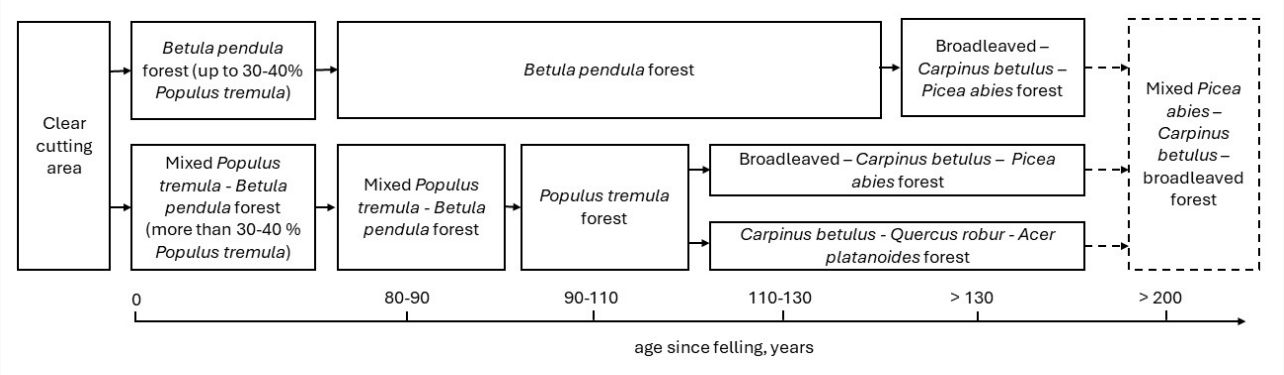

Figure 5. The main types of successions in *Betula pendula* forests in the Belavezhskaya Pushcha National Park

Betula pendula-to-*Populus tremula* forest transition phase (83 years). BPBP02 (95 years) represents the *Populus tremula* forest phase, while BPBP03 (109 years) marks the *Picea abies* forest phase, with few remaining *Betula pendula* and *Populus tremula* trees. Subsequently, succession diverges based on the second layer composition: 1) transitioning into a mixed *Carpinus betulus-Quercus robur-Acer platanoides* stand (BPBP02), or 2) evolving into a *Carpinus betulus-Picea abies* (BPBP03, BPBP09) stand with a minor presence of *Quercus robur* and *Acer platanoides*. In the latter case, given the presence of *Quercus robur* and *Acer platanoides* trees and saplings in the lower layers, a regeneration of broadleaved stands through the *Picea abies* phase is foreseeable within a few decades.

The forest stands BPBP01 and BPBP04 exhibit different patterns. The proportion of *Populus tremula* in the upper layer was insignificant, less than 30%, allowing *Betula pendula* to dominate for more than 120 years, until its natural demise, likely extending up to 130–140 years. *Betula pendula* accounts for 90% of the first layer at 70–80 years (BPBP01 in 1982 and BPBP04 in 2022), diminishing to 60% at 110 years (BPBP01 in 2022). *Picea abies* dominates in the lower layers, accompanied by *Carpinus betulus* and *Quercus robur*. The transition to spruce forests here is expected 20–30 years later than in birch forests with a high *Populus tremula* ratio. Consequently, broadleaved forest regeneration through the *Picea abies* phase is likely to span a longer period.

Forest stand BPBP08 belongs to a different association, *Querco roboris-Pinetum sylvestris*. Unlike most of the other studied phytocenoses, most *Picea abies* trees emerged here under the canopy of *Betula pendula*. In a 40-year-old forest, *Picea abies* comprised only 20% of the sparse second layer. Only at the age of 80 there were two layers clearly distinguished here. *Betula pendula* predominated in the first layer, with *Carpinus betulus* and *Picea abies* dominating the second layer. The low proportion of broadleaved species in the lower layers and understory suggests a future *Carpinus betulus-Picea abies* forest formation, with broadleaved species present in the stands in moderation. Further succession is expected to resemble that of BPBP01 and BPBP04 stands, but with reduced participation of broadleaved species.

The subsequent dynamics of the stands and the timing of the broad-leaved forest restoration will be determined by massive invasions of the bark beetle, which damages spruce (*Picea abies*) after prolonged dry climatic periods. Periodic mass mortality of *Picea abies* forests exhibits a distinct 7-year cyclicity in Belarus (Puhacheuski et al. 2020), often affecting Belavezhskaya Pushcha (Yermokhin 2010), situated near the southern border of *Picea abies* forest distribution. The demise of *Picea abies*, typically forming a dense upper stand layer, encourages the growth of broadleaved trees beneath its canopy. Climate warming could accelerate these processes. According to climate forecasts, by 2050, the growth of spruce in the southern regions of Belarus is likely to decrease by 20% (Yermokhin and Puhacheuski 2010), which will lead to a reduction in its competitiveness. Therefore, natural broadleaved forest regeneration is likely to progress through *Betula pendula*/*Populus tremula* and *Picea abies*/*Carpinus betulus* forest phases, spanning at least 200–300 years. However, broadleaved forests may arise directly after the *Betula pendula* or *Populus tremula* phase on more fertile soils.

Conclusion

The secondary *Betula pendula* forests of Belavezhskaya Pushcha, emerging from extensive clear-cuttings at the onset of the 20th century, have now reached an age of decay (100–130 years). By approximately 100 years, unmanaged *Betula pendula* forests typically exhibit 3–4 tree stand layers: *Betula pendula* and *Populus tremula* dominate the upper layer, while *Carpinus betulus* and/or *Picea abies* dominate the lower layers. *Acer platanoides*, *Quercus robur*, and *Tilia cordata* are also present in the lower layers, indicative of the rich soils and diverse tree species.

In most scenarios, *Betula pendula* forests transition into *Picea abies* forests, whilst broad-leaved forests may emerge no sooner than 200 years post-clearcutting, coinciding with the decline of *Picea abies* due to droughts and bark beetle outbreaks. Exceptions include forest phytocenoses on the most nutrient-rich soils, where *Quercus ro-*

bur and/or *Acer platanoides* can promptly replace mixed *Populus tremula-Betula pendula* stands after 100 years of development. Unlike the more northern *Betula pendula* forests in Belarus, *Carpinus betulus*, *Acer platanoides*, and *Quercus robur* are prevalent in the forest stands and understory of Belavezhskaya Pushcha. Additionally, the probability of *Picea abies* mortality at the southern border of its distribution range is significantly higher than in northern regions, increasing the likelihood of *Betula pendula* forests transitioning directly into broad-leaved forests. Nonetheless, the most probable succession pathway involves the regeneration of broadleaved forests from *Betula pendula* forests through the *Picea abies* phase, albeit at an accelerated pace compared to northern regions.

The results of the study indicate a significant reduction in the area of *Betula pendula* forests in Belavezhskaya Pushcha in the coming decades and their gradual replacement by spruce and mixed-broadleaved forests. Understanding and knowing this trend can help predict the structure, biodiversity and carbon sequestration potential of unmanaged forests.

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