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Altitudinal patterns of Norway spruce stands structure and productivity in the Ukrainian Carpathians

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Abstract. Elevation above sea level is one of the key orographic factors determining the spatial distribution, structure, and productivity of Norway spruce stands in the Ukrainian Carpathians. This study aimed to identify patterns of altitudinal differentiation in their stands structure and productivity and to define analytical groups for further investigation of assortment structure. The study was based on the forest compartment database of the Ukrainian State Forest Management Planning Association "Ukrderzhlisproekt" as of 1 January 2022. A total of 96,876 first layer forest inventory compartments covering 320,679.9 ha were analysed; in each compartment, spruce accounted for at least three units of the stand composition and elevation above sea level had been recorded. Area-weighted mean values, quantile characteristics of growing-stock distributions, and the non-parametric Kruskal-Wallis test were used in the analysis. The largest area of spruce stands was concentrated within the elevation range of 1,000-1,149 m above sea level, amounting to 83,760.3 ha, or 26.1%. This elevation range also had the highest area-weighted mean growing stock for the entire set of stands, at 377 $m^3 \cdot ha^{-1}$, and for mature stands, including overmature stands, at 479 $m^3 \cdot ha^{-1}$. The total area of mature and overmature stands was 64,699.0 ha, with their highest proportion within an individual elevation range occurring at high elevations. Differences in the growing stock of mature and overmature stands among elevation ranges were statistically significant, while the highest median and quartile values were likewise recorded at 1,000-1,149 m. Records for which elevation had not been established accounted for 7.6% of the area in the initial dataset and were excluded from the analysis of altitudinal differentiation. Changes

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in growing stock along the altitudinal gradient were also associated with the trophic status of forest-site conditions, age structure, relative stocking, and the proportion of spruce in the stand. The highest area-weighted mean growing stocks of mature and overmature spruce stands were recorded under fairly fertile and fertile site types, whereas values were substantially lower under infertile pine and fairly infertile pine site types. The practical significance of the findings lies in substantiating an elevation-, age-, and site type-based approach to selecting stands and model trees for assessing the assortment potential of Norway spruce

Keywords: *Picea abies*; orographic gradient; stand growing stock; trophotope; mature stands; forest mensuration; assortment potential

Introduction

Norway spruce (*Picea abies* (L.) Karst.) is one of the principal forest-forming species of the Ukrainian Carpathians, and its distribution, structure, and productivity vary considerably along the altitudinal gradient. Forest compartment data indicate that the most productive spruce stands in the region are concentrated mainly under moist, fairly fertile and fertile site types in the middle-mountain zone, whereas at higher elevations growing-stock accumulation is constrained by harsher climatic and edaphic conditions (Lavnyy & Matusevych, 2022). An analysis of changes in the area and structure of spruce stands in the Ukrainian Carpathians between 1988 and 2018 also demonstrated increasing altitudinal differentiation and a growing proportion of stands situated above 800 m above sea level (Lavnyy *et al.*, 2025).

Recent studies in the Eastern Carpathians have shown that the response of Norway spruce to climate change varies with elevation. At lower elevations, moisture deficits and high temperatures increasingly constrain growth, whereas in upper elevation zones growth depends to a greater extent on temperature conditions and the duration of the growing season (Sedmáková *et al.*, 2019; Popa *et al.*, 2024a). J. Schurman *et al.* (2024) noted that the distribution limits of spruce along the Carpathian altitudinal gradient are also shaped by interspecific competition, particularly with European beech.

In addition to climate, the productivity of spruce stands is determined by mountain topography, site conditions, and their stands structure. In the Romanian Carpathians, spruce stand growing stock has been found to depend on landscape spatial structure and the combined effects of local site conditions (Crişan *et al.*, 2023). A study by J. Kermavnar *et al.* (2023) in Central Europe showed that the vulnerability of *Picea abies* to dieback depends substantially on parent material, soil properties, and the degree of forest naturalness. An experimental study by D.J. Chmura & J. Modrzyński (2023) on Norway spruce provenances from the Carpathians and Sudetes showed that differences in growth and phenology reflect the adaptation of populations to the climate of their place of origin, while further warming and increasing aridity may reduce their productivity.

The adverse effects of warming are not confined to lower elevation zones. In high-elevation spruce forests of the High Tatras, large trees were found to be increasingly sensitive to drought in the preceding year, indicating that water limitation is becoming more pronounced even under traditionally cool high-mountain conditions (Märker *et al.*, 2025). In subalpine spruce forests of the Dinaric Alps, M. Orešković *et al.* (2024) found spatially heterogeneous growth responses to temperature and precipitation, as well as greater tree resilience at higher elevations. For the Ukrainian Carpathians, these broader European patterns need to be considered in the context of the regional characteristics of both natural and human-modified spruce forests. Studies of natural spruce forests in the Pokuttia Carpathians conducted by V.P. Losyuk *et al*. (2021) revealed considerable structural heterogeneity among stands and demonstrated the need to account for stand age, species composition, and forest site conditions when assessing productivity. At the same time, findings by G. D'Andrea *et al*. (2023) in Central Europe confirm the increasing climatic sensitivity of Norway spruce outside its optimal growing conditions.

Despite the available research, the altitudinal differentiation of the actual stands structure of spruce stands across the entire Ukrainian part of the Carpathians has not yet been synthesised using a comprehensive quantitative analysis. Most studies focus on particular forest types or individual forest tracts, or are based on tree-ring analysis, whereas compartment-level analysis makes it possible to assess area, age, growing stock, height, diameter, relative stocking, spruce proportion, and the trophic status of forest site conditions simultaneously. The scientific novelty of this study lies in combining altitudinal, age-related, and typological levels of analysis for all available forest inventory compartments within the Carpathian forest-growing zone that met the specified criteria. This approach made it possible to refine the elevation range associated with maximum growing stock, separately assess patterns related to age structure and the trophic status of forest site conditions, and establish well-founded groups for subsequent analysis of assortment structure. This study aimed to identify patterns of altitudinal differentiation in the stands structure and productivity of spruce stands in the Ukrainian Carpathians and to substantiate altitudinal and typological groups for planning further research into their assortment structure. To achieve this aim, three key objectives were defined: to characterise the spatial distribution of spruce stands and compare their principal mensuration parameters across elevation ranges; to analyse mature and overmature stands separately; and to assess the relationship between their productivity and the trophic status of forest site conditions.

Materials and Methods

The study was conducted in 2026 using a compartment-level dataset in XLSX format compiled by the Ukrainian State Forest Management Planning Association "Ukrderzhlisproekt" in response to an official request from the authors. The dataset was provided to the authors in 2026 and describes the state of the forest estate as of 1 January 2022. At the time of analysis, it was the most recent complete dataset available to the authors with a single common inventory date. The use of a single inventory date ensured the comparability of stands parameters across the study dataset. The study focused on firstlayer spruce stands within the Carpathian forest-growing zone in Zakarpattia, Ivano-Frankivsk, Lviv, and Chernivtsi regions. The initial dataset comprised all available forest inventory compartments in which spruce accounted for at least three units of the firstlayer stand composition. This threshold was applied to identify stands in which spruce had substantial coenotic and mensurational significance.

The initial dataset formed according to these criteria comprised 105,952 forest inventory compartments with a total area of 347,018.0 ha. Elevation data were available for 96,876 compartments covering 320,679.9 ha, representing 92.4% of the total area of the initial dataset. For 9,076 compartments covering a total area of 26,338.1 ha, or 7.6%, elevation above sea level was not specified in the source dataset; these records were therefore excluded from the calculations of altitudinal differentiation. To assess potential bias, the included and excluded records were compared in terms of their principal stands parameters. The source dataset contained spatial, administrative, and stands parameters for each forest inventory compartment: administrative region, forest enterprise, forest district, forest quarter and compartment, area, elevation above sea level, layer number, stand composition and origin, stand age and age group, site index class, forest site conditions, mean height and diameter, relative stocking, and growing stock per hectare. The combination "forest district-quarter-compartment" was used to identify records unambiguously, while data on stand origin and site index class were used for initial quality control and general characterisation of the dataset. Separate analytical breakdowns by the latter two variables were not presented in the article.

The following notation was used in the calculations: S – area of the forest inventory compartment, ha; M – stand growing stock, $m^3 \cdot ha^{-1}$; A – stand age, years; H – mean height, m; D – mean diameter, cm; P – relative stocking; K – proportion of spruce in the stand composition, expressed in composition units; and E – elevation above sea level, m. In this study, stand productivity was assessed using growing stock per hectare, as this indicator was available for the entire compartment-level dataset. In all summary tables, mean values of growing stock, age, height, diameter, relative stocking, proportion of spruce in the stand composition, and elevation above sea level were calculated as area-weighted means based on the area of each forest inventory compartment. This method of averaging characterises the mean value of a given variable across the corresponding area rather than the mean compartment based on the number of records:

$$\bar{X}_s = (\textstyle\sum_i X_i \cdot S_i)/(\sum_i S_i), \qquad (1)$$

where $\bar{X}_s$ – the area-weighted mean of the respective variable; X_i – the value of the variable in the ith forest inventory compartment; and S_i is the area of the i-th forest inventory compartment, ha. The classification of forest inventory compartments as young, middle-aged, premature, mature, or overmature stands was based on the corresponding attribute in the source dataset. In the forest management planning data, the boundaries of age groups were established with regard to the age of maturity, stand origin, and forest category; therefore, no single set of universal age limits was applied to the entire dataset. For a separate analytical assessment, mature and overmature stands were combined into one group, while the original age-group classification of each compartment was retained.

Six elevation ranges were distinguished for the analysis of altitudinal differentiation: below 700 m; 700-849 m; 850-999 m; 1,000-1,149 m; 1,150-1,299 m; and 1,300 m and above. This classification provided a more detailed characterisation of middle- and upper-mountain conditions, enabled identification of the elevation range with the highest growing stock, and distinguished high-elevation stands developing under more severe environmental conditions. According to the trophic status of forest-growing conditions, site types were grouped into infertile, fairly infertile, fairly fertile, and fertile site types. These site types are called trophotopes. Statistical analysis was performed using GNU PSPP 2.1.1. Forest inventory compartment area was used as a weighting variable for summary statistics. The standard deviation, 10th and 90th percentiles, quartiles, and median growing stock of mature and overmature stands were calculated from unweighted values for individual compartments. These statistics describe the distribution of compartments, whereas the area-weighted mean represents the mean growing stock across the corresponding area. Differences in growing stock among elevation ranges were tested using the non-parametric Kruskal-Wallis test based on unweighted M values; statistical significance was set at $p < 0.05$. Effect size was estimated using the formula:

$$\varepsilon^2 = (H_k w - k + 1)/(n - k), \qquad (2)$$

where H_kw – the Kruskal-Wallis statistic, k – the number of groups, and n is the total number of observations. Given the large size of the dataset, p-values were interpreted together with effect size and the direction of changes in the median, quartiles, and area-weighted mean values. Post hoc pairwise comparisons were not performed because the aim was to establish the overall pattern of the altitudinal gradient, and with a large number of observations even small differences may reach statistical significance.

Results and Discussion

Comparison of records with available and missing elevation data showed that the compartments excluded from the altitudinal analysis had lower area-weighted mean values for age, height, diameter, growing stock, and spruce proportion (Table 1). Thus, the results of the altitudinal analysis apply to 92.4% of the area in the initial dataset; the proportion of missing records and the potential direction of bias were taken into account when interpreting the results.

Table 1. Comparison of records according to the availability of elevation data

Record group	Number of compartments	Area		Area-weighted mean parameters of stands					
		ha	%	M, $m^3 \cdot ha^{-1}$	A, years	H, m	D, cm	P	K, units
Included in the analysis	96,876	320,679.9	92.4	348	68	20.1	23.3	0.74	8.0
Excluded because elevation data were unavailable	9,076	26,338.1	7.6	256	49	16.9	19.8	0.72	7.1
Complete dataset	105,952	347,018.0	100.0	341	66	19.9	23.0	0.74	7.9

Note: M – growing stock, $m^3 \cdot ha^{-1}$; A – age, years; H – mean height, m; D – mean diameter, cm; P – relative stocking; K – proportion of spruce in the stand composition, expressed in composition units. Means are presented as area-weighted values

Source: developed by the authors

The study dataset comprised 96,876 forest inventory compartments of firstlayer spruce stands with a total area of 320,679.9 ha. The general stands parameters of spruce forests by administrative region are presented in Table 2. Ivano-Frankivsk Region accounted for the largest share of the total area, at 178,054.6 ha, or 55.5%. The areas of spruce stands in Zakarpattia and Chernivtsi regions were similar, at 58,806.5 and 57,812.7 ha, respectively. The smallest area was recorded in Lviv Region, at 26,006.1 ha, or 8.1%.

Table 2. General stands parameters of spruce forests by administrative region of the Ukrainian Carpathians

Region	Number of compartments	Area		Area-weighted mean parameters of stands						
		ha	%	M, $m^3 \cdot ha^{-1}$	A, years	H, m	D, cm	P	K, units	Elevation, m
Ivano-Frankivsk	52,891	178,054.6	55.5	368	72	20.4	23.5	0.77	8.1	1,029
Zakarpattia	15,051	58,806.5	18.3	321	68	19.7	23.5	0.71	8.0	1,044
Chernivtsi	20,461	57,812.7	18.0	335	60	19.8	22.7	0.72	8.0	978
Lviv	8,473	26,006.1	8.1	303	57	19.6	22.1	0.69	7.1	804
Total/area-weighted mean	96,876	320,679.9	100.0	348	68	20.1	23.2	0.74	8.0	1,004

Source: developed by the authors

The overall area-weighted mean growing stock was 348 m³·ha⁻¹. The highest value was recorded in Ivano-Frankivsk Region, at 368 m³·ha⁻¹. The area-weighted mean growing stock was 335 m³·ha⁻¹ in Chernivtsi Region and 321 m³·ha⁻¹ in Zakarpattia Region, while the lowest value, 303 m³·ha⁻¹, was recorded in Lviv Region. These values describe the overall characteristics of the spruce stands studied within each administrative region, but do not yet directly reflect the productivity of mature and overmature stands, as they include all age groups. Figure 1 shows the distribution of spruce stand area across elevation ranges. It demonstrates that spruce stands are concentrated within the middle-mountain elevation ranges of 850-999 and 1,000-1,149 m above sea level, which together account for more than half of the study area. The results indicate marked spatial heterogeneity among spruce stands. Ivano-Frankivsk Region contains the largest area of spruce stands and has the highest area-weighted mean values of growing stock and relative stocking, together with a substantial proportion of spruce in the stand composition. Zakarpattia Region has the highest area-weighted mean elevation but a lower growing stock, which may be associated with differences in age and typological structure, relative stocking, and the greater proportion of high-elevation stands (Fig. 1).

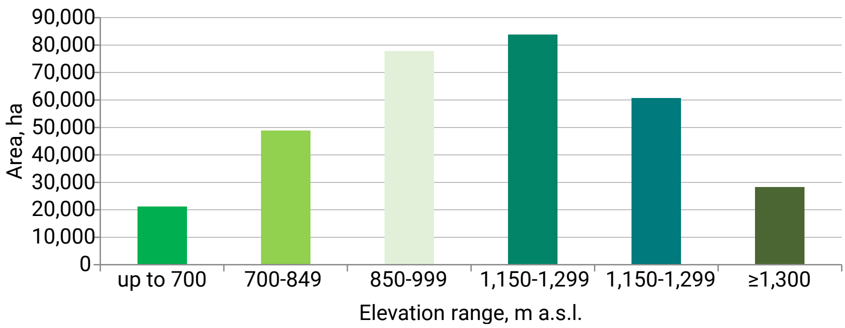

Figure 1. Distribution of spruce stand area by elevation range

Source: developed by the authors

A more detailed division into six elevation ranges was used to examine the altitudinal structure of spruce stands. The largest area of spruce stands occurred at 1,000-1,149 m above sea level, amounting to 83,760.3 ha, or 26.1%. The 850-999 m range was similar in area, comprising 77,862.4 ha, or 24.3%. Together, these two ranges account for more than half of the total area of the spruce stands studied, confirming their pronounced concentration within the middle-mountain zone (Table 3).

Table 3. Stands parameters of spruce forests by elevation range

Elevation range	Number of compartments	Area		Area-weighted mean parameters of stands						
		ha	%	Elevation, m	M, m³·ha⁻¹	A, years	H, m	D, cm	P	K, units
up to 700	9,542	21,088.4	6.6	592	302	58	19.6	22.9	0.68	6.9
700-849	18,777	48,895.1	15.2	775	317	55	18.8	21.7	0.72	7.3
850-999	24,882	77,862.4	24.3	915	355	58	19.4	21.8	0.75	7.5
1,000-1,149	24,794	83,760.3	26.1	1,060	377	63	20.0	22.4	0.78	8.0
1,150-1,299	13,603	60,764.6	18.9	1,201	359	77	21.6	25.0	0.76	8.8
1,300 m and above	5,278	28,309.1	8.8	1,365	311	117	21.8	28.8	0.65	9.3

Source: developed by the authors

The separate treatment of mature and overmature spruce stands was justified by the fact that, within this age group, growing stock is less strongly affected by incomplete stand development associated with younger ages. The overall dataset includes all age groups; therefore, its area-weighted mean growing stock is determined to a considerable extent by the proportions of young, middle-aged, and premature stands within each elevation range. Separate analysis of mature and overmature stands allows accumulated growing stock to be compared more appropriately across elevation ranges and helps identify stands suitable for subsequent investigation of assortment structure. Figure 2 presents the area-weighted mean growing stock for the entire dataset and for mature and overmature spruce stands across the elevation ranges. In both groups, growing stock reaches its maximum at 1,0001,149 m above sea level and then declines in the upper elevation zones.

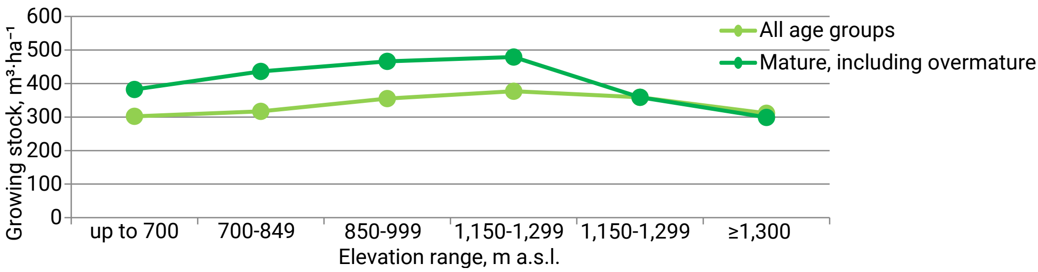

Figure 2. Area-weighted mean growing stock of the entire dataset and of mature and overmature spruce stands by elevation range

Source: developed by the authors

The area-weighted mean growing stock reaches a maximum of 377 m^3·ha^{-1} at 1,000-1,149 m above sea level. At lower elevations, growing stock is markedly lower: 302 m^3·ha^{-1} below 700 m and 317 m^3·ha^{-1} at 700-849 m. It increases to 355 m^3·ha^{-1} at 850-999 m and then reaches its maximum at 1,000-1,149 m. At higher elevations, it decreases slightly to 359 m^3·ha^{-1} at 1,150-1,299 m and to 311 m^3·ha^{-1} in the high-elevation range of 1,300 m and above. At the same time, the altitudinal gradient affects more than growing stock alone. Mean stand age gradually increases from 55-58 years in the lower and middle-mountain elevation ranges to 117 years at 1,300 m and above. The proportion of spruce in the stand composition also increases with elevation, from 6.9 composition units below 700 m to 9.3 units in the high-elevation zone. This pattern reflects a transition from mixed stands at lower elevations to purer or nearly pure spruce stands in the upper zones. Age structure is one of the principal factors determining stand growing stock and productivity. Middle-aged stands predominate in the study dataset, covering 136,194.3 ha, or 42.5% of the total area. Young stands occupy 71,169.7 ha, premature stands 48,616.9 ha, and mature stands, including overmature stands, 64,699.0 ha, or 20.2%. Thus, the overall area-weighted mean growing stock largely reflects the predominance of middle-aged stands. The distribution of spruce stand area by age group within the elevation ranges is presented in Table 4.

Table 4. Distribution of spruce stand area by age group within elevation ranges

Elevation range	Young stands, ha	Middle-aged stands, ha	Premature stands, ha	Mature and overmature stands, ha	Total, ha
up to 700	3,256.9	6,250.2	4,130.3	7,451.0	21,088.4
700-849	13,437.7	16,212.8	7,462.7	11,781.9	48,895.1

Table 4, Continued

Elevation range	Young stands, ha	Middle-aged stands, ha	Premature stands, ha	Mature and overmature stands, ha	Total, ha
850-999	22,152.7	25,860.7	15,344.1	14,504.9	77,862.4
1,000-1,149	19,963.9	37,352.9	14,069.5	12,374.0	83,760.3
1,150-1,299	10,024.1	39,281.3	4,505.3	6,953.9	60,764.6
1,300 m and above	2,334.4	11,236.4	3,105.0	11,633.3	28,309.1
Total	71,169.7	136,194.3	48,616.9	64,699.0	320,679.9

Source: developed by the authors

The distribution of spruce stands among age groups changes considerably along the altitudinal gradient. Most of the spruce stand area is concentrated in the middle-mountain zone, whereas the proportion of mature and overmature stands increases markedly in the upper elevation ranges (Table 4). Consequently, the area-weighted mean growing stock of the entire dataset reflects not only the effect of elevation above sea level but also differences in age structure. Mature and overmature stands were therefore analysed separately to provide a more appropriate assessment of the altitudinal differentiation of productivity. The total area of mature and overmature spruce stands is 64,699.0 ha. The largest area occurs at 850-999 m above sea level, where these stands occupy 14,504.9 ha. Slightly smaller areas were recorded at 1,000-1,149 m, with 12,374.0 ha, and in the high-elevation range of 1,300 m and above, with 11,633.3 ha. Although the total area of spruce stands in the high-elevation zone is smaller, the proportion of mature and overmature stands within this zone is the highest among all elevation ranges. The stands parameters of this age group by elevation range are presented in Table 5.

Table 5. Stands parameters of mature and overmature spruce stands by elevation range

Elevation range	Number of compartments	Area		Area-weighted mean parameters of stands						
		ha	%	Elevation, m	M, $m^3 \cdot ha^{-1}$	A, years	H, m	D, cm	P	K, units
up to 700	3,422	7,451.0	11.5	581	382	75	24.7	29.2	0.61	7.2
700-849	4,165	11,781.9	18.2	771	436	81	25.7	30.2	0.65	7.2
850-999	4,629	14,504.9	22.4	912	466	92	26.7	31.3	0.65	7.4
1,000-1,149	3,991	12,374.0	19.1	1,051	479	113	27.2	32.9	0.64	7.9
1,150-1,299	1,480	6,953.9	10.7	1,214	359	158	26.0	34.5	0.58	8.9
1,300 m and above	1,608	11,633.3	18.0	1,378	299	170	23.8	34.9	0.54	9.2

Source: developed by the authors

Analysis of the data in the table confirms that the elevation range of 1,000-1,149 m above sea level is the most productive among the elevation groups studied. The area-weighted mean growing stock in this zone is 479 $m^3 \cdot ha^{-1}$, the highest value recorded across all elevation ranges. A similar but slightly lower value of 466 $m^3 \cdot ha^{-1}$ was found at 850-999 m. At 700-849 m, the area-weighted mean growing stock decreases to 436 $m^3 \cdot ha^{-1}$, while below 700 m it is 382 $m^3 \cdot ha^{-1}$. In the upper elevation ranges, the productivity of mature and overmature spruce stands declines substantially. Growing stock is 359 $m^3 \cdot ha^{-1}$ at 1,150-1,299 m and 299 $m^3 \cdot ha^{-1}$ at 1,300 m and above. This decline occurs despite increases in mean stand age and diameter. At 1,300 m and above, mean age reaches 170 years and mean diameter 34.9 cm, while mean relative stocking decreases to 0.54 and mean height to 23.8 m. To provide a more detailed description of the growing-stock distribution in mature and overmature stands, quantile statistics, which are less sensitive to individual extreme values, were used alongside the area-weighted mean (Table 6).

Table 6. Descriptive statistics of growing stock in mature and overmature spruce stands by elevation range

Elevation range	Number of compartments	Area, ha	$\bar{M}S$, $m^3 \cdot ha^{-1}$	SD, $m^3 \cdot ha^{-1}$	P10, $m^3 \cdot ha^{-1}$	Q1, $m^3 \cdot ha^{-1}$	Median, $m^3 \cdot ha^{-1}$	Q3, $m^3 \cdot ha^{-1}$	P90, $m^3 \cdot ha^{-1}$
up to 700	3,422	7,451.0	381.6	124.2	220.0	283.0	370.0	456.0	537.9
700-849	4,165	11,781.9	435.8	128.9	244.0	319.0	412.0	506.0	586.0
850-999	4,629	14,504.9	466.0	120.9	281.0	356.0	449.0	530.0	602.0
1,000-1,149	3,991	12,374.0	478.8	120.3	310.0	385.0	470.0	552.0	627.0
1,150-1,299	1,480	6,953.9	358.9	97.7	220.0	291.0	352.0	421.0	482.0
1,300 m and above	1,608	11,633.3	298.8	88.8	170.0	224.0	296.0	352.0	411.0

Note: $\bar{M}S$ – area-weighted mean growing stock, $m^3 \cdot ha^{-1}$; SD – standard deviation of unweighted compartmentlevel growing-stock values; P10 and P90 – 10^{th} and 90^{th} percentiles; Q1 and Q3 – first and third quartiles; median – 50^{th} percentile. Quantiles and SD were calculated from individual forest inventory compartments without weighting by area

Source: developed by the authors

The quantile distribution confirms that growing stock in mature and overmature spruce stands reaches its maximum at 1,000-1,149 m above sea level: this range has the highest area-weighted mean growing stock, as well as the highest median, first quartile, and third quartile values. The nonparametric test (Formula 2) showed statistically significant differences in growing stock among elevation ranges for mature and overmature stands ($H_k w = 2{,}988{,}0$; $p < 0.001$; $\varepsilon^2 = 0.155$). Given the large size of the dataset, the p-value alone is not the principal consideration; equally important is the consistent increase in the central quantiles up to the 1,000-1,149 m range, followed by their decline above 1,150 m above sea level. The productivity of spruce stands varies substantially depending on forest-site conditions, elevation, age, relative stocking, species composition, and site index class. For the Ukrainian Carpathians, the mean growing stock of mature spruce stands has been reported at approximately 300-400 $m^3 \cdot ha^{-1}$ under fairly infertile pine site types, 400-450 $m^3 \cdot ha^{-1}$ under fairly fertile site types, and approximately 500 $m^3 \cdot ha^{-1}$ under fertile site types (Lavnyy & Matusevych, 2022). In the study dataset, mature and overmature spruce stands are most extensively represented under fairly fertile site types. Their area is 46,356.2 ha, accounting for 71.6% of the total area of mature and overmature spruce stands. Fertile site types account for a considerably smaller area of 9,655.2 ha (14.9%), while fairly infertile pine site types cover 8,378.3 ha (12.9%). Infertile pine site conditions are represented by only 309.3 ha, or 0.5%. The results of the analysis are presented in Table 7.

Table 7. Stands parameters of mature and overmature spruce stands by trophotope

Trophotope	Number of compartments	Area		Area-weighted mean parameters of stands						
		ha	%	Elevation, m	M, $m^3 \cdot ha^{-1}$	A, years	H, m	D, cm	P	K, units
Infertile site types	42	309.3	0.5	1,352	221	157	17.1	26.9	0.64	8.3
Fairly infertile site types	1,483	8,378.3	12.9	1,303	306	162	22.2	31.5	0.59	9.1

Table 7, Continued

Trophotope	Number of compartments	Area		Area-weighted mean parameters of stands						
		ha	%	Elevation, m	M, $m^3 \cdot ha^{-1}$	A, years	H, m	D, cm	P	K, units
Fairly fertile site types	14,594	46,356.2	71.6	966	423	110	26.2	32.4	0.62	7.8
Fertile site types	3,176	9,655.2	14.9	828	453	86	27.0	31.8	0.64	7.3

Source: developed by the authors

According to the table, the area-weighted mean growing stock of mature and overmature spruce stands increases consistently along the trophic gradient, from 221 $m^3 \cdot ha^{-1}$ under infertile pine site types and 306 $m^3 \cdot ha^{-1}$ under fairly infertile pine site types to 423 $m^3 \cdot ha^{-1}$ under fairly fertile site types and 453 $m^3 \cdot ha^{-1}$ under fertile site types. The largest difference occurs between fairly infertile pine and fairly fertile site types. This pattern indicates a close relationship between the trophic status of forest-site conditions and the growing stock of mature and overmature spruce stands, and confirms the need to account for typological conditions when analysing altitudinal differentiation. It is also important that the trophotopes differ in their altitudinal distribution. Infertile pine and fairly infertile pine site types are associated mainly with higher elevations, with area-weighted mean elevations of 1,352 and 1,303 m, respectively. The corresponding value is 828 m for fertile site types and 966 m for fairly fertile site types. This helps explain why the altitudinal differentiation of productivity cannot be considered independently of typological structure.

Recent studies of the Carpathian region indicate that the altitudinal differentiation of spruce stand productivity is closely related to interspecific competition, stand composition, forest naturalness, and disturbance regime. According to J. Schurman *et al*. (2024), the distribution limits and growth responses of spruce and beech in the Carpathians are shaped by the interaction between climatic constraints and competition along the altitudinal gradient. Studies in the Romanian Carpathians confirm that spruce stand volume depends on landscape configuration and local site conditions (Crişan *et al.*, 2023). Analysis of forest management planning data for the Ukrainian Carpathians for 1988-2018 revealed a reduction in the area of spruce stands, changes in their age and species structure, and an increase in the proportion of spruce stands occurring above 800 m above sea level (Lavnyy *et al.*, 2025). Taken together, these findings support the use of an analytical framework combining altitudinal, age-related, and typological dimensions. The distribution by trophotope revealed substantial differences in the growing stock of mature and overmature spruce stands, although the magnitude of these differences varied among the mountainous areas. Regional differences in spruce stand productivity within the predominant forest types have also been reported in previous studies (Lavnyy & Matusevych, 2022). The characteristics of mature and overmature spruce stands by regions and trophotope are presented in Table 8.

Table 8. Stands parameters of mature and overmature spruce stands by region and trophotope

Region	Trophotope	n	Area		Area-weighted mean parameters of stands						
			ha	%	Elevation, m	M, $m^3 \cdot ha^{-1}$	A, years	H, m	D, cm	P	K, units
Zakarpattia	Fairly infertile site types	123	1,117.1	1.7	1,413	235	162	21.0	37.0	0.53	8.4
Zakarpattia	Fairly fertile site types	1,676	8,586.3	13.3	1,170	363	151	27.3	37.6	0.52	8.5

Table 8, Continued

Region	Trophotope	n	Area		Area-weighted mean parameters of stands						
			ha	%	Elevation, m	M, m³·ha⁻¹	A, years	H, m	D, cm	P	K, units
Zakarpattia	Fertile site types	978	2,891.5	4.5	801	441	83	27.7	32.7	0.61	7.4
Zakarpattia	Total	2,777	12,594.9	19.5	1,107	370	137	26.8	36.4	0.54	8.2
Ivano-Frankivsk	Infertile site types	42	309.3	0.5	1,352	221	157	17.1	26.9	0.64	8.3
Ivano-Frankivsk	Fairly infertile site types	1,344	7,228.9	11.2	1,287	317	162	22.4	30.6	0.60	9.2
Ivano-Frankivsk	Fairly fertile site types	8,875	27,007.7	41.7	954	436	103	25.6	30.9	0.66	7.7
Ivano-Frankivsk	Fertile site types	1,041	3,046.6	4.7	888	477	89	26.4	30.8	0.68	7.4
Ivano-Frankivsk	Total	11,302	37,592.5	58.1	1,016	415	114	25.0	30.8	0.65	8.0
Lviv	Fairly infertile site types	5	6.9	0.0	1,220	213	164	20.8	29.3	0.41	10.0
Lviv	Fairly fertile site types	1,591	4,378.2	6.8	756	383	82	25.2	29.5	0.58	7.4
Lviv	Fertile site types	865	2,593.9	4.0	777	427	83	26.6	31.1	0.61	7.3
Lviv	Total	2,461	6,979.0	10.8	765	399	82	25.7	30.1	0.59	7.4
Chernivtsi	Fairly infertile site types	11	25.4	0.0	995	421	128	26.1	31.1	0.57	8.7
Chernivtsi	Fairly fertile site types	2,452	6,384.0	9.9	888	480	98	28.2	33.9	0.61	7.4
Chernivtsi	Fertile site types	292	1,123.2	1.7	850	478	90	27.7	33.2	0.65	6.5
Chernivtsi	Total	2,755	7,532.6	11.6	883	479	97	28.1	33.8	0.62	7.3

Note: n – number of forest inventory compartments; the proportion of area was calculated relative to the total area of mature and overmature spruce stands (64,699.0 ha). Groups with $n < 30$ were retained to provide a complete representation of the source dataset; however, owing to the small number of observations, they were not used for comparative conclusions

Source: developed by the authors

The largest area of mature and overmature spruce stands is represented by stands under fairly fertile site types in Ivano-Frankivsk Region, covering 27,007.7 ha, or 41.7% of the total area of this age group. This is the largest regional-typological group in the study dataset. It has an area-weighted mean growing stock of 436 $m^3 \cdot ha^{-1}$, a mean height of 25.6 m, a mean diameter of 30.9 cm, a relative stocking of 0.66, and a spruce proportion of 7.7 composition units. The highest area-weighted mean growing-stock values among adequately represented groups were recorded under fairly fertile and fertile site types in Chernivtsi Region, at 480 and 478 $m^3 \cdot ha^{-1}$, respectively, and under fertile site types in Ivano-Frankivsk Region, at 477 $m^3 \cdot ha^{-1}$. These groups are characterised by relatively favourable altitudinal positions, together with high mean values of height, diameter, and relative stocking.

Maximum growing-stock values occur at 1,000-1,149 m above sea level, although their magnitude depends on stand age and typological structure. In mature and overmature stands, growing stock declines sharply above 1,150 m after reaching its middle-mountain maximum. At the regional-typological level, the highest growing stocks are characteristic of adequately represented groups under fairly fertile and fertile site types in Ivano-Frankivsk and Chernivtsi regions. The small groups occurring under fairly infertile pine site types in Lviv and Chernivtsi regions were excluded from comparative conclusions.

Regional studies by H.H. Hrynyk (2011) demonstrated pronounced altitudinal zonation in Carpathian spruce stands and showed that their stands parameters depend on topography and forest-site conditions. The present study provides a quantitative refinement of these patterns using compartment-level data as of 1 January 2022: both the largest area and the highest area-weighted mean growing stock were recorded at 1,000-1,149 m above sea level. The identified altitudinal optimum is consistent with the current assessment of the region's typological structure. V. Lavnyy & O. Matusevych (2022) noted that highly productive, well-stocked spruce stands are concentrated mainly at elevations of 750-1,150 m above sea level, whereas the present study refines the maximum growing stock of mature and overmature stands to the 1,000-1,149 m range. Thus, different criteria for defining the study population – either the type-forming role of spruce or its actual proportion of at least three composition units – reveal a similar spatial pattern, although they produce different absolute area estimates.

Dendroclimatic studies help explain the ecological basis of the non-linear change in productivity along the altitudinal gradient. C.G. Sidor *et al*. (2015) reported that, in the Eastern Carpathians, spruce growth at lower elevations is more strongly dependent on water availability, whereas temperature limitation becomes more pronounced in the upper elevation zones. Temporal variation in climatic sensitivity along the altitudinal gradient has also been identified in Central Europe (Kolář *et al*., 2017). Studies by J. Schurman *et al*. (2024) and F. Märker *et al*. (2025) confirm increasing water stress at lower elevations and the emergence of drought sensitivity even at high elevations. These findings are consistent with the decline in growing stock above 1,150 m identified in the present study, despite increases in mean stand age and diameter. An analysis of more than 3,000 trees in the Eastern Carpathians showed that Norway spruce has the lowest drought resistance below 800 m, whereas above 1,400 m greater resistance is accompanied by slower recovery (Popa *et al*., 2024b). Data from J. Rybar *et al*. (2023) for the Western Carpathians likewise showed reduced radial growth of the principal forest-forming species during dry years, with the magnitude of this response partly dependent on elevation and soil conditions.

Age structure substantially affects productivity estimates. For the entire dataset, the maximum area-weighted mean growing stock at 1,000-1,149 m was 377 $m^3 \cdot ha^{-1}$, compared with 479 $m^3 \cdot ha^{-1}$ for mature and overmature stands. The mean value across all age groups therefore cannot be interpreted directly as the realised productivity potential of the site conditions. The need to account for age structure when analysing compartment-level data was previously emphasised in a study of modal spruce stands in Ukraine (Garmash *et al*., 2023). Assessments of the bioproductivity of coniferous stands in the Ukrainian Carpathians based on phytomass, net primary production, and sequestered carbon indicate that growing stock represents only one dimension of productivity (Vasylyshyn, 2013). In the present study, productivity was operationally assessed using growing stock per hectare, which was available for the entire compartment-level dataset; accordingly, the findings primarily concern patterns of stand growing-stock accumulation.

The typological analysis confirmed a consistent increase in growing stock from infertile pine to fertile site conditions. Values for fairly infertile pine, fairly fertile, and fertile site types generally correspond to the ranges previously reported for spruce forests in the Ukrainian Carpathians (Lavnyy & Matusevych, 2022). At the same time, the mean elevations of the trophotopes differ considerably: infertile pine and fairly infertile pine are concentrated predominantly at higher elevations than fairly fertile and fertile site types. Thus, elevation and trophic status are interrelated within the study dataset, and the identified maximum growing stock reflects their joint variation with relative stocking, stand age, and species composition. Typological grouping was used as a separate analytical level; however, the resulting area-weighted means describe the actual condition of the stands rather than the potential productivity of a forest type. This distinction is particularly important under nutrient-poor high-elevation conditions, where a high proportion of spruce does not compensate for lower mean stand height and relative stocking. Regional differences should also be interpreted with caution: groups with $n < 30$ were retained in Table 8 solely to provide a complete representation of the dataset, whereas substantive conclusions are based on groups with adequate representation.

The use of a compartment-level database made it possible to cover a large geographical area, but it also introduced several limitations. Forest compartment inventory data are not equivalent to data obtained from a standardised network of experimental sample plots; records without documented elevation above sea level accounted for 7.6% of the initial study area and differed in their mean mensurational characteristics. In addition, the inventory status as of 1 January 2022 does not reflect possible changes that occurred during 2023-2026. The identified patterns should therefore be regarded as a regional basis for stratifying subsequent field studies rather than as an unchanging description of the current condition of every individual forest tract. Further assessment of assortment structure requires the selection of model trees within the established altitudinal, age, and typological groups. Approaches to such selection are described by M.V. Lubchich *et al*. (2008). The results obtained make it possible to establish contrasting field groups and avoid combining stands that differ substantially in elevation, age, trophotope, and actual growing stock.

Conclusions

The largest area of spruce stands is concentrated at 1,000-1,149 m above sea level, covering 83,760.3 ha, or 26.1%, followed closely by the 850-999 m range, which accounts for 77,862.4 ha, or 24.3%. These elevation ranges form the principal middle-mountain core of spruce stands in the Ukrainian Carpathians. The area-weighted mean growing stock of the entire study dataset reaches its maximum at 1,000-1,149 m above sea level, at 377 $m^3 \cdot ha^{-1}$. Above 1,150 m, growing stock declines to 359 $m^3 \cdot ha^{-1}$ at 1,150-1,299 m and to 311 $m^3 \cdot ha^{-1}$ at 1,300 m and above.

Analysis of mature and overmature spruce stands confirmed that the altitudinal optimum for productivity occurs at 1,000-1,149 m above sea level. Within this range, the area-weighted mean growing stock of mature and overmature spruce stands is 479 $m^3 \cdot ha^{-1}$, while the median growing stock is 470 $m^3 \cdot ha^{-1}$. Above 1,150 m, growing stock in this age group declines markedly despite increases in mean stand age and diameter. The productivity of mature and overmature spruce stands also differs substantially among forest-site conditions. The largest area of this age group occurs under fairly fertile site types, covering 46,356.2 ha, or 71.6%. The area-weighted mean growing stock is 423 $m^3 \cdot ha^{-1}$ under fairly fertile site types and 453 $m^3 \cdot ha^{-1}$ under fertile site types, whereas fairly infertile pine and infertile pine site types are characterised by lower values of 306 and 221 $m^3 \cdot ha^{-1}$, respectively.

The findings support the use of a combined altitudinal, age-based, and typological approach in further studies of the assortment structure of spruce stands. The core sample should preferably comprise mature and overmature spruce stands under fairly fertile site types at elevations of 8501,149 m above sea level, particularly in Ivano-Frankivsk Region. Stands under fertile site types in Ivano-Frankivsk and Chernivtsi regions may be included as high-productivity variants, while upper-mountain stands under fairly infertile pine and fairly fertile site types may serve as contrasting groups.

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Conflict of Interest

None.

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Висотна диференціація лісівничо-таксаційної структури та продуктивності ялинових деревостанів Українських Карпат

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Анотація. Висота над рівнем моря є одним із ключових орографічних чинників, що визначає просторове поширення, структуру та продуктивність ялинових деревостанів Українських Карпат. Метою дослідження було встановити закономірності висотної диференціації їх лісівничо-таксаційної структури й продуктивності та визначити аналітичні групи для подальшого вивчення сортиментної структури. Дослідження виконано за матеріалами повидільної бази даних Українського державного проєктного лісовпорядного виробничого об'єднання «Укрдержліспроект» станом на 1 січня 2022 року. Проаналізовано 96 876 таксаційних виділів першого ярусу загальною площею 320 679,9 га, у яких частка ялини у складі насадження становила не менше трьох одиниць і було встановлено висоту над рівнем моря. Для аналізу застосовано середньозважені за площею показники, квантильні характеристики розподілу запасу та непараметричний критерій Краскела-Волліса. Найбільша площа ялинових деревостанів зосереджена в інтервалі 1000-1149 м над рівнем моря – 83 760,3 га, або 26,1 %. У цьому ж інтервалі встановлено найвищий середньозважений запас усієї сукупності деревостанів – 377 $м^3 \cdot га^{-1}$, а серед стиглих, включно з перестійними, – 479 $м^3 \cdot га^{-1}$. Загальна площа стиглих і перестійних деревостанів становила 64 699,0 га, причому їхня найбільша частка у структурі відповідного висотного інтервалу спостерігалася у високогір'ї. Відмінності запасу стиглих і перестійних деревостанів між висотними інтервалами були статистично значущими, а найбільші значення медіани та квартилів також зафіксовано в межах 1000-1149 м. Записи без установленої висоти охоплювали 7,6 % площі первинної сукупності й були виключені з розрахунків висотної диференціації. Характер зміни запасу вздовж висотного градієнта був пов'язаний також із трофічністю лісорослинних умов, віковою структурою, відносною повнотою та часткою ялини. Найвищі середньозважені запаси стиглих і перестійних ялинників виявлено у сугрудових і грудових умовах, тоді як у борах і суборах вони були істотно нижчими. Практичне значення результатів полягає в обґрунтуванні висотно-віково-типологічного підходу до добору деревостанів і модельних дерев для дослідження сортиментного потенціалу ялини європейської

Ключові слова: *Picea abies*; орографічний градієнт; запас деревостану; трофотоп; стиглі насадження; лісова таксація; сортиментний потенціал