Ann. For. Res. 68(2): 41-54, 2025
https://doi.org/10.15287/afr.2025.3845

ANNALS OF FOREST RESEARCH
www.afrjournal.org

How dynamic are structural and compositional changes at different scales? An example from the strictly protected forests of Roztocze National Park in Poland

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Keren S., Ochał W., Maciejewski Z., 2025. How dynamic are structural and compositional changes at different scales? An example from the strictly protected forests of Roztocze National Park in Poland. Ann. For. Res. 68(2): 41-54.

Abstract In certain instances, forest managers are expected to emulate the structural patterns and disturbance regimes of primary forests. In this context, the forest cycle theory, established during the 20th century and widely adopted by many forest researchers and practitioners with little or no critique, suggests that particular patches (groups of trees) within an old-growth stand develop unidirectionally, progressing through stages from regeneration and initial growth to optimal and, finally, breakdown stage. However, due to the lack of long-term observations with detailed tree position data, little research has been conducted on this subject. Our study focused on proxy small-scale spatial dynamics based on patches of living trees for which exact positions and diameters were recorded from 1993 to 2023. First, we analyzed changes at the stand level in terms of diameter distributions and tree species composition over three decades. The distributions of European beech and silver fir remained relatively stable, while the cumulative distribution changed significantly due to a noticeable decrease in young trees of minor species. Secondly, we investigated the dynamics of basal area (BA) changes at the sub-stand level on small patches ranging from 0.01 ha to 0.0625 ha for each decade and over the entire observation period. At the decadal level, the values of Clark-Evans index indicated spatially random single-tree mortality as the predominant disturbance pattern. However, over a longer period, some of these small disturbances repeatedly occurred and concentrated at the same microlocations within the forest, which eventually resulted in spatially aggregated losses of BA by the end of the observation period. Another important finding from this study was that patches with non-directional BA dynamics were more common than those with continual positive BA accretion and/or continual negative BA trajectories. This finding significantly challenges the premises of unidirectional patch development.

Keywords: forest dynamics, fine-scale patches, basal area trajectories, primary forests.

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Manuscript: received September 25, 2024; revised July 12, 2025; accepted July 21, 2025.

Introduction

With the growing concerns about how to adapt managed forests to ongoing climate changes, the structural dynamics and changes in tree species composition of primary forests have been drawing ever greater attention from forest researchers since the beginning of 21st century. In Europe, the remnants of these forests are mostly composed of shade-tolerant species such as European beech (*Fagus sylvatica* L.), silver fir (*Abies alba* Mill.) and/or Norway spruce (*Picea abies* (L.) H. Karst.) (Sabatini et al. 2021, Motta et al. 2024). Studying the intricacies of their structure and species composition is crucial as they serve as solid indicators of site naturalness (Meyer et al. 2021) and are thus often used as a reference for close-to-nature forest management (Krumm et al. 2023). Although large-scale disturbances occasionally affect these forests and may abruptly change their structure and composition (Hobi et al. 2015, Jaloviar et al. 2017, Feldmann et al. 2018), such events are usually of a local character. In most cases, primary forests have been found to be resistant and resilient, typically experiencing single-tree mortality, with canopy openings often filled by advanced regeneration (Nagel et al. 2010; Feldmann et al. 2018a, 2020; Petrovska et al. 2023).

Over time, typically over the span of a few decades, primary mixed beech-coniferous forests tend to undergo gradual changes in structure (Diaci et al. 2011, Keren et al. 2014, Kulha et al. 2020) and tree species composition (Vrška et al. 2009, Szwagrzyk et al. 2012, Kulla et al. 2023). Most studies on this topic have been conducted at the stand level, whereby the structural and compositional changes that these forests experience have been ascribed to a variety of different factors including air pollution (Diaci 2011), browsing (Diaci et al. 2022) and climate change (Kulla et al. 2023). In addition, the processes of masting, competition and facilitation among different tree species are very complex and difficult to fully understand due to the unavailability of detailed long-term data, suggesting that much work remains for forest researchers. Even structural data spanning several decades are often unavailable for many primary stands. Therefore, when such data are available, it is important to analyze them to describe structural and compositional changes in primary forests in different parts of Europe. In this context, several studies over the last three decades have indicated the progression of beech and decline of silver fir in European primary forests (Korpel 1995, Diaci 2011, Maciejewski & Szwagrzyk 2011, Keren et al. 2014, Diaci et al. 2022). Such reports from different countries are crucial for gaining an insight into whether there is a trend at the continental level regarding changes in the structure and tree species composition of unmanaged beech-conifers stands.

In forest research and forestry practice, structural changes are typically described at the stand or landscape level. In Poland, stand areas usually exceed one hectare, typically ranging between a few to several dozen hectares. While observing structural and species changes at the stand level is important, large changes may not be apparent over one or even a few decades (Stillhard et al. 2022), unless impactful canopy disturbances occur (Nagel et al. 2017). The consequences of medium- and large-scale disturbances are immediately detectable and can be relatively easily quantified. However, the underlying structural changes at the sub-stand level that occur due to small-scale mortality are much more subtle and difficult to detect. Additionally, the dynamics and direction of these changes are not yet thoroughly understood due to the scarcity of spatio-temporal data from unmanaged forests. A rich body of valuable studies has been conducted with regard to the spatial delineation and identification of developmental phases/stages (sub-stand patches) in primary forests (Meyer 1999, Drößler & Meyer 2006, Winter & Brambach 2011, Feldmann et al. 2018b, Glatthorn et al. 2018, Zenner & Peck 2021). However, only few studies in Europe have addressed the issue of patch development through a period of a few decades (Král et al. 2018, Meyer et al. 2021). At the patch level, spanning a few hundred square meters, changes in primary forests are often believed to follow a straightforward cyclical pathway, wherein a given patch develops unidirectionally from the initial growth stage to the optimal stage, eventually culminating in the breakdown stage (Leibundgut 1982, Mayer 1984, Korpel 1995). However, in this long-term process, the steady (selection) stage occurs more often than previously thought (Král et al. 2014, 2016, Keren et al. 2017). Moreover, Král et al. (2018) found that a large percentage of patches at the sub-stand level do not develop linearly from the initial to breakdown stage, but rather experience various trajectories. These authors showed that during their development, sub-stand patches may undergo larger or smaller disturbances, or conversely, tree growth may be unexpectedly accelerated. While patch development trajectories can be cyclical, following the growth–optimum–breakdown sequence without interruptions, they can also be acyclic and non-linear. Acyclic development trajectories vary; for instance, some patches may reach the breakdown phase more quickly, while others may experience only slight disturbances before continuing to accumulate biomass. Král et al. (2018) found that more than 60% of the transitions in Czech old-growth forests were acyclic (moving across or backward in the model cycle). Thus, it not yet clear whether one-directional cyclic development at the patch level in old-growth forests should be considered a general rule, as suggested by some authors (Leibundgut 1982, Remmert 1992, Korpel 1995). Based on premises and knowledge from the 20th century, this trajectory has been adopted by foresters and applied to most European managed forests, even those composed of shade-tolerant tree species. However, is this the only trajectory that should be pursued if the goal is to manage forests in a way that is “closer to nature”?

Considering the need to monitor structural and compositional changes in primary forests at the stand level, along with the scarcity of knowledge regarding patch development at the sub-stand level, the objectives of this study were to (1) identify significant structural and compositional changes in the Roztocze primary forest over three consecutive decades, based on three 0.5 ha permanent plots and (2) analyze and explain the direction of these changes in smaller subplots. Specifically, we focused on microscales ranging from 0.01 ha to 0.0625 ha, as these scales are often considered when marking trees for cutting within the context of single-tree and group selection silviculture. Forest managers typically have insights into what the structure should look like at stand level or per hectare, but there is limited information on how this structure is built and how it changes over time at smaller spatial scales. Such information may be of practical use to forest managers and conservationists, at least in areas where close-to-nature silviculture aims to emulate disturbance regimes and structural patterns that occur in reference unmanaged forests.

Materials and Methods

Study area

Roztocze National Park (RNP) is situated in the central part of the meta-Carpathian upland known as the Roztocze Highlands in the southeastern part of Poland (50°31' to 50°40' N and 22°53' to 23°07' E, Fig.1). The landscape of the RNP is characterized by long chains of upper Cretaceous limestone hills reaching 366 m a.s.l., surrounded or partially covered by thick layers of postglacial deposits, sand or loess. The most common soil types in the RNP are Podzols and Cambisols (Maciejewski 2010). The study area is considered a climatic border between the maritime (Atlantic) climate and the continental climate. Based on the observations from 2012 to 2024 mean annual temperature is 8.8°C, while mean annual precipitation amounted to 690 mm (unpublished report Maciejewski 2025).

The RNP was officially established in 1974, but the studied stands have been strictly protected since 1957 in the frame of smaller forest reserve Nart-Czerkies. Thus direct human impact has been absent in the study area for at least seven decades. We cannot completely exclude the possibility of very light single-tree removals during large conflicts such as WWII, however there is no physical or written evidence of such interventions. Currently, strictly protected forest stands cover almost 33% of the RNP area. From the end of the 16th century until the park's establishment, the forests growing in the current RNP area belonged to a large aristocratic estate, and a large portion of them was used as the great game reserve known as "Zwierzyniec". This helped prevent the fragmentation of the forest complex and also helped to maintain the natural character of many forest stands of the study area (Maciejewski 2010). According to classification definitions (Buchwald 2005) some parts of the strictly protected forests of the RPN have the character of old-growth stands, so they have consequently been recognized as remnants of European primary forests (Szwagrzyk et al. 2012, Sabatini et al. 2021). The forests of the RPN are characterized by high species diversity and are located near the natural range limits of major forest tree species such as European beech, Norway spruce and silver fir (Szwagrzyk et al. 2018). These circumstances make the area ideal for investigating spontaneous development of natural forest structure and dynamics.

Data collection

Three sample plots, each measuring 0.5 ha (100 x 50 m), were measured four times over the last three decades (1993, 2003, 2013, and 2023). Although there are a few more such plots in the study area, we selected these three because they were dominated by beech and fir, the main species of interest, and because they were located in the best-preserved part of the RNP. The following information was recorded: tree species, DBH (callipering with 0.1 cm precision) and the position of each tree (x and y coordinates) within each sample plot. The diameter at breast height (DBH) was measured for all living trees that exceeded the inventory threshold of 7.0 cm. For each tree, the diameter was measured twice (in two perpendicular positions) at 1.30 m above the ground, and the

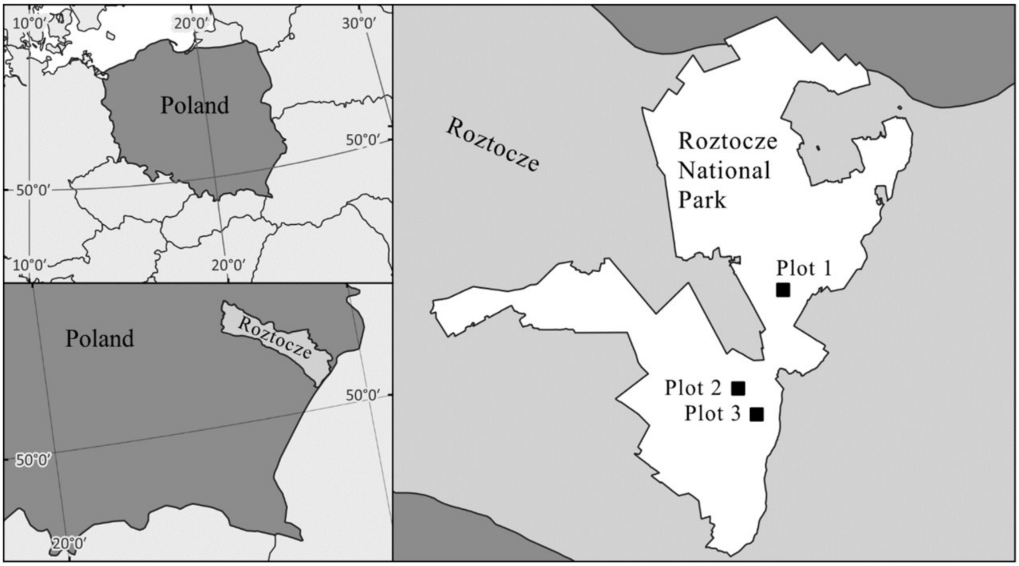

Figure 1 The coarse and detailed map of study site location (Roztocze National Park) and the position of investigated plots within it.

average value of the two measurements was used in the analysis. When the first inventory was conducted in 1993 each 100 x 50 m plot was divided into 10 x 10 m subplots by physically marking the corners of those subplots with wooden sticks. Then by using measuring tape the position of each tree within a subplot (tree coordinates x, y) was measured as a distance from the subplot sides that basically represent x and y axis. Finally, the data from each subplot were calculated in the frame of one coordinate system at the level of whole 0.5 ha plot.

Data analysis

In the first step, we analyzed changes in diameter at breast height (DBH) and basal area (BA) distribution, as well as species composition across the study area over the 30-year observation period. Frequency distributions of DBH and basal area were constructed using 5-cm wide classes and analyzed for the years in which the measurements were taken. The χ^2 test with a significance level of $\alpha = 0.05$ was used to check if there were significant structural and compositional changes in the Roztocze primary forest on three 0.5 ha permanent plots between the beginning and end of the observation period.

Next, detailed tree coordinate data were used to subdivide the 0.5 ha plots into smaller square subplots with dimensions of 10 x 10 m (0.01 ha), 12.5 x 12.5 m (0.0156 ha), 16.67 x 16.67 m (0.0278 ha) and 25 x 25 m (0.0625 ha) to analyze the dynamics of stand structural features at fine spatial scales. For each subplot size, we defined two trajectories of BA dynamics: positive ($BA_t - BA_{t-1} \geq 0$) and negative ($BA_t - BA_{t-1} < 0$) change in BA on a decadal scale, where t refers to a specific end of inventory period and t-1 stands for the beginning of that inventory period. We then calculated the proportion of subplots with the identified trajectory of BA dynamics for each of the four spatial scales. While it might be appealing to introduce a neutral state with small changes in basal area on decadal level, any threshold in our opinion would be subjective. Instead of using a neutral state, for a deeper insight in small changes we provided detailed information about gains and losses of BA per hectare at decadal level for different size of subplots by using class width of 2 $m^2 \cdot ha^{-1}$ (Fig. 4).

Based on the BA dynamics observed between adjacent decades, we further distinguished four scenarios of BA development over the 30-year observation period. These scenarios, or trajectories, were categorized as follows: +3BA (denoting three consecutive periods of BA growth), +2BA (two periods of BA growth and one of BA decline), -2BA (two periods of BA decline and one of BA growth) and -3BA (three consecutive periods of BA decline). In the frame of the -2BA scenario we additionally distinguished the loss→gain→loss trajectory, and likewise in the frame of the +2BA scenario the gain→loss→gain trajectory was distinguished as they show interchangeable dynamics of BA development. In this part of the analysis, we examined the frequency of individual BA development scenarios at each of the spatial scales.

To assess the spatial pattern of tree mortality for each decade and for the entire analyzed period, we calculated the aggregation index R (Clark & Evans 1954) with edge correction according to (Donnelly 1978) using the “clarkevans” function from the r package “spatstat” (R Core Team 2021). The significance of the null hypothesis was tested assuming complete spatial randomization by calculating the *p*-value for the two-sided test using the standardized R-value (Clark & Evans 1954). The *p*-value computation was conducted by using the “clarkevans.test” function from the r package “spatstat.explore” (R Core Team 2021).

In the final step, we compiled detailed BA change distributions, showing the frequency and magnitude of observed absolute BA changes at the different spatial scales. Based on the frequency and magnitude of BA changes over the 30-year observation period, we described the direction and intensity of changes in the spatio-temporal structure of the Roztocze forest.

Results

Changes in diameter distribution, basal area distributions and tree species composition

For the combined three permanent plots of 0.5 ha (a cumulative total of 1.5 ha), significant changes occurred in DBH distributions over the observed period from 1993 to 2023 with respect to the total number of trees (χ^2 = 37.4, p = 0.0001; Fig. 2a). The number of beech trees slightly increased, while the number of silver fir trees slightly decreased, indicating that the distributions of these species remained relatively stable during this period. However, a significant change was detected for hornbeam (χ^2 = 83.4, p = 0.0000), primarily due to a large decrease in the number of small trees of this species. Significant changes in tree species composition, based on the number of trees, were also observed during the study period (χ^2 = 20.5, p = 0.0002; Table 1). On the other hand, the basal area distribution for individual tree species, as well as cumulatively for all species at the stand level, remained relatively stable over the three decades (Fig. 2b).

On the entire observed area of 1.5 ha, the total BA gradually increased from 32.8 $m^2 \cdot ha^{-1}$ to 38.7 $m^2 \cdot ha^{-1}$ during first two decades (1993 to 2013). However, in the last decade (2013-2023), it slightly decreased to 36.1 $m^2 \cdot ha^{-1}$ (Table 1). The overall increase in BA was mainly contributed by beech (from 13.1 $m^2 \cdot ha^{-1}$ to 18 $m^2 \cdot ha^{-1}$). The slight decline in the last decade was largely due to a 12.8% drop in silver fir BA, which reduced its share in tree species composition for 3%. Additionally, the shares of other species (hornbeam, oak, Scots pine, Norway spruce), which already played a minor role at the beginning of the observation period (cumulatively accounting for 15% in 1993), continuously decreased, with their cumulative share dropping to only 9% by 2023. After the three decades, only beech increased its share in BA, rising from 40% to 50% (Table 1). In the Table 2 the information about the ingrowth of small trees exceeding the inventory threshold of 7.0 cm in DBH and the number of trees that died (regardless of the cause of their death as such information was not collected in the past) is provided for particular decades.

Small-scale dynamics of BA from 1993 to 2023

The percentages of negative changes in basal area differed across particular decades (Figure 3). Interestingly, smaller subplots of 0.01 ha and 0.0156 ha exhibited a higher percentage of negative BA changes over the entire three-decade period than within individual decades. Conversely, the subplots of 0.0278 ha and 0.0625 ha tended to experience larger percentage of negative BA changes during particular decades, but by the end of the total observation period (1993-2023), these changes appeared to even out as the decadal highs and lows averaged out. Dying of a single tree or a few trees rules out the increases of a single 10-year period more easily than increases of the whole 30-year period. Depending on the subplot size, negative BA changes over the entire observation period ranged from 29% to 35% (Figure 3).

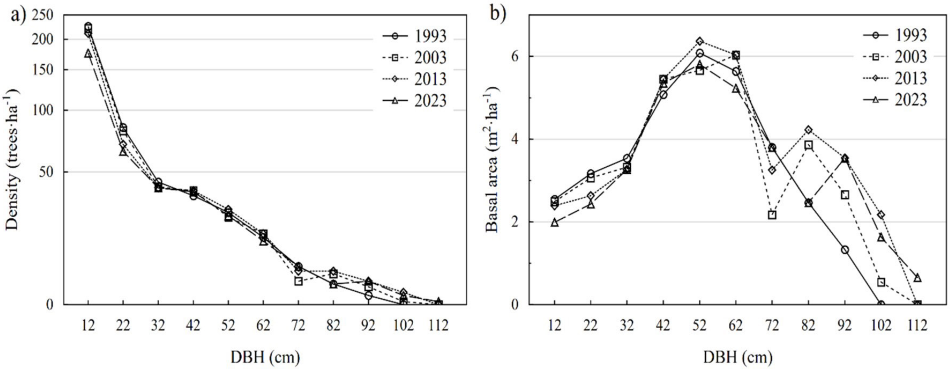

Figure 2 Structure of tree diameter (a) and basal area distribution (b).

Table 1 The main dendrometric characteristics of the studied forest in the Roztocze National Park based on three 0.5 ha permanent plots in consecutive inventory years.

Species	Quadratic mean diameter (cm)				Stand density (trees ha^{-1})				Basal area (m^{2}ha^{-1})			
	1993	2003	2013	2023	1993	2003	2013	2023	1993	2003	2013	2023
Abies alba	35.3	36.3	37.8	37.9	151	147	152	132	14.83	15.22	17.04	14.86
Fagus sylvatica	31.0	32.2	34.3	35.4	173	189	193	183	13.05	15.37	17.79	18.00
Carpinus betulus	16.9	18.0	19.4	20.7	105	93	76	60	2.36	2.37	2.24	2.03
Pinus silvestris	46.5	49.4	50.0	48.7	10	7	6	5	1.70	1.41	1.18	0.87
Quercus robur	35.8	32.6	30.4	32.4	7	4	3	2	0.74	0.33	0.19	0.17
Picea abies	17.0	19.4	23.0	26.1	7	6	5	4	0.15	0.18	0.22	0.21
Total	30.4	31.6	33.7	34.5	453	446	435	386	32.83	34.88	38.66	36.14

Table 2 The ingrowth of small trees exceeding the inventory DBH threshold and trees that died (regardless of death cause) expressed in numbers per hectare, with basal area (m2·ha-1) in parentheses.

Species	1993-2003		2003-2013		2013-2023	
	Ingrowth	Mortality	Ingrowth	Mortality	Ingrowth	Mortality
Abies alba	15 (0.09)	19 (2.26)	19 (0.10)	15 (1.07)	3 (0.02)	23 (3.65)
Fagus sylvatica	26 (0.13)	10 (0.48)	19 (0.09)	15 (0.55)	5 (0.02)	14 (1.95)
Carpinus betulus	4 (0.02)	16 (0.37)	3 (0.01)	19 (0.46)	0 (0)	16 (0.44)
Pinus silvestris	0 (0)	3 (0.31)	0 (0)	1 (0.25)	0 (0)	1 (0.33)
Quercus robur	0 (0)	3 (0.42)	0 (0)	1 (0.16)	0 (0)	1 (0.03)
Picea abies	0 (0)	1 (0.01)	0 (0)	1 (0)	0 (0)	1 (0.03)
Total	45 (0.24)	52 (3.85)	41 (0.2)	52 (2.49)	8 (0.04)	56 (6.43)

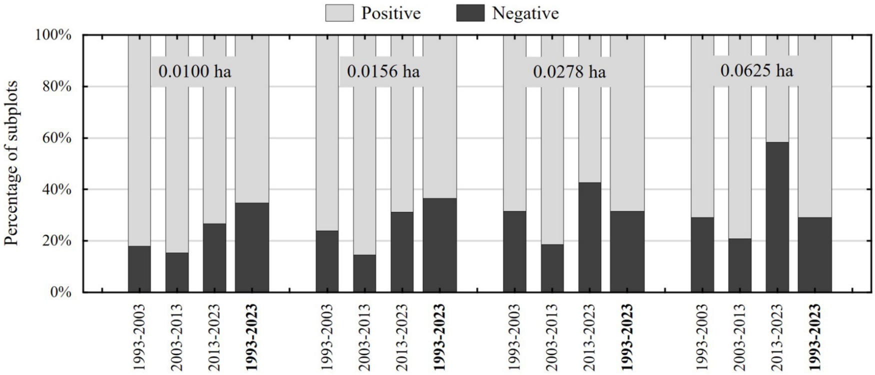

Figure 3 Percentage of subplots from 0.01 ha to 0.0625 ha on which positive and negative changes of basal area were observed, aggregating all plots in particular decades (consecutive observation periods).

However, here it is also important to pay attention to BA losses and gains in absolute terms. Namely, despite the fact that negative BA changes in absolute terms were rather large in a few instances, the median of BA losses within individual decades was fairly small on the largest subplots amounting to 4.8 m^2·ha^{-1} and moderately high with 12.1 m^2·ha^{-1} on the smallest subplots. Considering positive BA changes the impact of subplot size was obviously smaller as the median in this case amounted to 4.4 m^2·ha^{-1} and 5.2 m^2·ha^{-1} on largest and smallest subplots, respectively. The full spectrum of BA losses and gains in absolute terms is shown in the Figure 4. Based on this Figure, the outcomes further showed that small BA fluctuations in the range of ± 2 m^2·ha^{-1} occurred on 24.7% and 23.6% of the smallest and largest subplots, respectively.

For illustrative purposes four main scenarios of BA changes through time are shown at different spatial scales in the form of a map in the Figure 5.

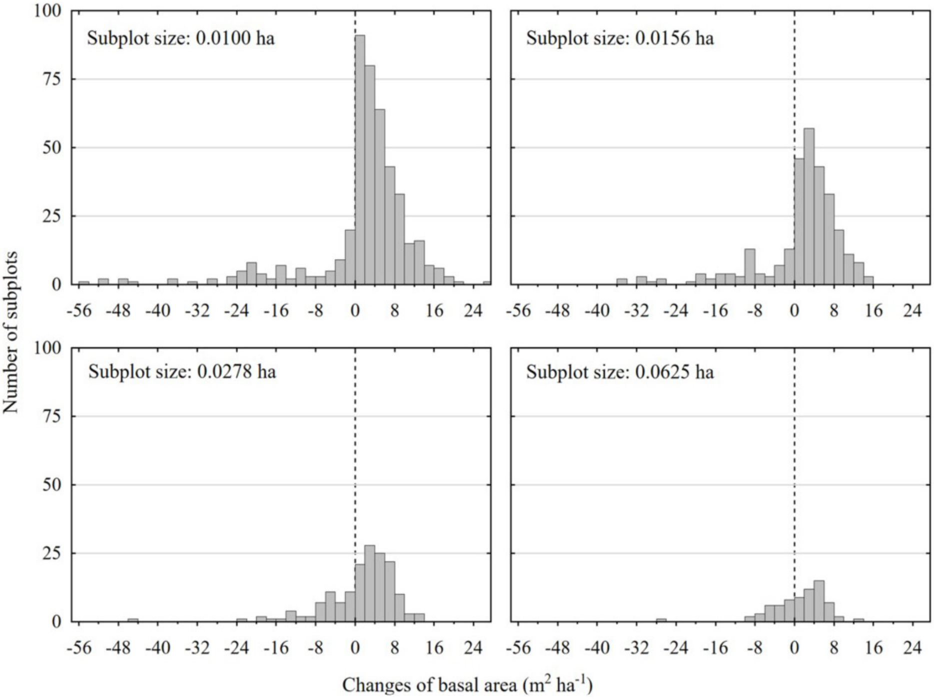

Figure 4 Distribution of basal area losses and gains on a decadal level (without averaging over studied decades) for different subplot sizes, expressed in absolute terms per hectare.

The subplots that experienced a continual decrease in BA over the three consecutive decades were rare, ranging from 0.7% to 4.2%, depending on subplot size (Fig. 6). The scenario involving two negative decades and one positive decade in terms of BA dynamics occurred in 6% to 25% of the cases, out of which the loss-gain-loss trajectory ranged from 2% to 16.7% on the smallest and largest subplots, respectively. Conversely, the trajectory with two positive decades and one negative decade was the most frequently occurring, ranging from 41.7% to 48.1%, out of which the gain-loss-gain trajectory amounted to 10.7% on the smallest- and 8.3% on the largest subplots. Finally, the continual increase in BA over the three consecutive decades (directional positive development) was still a relatively frequent trajectory, occurring in 25% to 47.3% of possible cases, depending on subplot size (Fig. 6). In summary, combined non-directional BA dynamics with one and/or two decades of negative changes within the 30-year period were more common than cases of positive continual BA accretion, whereas the scenario of three consecutive decades of negative BA dynamics was exiguous.

Considering the mortality of trees at decadal level and across the period of all three decades, random spatial pattern was predominant as most calculated R values of the Clark-Evans test were close to 1. Only in one of the three studied plots the aggregate mortality pattern was found regarding the last decade (2013-2023) and the overall period from 1993 to 2023 (Table 3).

Table 3 The test outcomes of point pattern analysis based on the Clark-Evans R index.

Plots	Period	R	*p*-value
Plot 1	1993-2003	1.0205	0.8199
	2003-2013	0.9721	0.7650
	2013-2023	0.8716	0.1482
	1993-2023	0.9998	0.9964
Plot 2	1993-2003	0.9952	0.9652
	2003-2013	0.9723	0.8267
	2013-2023	1.1160	0.1985
	1993-2023	0.9890	0.8635
Plot 3	1993-2003	0.8738	0.1373
	2003-2013	0.8876	0.1476
	2013-2023	0.8132	0.0384
	1993-2023	0.7873	0.0000

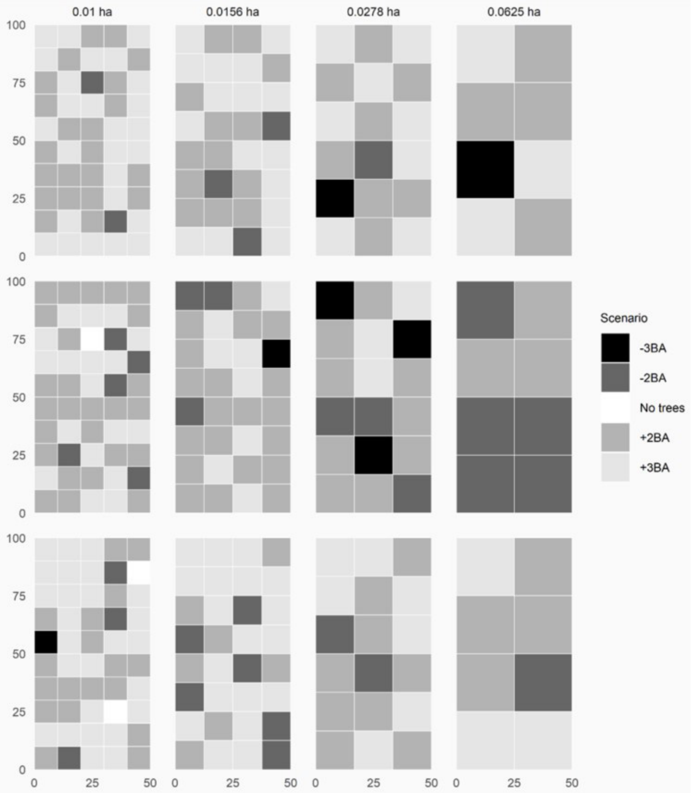

Figure 5 The scenarios of basal area changes at decadal level over three decades (+3BA — light gray, +2BA — gray, -2BA — dark gray, -3BA — black, no trees — white) observed in the study plots (plot 1 — top, plot 2 — middle, plot 3 — bottom) at spatial scales from 0.01 ha (left) to 0.0625 ha (right).

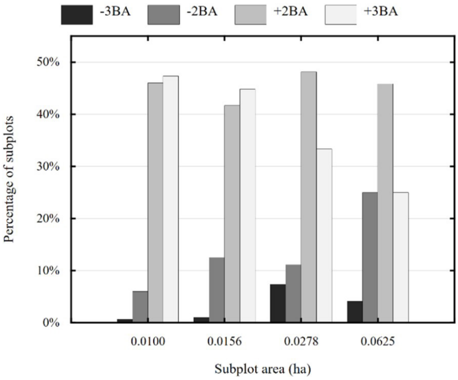

Figure 6 Percentage of subplots of different sizes with respect to developmental trajectories of basal area. The legend of trajectories is provided below: -3BA — three consecutive decades with a decrease in basal area in each decade; -2BA — two decades with negative changes and one decade with a positive change in basal area; +2BA — two decades with positive changes and one with a negative change in basal area; +3BA — three consecutive decades with an increase in basal area in each decade.

Discussion

Structural and compositional changes in a 1.5 ha monitored area over a three-decade period

The DBH distributions, considering the total number of trees in the RNP, significantly changed primarily due to a considerable decrease in the number of young hornbeam trees between 1993 and 2023. Although some admixed tree species, such as hornbeam, oak, pine and spruce, naturally occur in the RNP, their decline in species composition from 15% to 9% over the last three decades suggests their smaller competitive ability compared to shade-tolerant beech and fir. Although there is no clear evidence about direct human influence in the past in the study area, we do not completely exclude the possibility of low-intensity logging. For instance, during historical conflicts such as WWII, it is unclear whether there was any minor direct human impact on these forests or not. If any logging took place, it may have to a smaller degree helped the regeneration and ingrowth of less shade-tolerant species at the cost of beech and fir. However, even a small change in the share of minor species due to direct human impact would skew our proper understanding of the dynamics of these forests. Unfortunately, for many European primary forests, it is difficult, and sometimes impossible, to determine the exact degree of human influence prior to official strict protection, which questions their real status, so the caution is certainly advised when drawing conclusions in this regard.

Even if there was no direct human influence, little or no information exists regarding the impact of natural disturbances, as they were not accurately investigated or even recorded in the past. Disturbances have the potential to greatly impact forest dynamics (Nagel et al. 2014, Cerioni et al. 2024, Rodrigo et al. 2024) which is why gathering data and studying their effects is crucial for understanding the dynamics of primary forests. Recent evidence shows that more intensive disturbances occasionally occur in some parts of the RNP, after which hornbeam as a mid-shade tolerant species might play a role in tree species composition along with more shade-tolerant beech and fir. However, more light-demanding species struggle to compete with established advanced regeneration of shade-tolerant species (Szwagrzyk et al. 2018) and their share in the study area remains rather small. Small admixture of light-demanding tree species was also observed in other primary forests in Europe (Hobi et al. 2015, Feldmann et al. 2018a). While some recent changes in primary forests may be attributed to ongoing climate change (Kulla et al. 2023), it is also quite possible that following the strict protection of investigated stands since 1957, beech naturally started to suppress and more decisively dominate over shade-intolerant tree species. Consequently, beech, along with silver fir, which still plays a significant role, remain the major tree species on our plots, similar to other European primary forests that have been strictly protected for long periods (Paluch et al. 2021, Motta et al. 2024).

If large disturbances continue to be absent in the future, we may expect further reductions in minor tree species in the tree species composition. The share of silver fir in total stand BA decreased by 3% over the last decade. Due to the overall increase in total BA, the relative share of silver fir decreased from 45% to 41% over the entire three-decade period, although its absolute share remained stable at 22.3 $m^2 \cdot ha^{-1}$. Reports from other European countries (Diaci et al. 2022, Kulla et al. 2023) suggest that in the near future, beech may become the only major tree species in primary forests, with silver fir declining to a minor species. Currently, silver fir's "position" in the RNP remains stable, but the overall changes in tree species composition in our study indicate that intensive dynamics are still ongoing. Therefore, it will be interesting to monitor these changes in the future to determine the extent to which they correspond with developments in other similar sites in Poland and across Europe.

Temporal dynamics of BA at fine spatial scales

Considering the concept of cyclic development of primary forests, there is a general assumption that basal area or biomass of sub-stand patches in these forests develops unidirectionally through time (Leibundgut 1982, Remmert 1992, Korpel 1995). A few recent studies applying different methodological techniques indicated biomass build up over decades followed by saturation, but they were conducted at the stand scale in forest reserves with background management (Meyer et al. 2021, Nagel et al. 2023, Idoate-Lacasia et al. 2024). However, Král et al. (2018) found that sub-stand patches mostly do not follow a unidirectional pattern as they undergo temporary setbacks following larger or smaller disturbances through time. In this regard our results strongly corroborate the findings by Král et al. (2018). These findings suggest that one-directional cyclic development in primary forests, although it occurs, should not be considered a general rule. Consequently, in those areas where silviculturalists tend to emulate natural processes, there is no justification to pursue only a unidirectional development of forests.

Similar to other European primary forests (Trotsiuk et al. 2012, Petritan et al. 2015, Paluch 2021), single-tree mortality was the predominant disturbance pattern in our study area, as negative BA changes were small in absolute terms and occurred locally, following a random spatial mortality pattern in most cases based on Clark-Evans test. Therefore, random single-tree removals seem to be the most appropriate silvicultural technique for emulating natural processes. Nonetheless, it is also important to note that the share of negative BA changes in our study decreased with increasing subplot size (about 35% and 29% for subplots of 0.01 ha and 0.0625 ha in size, respectively), which suggests that negative BA changes over longer periods, to a degree, tend to occur in an aggregated manner at certain locations within a stand. The outcomes of Clark-Evans test confirmed the tendency to group mortality of trees in one of the three studied plots over the period of three decades. Consequently, this outcome suggests that creating patches with a unidirectional BA development should not be excluded from close-to-nature forest management altogether, but rather applied in a reasonable manner as a complementary technique to single-tree removals.

Conclusion

The fact that, on a decadal level, most BA losses in the RPN primary forest were fairly small supports the idea that single-tree selection system should be predominantly applied, at least in forests composed of shade-tolerant tree species where the aim is to emulate natural processes. However, group-selection system and potentially irregular shelterwood should also play a role as directional BA dynamics turned out to be consecutively negative and/ or positive at the largest observed scale of 0.0625 ha across three decades. Another potentially useful insight for forest managers stems from the finding that wave-like BA dynamics characterized by loss-gain-loss and gain-loss-gain trajectories were partly present in our study area at small spatial scales. Thus, contrary to forestry practices that are based purely on unidirectional patch development, where continual BA accretion is typically pursued in even-aged managed stands until the final cut, our results suggest that forest managers could allow more flexibility in applying silvicultural interventions. Under this approach, BA at small spatial scales may fluctuate slightly from decade to decade rather than grow unidirectionally. This conclusion applies specifically to small-scale BA dynamics and should not be generalized or readily extrapolated. Namely, if significant tree mortality occurs at subplot level, it can indicate a temporary developmental „setback" when recalculated per hectare, which does not necessarily fit the reality of that larger scale. Therefore, to reliably quantify and describe long-term BA or biomass dynamics at the stand level, future research in primary forests should focus on larger scales, where the data from permanent plots of greater size would be thoroughly examined.

Conflict of interest

The authors declare no financial or personal interests could influence the work presented in this paper.

Acknowledgement

This research was supported by the National Science Centre in Poland (NCN) in the frame of the project nr 2021/43/D/NZ9/00645.

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