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Altitudinal Variation in Species Diversity, Distribution, and Regeneration Status of a Secondary *Picea* Forest in Guandi Mountain, Northern China

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Abstract: Altitude plays a crucial role in shaping the diversity and distribution of species in forest landscapes in mountainous regions. However, existing studies often lack comprehensive analysis of the intricate relationships among environmental factors, disturbances, and species diversity. This study aims to address this gap by thoroughly analyzing major species' diversity, distribution, and regeneration status, along with their influencing factors, across different altitudinal gradients (1850 to 2350 m). Field surveys were conducted to examine the major species in different vegetation layers of the secondary *Picea* forest in Guandi Mountain. The key findings from the study include the following: (1) the study area recorded a total of nine species of adult trees, belonging to eight genera in five families, fourteen species of shrubs from eight genera in five families, and fifty-two herb species representing forty-eight genera in twenty-six families. Dominant species varied across layers, with *Picea asperata* Mast. and *Larix principis-rupprechtii* Mayr. dominating the arborous layer, *Lonicera ferdinandii* Franch. and *Cotoneaster acutifolius* Turcz. in the shrub layer, and *Poa pratensis* L. and *Duchesnea indica* (Andrews.) Focke in the herb layer. (2) Altitude significantly influenced species diversity, with the most pronounced effects observed in the shrub and herb layers. (3) Tree species regeneration varied with altitude, with *Picea asperata* exhibiting the highest regeneration performance, particularly in the high-altitude zone (2250–2350 m). Regeneration parameters were significantly correlated with species diversity indices in both tree and shrub layers. (4) Redundancy analysis revealed that, apart from altitude, cutting ($p = 0.015$) influenced the species diversity of the tree layer, while annual precipitation ($p = 0.006$) and temperature ($p = 0.01$) determined the diversity of the shrub layer. Grazing ($p = 0.042$) was identified as a determining factor for species diversity in the herb layer. Overall, these findings provide valuable insights into the sustainable management of forest ecosystems in the study area and offer practical guidance for forest management in similar mountainous landscapes worldwide.

Keywords: secondary *Picea* forest; vegetation layers; altitudinal gradient; environment factors

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1. Introduction

The health and ecological benefits of forest ecosystems hinge on the critical aspects of biodiversity, distribution, and regeneration status. These factors play vital roles in predicting future forest dynamics and enhancing ecological advantages [1–4]. Different vegetation layers, including herbs, shrubs, and trees, contribute significantly to the biodiversity of forest ecosystems [5–7]. Understanding the diversity and distribution patterns across these layers forms a rational basis for devising effective biodiversity protection strategies.

Regeneration stands out as a pivotal process influencing the survival and persistence of species within communities [8]. The maintenance of forest community structure relies heavily on species composition, stand structure, and the regeneration status of tree species in the dry Afromontane forests of Awi Zone, northwestern Ethiopia, and heavily on the regeneration capacity of typical tree species [9,10]. This regeneration capacity is crucial for conserving and preserving forest biodiversity [11]. The successful regeneration of tree species depends on the ability of seedlings and saplings to survive and grow, ensuring the long-term sustainability of forests [12–14]. Consequently, effective management and conservation of natural forests necessitate reliable data on regeneration trends [3]. Natural disturbances and environmental factors play pivotal roles in shaping plant diversity patterns in mountainous areas [15,16]. A comprehensive analysis of plant community diversity, distribution, regeneration, environmental impact factors, and related aspects is a valuable tool for effectively managing forest ecosystems.

Species diversity distribution results from prolonged interactions among species and between species and their environments [17]. The relationship between changes in species diversity and environmental factors is closely intertwined. An analysis of vegetation alongside ecological aspects like topography, soil, and climate can reveal the stability of plant communities and the extent of their interaction with these environmental factors [18]. Altitude significantly influences the distribution of plant species, effectively shaping the regional climate and, consequently, the dispersal of flora [19,20]. Therefore, researchers from diverse disciplines contemplate species diversity through the lens of various environmental elements, including elevation, climate, inclination, and direction [21]. Additionally, spatial changes in climatic conditions (such as temperature and rainfall) have been suggested to play a fundamental role in controlling species diversity [22–24], impacting species coexistence and persistence. Maintaining species diversity stands as the primary goal of ecological management. Effective ecosystem management requires identifying the factors that influence species distribution and diversity, along with the patterns of species diversification linked to ecological traits [25].

The Guandi Mountain Forest Area, a vital distribution area of forest resources in North China, hosts a predominant secondary cold–temperate *Picea* forest. *Picea asperata* Mast. is instrumental in soil stabilization and water conservation and plays a pivotal role in safeguarding biodiversity within North China's mountainous secondary forests and in rehabilitating degraded ecosystems [26]. Unsustainable cutting and grazing have significantly affected the long-term diversity of local plants. Although some studies discussed the determinants of species diversity and regeneration in the Guandi Mountain complex, few have comprehensively assessed the interconnectedness between biodiversity analysis, ecosystem regeneration, and environmental variables, and results remain scant [27–29]. The aim of this investigation is to explore the species diversity across various altitudinal zones within Guandi Mountain's secondary *Picea* forests, along with the influencing environmental factors and the regeneration dynamics of arboreal species. The findings offer a theoretical base for the conservation of biodiversity and ecological restoration of forest ecosystems in Guandi Mountain, facilitating sustainable forest management in the study area.

2. Materials and Methods

2.1. Study Area

The study area was situated in the Guandi Mountain Forest Area, located in the central part of the Lvliang Mountains in the western region of Shanxi Province (37°50′–38°02′ N, 111°24′–112°37′ E) (Figure 1). The Koppen climate classification in this mountainous region is Dwb, characterized by a monsoon-influenced warm-summer humid continental climate. The annual average temperature is 3–4 °C, with an average frost-free period of 115 days and an annual precipitation of 600–800 mm [30]. Rainfall generally decreases from the high to low mountain areas, accompanied by an annual evaporation of 1100–1500 mm. The soil types in the area follow a vertical distribution pattern from low to high, including yellow moorland soil, mountain cinnamon soil, mountain eluviated brown soil, brown mountain soil, and sub-alpine meadow soil [31]. The dominant tree species in the sample plot was *Picea asperata*, a cold–temperate conifer native to western China with several varieties. Other common trees included *Larix principis-rupprechtii* Mayr., *Betula albosinensis* Burk., and *Betula platyphylla* Suk., etc. Shrubs beneath the canopy mainly consisted of *Lonicera ferdinandii* Franch., *Cotoneaster acutifolius* Turcz., and *Rosa bella* Rehd.et Wils., etc. The herbaceous layer mainly included *Poa pratensis* L., *Duchesnea indica*(Andrews.) Focke, and *Chimaphila japonica* Miq., etc.

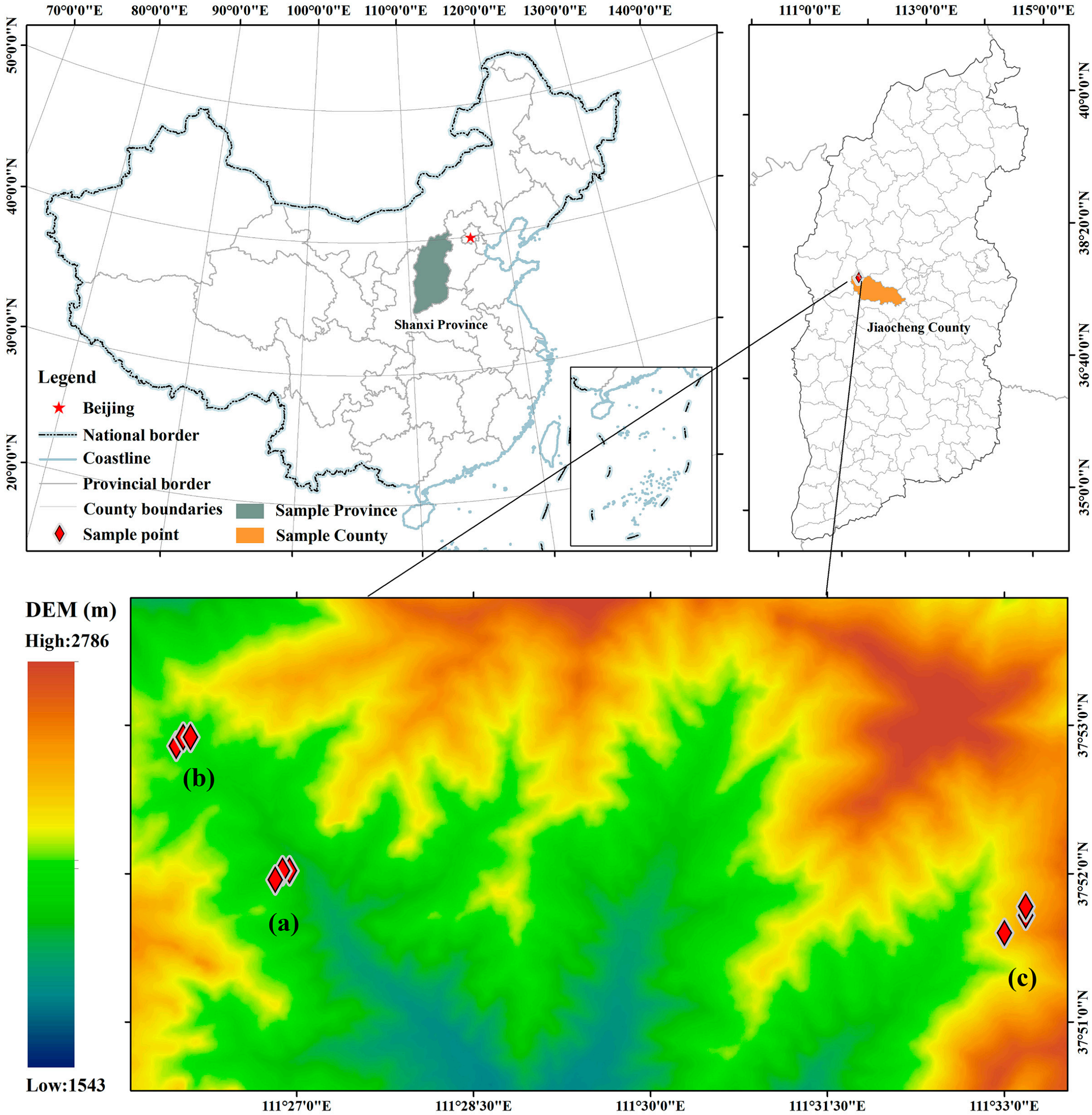

Figure 1. Map of the Guandi Mountain Forest Area indicating the sampling sites along the altitudinal gradient in the study area. Note: (**a**) represents low-altitude sample sites, (**b**) indicates middle-altitude sample sites, and (**c**) denotes high-altitude sample sites.

2.2. Field Sampling and Measurements

In July 2022, we established three altitude gradients in both intact and lightly disturbed areas of secondary *Picea* forests in the Guandi Mountain Forest Area, ranging from 1850 to 2350 m. These altitude zones included the low-altitude zone (1850–1950 m), middle-altitude zone (2050–2150 m), and high-altitude zone (2250–2350 m). For each altitude gradient, three plots measuring 50 m × 50 m were established at the center and at the four corners. Additionally, five 5 m × 5 m shrub-layer survey plots and 10 1 m × 1 m herb-layer survey plots were set up in each sample plot using the diagonal method. In total, we surveyed 9 tree plots, 45 shrub-layer plots, and 90 herb-layer plots.

All living trees with a diameter at breast height (DBH) of ≥1 cm were categorized as seedlings (DBH 1–5 cm), saplings (DBH 6–10 cm), and adult trees (DBH > 10 cm) [32]. Measurements were taken for tree species, density, DBH, and height. Simultaneously, species identity, density, height, and coverage (%) were recorded for shrub and herb plots. The number of tree seedlings and saplings reflected the regeneration status, while the ratio of seedlings and saplings to adult trees determined regeneration performance [33]. Environmental factors, including elevation, latitude, longitude, and slope of the sample plots, were also recorded.

Based on on-site plot investigation results, the slope aspect was categorized as follows: 0.2 represented a shady slope (0° to 45° clockwise rotation from true north), 0.4 represented a semi-shady slope (45° to 135°), 0.6 represented a sunny slope (135° to 225°), and 0.8 represented a semi-sunny slope (225° to 315°). We employed a semi-quantitative scale to measure the degree of anthropogenic disturbance, including cutting intensity, grazing intensity, and tourism disturbance intensity. The level of anthropogenic disturbance was recorded through visual assessment near each sample site using a three-point scale (0 = no/low, 1 = moderate, 2 = high) [34] (Table 1).

Table 1. Disturbance Status of Sample Plots.

Interference Intensity	Interference Level	Interference Category		
		Cutting	Grazing	Traveling
No/Low	0	Relative pile density < 0.1	Livestock carrying capacity 0.5 to 1.5 sheep·ha^{-1}·a^{-1}	Traces of plant loss are identified after trampling by tourists; there are dense bare patches within the transect, with widespread livestock feces visible; there are many types and quantities of garbage.
Moderate	1	0.1 ≤ Relative pile density ≤ 0.2	Livestock carrying capacity 1.5 to 2.5 sheep·ha^{-1}·a^{-1}	The density of trampling marks decreases and is nearly nonexistent; scattered bare spots within the sample strip are not very noticeable, with occasional occurrences of livestock feces; there is a relatively small amount of garbage.
High	2	Relative pile density > 0.2	Livestock carrying capacity 2.5 to 4.5 sheep·ha^{-1}·a^{-1}	No obvious bare spots, livestock feces are hardly visible, no tourist garbage.

The relative stand density and relative crown density of the stand factors were calculated according to the relative impact method [35]. Relative stand density is the ratio of the stand density of each sample site to the sum of the stand densities of all sample sites, and relative crown density is the ratio of the crown density of each sample site to the sum of the crown density of all sample sites. Cutting intensity was determined based on relative stump density, grazing intensity based on the number of cattle, sheep, and horses per hectare per unit time [36], and tourism disturbance intensity based on the density of trampling marks, bare patches, and the quantity of tourist litter [37]. Characteristics of the sample plots and the degree of disturbance are detailed in Table 2.

Table 2. Features and degree of disturbance across each sample plot. LA indicates low altitude, MA indicates middle altitude, and HA indicates high altitude. MAT indicates mean annual temperature. MAP indicates mean annual precipitation.

Altitude Gradient/m	Plot /NO.	Forest Stand Factor				Terrain Factor		Climate Factor		Interference Factor		
		Relative Stand Density	Relative Canopy Density	Average Height/m	Average DBH/cm	Aspect/°	Slope	MAT/°C	MAP/mm	Cutting	Grazing	Traveling
LA (1850–1950)	L1	0.16	0.11	24.11	24.63	180	0.23	4.1	674	1	1	0
	L2	0.13	0.12	25.31	27.05	180	0.24	4.1	674	1	1	1
	L3	0.14	0.11	19.56	23.44	181	0.24	4.2	674	0	1	0
MA (2050–2150)	M4	0.10	0.11	21.79	26.41	298	0.35	4.1	670	2	0	1
	M5	0.08	0.12	24.02	29.49	226	0.35	4.1	669	1	0	1
	M6	0.11	0.11	18.04	25.07	312	0.35	4.1	669	1	0	1
HA (2250–2350)	H7	0.09	0.11	15.24	24.31	230	0.26	5.6	662	2	1	1
	H8	0.10	0.10	17.82	23.14	90	0.30	5.5	659	2	1	2
	H9	0.10	0.10	15.60	20.36	300	0.26	5.5	660	2	1	2

2.3. Data Collection and Analysis

The Importance Value Index (IVI) serves as a comprehensive indicator to depict the status and role of a species within a community. Due to its straightforward calculation and inherent capability of elucidating a species' dominance in a community, IVI has found broad applications across various ecological fields [38]. Our calculation of IVI for each tree species involved considering relative density, relative dominance, and relative frequency, and a parallel calculation was conducted for the shrub and herb layers [39]. Dominant species were selected based on IVI and frequency; refer to Supplementary File S1. The formulae are the following:

(1) IVI of tree layer = (relative density + relative dominance + relative frequency)/3;
(2) IVI of shrub and herb layer = (relative density + relative dominance + relative coverage)/3.

Distinct diversity indices were found to be sensitive to spatial scale and other factors. Therefore, we used the following diversity indices to contrast the research results.

(1) The Shannon diversity index: $H' = -\sum_{i=1}^{S} P_i(lnP_i)$
(2) Simpson's dominance index: $D = 1 - \sum_{i=1}^{S} P_i^2$
(3) Pielou's evenness index: $J = H'/lnS$
(4) The Margalef richness index: $R = (S-1)/lnN$
(5) Fisher's alpha: $S = a \times ln(1 + n/a)$

Where Pi is the proportion of the number of individuals of the species divided by the total number of individuals in the plot; S is the number of species present in the sample plot; N is the total number of species in the plot, and α represents Fisher's alpha. Diversity survey data refer to Supplementary File S2.

This study mainly employed several analytical approaches: (1) data organization and calculation of species importance values were performed using Microsoft Excel 2019, while diversity indices were computed using Past 4.07b [40]. (2) One-way ANOVA [41] was utilized to assess differences in various diversity indices across distinct gradients. (3) The Pearson correlation analysis was conducted to evaluate the relationship between species diversity indices and regeneration parameters. (4) Correlation coefficients between environmental factors and different vegetation layers were computed using the 'Hmisc' and 'corrplot' packages in R 4.2.2 [42]. Subsequently, by selecting relevant environmental factors and using those with a significant impact, redundant analysis (RDA) [43] was conducted with the species diversity index as the response variable and environmental and disturbance factors as explanatory variables, using the 'Vegan' package in R 4.2.2. The plots were generated using R 4.2.2 and Origin 2022 "https://www.originlab.com/ (accessed on 10 April 2023)".

3. Results

3.1. Distribution of Species along Altitudes

The survey identified ten tree species belonging to five families and nine genera, fourteen shrub species from five families and eight genera, and fifty-two herb species spanning twenty-six families and forty-eight genera across the sample plots.

Dominant species were determined based on their IVIs and frequencies (Supplementary File S1). In the tree layer, *Picea asperata*, *Larix principis-rupprechtii*, *Betula albosinensis*, and *Betula platyphylla* were identified as dominant. The shrub layer was dominated by *Lonicera ferdinandii*, *Cotoneaster acutifolius*, and *Rosa bella*, while the herb layer was dominated by *Poa pratensis*, *Duchesnea indica*, and *Chimaphila japonica*.

The IVI of species exhibited notable variations across different altitudinal zones (Figure 2). *Larix principis-rupprechtii* and *Betula platyphylla* showed increased dominance in the tree layer at higher altitudes. In the shrub layer, *Cotoneaster acutifolius*, *Rosa bella*, and *Spiraea trilobata* L. displayed increased dominance at higher altitudes. Conversely, *Corylus mandshurica* Maxim. and *Cotoneaster multiflorus* Bge. were dominant shrubs at lower altitudes. In the herb layer, *Poa pratensis*, *Chimaphila japonica*, and *Myosotis alpestris* were most dominant at lower altitudes, *Adoxa moschatellina*, *Duchesnea indica*, and *Allium ramosum* L. were most dominant in the middle-altitude zones, and *Anthriscus sylvestris* (L.) Hoffm. and *Ligusticum jeholense* Nakai et Kitag. appeared only in the higher-altitude zones. Species such as *Larix principis-rupprechtii*, *Lonicera ferdinandii*, *Cotoneaster acutifolius*, *Poa pratensis*, and *Duchesnea indica* exhibited a wide altitudinal range, with more shrub species in the middle-altitude zones and herb species in both middle- and high-altitude zones.

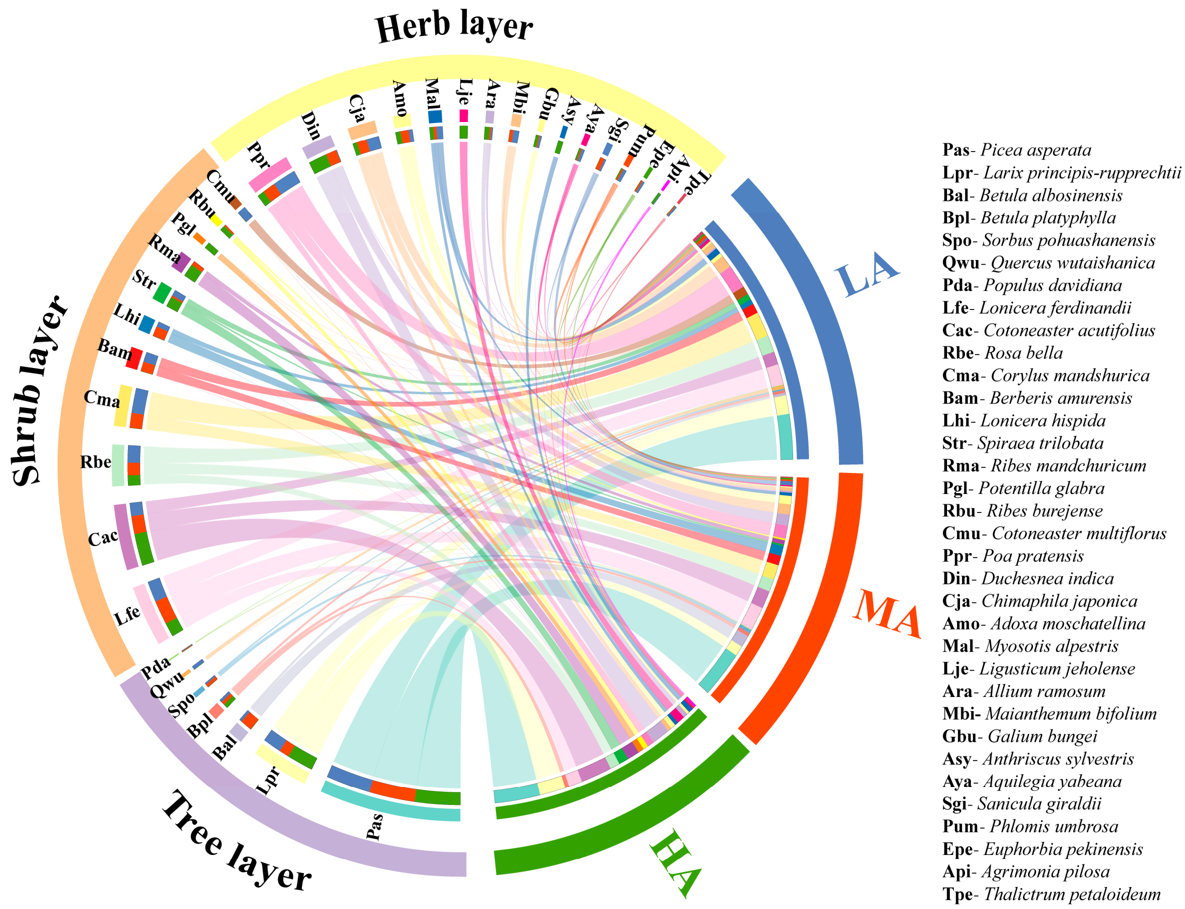

Figure 2. Major species distributed across various altitudes of the secondary *Picea* forest in the study area. (The direction of the lines illustrates the dominant species presented along altitudes in these samples, and the thickness of each bar denotes the importance value of the dominant species in each sample. Three-letter codes were utilized to denote each species.).

3.2. Analysis of Species Diversity along Altitudes

The species diversity across different vegetation layers exhibited notable variations along altitudinal gradients. In the arborous layer, the Margalef index and Fisher's alpha displayed a trend of low-altitude zone > middle-altitude zone > high-altitude zone, with a significant difference observed in the Margalef index. The Shannon diversity index and Simpson's dominance index showed a single-peaked trend, with the highest values recorded in the middle-altitude zone. Additionally, Pielou's evenness index demonstrated a pattern of high-altitude zone > middle-altitude zone > low-altitude zone.

For the shrub layer, the Shannon diversity index, Simpson's dominance index, the Margalef index, and Fisher's alpha at different elevations exhibited a trend of low-altitude zone > middle-altitude zone > high-altitude zone, with significant differences.

Similarly, the herb layer displayed a pattern of low-altitude zone > middle-altitude zone > high-altitude zone for the Shannon diversity index and Simpson's dominance index. However, no statistical significance was observed for the Margalef index and Fisher's alpha (Figure 3).

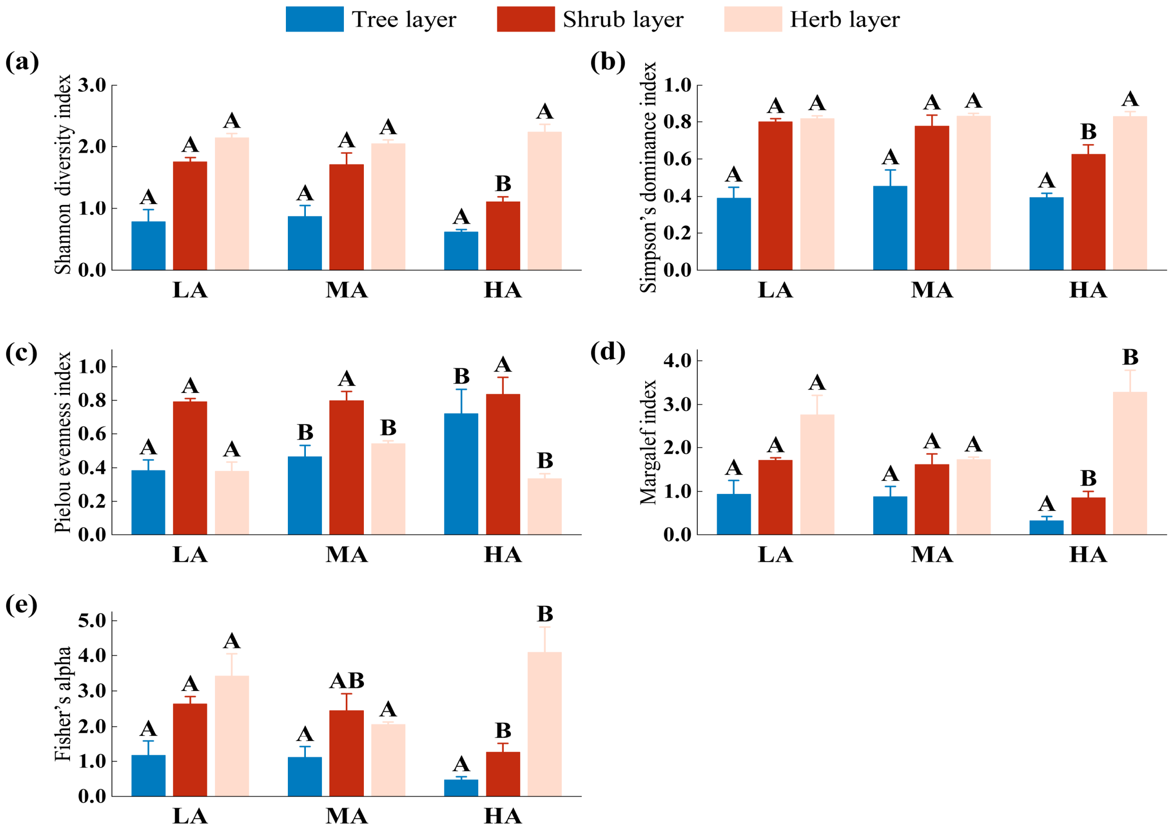

Figure 3. Diversity indices of various vegetation layers along altitudes. Note: different capital letters (A, B) indicate significant differences in species diversity in the same vegetation layers at different altitudes, with a significance level of $\alpha = 0.05$. (**a**): Shannon diversity index, (**b**): Simpson's dominance index, (**c**): Pielou evenness index, (**d**): Margalef index, (**e**): Fisher's alpha.

3.3. Forest Tree Regeneration Status along Altitudes

Across all sample plots, the average tree density was 522 trees/ha, ranging from 844 trees/ha at low altitudes to a minimum of 348 trees/ha at high altitudes. The average total basal cover was 24.04 m^2/ha, varying from 33.13 m^2/ha at low altitudes to a minimum of 16.86 m^2/ha at high altitudes (Table 3).

Table 3. Regeneration attributes of secondary *Picea* forest in the study area across distinct altitudinal gradients. SED = Seedling Density, SAD = Sapling Density, Se/At = Seedling/Adult tree ratio, Sa/At = Sapling/Adult tree ratio, TBC = Total Basal Cover, TDN = Tree Density.

Altitude Gradient/m	Plot/NO.	SED/(Plant·ha)	SAD/(Plant·ha)	Se/At	Sa/At	TBC/(m^2·ha)	TDN/(Plant·ha)
LA (1850–1950)	L1	20	88	0.02	0.10	30.13	844
	L2	12	48	0.02	0.07	33.13	732
	L3	56	92	0.09	0.14	24.58	656
MA (2050–2150)	M4	92	44	0.20	0.10	25.15	460
	M5	28	52	0.08	0.14	28.40	368
	M6	52	104	0.11	0.22	20.73	472
HA (2250–2350)	H7	116	36	0.32	0.10	16.86	364
	H8	96	36	0.21	0.08	17.51	456
	H9	240	32	0.69	0.09	19.90	348

In the seedling layer of the secondary *Picea* forest, the highest density was 240 trees/ha in the high-altitude area, while the minimum density was 12 trees/ha in the low-altitude area. The maximum and minimum densities of the sapling layer occurred in the middle- and high-altitude zones, with 104 trees/ha and 32 trees/ha, respectively. The regeneration performance of tree species differed under different altitude gradients (Table 3). The average value of Se/At was 0.19, ranging from a maximum of 0.69 in the high-altitude zone to a minimum of 0.02 in the low-altitude zone. Compared to Se/At, the Sa/At values were higher in the high-altitude zone, while the Sa/At values were lower in the middle- and low-altitude zones (Table 3).

Picea asperata in the high-altitude zone, *Betula albosinensis* in the middle-altitude zone, and *Quercus wutaishansea* Mayr. in the low-altitude zone exhibited high regeneration performance, with *Picea asperata* showing the relatively greatest regeneration performance. *Larix principis-rupprechtii* displayed lower regeneration performance along all three altitudinal gradients (Table 4).

Table 4. Regeneration attributes of primary species found in secondary *Picea* forest across the study area under distinct altitudinal gradients.

Altitude Gradient/m	Species	SED/(Plant·ha)	SAD/(Plant·ha)	TDN/(Plant·ha)	Se/At	Sa/At
LA (1850–1950)	*Picea asperata*	8	132	1796	0.004	0.07
	Larix principis-rupprechtii	4	8	400	0.01	0.02
	Betula platyphylla	4	16	20	0.20	0.80
	Quercus wutaishansea	24	32	8	3	4
MA (2050–2150)	*Picea asperata*	48	32	1080	0.04	0.03
	Larix principis-rupprechtii	8	8	116	0.07	0.07
	Betula albosinensis	116	156	52	2.23	3
HA (2250–2350)	*Picea asperata*	436	100	736	0.59	0.136
	Larix principis-rupprechtii	16	4	408	0.04	0.01

3.4. Pearson Correlation Analysis of Species Diversity Indices and Regeneration Parameters

The Pearson correlation results between the species diversity index and the regeneration parameters of the secondary *Picea* forest revealed that the correlation was primarily observed in the tree layer and the shrub layer, with the relationship between the regeneration parameters and the species diversity of the understory herbs not reaching a significant level (Figure 4).

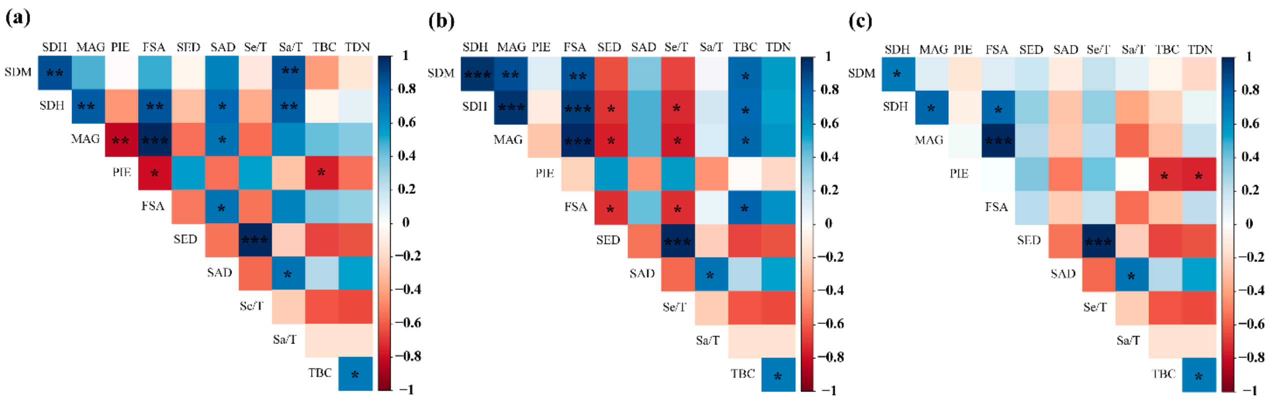

Figure 4. Heatmap results of correlations between diversity index and regeneration parameters of various vegetation layers in a secondary *Picea* forest throughout the study area. Note: (**a**) denotes the tree layer, (**b**) indicates the shrub layer, and (**c**) indicates the herb layer; SDH = Shannon diversity index, SDM = Simpson's dominance index, PIE = Pielou's evenness index, MAG = Margalef index, FSA = Fisher's alpha; SED = Seedling Density, SAD = Sapling Density, Se/At = Seedling/Adult tree ratio, Sa/At = Sapling/Adult tree ratio, TBC = Total Basal Cover, TDN = Tree Density, * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$.

In the tree layer, the total basal coverage (TBC) was significantly negatively correlated with Pielou's evenness index (PIE). The value of Sa/At positively correlated with Simpson's dominance index (SDM) and the Shannon diversity index (SDH). Sapling density significantly and positively correlated with the Shannon diversity index, the Margalef richness index (MAG), and Fisher's alpha (FSA). The greater the regenerative performance, the more complex the species diversity of the trees (Figure 4a).

In the shrub layer, the total basal cover (TBC) exhibited substantial positive correlations with Simpson's dominance index (SDM), the Shannon diversity index (SDH), the Margalef richness index (MAG), and Fisher's alpha (FSA). The seedling density was significantly negatively correlated with the Shannon diversity index, the Margalef richness index, and Fisher's alpha. The greater the regeneration performance, the more monotonous the species diversity of the shrubs (Figure 4b).

3.5. Role of Disturbance and Environmental Variables

The redundancy analysis (RDA) findings highlight the first principal component's superior explanatory power for the diversity indices of the three vegetation layers. In the tree layer, the Shannon diversity index, the Margalef index, Fisher's alpha, and Simpson's dominance index exhibit positive correlations with the first principal component, while Pielou's evenness is negatively correlated. Fisher's alpha shows the highest correlation with the first principal component, followed by the Margalef index. Moving to the shrub layer, Simpson's dominance index, the Shannon diversity, the Margalef richness index, and Fisher's alpha all correlate negatively with the first principal component, with Pielou's evenness exhibiting a similar negative correlation. The Margalef index demonstrates the highest correlation with the first principal component in the shrub layer. As for the herb layer, Simpson's dominance index, the Shannon diversity index, the Margalef index, Fisher's alpha, and Pielou's evenness all show positive correlations with the first principal component. The Margalef index and Fisher's alpha particularly stand out, with higher correlations.

Comprehensively interpreting the heatmap and RDA results, altitude (p = 0.041) and cutting (p = 0.015) emerge as significant factors influencing the species diversity of the tree layer. Altitude and cutting factors exhibit negative correlations with the Margalef index and Fisher's alpha, while demonstrating positive correlations with Pielou's evenness. In the shrub layer, annual precipitation (p = 0.006), annual temperature (p = 0.01), elevation (p = 0.012), and average tree height (p = 0.033) significantly impact species diversity. The Shannon diversity index, the Margalef index, Fisher's alpha, and Simpson's dominance index negatively correlate with average tree height and annual precipitation, while positively correlating with elevation and annual temperature. For the herbaceous layer, elevation (p = 0.018) and grazing (p = 0.042) are significant influencers of species diversity. The Margalef index and Fisher's alpha correlate positively with grazing and elevation factors (Figure 5).

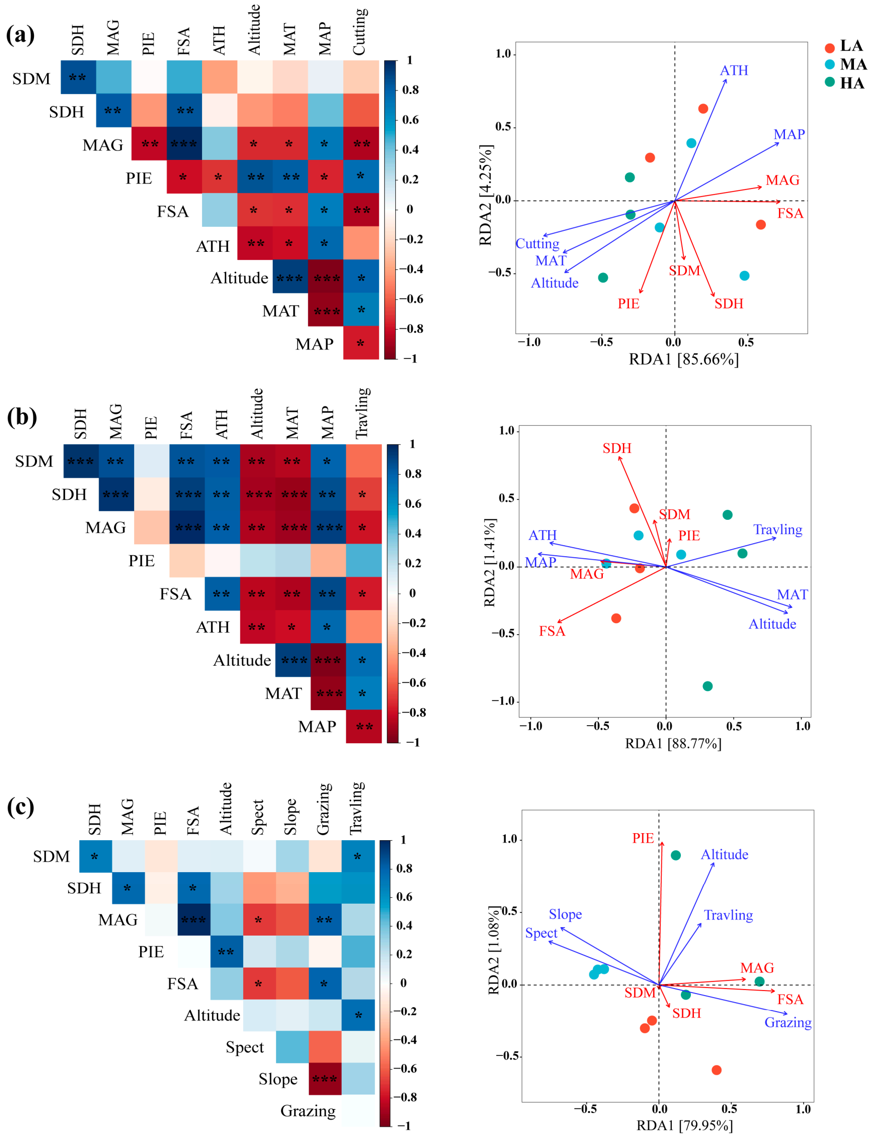

Figure 5. Correlation heatmap and redundancy analysis of species diversity characterized by the disturbance and environmental variables in the secondary *Picea* forest vegetation layers. Note: (**a**) denotes the tree layer, (**b**) indicates the shrub layer, and (**c**) indicates the herb layer; SDH = Shannon Diversity Index, SDM = Simpson's dominance index, PIE = Pielou's evenness index, MAG = Margalef index, FSA = Fisher's alpha, ATH = average tree height. * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$.

4. Discussion

4.1. Composition Characteristics, Diversity, and Distribution of Species along Altitudes

This study underscores significant disparities in species composition across distinct vegetation layers at various altitudes. These differences are likely shaped by site-specific conditions [44], interlinked with geographical location, climate nuances, and human-induced disturbances [45–48].

The importance value index serves as a reflective measure of variation and distribution characteristics within plant communities along altitude gradients [49,50]. Notably, dominant species diverged among elevations within different vegetation layers, and the importance values of identical species exhibited altitude-dependent variations that were not the same at different elevations. Species such as *Lonicera ferdinandii*, *Cotoneaster acutifolius*, and *Rosa bella* in the shrub layer, and *Poa pratensis* and *Chimaphila japonica* in the herb layer demonstrated wider distribution altitudes, indicative of broader ecological niches and enhanced resistance to biotic pressures. This adaptability might be attributed to the ecological and physiological traits of vegetation, enabling species to endure extreme environmental conditions and acclimate to challenging climates. Altitude-induced microclimatic variations influenced plant microhabitats, aligning with Wang et al. [51].

Species diversity, intricately linked with forest structure and species composition [52], displayed significant altitude-driven differences across distinct vegetation layers. Tree- and shrub-layer diversities diminished markedly with increasing altitudes, while herb-layer diversity exhibited a conspicuous rise. The consistent Pielou's evenness index across altitude gradients suggests an equitable distribution of individuals within each vegetation layer. The heightened richness of herbaceous vegetation at high altitudes can be attributed to a more favorable and predictable environment for herbaceous species [53,54], aligning with several other studies by [55–57].

In the tree layer, a limited number of tree species dominate high-altitude forest vegetation as elevation increases, potentially linked to slower evolution and diversification rates, aligning with findings by Chen [58]. This contrasts with Gao et al.'s research suggesting peak species richness and diversity at intermediate altitudes, declining at lower and higher altitudes [30]. This discrepancy may be attributed to the pronounced influence of climate change associated with altitude rise on species diversity. McCain [59] proposed a climate model that suggests that moderate temperature and precipitation at middle altitudes foster higher plant diversity. In sum, the marked shifts in geographical and climatic conditions with altitude elevation contribute to species diversity and distribution variations influenced by topography, climate, soil, and biotic interactions [60,61].

4.2. Regeneration Status of the Secondary Picea Forest along Altitudes

Regeneration stands as a pivotal process in shaping the floristic components of communities. For the enduring management of forest biodiversity, the natural regeneration of tree species within forest ecosystems assumes paramount importance [62]. The regeneration performance of trees in forest ecosystems hinges on the population structure, with the emergence of sufficient seedlings and saplings serving as crucial indicators of a forest's regeneration potential [63]. Simultaneously, tree density and basal area constitute vital factors influencing forest structure [64].

In this study, seedling densities ranged from 12 to 240 trees/ha, while sapling densities ranged from 32 to 104 trees/ha across different altitudes. These variations in densities may be attributed to factors such as altitude and anthropogenic disturbances [30]. The relatively lower average values of total basal cover (TBC) observed at low altitudes could be linked to the more mature stands prevalent in these areas.

Moreover, the seedlings/adult trees (Se/At) ratio at lower altitudes was notably low compared to other altitude zones, potentially indicating more pronounced disturbance conditions. *Picea asperata* exhibited a high regeneration rate at high altitudes while facing impediments at lower and middle altitudes. This hindrance might be attributable to disturbances rendering microhabitat conditions unfavorable for *Picea asperata* survival, consequently offering ecological niches for the establishment of broad-leaved tree species like *Quercus wutaishansea* and *Betula albosinensis*. This observation aligns with the Janzen–Connell theory, suggesting elevated mortality rates in proximity to mature trees [65,66]. Additionally, prevalent anthropogenic disturbances such as tourism, cutting, and grazing in the study area likely contribute to the overall low density of seedlings [32].

4.3. Relationship between Species Diversity Index and Regeneration Parameters

The natural regeneration process is paramount in safeguarding and perpetuating biodiversity [11]. Consequently, assessments of forest vegetation offer valuable insights into tree population status, regeneration dynamics, and overall diversity, aiding in the pursuit of effective conservation goals [67].

In this study, the regeneration performance of tree species exhibited a positive correlation with tree species diversity. This suggests that the intricate diversity of tree species enhances the regenerative potential of forests, potentially attributed to distinct nutrient and resource requirements among various tree species. Increased diversity, therefore, augments the survival prospects of forest communities. Different tree species find suitable ecological niche spaces in undisturbed natural forests, contributing to enhanced regeneration [68]. The relationship between shrub species diversity and tree regeneration performance revealed a contrasting pattern, indicating that higher regeneration performance in tree species is associated with lower shrub diversity. This may stem from the inhibitory effects of many shrubs on the growth of tree seedlings and saplings [69]. Studies suggest juvenile trees often compete with shrubs and herbaceous plants beneath the canopy, intensifying competition for resources and space [70].

While a substantial and direct correlation between seedling and sapling density is typically anticipated [71], the lack of significance in this study could be attributed to the reduced canopy cover resulting from human disturbance. This alteration may impact the regeneration performance of tree species [72], leading to a relatively lower success rate of seedling recruitment into saplings. Conversely, in areas with favorable regeneration conditions, *Picea asperata* in high-altitude zones may be in the early regeneration stage, resulting in a relatively lower density of saplings compared to seedlings [73].

4.4. Role of Anthropogenic and Environmental Factors on Species Diversity

Anthropogenic disturbance, environmental factors, and biological interactions collectively shape the diversity and distribution patterns of species [74,75]. This study underscores the prominent influence of elevation on species diversity across diverse vegetation layers (Figure 5). As altitude increases, there is a marked decline in tree diversity, consistent with the findings of Pausas et al. [76], which could be attributed to the significant impact of temperature on the physiology of woody plants. Qin et al. [77] reported a consistent decline in the species richness index of the herb layer in Guan Di Mountain, concomitant with rising altitude. Despite these trends, our analysis revealed that the Margalef richness index for the herb layer peaked within the high-altitude zones. Various factors, including temperature, moisture, and soil conditions, likely contribute to the observed variations in species diversity within the herbaceous layer across different altitudes [78].

Furthermore, factors such as altitude, slope, and latitude play crucial roles in shaping vegetation and community types [79,80]. Plant growth is intricately linked to biological, climatic, and various environmental factors, with climate itself being influenced by topographical features like altitude, slope, and aspect [81].

In recent years, the forest vegetation within the study area has experienced varied forms of disturbance, significantly impacting the stability of the local forest ecosystem. Existing research suggests that human-induced disturbance strongly affects plant communities' species composition and diversity, while natural disturbance is often associated with specific natural conditions [82–84].

In addition to altitude, human-induced cutting activities emerge as a significant factor influencing species diversity within the tree layer. Cutting practices alter the spatial structure and density distribution of trees, leading to shifts in plant competition dynamics [85]. Weaker tree species may struggle to coexist with more competitive counterparts, thereby impacting overall tree species diversity [86]. Different tree species exhibit varying water requirements, and temperature also affects species' tolerance and adaptability. Alterations in altitude and terrain result in changes in temperature and precipitation. Consequently, under distinct annual temperature and precipitation conditions, variations in shrub species diversity are observed [87]. Grazing activities in the study concurrently contribute to the increased richness of herbaceous plants. This phenomenon may be attributed to grazing activities balancing the species composition of herbaceous plant communities, thereby fostering greater diversity [88].

5. Conclusions

Based on data from the secondary *Picea* forest along three consecutive altitudinal gradients in Guandi Mountain, we analyzed the species distribution of the secondary *Picea* forest, evaluated tree species' regeneration, and identified environmental conditions impacting species diversity. The main conclusions can be summarized as follows: elevation influences the dominance of species across the various vegetation layers in secondary *Picea* forests. Variations in species diversity with elevation are primarily observed in the shrub and herb layers. In the shrub layer, species diversity declines as elevation rises, whereas in the herb layer it peaks at higher elevations. The study highlights that, aside from elevation, cutting as a disturbance factor primarily affects species diversity within the tree layer, with grazing chiefly influencing the diversity of the herb layer. Climatic factors exert the greatest impact on the shrub layer, with stand dynamics being the secondary influence. Simultaneously, the study identifies the variability in the regeneration potential of dominant tree species with changing altitudes. Notably, *Picea asperata* and certain broad-leaved tree species, such as *Betula albosinensis* and *Quercus wutaishanica*, exhibit promising regeneration potential. Therefore, *Picea asperata* can be regarded as an essential species for forest restoration in the elevated regions of Guandi Mountain. The study proposes a scientific approach to planning and the judicious allocation of saplings and seedlings of tree species with higher regeneration potential. This serves as a crucial foundation for restoring forest vegetation in the region, contributing significantly to the exploration of sustainable forest management practices.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/f15050771/s1. File S1. Species composition and quantitative characteristics of main species in different forest layers. File S2. Species diversity indices of different vegetation layers at three altitude gradients.

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