



Ecological relations of natural regeneration of forest phytocoenoses in the Left-Bank Polissia of Ukraine

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ABSTRACT: This study aimed to identify the factors affecting the population density, viability, and structural stability of natural regeneration in leading forest species (*Pinus sylvestris*, *Quercus robur*, *Acer platanoides*) in the Left-Bank Polissia of Ukraine. The research focused on four forest formations: *Pineta sylvestris*, *Querceta roboris*, *Betuleta pendulae*, and *Populeta tremulae*. Field surveys used stratified random sampling and elemental accounting of self-seeding cohorts. Key environmental factors influencing cohort conditions included soil water regime, nitrogen content, carbonates, habitat illumination, and thermal regime. The study revealed how cohort traits respond to gradients of these factors, showing both diversity and individuality, which are crucial for enhancing adaptive potential and environmental sustainability. The response of these young cohorts to ecological factors reflects species-specific regeneration requirements and their ability to adapt. In *Pineta sylvestris hylocomiosa* forests, conditions for successful natural regeneration were found to be favorable. However, anthropogenic pressure led to a 35-55% reduction in regeneration density, decreased vitality, and cohort imbalance. The study also found that natural regeneration is more cost-effective than plantation forestry, reducing costs by 2.3-3.5 times per hectare. These findings can inform sustainable forest management and predict forest ecosystem adaptability to climate change.

Keywords: biodiversity; ecosystems; natural regeneration; integrated population analysis; population structure; mathematical modelling.

Relações ecológicas da regeneração natural de fitocenoses florestais na Polísia da Margem Esquerda da Ucrânia

RESUMO: Este estudo teve como objetivo identificar os fatores que afetam a densidade populacional, a viabilidade e a estabilidade estrutural da regeneração natural de espécies florestais importantes (*Pinus sylvestris*, *Quercus robur*, *Acer platanoides*) na Polissia da Margem Esquerda da Ucrânia. A pesquisa concentrou-se em quatro formações florestais: *Pineta sylvestris*, *Querceta roboris*, *Betuleta pendulae* e *Populeta tremulae*. Os levantamentos de campo utilizaram amostragem aleatória estratificada e análise elementar de coortes de regeneração espontânea. Os principais fatores ambientais que influenciam as condições das coortes incluem o regime hídrico do solo, o teor de nitrogênio, os carbonatos, a luminosidade do habitat e o regime térmico. O estudo revelou como as características das coortes respondem aos gradientes desses fatores, demonstrando diversidade e individualidade, cruciais para o aumento do potencial adaptativo e da sustentabilidade ambiental. A resposta dessas coortes jovens aos fatores ecológicos reflete as necessidades específicas de regeneração de cada espécie e a capacidade de adaptação de cada uma. Nas florestas de *Pineta sylvestris hylocomiosa*, as condições para o sucesso da regeneração natural foram consideradas favoráveis. No entanto, a pressão antropogênica levou a uma redução de 35 a 55% na densidade de regeneração, à diminuição da vitalidade e ao desequilíbrio entre as coortes. O estudo também constatou que a regeneração natural é mais rentável do que o plantio florestal, reduzindo os custos em até 3,5 vezes por hectare. Essas descobertas podem orientar o manejo florestal sustentável e prever a capacidade de adaptação dos ecossistemas florestais às mudanças climáticas.

Palavras-chave: biodiversidade; ecossistemas; regeneração natural; análise populacional integrada; estrutura populacional; modelagem matemática.

1. INTRODUCTION

Natural regeneration of forests in the Polissia region plays a key role in conserving biological diversity, maintaining hydrological balance, restoring soil cover, and building ecosystem resilience in the face of climate change. This

process is the primary mechanism for maintaining the forest ecosystem in an equilibrium state without the need for considerable inputs, which is essential in the context of global warming, land degradation, and reduced funding for reforestation. The relevance of investigating natural

regeneration has grown in the context of the need to reduce the cost of artificial reforestation, minimise the anthropogenic impact, and ensure the adaptive plasticity of forest communities.

The environmental and economic benefits of self-seeding indicate its feasibility as a basic strategy in sustainable forest management systems, which involves the reproduction of stands with high internal resistance to climatic and anthropogenic challenges. In this context, the analysis of the links between the structure of regeneration and the action of abiotic and phytocoenotic factors that formed the mosaic of ecological niches and determined the viability of populations of the key forest-forming species has gained relevance. Consideration of the interaction of water regime, acidity, temperature, carbonate balance, and the impact of associated vegetation is necessary to understand the mechanisms of formation of sustainable phytocoenoses and the spatial organisation of their restoration.

The results of the assessment of the success of natural regeneration of forests in the Left-Bank Polissia, performed according to a set of population traits of the young generation of forest-forming species, including indicators of its population density, ontogenetic development, age, size, and vitality structure, are presented in the publication by Skliar; Sherstiuk (2022). The researchers determined the levels of structural stability of populations depending on the type of stand and the ecological condition of the sites.

The review of the retrospective state of Ukrainian forests proposed by Yakuba (2022) focused on the need for systematic monitoring to preserve the forest fund and develop adaptive management strategies. The researcher noted that without accounting for the dynamics of age composition and anthropogenic impact, the effectiveness of forest management is limited. Davydov (2020) summarised the data on the distribution of the alien species *Physocarpus opulifolius* in the territory of the Left Bank of Ukraine. The researcher found that this species is often cultivated and runs wild in the Polissia and Forest-Steppe zones, particularly in Kyiv, Poltava, Sumy, Cherkasy, and Chernihiv regions. Davydov also described the new shrub association *Elymo repenti-Physocarpetum opulifolii*, where *Physocarpus opulifolius* is the diagnostic and dominant species.

The relevance of studying the ecological relations of natural regeneration of phytocoenoses of the Left-Bank Polissia was confirmed by the observations of Grybovych (2022). Specifically, the analysis results on the growth of pine forests in Ukrainian Polissia revealed greater viability and productivity of mixed pine-birch crops compared to pure stands, which confirmed the stabilisation of regeneration due to phytocoenotic diversity. Danylchenko; Zhorniak (2025) showed the impact of military operations on the national nature parks of the Sumy region. The researchers demonstrated large-scale degradation of forest ecosystems, including loss of biodiversity, chemical contamination of soils, and complications of natural regeneration processes. These data reflect the extreme environmental factors that determine the sustainability and regeneration of forest phytocoenoses in the Polissia border regions.

In the context of the socio-ecological approach, Mañas-Navarro et al. (2023) found that the effectiveness of ecological restoration is markedly affected by management and communication barriers. A network model for analysing the interaction between actors was proposed as a tool for

increasing institutional capacity in environmental protection measures.

Using the example of the Chinese city of Xuzhou, Qiu et al. (2023) investigated how the configuration of green spaces and their spatial location affect the carbon balance of territories. The researchers emphasised the significance of the structural continuity of the ecological network. Zhao et al. (2023) proposed a multifunctional approach to restoring degraded landscapes in mining regions by integrating water, climate, and biodiversity functions within a spatial optimisation framework. The study was an example of the practical application of the ecosystem approach in complex anthropogenic conditions. Wan et al. (2024) conducted an empirical assessment of the ability of urban green networks to accumulate carbon, which indirectly confirms the effectiveness of natural regeneration as a mechanism of climate stabilisation. Thus, the scientific discourse confirmed the need for a comprehensive approach to assessing natural regeneration using data on abiotic gradients, phytocoenotic interactions, microclimatic factors, and the socio-ecological context. The theoretical and empirical findings obtained necessitate research that combines population, spatial, and economic levels of analysis.

The purpose of the present study was to identify the relationships between abiotic ecological gradients, phytocoenotic interactions, and population characteristics of natural regeneration of forest phytocoenoses in the Left-Bank Polissia of Ukraine.

The objectives of the study were to analyse the quantitative and qualitative characteristics of the young generation of the leading forest-forming species (*Pinus sylvestris* L., *Quercus robur* L., *Acer platanoides* L.) in the region within typical phytocoenoses, to assess the impact of ecological gradients and biotic interactions on the viability and structural diversity of regeneration, to identify typical models of regeneration considering anthropogenic pressure, and to propose economic guidelines for sustainable forest management.

2. MATERIALS AND METHODS

The study was based on the materials of field research conducted on the territory of the Left-Bank Polissia of Ukraine during 2002-2024, with regular observations conducted annually within Chernihiv and Sumy regions, particularly in the territories of Novgorod-Siverskyi, Shostka, and Koryukiv districts, in the forests of the state enterprises Novgorod-Siverskie Forestry, Krolevets Forestry, and Seredina-Budske Forestry.

Data collected after February 2022 were obtained under the conditions of the armed conflict in Ukraine. Although certain logistical challenges related to access and field organisation occurred, the established sampling design and data collection protocol were maintained without methodological changes. The same assessment procedures and indicators were applied throughout the entire study period, ensuring comparability between observations obtained before and after 2022.

The spatial distribution of the investigated sample plots across the Left-Bank Polissia region is presented in Figure 1. The spatial arrangement of plots reflects the stratified sampling design used to characterise natural regeneration patterns under different ecological conditions.

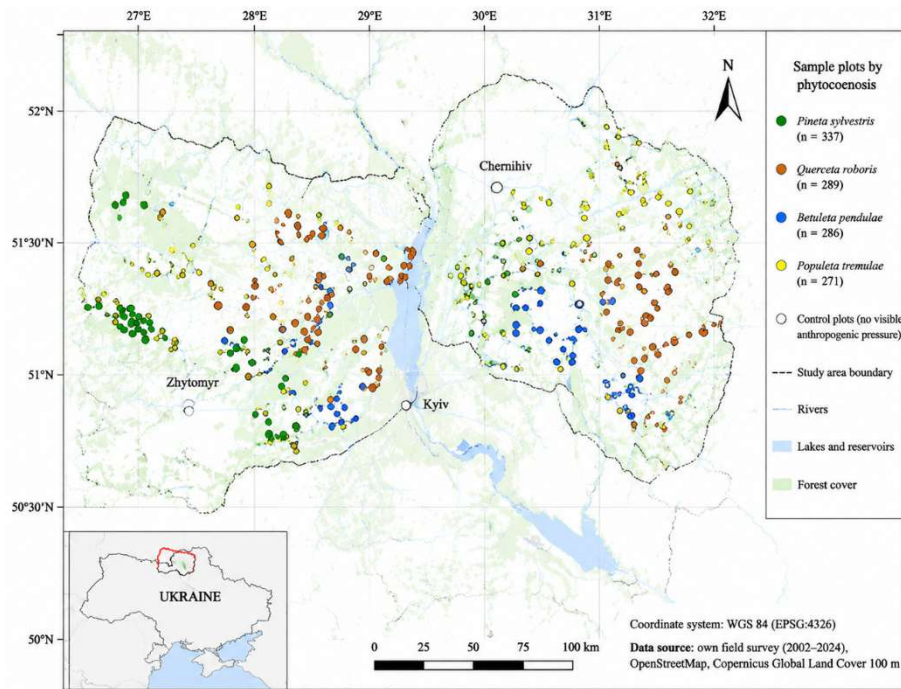


Figure 1. Spatial distribution of sample plots across the Left-Bank Polissia region by major phytocoenoses.

Figura 1. Distribuição espacial das parcelas amostrais na região da Polissia da Margem Esquerda por principais fitocenoses.

The study design was longitudinal, as the established sample plots were monitored repeatedly during the observation period. Annual surveys were conducted on the same permanent plots to track temporal changes in regeneration density, vitality structure, and cohort development. Data collected across different years were integrated into a unified dataset, where repeated observations were used to characterise long-term patterns of regeneration dynamics. For regression and comparative analyses, annual measurements were aggregated by plot and phytocoenosis type to obtain representative values of population characteristics and associated ecological parameters.

The study covered forest phytocoenoses typical for the Left Bank Polissia of Ukraine. They belong to 42 associations, 24 groups of associations, and 4 formations (*Pineta sylvestris*, *Querceta roboris*, *Betuleta pendulae*, *Populeta tremulae*) of forest vegetation. Although the study dataset included 42 forest associations, the detailed analysis was conducted at the level of four dominant forest formations. These formations were selected because they represent the main forest types of the Left-Bank Polissia region and include the largest number of sample plots, allowing reliable statistical analysis and comparison of regeneration patterns. Data from the remaining associations were included in the overall assessment of regeneration characteristics and ecological conditions but were not analysed separately due to their lower representation and insufficient replication for independent statistical comparisons. A stratified random sampling was used, covering from 20 to 50 sample plots in each type of phytocoenosis, accounting for microrelief, canopy structure, and the degree of anthropogenic pressure.

Control plots were selected from areas without visible signs of direct anthropogenic disturbance, including recent logging, grazing, mechanical soil disturbance, or other forest management interventions. The selection of control sites was based on field assessments of stand condition, disturbance indicators, and similarity of ecological characteristics to impacted plots. Control plots were located within comparable forest formations and under similar environmental conditions (soil characteristics, moisture regime, canopy structure, and relief) to ensure that differences in regeneration characteristics were primarily associated with anthropogenic pressure rather than habitat variation. The same sampling protocol and regeneration assessment methods were applied in both impacted and control plots.

Additionally, each formation was divided by the number of sample plots for each phytocoenosis type to ensure data representativeness. Each sample plot had an area of 400 m² (20 × 20 m), which was considered sufficient to characterise the structure of natural regeneration cohorts while maintaining comparability among different phytocoenoses. To ensure spatial independence of observations, sample plots were located at a minimum distance of 100 m from each other and were established in areas representing different microhabitat conditions, canopy characteristics, and levels of anthropogenic disturbance. The spatial arrangement of plots was determined using a stratified random approach, preventing clustering of observations within a single local site and reducing the risk of spatial autocorrelation. For *Pineta sylvestris*, 50 sample plots were allocated (about 40% of the total); for *Querceta roboris* and *Betuleta pendulae*, 30 sample plots were allocated for each formation; and for *Populeta tremulae*, 20 sample plots were allocated. The images of species *Pinus sylvestris* L. (a), *Quercus robur* L. (b), and *Acer platanoides* L. (c) are presented in Figure 2.

The study was based on the system of dividing woody plant populations into intrapopulation structural groups – cohorts, formed considering population and silvicultural approaches. The following cohorts were identified within the populations of the leading forest-forming species: germinating seedlings, seedlings, small understory, medium understory, large understory, young trees, and generative trees of the upper forest layer.



Figure 2. a) *Pinus sylvestris* L.; b) *Quercus robur* L.; c) *Acer platanoides* L.
 Figura 2. a) *Pinus sylvestris* L.; b) *Quercus robur* L.; c) *Acer platanoides* L.

The study employed stratified sampling. A random grid method was used to select trees/individuals within each sample area. The grid was superimposed on the area with a uniform distribution of survey points, which enabled random selection of individuals for more detailed analysis. Each sampling element included trees/individuals of different age groups, which ensured that the data were representative of all cohorts of forest-forming species.

Within each plot, the study recorded the number and population density (pcs/ha) of self-seeding, with division into cohorts (small, medium, large, and young trees) of the young generation according to Site class standards and the methodology of field bioecological research (ORDER OF THE MINISTRY OF ECOLOGY AND NATURAL RESOURCES OF UKRAINE NO. 161 “On Approval of the Methodology for Determining the Classification of Forest Areas as Primeval Forests, Quasi-Primeval Forests and Natural Forests”, 2018; YAKUBENKO et al., 2020). For each individual, coordinates and morphometric parameters (height, diameter, number of shoots, etc.) were recorded, and vitality was determined according to the scale of vitality classes, which has three gradations. The vitality class was determined according to the morphometric parameters of plants (height, trunk diameter, number of shoots, etc.) and, additionally, by visual signs of their condition. High vitality class (class a) – specimens with high values of morphological parameters, showing optimal growth rates and no signs of disease or damage. Medium vitality class (class b) – specimens with moderate growth and size, and possibly with minor damage or signs of stress. Low vitality class (class c) – weak specimens with reduced size and growth and possibly substantial damage.

A generalised indicator of cohort vitality, the quality index Q , was calculated using the following formula 01:

$$Q = \frac{1}{2}(a + b), \quad (1)$$

where: a is the proportion of individuals in the high vitality class; b is the proportion of individuals in the middle class.

The resulting value was used to determine the type of cohort: depressed ($Q < 0.1667$), balanced ($0.1667 - 0.3333$), and prosperous ($Q > 0.3333$). These threshold values were adopted because the Q index reflects the proportion of individuals with sufficient vitality for further development. The value of 0.1667 represents the critical boundary

separating cohorts dominated by low vitality individuals from those capable of maintaining regeneration processes. The Index of the Diversity of the Size Structure (IDSS) was employed to assess the diversity of the size structure of the cohorts (2):

$$IDSS = \frac{N_f}{N_t} \times 100\%, \quad (02)$$

where: N_f is the number of factually detected combinations of height and diameter classes; N_t is the number of all theoretically possible combinations. The optimal IDSS values are within 25-50%. This interval was considered optimal because it indicates a balanced representation of different size classes and prevents both structural simplification and excessive fragmentation of regeneration cohorts.

To identify changes in the state of regeneration over time, the Index of Vitality Dynamics (IVD) was calculated as follows (3):

$$IVD = \frac{Q_n - Q_p}{0.166}, \quad (03)$$

where: Q_n is the quality index in the next cohort; Q_p is the quality index in the previous cohort; 0.166 is the value of the quality index at which the cohort transitions from one quality type to the next.

If $IVD = 0$, there are no changes in the value of the quality index Q in the cohorts by stages of natural recovery. IVD values with a minus sign signify a deterioration in the vitality of the cohort, while those with a plus sign signify its improvement.

Overall, IVD values are in the range from -3.012 to +3.012. The standardisation by the transition value of $Q = 0.166$ allows comparison of changes between cohorts with different initial vitality states and provides a consistent measure of regeneration improvement or decline. The assessment of the age structure of the cohorts was accompanied by the determination of the Index of Cohort Discreteness (KD) (4):

$$KD = \frac{P_0}{P_{zag}}, \quad (04)$$

where: P_0 is the number of age gradations with the number of sub-grades equal to zero; P_{zag} is the total number of gradations in the age spectrum.

If $KD=0$, the age spectrum of the cohort is continuous; if $KD>0$, it is discrete. The closer the value of KD is to 1, the more discrete the age spectrum is. Optimal values of KD do not exceed 0.15. The threshold of 0.15 was used as an indicator of acceptable age continuity, since lower KD values correspond to more continuous regeneration and reduced gaps between age classes.

The ecological parameters of habitats where natural regeneration of *Pinus sylvestris*, *Quercus robur*, and *Acer platanoides* occurs were determined by phytosociological methods using ecological scales. The following abiotic environmental factors were included in the analysis: soil water regime (Hd), soil moisture variability (fH), soil acidity (Rc), soil carbonate content (Ca), soil nitrogen content (Nt), thermal regime of the territory (Tm), continental climate (Kn), cryo regime (Cr), and light (Lc). Illumination was also measured using a digital luxmeter Extech LT300 (USA) in three horizons (soil, undergrowth, and above the undergrowth), which helped to assess the actual photoperiod of the territory.

The study employed gradient analysis (DCA – detrended correspondence analysis), correlation and regression modelling with the construction of linear, exponential and logarithmic trends to establish relations between the population characteristics of cohorts of the young generation (self-seeding) of forest-forming species and ecological parameters of phytocoenoses. The reliability of regression models was evaluated using goodness-of-fit statistics. The coefficient of determination (R^2) was calculated to estimate the explanatory capacity of each model. The overall significance of regression equations was assessed using ANOVA-based global p-values, while the significance of individual predictors was determined using coefficient p-values. Multicollinearity among ecological predictors was assessed using the variance inflation factor (VIF).

The reliability and predictive stability of the regression models were assessed using 10-fold cross-validation and residual analysis. During cross-validation, the dataset was divided into training and validation subsets, and model performance was evaluated by comparing predicted and observed values. The cross-validated coefficient of determination ($CV-R^2$) ranged from 0.61 to 0.75, indicating that the models retained satisfactory explanatory capacity when applied to independent subsets of the data. The difference between the original and cross-validated R^2 values remained within acceptable limits, suggesting limited overfitting. Residual analysis was performed to assess model assumptions, including the presence of systematic deviations, heteroscedasticity, and influential observations. The residual patterns did not reveal pronounced deviations, confirming the suitability of the regression models for describing relationships between ecological gradients and regeneration characteristics.

Threshold responses were analysed using the broken-stick model to identify critical points in the gradient at which a sharp decrease in viability or density was observed. The combined effect of two environmental factors was modelled using a second-order response surface equation (5):

$$z = a + b \times x + c \times y + d \times x^2 + e \times y^2 + f \times xy \quad (05)$$

where: z is the predicted regeneration indicator (Q or IDSS), x and y are ecological gradients, where a is the intercept, b and c are linear effects of environmental factors, d and e

represent quadratic effects, and f represents the interaction between the two factors, and xy represents the interaction effect between environmental factors.

The constructed response surfaces helped to visualise the optimal ecological windows for each species. The threshold values used for interpretation of the indices were selected based on the ecological meaning of the indicators rather than statistical optimisation. For the Q index, the value of 0.1667 represents the minimum proportion of viable individuals required to classify a cohort as capable of further regeneration. The IDSS interval of 25–50% corresponds to a structurally balanced cohort with sufficient representation of different size classes. The IVD threshold is derived from the transition value between Q categories (0.166), allowing standardised comparison of changes in vitality between successive cohorts. The KD threshold of 0.15 reflects the acceptable level of discontinuity in age structure, above which gaps between age groups indicate unstable regeneration.

The experimental flow of the research is visualised in Figure 3.

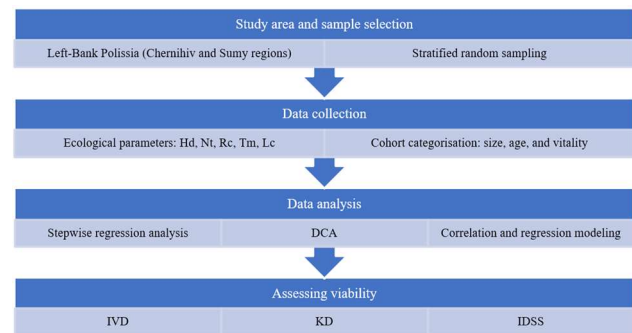


Figure 3. The experimental flowchart of the research.

Figure 3. O fluxograma experimental da investigação.

Phytocoenotic interactions were studied by comparing the vital parameters of the primary species in different types of associations and microhabitats, particularly in the presence of associated vegetation. The impact of anthropogenic pressure was analysed by comparing the regeneration rates in areas with traces of mechanical intervention (felling, grazing, skidding) with control natural areas.

The statistical significance of the differences was assessed by analysis of variance (ANOVA) and the Kruskal-Wallis test for non-parametric samples. Temporal replication across years was considered as repeated observations of the same ecological units, allowing assessment of long-term regeneration trends rather than independent cross-sectional comparisons. The study was conducted following the ethical standards specified in the Convention on Biological Diversity (1992). To verify the adaptive feasibility of natural regeneration in the context of climate change, a comparative analysis of the costs of natural and artificial reforestation was conducted based on surveys of sites with different management regimes. This approach helped to integrate structural-ecological, population, and economic levels of analysis, ensuring that the methodology fully met the stated objectives and obtained results.

The economic analysis compared the costs associated with natural regeneration and artificial reforestation approaches. The assessment included the main operational cost components of forest establishment, including site preparation, soil treatment, planting material production and

procurement, planting operations, labour inputs, and subsequent tending activities required during the early stages of stand development. For natural regeneration, the analysis considered monitoring, protection, and silvicultural maintenance costs associated with naturally established cohorts. Cost data were obtained from forestry management records, operational documentation of the investigated forest enterprises, and current regional estimates for forestry activities during the study period. The total cost per hectare was calculated for each regeneration approach, allowing comparison of economic efficiency under the conditions of the Left-Bank Polissia region.

3. RESULTS

The detailed analysis focused on the four dominant formations, while observations from other associations were incorporated into the general assessment of regeneration variability across the study region. Based on the stepwise regression analysis, the study found that the most substantial and statistically significant influence on the condition of young *Pinus sylvestris*, *Quercus robur*, and *Acer platanoides* cohorts is exerted by such factors as soil water regime (Hd), nitrogen (Nt) and carbonate (Ca) content, as well as site illumination (Lc) and temperature (Tm). Table 1 presents the results of

stepwise regression analysis for the primary population characteristics using the example of small understory cohorts.

The results of the regression analysis revealed that population traits demonstrate a prominent level of individuality in response to changes in the scores of the leading abiotic factors. The goodness-of-fit assessment confirmed the reliability of the obtained regression models. The models explained a substantial proportion of variation in regeneration characteristics, while ANOVA results confirmed their statistical significance. VIF diagnostics demonstrated that the included environmental predictors did not produce critical multicollinearity, allowing reliable interpretation of the effects of individual ecological gradients. Validation analysis confirmed the stability of the regression models, with cross-validated estimates demonstrating consistent predictive performance. Residual diagnostics indicated no systematic errors, supporting the reliability of the identified relationships between ecological factors and regeneration characteristics.

Different variants of trends were observed: a) an increase in the values of population traits with an increase in the scores of factors; b) a decrease in the values of population traits with an increase in the scores; c) the traits reaching maximum values at the level of “intermediate” values of scores, etc.

Table 1. Results of the stepwise regression analysis for the small understory cohorts.

Tabela 1. Resultados da análise de regressão stepwise para as pequenas coortes do sub-bosque.

Population feature	Regression equation	R ²	Global p-value (ANOVA)	Significant coefficients (p-value)	VIF range
Density – <i>Pinus sylvestris</i>	$y = -3285.7 - 0.09Hd - 0.04Rc + 0.31Nt + 0.45Lc - 0.19Tm + 0.12Kn + 0.12Cr - 0.39Ca$	0.78	<0.001	Hd (0.012); Nt (0.018); Lc (0.004); Tm (0.031); Ca (0.022)	1.4–3.2
Quality index Q – <i>Pinus sylvestris</i>	$y = 22.4 - 0.94Hd - 0.66Rc + 0.87Nt + 0.82Lc - 0.25Fh + 0.42Tm - 0.60Kn - 0.21Cr + 0.67Ca$	0.74	<0.001	Hd (0.009); Lc (0.003); Tm (0.021); Ca (0.015)	1.3–3.5
IDSS – <i>Pinus sylvestris</i>	$y = 130.63 + 0.32Hd + 0.07Rc + 0.07Nt - 0.38Lc - 0.51Tm + 0.23Kn + 0.34Cr - 0.21Ca$	0.69	0.002	Hd (0.027); Lc (0.014); Tm (0.038); Ca (0.041)	1.2–3.1
KD – <i>Pinus sylvestris</i>	$y = -4.84 + 0.29Hd - 0.27Rc - 0.25Nt + 0.50Lc + 0.80Tm - 0.12Kn - 0.52Cr + 0.46Ca$	0.66	0.004	Tm (0.019); Cr (0.033); Ca (0.028)	1.3–3.0
Density – <i>Quercus robur</i>	$y = 20437.3 - 0.14Hd - 0.02Rc - 0.8Nt - 0.47Lc - 0.82Tm + 0.38Ca$	0.81	<0.001	Hd (0.006); Nt (0.013); Lc (0.022); Tm (0.011)	1.5–3.6
Quality index Q – <i>Quercus robur</i>	$y = 2.69 - 0.25Hd + 0.033Rc - 0.60Nt + 0.31Lc - 0.16Tm + 0.13Ca$	0.63	0.006	Hd (0.032); Nt (0.041); Ca (0.025)	1.2–2.8
IDSS – <i>Quercus robur</i>	$y = 1938.8 - 0.61Hd + 0.34Rc - 0.81Nt - 0.64Tm + 0.15Ca$	0.71	0.003	Hd (0.018); Nt (0.024); Tm (0.035)	1.4–3.3
KD – <i>Quercus robur</i>	$y = -6.75 + 0.37Hd + 0.22Rc + 0.50Tm - 0.36Cr - 0.19Ca$	0.65	0.005	Hd (0.028); Tm (0.017); Cr (0.039)	1.3–3.0
Density – <i>Acer platanoides</i>	$y = 115966.4 - 0.14Hd + 0.05Rc + 0.39Nt - 0.59Lc - 0.38Tm$	0.79	<0.001	Hd (0.011); Nt (0.020); Lc (0.005); Tm (0.029)	1.4–3.4
Quality index Q – <i>Acer platanoides</i>	$y = 16.69 - 0.57Hd + 0.43Nt + 0.61Lc - 0.63Tm + 0.59Ca$	0.76	<0.001	Lc (0.003); Tm (0.016); Ca (0.012)	1.2–3.1
IDSS – <i>Acer platanoides</i>	$y = -1172.7 + 0.27Hd - 1.46Nt + 0.62Tm + 0.31Ca$	0.68	0.004	Nt (0.019); Tm (0.034); Ca (0.027)	1.3–3.2
KD – <i>Acer platanoides</i>	$y = 6.63 - 0.24Hd + 1.19Nt - 0.68Tm - 1.22Ca$	0.64	0.006	Nt (0.023); Tm (0.037); Ca (0.018)	1.2–2.9

Note: In the regression equations, Hd – soil water regime; Nt – soil nitrogen content; Ca – soil carbonate content; Lc – habitat illumination/light regime; Tm – thermal regime; Rc – soil acidity; Fh – soil moisture variability; Kn – continentality of climate; Cr – cryo-climate regime. The dependent variables represent the analysed regeneration characteristics: Density – density of young tree cohorts; Q – vitality index; IDSS – index of dynamic structural stability; KD – coefficient of regeneration discreteness. R² represents the coefficient of determination and indicates the proportion of variance explained by each regression model. The global p-value was obtained from ANOVA testing and reflects the significance of the overall regression model. Individual coefficient p-values indicate the statistical contribution of individual ecological predictors. VIF values were calculated to assess multicollinearity among explanatory variables, with values below 5 indicating the absence of critical multicollinearity.

Nota: Nas equações de regressão, Hd – regime hídrico do solo; Nt – teor de nitrogênio no solo; Ca – teor de carbonatos no solo; Lc – regime de luminosidade/luz do habitat; Tm – regime térmico; Rc – acidez do solo; Fh – variabilidade da umidade do solo; Kn – continentalidade climática; Cr – regime crioclimático. As variáveis dependentes representam as características de regeneração analisadas: Density – densidade de coortes de árvores jovens; Q – índice de vitalidade; IDSS – índice de estabilidade estrutural dinâmica; KD – coeficiente de descontinuidade da regeneração. O R² representa o coeficiente de determinação e indica a proporção da variância explicada pelo modelo de regressão. O valor-p global foi obtido por meio de teste ANOVA e reflete a significância do modelo de regressão como um todo. Os valores-p dos coeficientes individuais indicam a contribuição estatística de cada preditor ecológico. Os valores de VIF foram calculados para avaliar a multicolinearidade entre as variáveis explicativas, sendo que valores inferiores a 5 indicam a ausência de multicolinearidade crítica.

Specifically, in the *Pinus sylvestris* understory, the study recorded a clear tendency for population density values to

increase against the background of increasing illumination (Figure 4a) and quality index Q values with increasing values

of thermal regime and, accordingly, radiation balance indicators (Figure 4b). In *Quercus robur*, against the background of increasing soil moisture, an increase in population density was observed (Figure 5). The young generation of *Acer platanoides* was characterised by an increase in the quality index Q with increasing illumination under the forest canopy (Figure 6a), as well as in the carbonate content of the soil (Figure 6b) and radiation balance indicators (thermal regime scores) (Figure 6c).

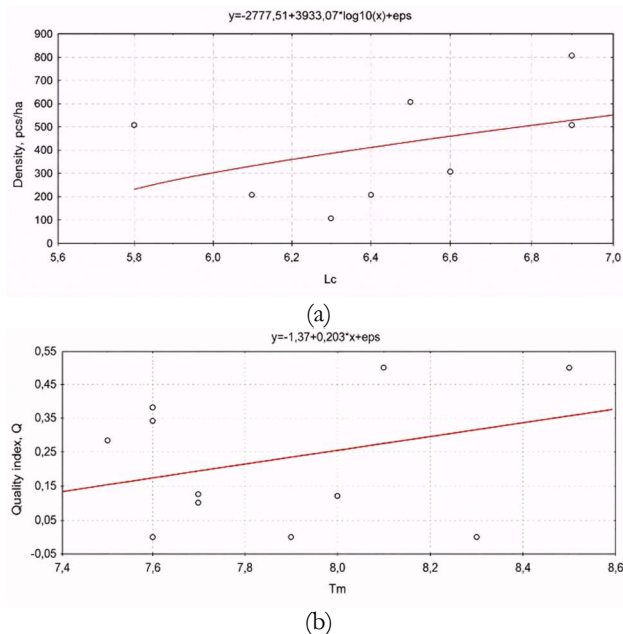


Figure 4. Changes in the cohorts of large understory of *Pinus sylvestris*: a) density along the light gradient (Lc); b) values of the quality index Q along the thermal regime gradient (Tm).

Figura 4. Alterações nas coortes de sub-bosque de *Pinus sylvestris*: a) densidade ao longo do gradiente de luz (Lc); b) valores do índice de qualidade Q ao longo do gradiente de regime térmico (Tm).

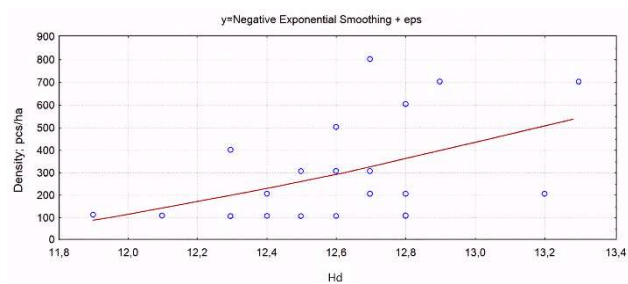


Figure 5. Changes in the density of cohorts of the medium understory of *Quercus robur* along the gradient of soil water regime (Hd).

Figura 5. Alterações na densidade de grupos do sub-bosque médio de *Quercus robur* ao longo do gradiente do regime hídrico do solo (Hd).

In the cohorts of young *Pinus sylvestris* trees, the population density decreases with increasing scores of soil water regime (Hd) (Figure 7a), soil nitrogen content (Nt) (Figure 7b), and IVD index values by soil acidity gradient (Rc) (Figure 7c). The same trend was recorded for the values of the quality index Q in the cohorts of the medium understory of *Quercus robur* in relation to the soil water regime (Hd) (Figure 7d).

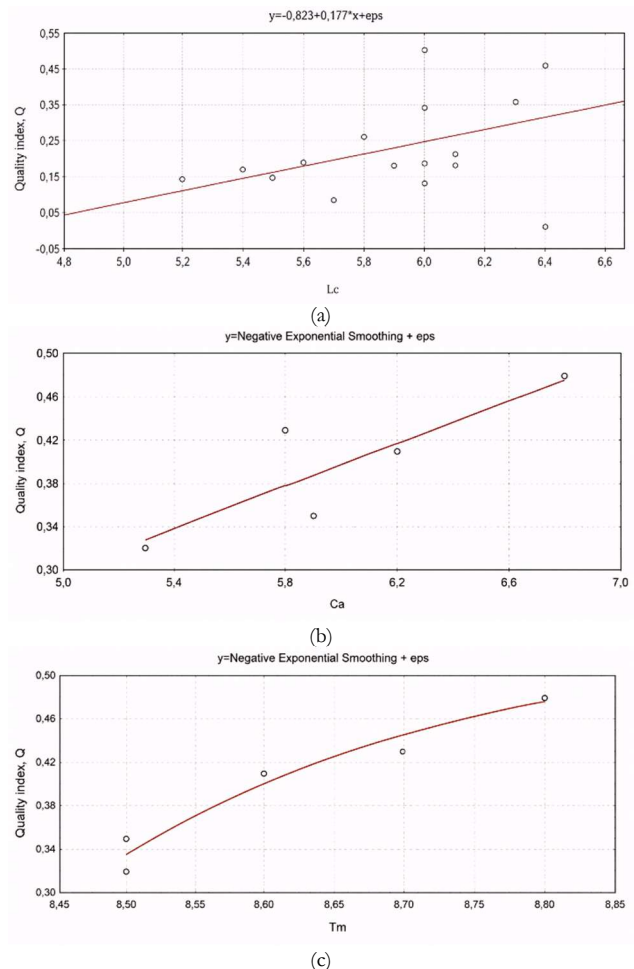


Figure 6. Changes in the values of the quality index Q in small understory cohorts of *Acer platanoides*: a) along the light gradient (Lc); b) along the gradient of soil carbonate content (Ca); c) along the temperature gradient (Tm).

Figura 6. Alterações nos valores do índice de qualidade Q em pequenos grupos de sub-bosque de *Acer platanoides*: a) ao longo do gradiente de luz (Lc); b) ao longo do gradiente de teor de carbonato no solo (Ca); c) ao longo do gradiente de temperatura (Tm).

In the younger generation of *Pinus sylvestris*, the largest values of the Q index were mostly recorded at the level of “intermediate” values of the water regime factor (Hd) (Figure 8a), soil acidity (Rc) (Figure 8b), soil carbonate content (Ca), and climate continentality indicators (Figure 8c). This feature, specifically, was also inherent in the dynamics of the index of size structure diversity (IDSS) in cohorts of the large understory of *Quercus robur* along the soil acidity gradient (Rc) (Figure 9).

Despite the diversity of the response of *Pinus sylvestris*, *Quercus robur*, and *Acer platanoides* cohorts and their population traits to changes in the scores of environmental factors, certain general features were also identified in this aspect. For the water regime of the soil, they were manifested in the fact that at different stages of recovery in young cohorts, the largest values of the quality index often fell within 12.4-12.8 points (conditions transitioning from dry forest to wet forest). In areas with a soil water regime that had a score over 13 points, all cohorts of the young generation had a substantial decrease in vitality. When the water regime was at 12.2-12.6 points, a series of cohorts had some of the largest density indicators.

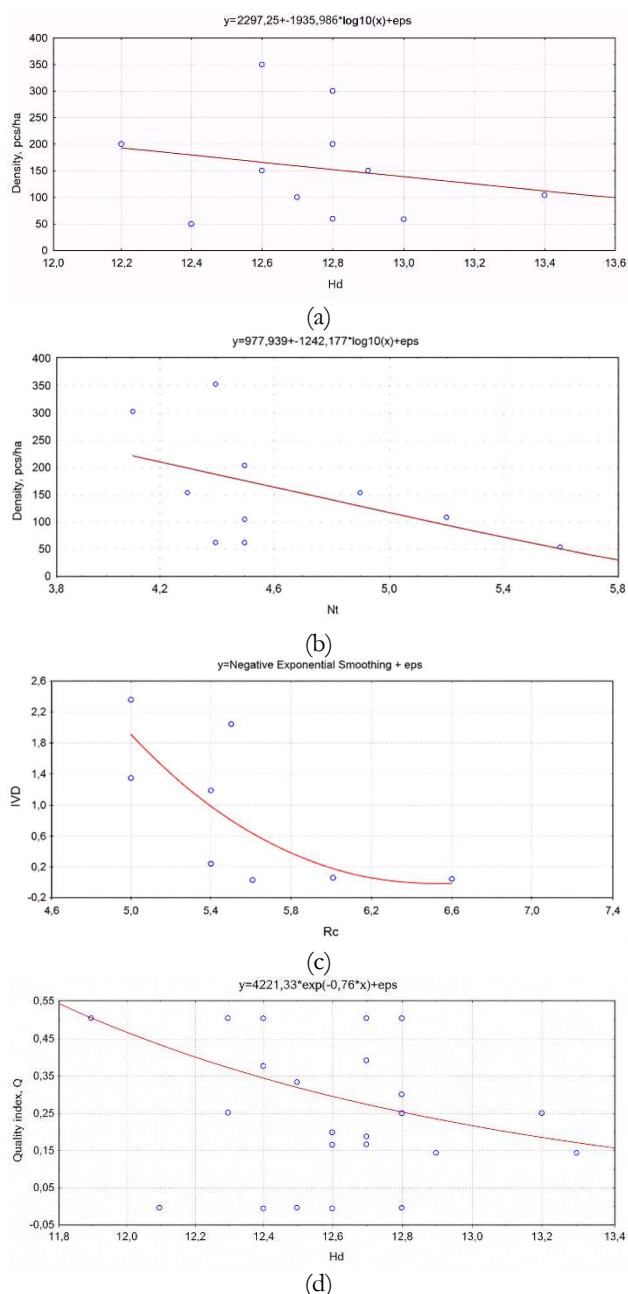


Figure 7. Changes in the density of cohorts of young *Pinus sylvestris* trees: a) along the gradient of soil water regime (Hd); b) along the gradient of soil nitrogen content (Nt); c) changes in the values of the IVD index along the gradient of soil acidity (Rc); d) changes in the values of the Q index along the gradient of soil water regime (Hd).

Figura 7. Alterações na densidade das coortes de árvores jovens de *Pinus sylvestris*: a) ao longo do gradiente do regime hídrico do solo (Hd); b) ao longo do gradiente do teor de nitrogênio no solo (Nt); c) alterações nos valores do índice IVD ao longo do gradiente de acidez do solo (Rc); d) alterações nos valores do índice Q ao longo do gradiente do regime hídrico do solo (Hd).

Most cohorts of the younger generation respond to an increase in light by increasing the quality index Q, as well as by decreasing or increasing the density of cohorts and the diversity of size structure (BEN MEFTAH et al., 2015; LEVCHENKO; GUMENIUK, 2022). Population density mostly has a clear tendency to decrease with increasing nitrogen content. This is a result of the fact that on more fertile soils, a more closed herbaceous layer (with a projected cover of more than 50%) is predominantly represented,

which negatively affects the survival and vitality of the undergrowth in the restoration areas.

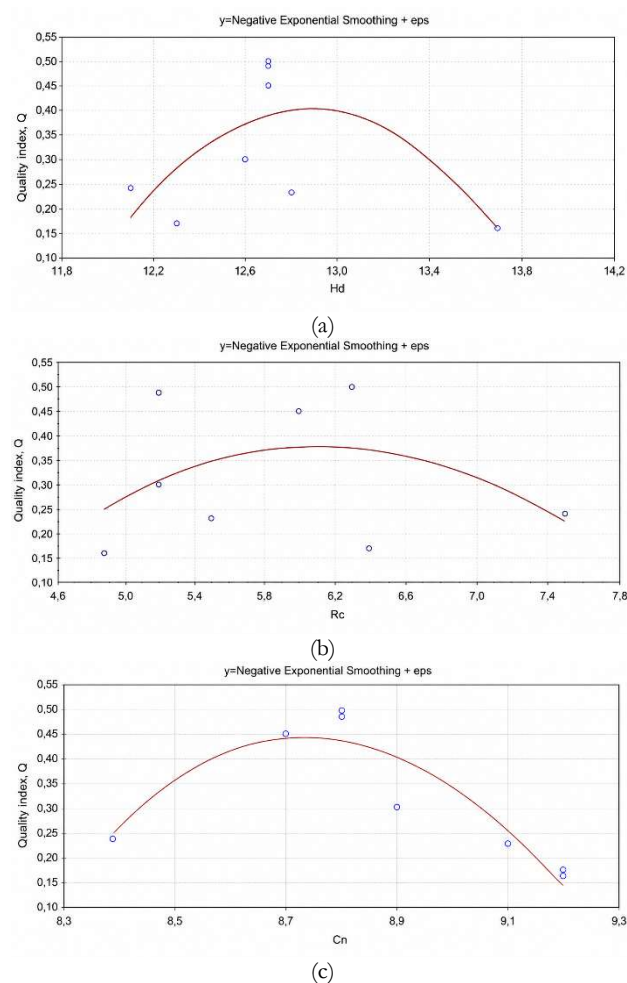


Figure 8. Changes in the cohorts of large understory of *Pinus sylvestris*: a) values of the quality index Q along the gradient of soil water regime (Hd); b) values of the quality index Q along the gradient of soil acidity (Rc); c) values of the quality index Q along the gradient of continentality (Kn).

Figura 8. Alterações nas coortes de sub-bosque de *Pinus sylvestris*: a) valores do índice de qualidade Q ao longo do gradiente de regime hídrico do solo (Hd); b) valores do índice de qualidade Q ao longo do gradiente de acidez do solo (Rc); c) valores do índice de qualidade Q ao longo do gradiente de continentalidade (Kn).

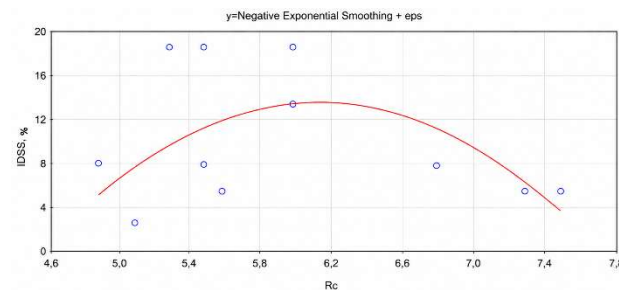


Figure 9. Changes in the index of size structure diversity (IDSS) of cohorts of large understory of *Quercus robur* along the soil acidity gradient (Rc).

Figura 9. Alterações no índice de diversidade da estrutura de tamanho (IDSS) de grupos de sub-bosque de grande porte de *Quercus robur* ao longo do gradiente de acidez do solo (Rc).

Along the thermal regime gradient, namely, as its indicators and, accordingly, the size of the radiation balance

increase, the values of the quality index Q mainly increase. Along the thermal regime gradient, the values of the population density and the IVD index both increase and decrease in the cohorts. Under natural conditions, not only is the influence of individual environmental factors essential, but also the result of their interaction (SAFAROVA; NOVRUZOVA, 2021; ANDREITSEV et al., 2024). Therefore, the study also addressed this issue and, accordingly, analysed the nature of the joint effect of different pairs of leading environmental factors on the state of *Pinus sylvestris*, *Quercus robur*, and *Acer platanoides* cohorts and their population parameters. The study found that five variants of effects are usually manifested:

Variant 1. The largest values of population characteristics (density, indices of quality or diversity of size structure, etc.) are achieved when the scores of both ecological factors reach the greatest values.

In *Pinus sylvestris*, this effect is manifested at the level of the middle understory when light and soil carbonate content or light and thermal conditions interact to influence the quality index of this young generation cohort (Figure 10). In *Quercus robur*, the interaction of light and carbonate content in the soil and their influence on the value of the quality index of the medium understory.

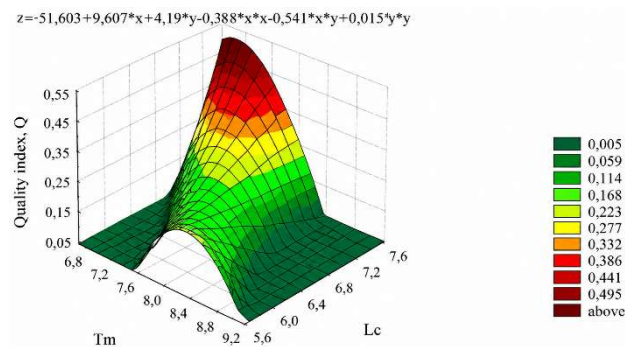


Figure 10. Changes in the quality index Q of cohorts of medium understory of *Pinus sylvestris* under the influence of light (Lc) and temperature (Tm) factors.

Figura 10. Alterações no índice de qualidade Q de grupos de sub-bosque médio de *Pinus sylvestris* sob a influência dos fatores de luz (Lc) e de temperatura (Tm).

Variant 2. The largest values of population characteristics are achieved when the scores of one environmental factor are at the greatest, and the other is at the smallest values. This effect is typical for *Pinus sylvestris*. In this species, this variant at the level of a small understory corresponds to a change in the quality index values against the background of changes in the water regime of soils and illumination; a change in density under the influence of illumination and the water regime of soils, as well as the thermal regime and the amount of nitrogen in the soil; a change in the diversity of the size structure under the influence of the thermal regime and the carbonate content in the soil.

In the middle understory of *Pinus sylvestris*, the change in the quality index under the influence of light and temperature regime, as well as under the influence of temperature regime and soil carbonate content; density under the influence of temperature regime and soil nitrogen content, as well as soil water regime and soil nitrogen content (Figure 11); and the diversity of the size structure under the influence of light and temperature regime factors.

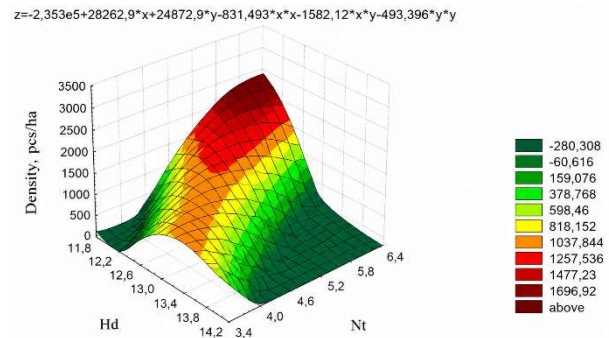


Figure 11. Changes in the density of cohorts of *Pinus sylvestris* medium understory under the influence of soil water regime (Hd) and nitrogen content (Nt).

Figura 11. Alterações na densidade dos grupos de *Pinus sylvestris* no sub-bosque médio sob a influência do regime hídrico do solo (Hd) e do teor de nitrogênio (Nt).

In *Quercus robur*, according to this variant, a change in the density of cohorts of small understory occurs under the influence of the water regime of soils and the content of carbonates in them. In the case of *Acer platanoides*, the density of small understory changes under the influence of light and nitrogen content in the soil, as well as changes in the quality index of young trees against the background of changes in the water regime of soils and their carbonate content.

Variant 3. The greatest values of population characteristics are achieved when the scores of both environmental factors are at their smallest values. This variant is manifested in changes in the density of the small understory of *Pinus sylvestris* under the influence of the factors of light and nitrogen content in the soil, light and temperature, light and carbonate content in the soil.

Variant 4. The greatest values of population characteristics are achieved when the scores of both environmental factors are at the level of average values. This variant is particularly typical for *Quercus robur*. In the case of a small understory, it is manifested in the quality index Q when the factor of soil water regime interacts with the factor of soil carbonate content, as well as with the factor of climate continentality (Figure 12). In *Quercus robur*, the combination of the average level of soil water regime and soil acidity is favourable for the formation of cohorts with a prominent level of size structure diversity. In the large understory, the density of cohorts changes against the background of the influence of soil nitrogen and carbonate content factors.

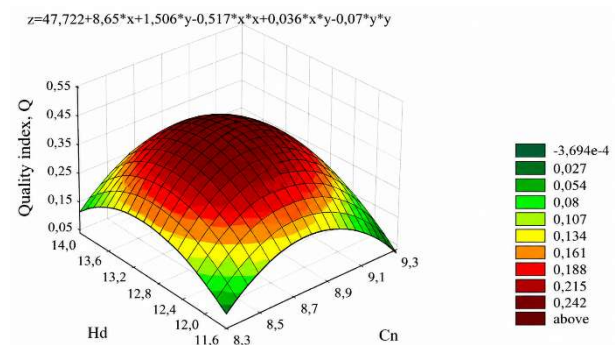


Figure 12. Changes in the values of the quality index Q in cohorts of the small understory of *Quercus robur* under the influence of climate continentality (Kn) and soil water regime (Hd).

Figura 12. Alterações nos valores do índice de qualidade Q em grupos de sub-bosque de pequeno porte de *Quercus robur* sob a influência da continentalidade climática (Kn) e do regime hídrico do solo (Hd).

In *Pinus sylvestris*, this variant is characterised by changes in the diversity of the size structure of the small understory against the background of the scores of soil carbonate and nitrogen content, as well as under the influence of soil water regime and thermal regime. In the medium understory – changes in the quality index Q under the influence of thermal regime and nitrogen content; density under the influence of thermal regime and soil carbonate content, soil carbonate and nitrogen content, soil water regime and the amount of carbonate in them; diversity of the size structure under the influence of illumination and the amount of carbonate in the soil.

Variant 5. The greatest values of population characteristics are achieved when the scores of one environmental factor are at the largest, and the other are at the average values.

In *Pinus sylvestris*, this variant corresponds to a change in the cohort quality index in the middle understory under the influence of soil water regime and light, as well as under the influence of light and the amount of nitrogen in the soil. In *Acer platanoides*, the change in the quality index of small understory under the influence of soil water regime and light. In *Quercus robur*, the combination of medium moisture and high light levels is favourable for the formation of cohorts of understory with a significant diversity of size structure.

Often, the nature of the response of population parameters to environmental conditions is a combination of the above effects. For example, this is typical for the change in the values of the quality index Q in the cohorts of the middle understory of *Pinus sylvestris* against the background of the influence of soil water regime and thermal regime factors (Figure 13).

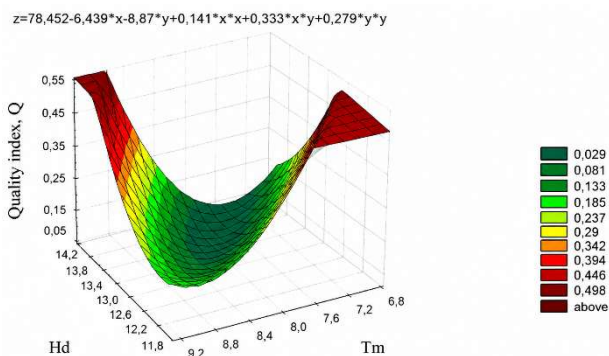


Figure 13. Changes in the quality index Q in cohorts of medium understory *Pinus sylvestris* under the influence of soil water regime (Hd) and thermal regime (Tm) factors.

Figura 13. Alterações no índice de qualidade Q em grupos de *Pinus sylvestris* de sub-bosque médio sob a influência dos fatores do regime hídrico do solo (Hd) e do regime térmico (Tm).

Source: developed by the authors of this study.

Areas with signs of anthropogenic pressure showed disturbances in the structure of phytocoenoses and characteristics of natural regeneration. Specifically, in areas with signs of mechanical intervention, logging, or traces of grazing pressure, a 35-55% reduction in self-seeding density was observed, especially in oak and birch associations. Under such conditions, *Pinus sylvestris* showed a decrease in the quality index Q to 0.05, and IDSS did not exceed 17%, which indicated instability of the formation of regeneration cohorts. In phytocoenoses with fragmented cover and litter damage, the predominance of undergrowth with signs of oppression

and a disturbed ratio of age classes was recorded. A high KD (>0.35) and negative IVD indicated a depressed nature of regeneration, with a low probability of transition to stable stands without external intervention. Thus, the anthropogenic impact was a destabilising factor for the regeneration processes, reducing the structural stability of phytocoenoses and disrupting natural selection based on microecological conditions.

Consequently, the younger generation of *Pinus sylvestris* responds most actively to light and humidity, demonstrating high adaptability at medium and large growth. The greatest density and quality of self-seeding was observed in *Pinus sylvestris* under conditions of optimal humidity and light. The *Quercus robur* understory is sensitive to light, as well as to soil acidity and carbonation, and was less competitive in shaded habitats and acidic soils. The young generation of *Acer platanoides* demonstrates stable regeneration under moderate thermal and carbonate parameters.

The population analysis showed that the forest phytocoenoses of the Left-Bank Polissia formed fundamentally distinct “portraits” of self-seeding, which was reflected in the whole range of indicators – from density to structural differentiation. This, specifically, is clearly evidenced by the data on natural regeneration in the forests of the *Pineta sylvestris hylocomiosa*, *Pineta sylvestris franguloso-vacciniosa*, *Querceta roboris convallariosa*, and *Betuleta pendulae vacciniosa* association groups, which are among the most widespread phytocoenoses within the area under study.

In *Pineta sylvestris hylocomiosa*, self-seeding of *Pinus sylvestris* provided the most complete age spectrum. The density of small understory reached 4,456 specimens/ha, medium understory – 3,213 specimens/ha, large understory – 1,606 specimens/ha, and young trees – ≈1,100 specimens/ha. The quality index (Q) of most cohorts reached values corresponding to “thriving” (0.33 and above) indicators. The IDSS value rose to 43.1%, recording a diverse size structure, while the IVD (+1.35- +1.57) showed steady improvements in vigour from small understory to young trees. KD stayed minimal (0.11-0.15), confirming the continuity of age groups and generation flow. The association of dense, viable cohorts with micro-depressions with optimal moisture created a variety of microhabitats that together maintained a high total density.

In *Pineta sylvestris franguloso-vacciniosa*, the total density of *Pinus sylvestris* was lower (2,875 specimens/ha). Small and medium-sized stands were mostly characterised by Q≈0.19-0.33 with IDSS≈23%, but in cohorts of large and young trees, the density fell below 900 specimens/ha, KD increased to 0.3, and Q in most cohorts decreased to 0.17-0.21. Although the positive IVD (+1.2) confirmed the overall recovery trend, localised gaps between the medium understory and the entry of young trees indicated temporal “pauses” in the generation flow, probably related to fluctuations in soil moisture and live canopy characteristics, as well as competition with *Vaccinium myrtillus*. In *Betuleta pendulae vacciniosa*, *Pinus sylvestris* regeneration was depressed. Although a strong small understory (3,631 specimens/ha) formed a dense cover, Q did not exceed 0.15, IDSS dropped to 6-12%, IVD was negative (-0.8), while KD exceeded 0.4. The loss of medium and large understory caused by the shading of the birch canopy and acidified litter caused fragmentation of the age spectrum and accumulation of small individuals with slow growth and development.

In the oak forests of the *Querceta roboris convallariosa* association group, the density of *Quercus robur* undergrowth mainly varied within 1,700-2,800 units/ha, but Q mostly stayed within 0.1-0.3, IDSS did not exceed 15%, and KD reached 0.33. Positive IVDs were observed only in micro-coenoses on lighter sandy loam soils, while in massive areas with acidic soil, the viability of small understory decreased sharply. Thus, oak coenoses were characterised by a reduced density of age classes with a discrete transition to the stand tier.

Overall, the analysis of the state of natural regeneration in various groups of associations of the Left-Bank Polissia of Ukraine revealed that the most favourable conditions for natural regeneration were recorded in mesotrophic *Pineta sylvestris hylocomiosa*, which provided high quantitative and qualitative characteristics of this process. The cohorts of the younger generation here had a balanced age and vital rate structure, with fairly high Q and IDSS combined with minimal depressive risks. A balanced but vulnerable nature of regeneration was characteristic of *Pinus sylvestris franguloso-vacciniosa* and some micro-pockets of oak forests. A depressed state with a predominance of small understory, low Q, and negative IVD was recorded in birch forests, where natural transition to greater cohorts was unlikely without intervention. The identified patterns of regeneration can be used as a basis for predicting forest regeneration dynamics and planning nature-based forest management.

The study confirmed that certain types of phytocoenoses in the Left-Bank Polissia of Ukraine have a prominent potential for sustainable functioning, particularly due to stable, continuous natural regeneration. The greatest level was demonstrated by pine forests of the *Pineta sylvestris hylocomiosa* type, where the combination of high self-seeding density, optimal age structure, and low level of fragmentation of age spectra (KD = 0.13) ensured sustainable reproduction of the primary tree species (*Pinus sylvestris*). Such areas should be considered as a priority for integration into sustainable forest management programmes, as they not only maintain intra-ecosystem balance but also require minimal anthropogenic intervention.

Phytocoenoses with high natural regeneration dynamics are a source of numerous ecosystem services (FEDONIUK et al., 2024; MAHARRAMOVA et al., 2026). They provide soil conservation, water balance regulation, microclimate stabilisation, biodiversity maintenance, and carbon sequestration without the need for maintenance and planting material. For example, within *Pineta sylvestris franguloso-vacciniosa*, although some complications with cohort formation were recorded, the IDSS level stayed sufficient (23%), which led to the maintenance of productive and sustainable stands with reduced maintenance costs. Natural regeneration proved to be more cost-effective than artificial reforestation. The economic comparison demonstrated that the lower costs of natural regeneration were mainly associated with reduced requirements for planting material, planting operations, and repeated establishment activities. The largest differences between approaches were observed in the initial establishment phase. According to empirical surveys, the average cost per hectare of areas with high self-regeneration was 2.3-3.5 times lower than in analogous areas with established cultures (Figure 14). In the context of limited budget funding and climate change risks, this strategy appears more rational in terms of resource conservation and payback of forestry measures. Reducing the need for soil preparation,

planting material, and crop care substantially reduces overall costs and minimises the anthropogenic impact on the ecosystem (PETROV et al., 2024; SHAHINI et al., 2025).

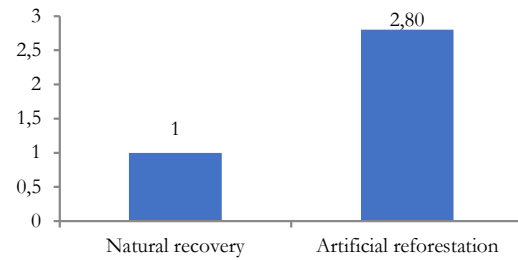


Figure 14. Comparison of average costs per hectare for natural and artificial restoration of phytocoenoses based on the results of empirical surveys.

Figura 14. Comparação dos custos médios por hectare entre a restauração natural e a artificial de fitocenoses, com base em levantamentos empíricos.

Note: the indicator for artificial reforestation (2.8) is an average value within 2.3-3.5 recorded during field surveys.

An additional argument in favour of natural regeneration is its role in increasing the climate resilience of forests. Self-seeding populations that form within local microclimatic conditions demonstrate increased adaptation to existing gradients of humidity, acidity, temperature, and light. For instance, *Acer platanoides* successfully regenerated only in a narrow range of optimal conditions, while *Pinus sylvestris* demonstrated plasticity to a wider range of environments. This reflects the expediency of preserving naturally adapted gene pools as a basis for the formation of climate-resilient landscapes. Thus, natural regeneration has not only ecological but also strategic value for forest management in the context of climate change. Its integration into forestry policy and practice can reduce costs, increase ecosystem stability, and ensure the long-term reproducibility of forest resources without disturbing the natural balance.

4. DISCUSSION

The obtained results demonstrate that natural regeneration of forest phytocoenoses in the Left-Bank Polissia is determined by the combined influence of abiotic gradients, phytocoenotic interactions, and anthropogenic pressure. The strongest relationships were associated with soil water regime (Hd), nitrogen availability (Nt), carbonate content (Ca), illumination (Lc), and thermal regime (Tm), confirming the multifactorial nature of regeneration processes. Similar patterns were reported in European and boreal forest ecosystems, where regeneration success depends on the interaction between moisture availability, light conditions, soil properties, and stand structure rather than on a single environmental factor (MARTIN et al., 2020; PETROKAS et al., 2024). The spatial mosaic of favourable ecological conditions observed in the present study corresponds with approaches based on ecological network analysis, which emphasise the importance of identifying areas with optimal restoration potential (KONDRATIUK, 2019; ZHAI; HUANG, 2022).

The most pronounced regeneration stability was observed in *Pineta sylvestris* association groups, where young cohorts demonstrated high density, vitality, and balanced age and size structures under moderate moisture and sufficient illumination. These findings agree with Martin et al. (2020), who showed that conifer regeneration in boreal forests is

strongly regulated by moisture conditions and shade intensity. Similarly, Petrokas et al. (2024) demonstrated that closer-to-nature management based on natural regeneration promotes continuity of age structure and regeneration stability in northern European hemiboreal forests. The present study extends these observations by showing that, in the Left-Bank Polissia, the regeneration success of *Pinus sylvestris* is additionally associated with the role of accompanying vegetation, including *Vaccinium myrtillus* and *Frangula alnus*, which contributes to the formation of favourable microenvironmental conditions. Comparable relationships between vegetation structure, hydrological stability, and restoration success have also been reported in other ecosystems (MOHAN et al., 2021; CASTELLANO et al., 2022).

In contrast, *Quercus robur* and *Acer platanoides* demonstrated more specific environmental responses and greater sensitivity to changes in ecological conditions. In oak associations, regeneration depression was associated with reduced structural continuity, anthropogenic disturbance, and unfavourable soil conditions. This corresponds with European studies showing that oak regeneration depends strongly on the availability of suitable microsites, seed sources, and disturbance regimes. Wijedasa et al. (2020) similarly demonstrated that spatial factors related to seed dispersal and proximity to mature stands influence regeneration success, while the present study indicates that fragmentation of regeneration in oak and birch associations may also reflect limitations in regeneration continuity. For *Acer platanoides*, the importance of illumination, thermal regime, and soil conditions confirms the species-specific character of regeneration responses and supports the need for differentiated management strategies.

The comparison of the proposed indices with international approaches demonstrates their compatibility with established concepts of forest vitality and structural diversity assessment. The Q index reflects vitality-based approaches that evaluate cohort condition and survival potential, whereas IDSS corresponds with structural complexity indicators based on tree-size differentiation and structural heterogeneity (MCELHINNY et al., 2005; MCELHINNY et al., 2006). The IVD and KD indices extend these approaches by incorporating temporal changes and continuity of cohort structure, which are essential for evaluating regeneration sustainability. Thus, the proposed index system provides a cohort-based framework that integrates vitality, structural diversity, and population dynamics.

Anthropogenic pressure represented a major factor limiting regeneration success. Mechanical disturbance, logging, and grazing reduced regeneration density by 35–55% and shifted cohorts towards depressed structural categories. Similar effects of ecosystem degradation and delayed recovery were reported in disturbed forest and mining landscapes (DONG et al., 2019; TIAN et al., 2025).

The observed threshold responses, including rapid declines in Q values under increased acidity or shading, correspond with findings on ecological degradation thresholds and ecosystem resilience (ROMANCHUK et al., 2018; HE; SHI, 2022). At the same time, the results confirm that natural regeneration can provide an economically efficient restoration pathway, with costs 2.3–3.5 times lower than artificial reforestation, supporting global assessments of natural regeneration as a biodiversity-friendly and cost-

effective restoration strategy (NYKYTIUK; KRAVCHENKO, 2024; CHAZDON et al., 2025).

The interpretation of regression models should consider the limitations of stepwise selection procedures. Although stepwise regression was useful for identifying the most influential ecological predictors, multiple correlated variables may increase the risk of overfitting and unstable coefficient selection. In the present study, this limitation was reduced through ecological interpretation of model outputs, multicollinearity assessment, and validation procedures. Nevertheless, the identified relationships should be considered associative, and future research should confirm them using independent datasets and alternative approaches, including mixed-effects or machine-learning models.

The findings also have broader implications for forest management. The ecosystem-based approach proposed by de Groot et al. (2016) emphasises maintaining structural complexity to support biodiversity, and the present study confirms that forests with higher structural diversity maintained greater regeneration stability. The application of natural regeneration strategies should therefore combine ecological effectiveness with social responsibility, considering biodiversity conservation, ecosystem services, and the interests of local communities. As highlighted by Barnaud et al. (2021) and Han et al. (2025), successful restoration requires consideration of both ecological and social dimensions. The integration of ecological gradients, regeneration indices, spatial analysis, and economic assessment provides a basis for developing regionally adapted strategies for sustainable forest management.

The generalisation of the literature analysis revealed that the findings of the study of natural regeneration of forest phytocoenoses of the Left-Bank Polissia were consistent with global trends recorded in different ecological and climatic zones. The established dependence of the viability and structural completeness of self-seeding on the combined effect of abiotic gradients, phytocoenotic interactions, and spatial factors confirmed the universality of the multifactorial nature of forest regeneration. The study also revealed a correlation between high cohort diversity and ecosystem stability within optimal microecological conditions. In a series of cases, analogous threshold responses, destabilising effects of anthropogenic impacts, and the significance of maintaining a mosaic structure of regeneration were observed. Comparison with international studies helped to interpret the results as part of a broader ecological pattern, which confirms the relevance of the chosen approach and substantiates recommendations for further spatial planning of sustainable forest management.

The implementation of the proposed management recommendations also has important ethical and social implications. Preference for natural regeneration approaches contributes to the conservation of native forest genetic resources, maintenance of biodiversity, and preservation of ecosystem functions, reducing unnecessary disturbance associated with intensive artificial regeneration practices. At the same time, forest management decisions should consider the interests of local communities, including access to forest resources, recreational values, and long-term ecosystem services. Therefore, the application of regeneration-based management strategies should combine ecological effectiveness with principles of responsible stewardship, transparency, and sustainable use of forest ecosystems.

5. CONCLUSIONS

Based on the results of studying the ecological relations of natural regeneration of the leading forest-forming species (*Pinus sylvestris*, *Quercus robur*, and *Acer platanoides*) of the Left-Bank Polissia of Ukraine based on a combination of synphytoindication using the unified eco-scales of J.P. Didukh and regression analysis, the study found that the key environmental factors that most significantly affect the state of young cohorts in the region include the water regime of soils (Hd), the content of nitrogen (Nt) and carbonates (Ca), as well as the conditions of illumination of habitats (Lc), and their thermal regime (Tm).

The nature of changes in cohort traits along simple gradients of nine abiotic factors (apart from Hd, Nt, Ca, Lc, Tm, variability of soil moisture (fH), soil acidity (Rc), continental climate (Kn), cryo regime (Cr)) and their joint action was determined. The study showed that this response is characterised by diversity and individuality, which is the result not only of species-inherent features of recovery, but also of specific environmental requirements of each cohort of the young generation. The diversity and individuality of response to environmental factors are significant mechanisms for increasing the adaptive potential of cohorts and enhancing their environmental sustainability, which ultimately has a positive impact on the success of natural regeneration and the ability of forests to sustain themselves.

Therewith, the study revealed certain general features and patterns of response of the characteristics of young cohorts of *Pinus sylvestris*, *Quercus robur*, *Acer platanoides* and their population traits to changes in the scores of environmental factors. Specifically, it was shown that against the background of a complex system of ecological and coenotic relationships inherent in forest phytocoenoses, conditions favourable enough for natural regeneration and ecosystem functioning are often formed in the forests of the *Pineta sylvestris hylocomiosa* association group. Here, the study recorded cohorts of the younger generation of the coenosis-creator with high population density and vitality, as well as a balanced age, size, and vital structure.

Anthropogenic pressure (felling, grazing, mechanical intervention) reduced the density of regeneration by 35-55%, led to a decrease in the vitality of the younger generation of trees and the formation of cohorts of the “depressed” category, and also disrupted the stability of their age structure. The identified patterns allow recommending the conservation and priority management of natural pine plots with high regeneration rates as centres of sustainable reproduction.

The study confirmed that natural regeneration is a cost-effective strategy: the average cost per hectare was 2.3-3.5 times lower than artificial reforestation. The prospect of further research is to expand the spatial coverage, integrate genetic markers of viability, and develop models for scenario forecasting of regeneration in changed climate conditions.

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