

Article

Optimization of Key Stand Structural Factors to Enhance Water-Holding Function, Soil Conservation, and Carbon Sequestration in *Schima superba* Forests: Insights from Subtropical Dongbai Mountain

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Abstract: Revealing the interactions between stand structure factors and ecosystem functions is crucial for enhancing forest soil and water conservation, as well as carbon storage. However, the optimal stand structure configuration for achieving superior ecological functions remains unclear, particularly in complex subtropical evergreen broad-leaved forests. Using *Schima superba* Gardn. et Champ. forests in Dongbai Mountain as a case study, this study investigated the effects of seven stand structure factors—stand density, canopy density, uniform angle index, and mixing degree—on three key ecosystem functions, water-holding function, soil improvement function, and carbon sequestration. Redundancy analysis (RDA) and structural equation modeling (SEM) were employed to quantify these relationships. The results identified stand density as the most influential factor, directly or indirectly affecting ecosystem functions by regulating other structural attributes. Optimal structural configurations were determined, including stand densities of 1228, 1532, and 1675 plants·hm^{−2} for maximizing water-holding function, soil improvement function, and carbon sequestration, respectively. Recommendations emphasize adjusting stand density, canopy density, uniform angle index, and mixing degree according to site-specific conditions. Practical strategies, such as replanting, intercropping, and introducing functionally complementary species, should aim to enrich vertical structure, maintain species randomness, and avoid dominance by a single species or excessive density. These findings offer actionable insights for improving the ecological functions of subtropical forests and have broader implications for sustainable forestry management, advancing regional carbon neutrality, and addressing global ecological challenges.

Keywords: stand density; structural optimization; subtropical forest ecosystems; ecosystem function indicators



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1. Introduction

Forests are a cornerstone of terrestrial ecosystems, providing essential ecological functions such as water retention, soil conservation, carbon sequestration, and biodiversity maintenance [1]. Subtropical evergreen broad-leaved forests, particularly *S. superba* forests, are vital ecosystems in southern China, contributing significantly to regional ecological

stability and carbon storage [2]. Stand structure is a core factor in forest ecosystem evolution and biodiversity formation. Its dynamics are crucial for analyzing and managing forest ecosystems, providing a scientific basis for enhancing their stability and productivity [3,4].

Increasing evidence has underscored the influence of forest structure on ecosystem functions and services, such as biodiversity, habitat quality, water retention, forest yield, carbon sequestration, and aboveground biomass [5–7]. The spatial characterization of stand structure is viewed as a critical determinant of forest development state and stability and is recognized by researchers as one of the most direct and promising regulatory factors [8]. Stand age can impact biomass and productivity by driving changes in stand structure throughout forest development and is closely related to stand density [9,10]. Sun et al. observed in temperate climate regions that carbon input exceeded carbon output in larch plantation forests with high stand densities, leading to higher soil carbon stocks [11]. Currently, in the process of afforestation and vegetation restoration, several ecological issues remain due to excessive planting density and improper species selection, including slow tree growth, soil moisture deficit, and deep soil dryness [12,13]. These challenges have resulted in a “dilemma” in forestry development. Simply increasing forest and vegetation cover may further exacerbate local soil moisture depletion, leading to soil dryness and even affecting the stability of vegetation [14]. While global studies have demonstrated the relationship between stand structure and ecosystem functions, research focusing on subtropical forest ecosystems—and specifically *S. superba* forests—remains insufficient. Addressing this gap is crucial for improving ecological services and achieving sustainable forest management in subtropical regions. Therefore, the key question for future global sustainable forestry development is how to scientifically adjust stand structure, enhance stand ecological functions, and avoid causing irreversible depletion of ecological resources or other new environmental problems. Recently, Wang et al. significantly enhanced soil and water conservation on the Loess Plateau by optimizing stand structural factors such as the uniform angle index of *Robinia pseudoacacia* L., highlighting the critical role of stand structure in regulating ecological functions [15]. In temperate forests, some scholars have studied the optimal stand density based on the principles of water balance [16] and suitable forest and grass vegetation cover [17]. Other scholars have focused on the environmental changes in vegetation, forest structure, and soil following forest management practices [18–20]. The impact of forest management measures such as thinning, stand soil preparation, and micro-topography modification on stand functions has been fully confirmed [21], and these measures can significantly improve stand functions. While forest management practices like thinning and structural adjustments have been widely studied in temperate and arid ecosystems, their application in subtropical *S. superba* forests remains poorly understood.

This is particularly true for subtropical forests, such as those dominated by *Castanopsis* spp. and *S. superba*, where the urgent challenge is to determine how to regulate stand structure to optimize multiple ecosystem functions. In these forests, managing canopy density, tree species composition, and stand density play a critical role in enhancing water retention, improving soil quality, and boosting carbon sequestration. By optimizing these structural elements, forests can better capture and retain water, promote nutrient cycling, and increase carbon storage capacity, all of which contribute to the overall resilience and sustainability of the ecosystem. This study aims to explore how the strategic adjustment of stand structure in subtropical forests can enhance these critical ecosystem services, offering both theoretical support and practical recommendations for forest management in similar subtropical regions.

Through plot surveys, model selection, and practical feasibility analysis, this study focused on four key stand structure factors (SSTFs)—stand density (SD), canopy density

(CD), uniform angle index (W), and mixing degree (M)—to evaluate their impacts on ecological function indicators ($EFFIs$). The objectives of this study are as follows:

- (1) To quantitatively evaluate the ecological functions of *S. superba* forest stands and determine the relative weights of different $EFFIs$;
- (2) To analyze the coupling relationships between $SSTFs$ and $EFFIs$, identifying the key structural factors that significantly influence ecological functions;
- (3) To develop an optimization model for the *S. superba* forest stand structure, proposing targeted management strategies to enhance the water-holding function (WF), soil improvement function (SF), and carbon sequestration (CS).

2. Materials and Methods

2.1. Site Description

The study site is located in a key area of a typical middle subtropical forest in Dongbai Mountain ($120^{\circ}39'–120^{\circ}42'$ E, $29^{\circ}50'–29^{\circ}59'$ N), Zhuji County, Shaoxing, China, within a subtropical monsoon climate transition zone (Figure 1). The region hosts a large, well-preserved coniferous-broadleaf mixed forest with a rich diversity of tree species. Among these, *S. superba* dominates as a highly adaptable evergreen species in subtropical regions. Known for its resilience to varying light, water, and soil conditions, *S. superba* is integral to forest ecosystems, providing essential services such as soil stabilization, erosion prevention, and biodiversity enhancement [22,23].

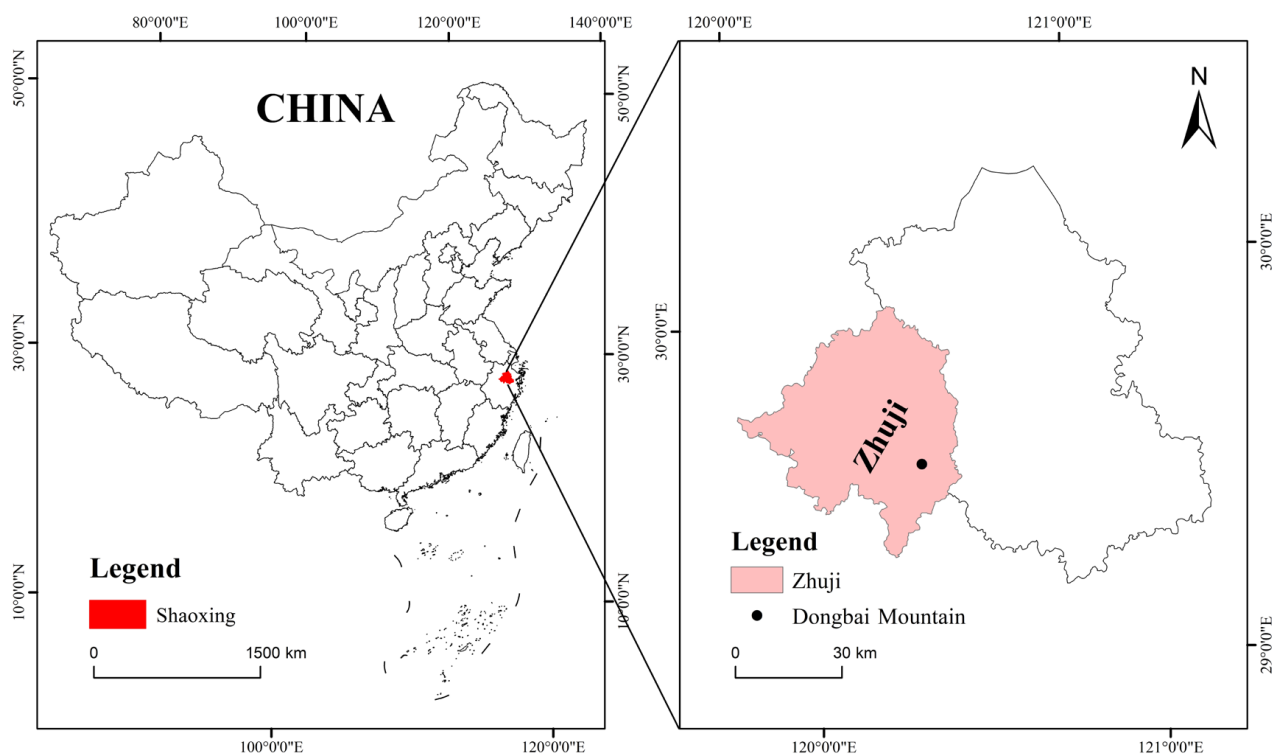


Figure 1. Location of the Dongbai Mountain Study Area.

Studying *S. superba* forests in Dongbai Mountain offers a valuable opportunity to analyze the ecological structure and functional dynamics of subtropical forest systems. As a representative species widely distributed across the subtropical monsoon climate zone, findings from this research contribute not only to the understanding of regional forest ecosystems but also to broader ecological restoration and management efforts. These characteristics affirm Dongbai Mountain's significance as an ideal site for investigating the traits of subtropical forest ecosystems.

In *S. superba* forests, the influence of the subtropical monsoon climate on stand structure and ecological functions is particularly significant. For example, during the wet season, higher precipitation promotes rapid tree growth, while the dry season intensifies water competition, especially under conditions of low soil moisture, which may restrict tree growth. This directly affects the carbon sequestration efficiency.

2.2. Plot Establishment and Survey

Twenty-four sample plots were established in an area free from human disturbance, and the following investigations were conducted: (1) The basic information of the standard plots, including the altitude, longitude, latitude, and azimuth of the center point of each sample plot, was recorded using an RTK instrument (Chcnv, Shanghai, China). Stand site conditions (such as air and soil temperature, moisture, soil characteristics, etc.) and canopy density were determined using traditional community survey methods [24]. (2) Tree species (as referenced in the Flora of Zhejiang Province), relative position, height, and diameter at breast height (DBH, measured at 1.3 m) of all living trees and snags were recorded. (3) Forest floor litter was collected to determine water-holding capacity by calculating the weight variation between full saturation and drying [25].

2.3. Survey and Calculation of Stand Structure Indicators

The main structural factors investigated within the sample plots established in this study included *SD*, mean *DBH*, mean tree height (*TH*), uniform angle index (*W*), neighborhood comparison (*U*), canopy density (*CD*), and mixing degree (*M*).

The local neighborhood spatial distribution was quantified using the uniform angle index (*W*) [26]. The uniform angle index was calculated as follows (1):

$$W_i = \frac{1}{n} \sum_{j=1}^4 Z_{ij} \quad (1)$$

with $Z_{ij} = \begin{cases} 1, & \text{the } a\text{-angle } j \text{ is smaller than } a_0 \\ 0, & \text{otherwise} \end{cases}$ and $0 \leq W \leq 1$.

W is a key metric for assessing forest stand spatial patterns, efficiently representing tree distribution using average and individual values without requiring direct measurements. The smaller the uniform angle index value, the more uniform the local neighborhood distribution around the focal tree, while a value between 0.475 and 0.517 suggests a random distribution.

U is commonly used to assess the strengths and weaknesses of individual trees within a forest stand [26]. In this study, *DBH* was used to calculate the neighborhood comparison using the following formula (2):

$$U_i = \frac{1}{n} \sum_{j=1}^4 K_{ij} \quad (2)$$

with $K_{ij} = \begin{cases} 1, & \text{the reference tree } i \text{ is larger than neighboring tree } j \\ 0, & \text{the reference tree } i \text{ is smaller than neighboring tree } j \end{cases}$.

M describes the species composition and spatial pattern in a multispecies forest, reflecting the probability that a reference tree belongs to the same species as its nearest neighbor [26]. It was calculated using the following Formula (3):

$$M_i = \frac{1}{n} \sum_{j=1}^n V_{ij} \quad (3)$$

with $V_{ij} = \begin{cases} 1, & \text{the reference tree } i \text{ is larger than neighboring tree } j \\ 0, & \text{the reference tree } i \text{ is smaller than neighboring tree } j \end{cases}$.

2.4. Survey and Calculation of Ecological Function Indicators

Three *EFFIs* including 13 secondary indicators—*WF*, *SF*, and *CS*—were investigated and monitored in the forest stands of the sample plots. For soil sample collection, sites with representative soils and minimal anthropogenic disturbance were selected near each sample plot, and soil profiles were excavated to a depth of 1 m. At each sample site, soil samples were collected using a stainless-steel cutting ring (5.0 cm in diameter and height) from the 0–20 cm soil layer, with three replicates per layer. These soil samples were weighed fresh in the field, transported to the laboratory, and dried at 80 °C to a constant weight for the calculation of soil volumetric weight and moisture content. In addition, approximately 500 g of soil carbon samples were collected from the five soil layers mentioned above. After natural air-drying, soil moisture content was determined by desiccation, and the soil samples were analyzed for soil organic carbon (SOC), total nitrogen (TN), total phosphorus (TP), ammonia-nitrogen (NH₃-N), and available phosphorus (AP).

Additionally, based on China's forestry industry standard document "Standing Wood Biomass Model and Carbon Measurement Parameters" and the research results of related scholars [27,28], biomass modeling was conducted to calculate the biomass of trees from the woody biomass of individual plants (Table S1). A biomass model applicable to Zhejiang and similar regions was selected. For tree species without specific biomass growth equations, equations from other similar species within the same genus and family were used instead. The biomass per unit area of the sample plot was calculated by summing the biomass of all individual trees within the plot, and the carbon density was determined by multiplying the biomass of the tree species (or group) by the carbon content rate (for both the tree and shrub layers) in the sample plot, using the following formula:

$$B = 10 \times \sum_{i=1}^n \frac{B_i}{S} \quad (4)$$

$$C = B \times CF \quad (5)$$

where B is the woody biomass per unit area (t·hm^{−2}); B_i is the biomass of the first i plant biomass (kg); S is the area of the sample plot (m²); n is the number of tree plants in the sample plot; i represents the index for individual trees in the sample plot; C is the carbon density of vegetation (t·hm^{−2}); and CF is the carbon content rate.

2.5. Statistical Analysis

The weights of the relevant parameters were calculated by evaluating the *EFFIs* of the *S. superba* forest using the entropy weight method (EWM). The raw data were normalized based on the sign of the index. For a positive index, the standardization equation used was (6); for a negative index, the standardization equation used was (7):

$$Z_{ij} = \frac{x_{ij} - \min(x_{ij})}{\max(x_{ij}) - \min(x_{ij})} \quad (6)$$

$$Z_{ij} = \frac{\max(x_{ij}) - x_{ij}}{\max(x_{ij}) - \min(x_{ij})} \quad (7)$$

where x_{ij} is the value of the j the sample plot corresponding to the i evaluation index, and z_{ij} the normalized value of the corresponding indicator.

In an assessment involving n evaluation indices and m sample plots, the entropy value for index i was calculated as shown in Equation (8):

$$H_j = -k \sum_{j=1}^m e_{ij} \ln e_{ij}, i = 1, \dots, n; j = 1, \dots, m \quad (8)$$

where $e_{ij} = \frac{z_{ij}}{\sum_{i=1}^m z_{ij}}$; when $k = \frac{1}{\ln m}$; when $e_{ij} = 0$ and $e_{ij} \ln e_{ij} = 0$
 The weights of the indicators are calculated as follows (9):

$$W_i = \frac{1-H_i}{m-\sum_{i=1}^n H_i} \quad (9)$$

where $0 \leq W_i \leq 1$; $\sum_{i=1}^m W_i = 1$.

2.6. Optimization of Stand Structure in the *S. superba* Forest

The SSTF parameters influencing the EFFIs were identified through redundancy analysis (RDA) using CANOCO v. 5.0 (Microcomputer Power Supply, Ithaca, NY, USA). To assess the significance of the eigenvalues, a Monte Carlo permutation test was conducted. Based on the RDA results, the variance explained by different SSTFs on EFFIs was determined. Factors with relatively high explanatory power and greater practical applicability for forestry practitioners were selected as optimization targets. Subsequently, a structural equation model (SEM) was constructed to examine the multifaceted relationships between SSTFs and EFFIs, using Amos v. 22.0 (IBM Corp., Armonk, NY, USA).

After the optimal SSTFs were determined by RDA and Pearson's correlation analysis, the structural equation model (SEM) was used to analyze the comprehensive effects of stand structure on ecosystem function indicators. SEM is commonly employed to quantify relationships among multiple factors, including path, causal, and both direct and indirect effects, thereby providing robust connections between theoretical and empirical concepts [29]. Compared with regression models, SEM offers the advantage of constructing all hypothesized causal relationships between predictor and dependent variables [30]. This approach facilitates the optimization of evaluation indicators under specific objective conditions, identifying their optimal combination and corresponding values. Using this optimized combination, selected stand structure factors were refined with SAS v. 9.4 (SAS Institute Inc., Cary, NC, USA) and the response surface method to derive the best response values for optimizing ecological function parameters.

While this study provides a robust framework for understanding the relationships between stand structure and ecological functions, certain methodological limitations should be acknowledged. First, the selection of sample plots, while representative of key ecological gradients, may not fully capture the heterogeneity of the entire study region. This limitation could affect the generalizability of our findings to other subtropical forest ecosystems. Second, potential sampling errors, such as insufficient sample size and spatial heterogeneity, may have introduced variability in the soil property measurements. For instance, the limited number of soil samples within each plot might underestimate the spatial variation of soil organic matter or moisture levels. Finally, the RDA and SEM models used in this study, while effective in elucidating relationships between structural indicators and ecological functions, are sensitive to variable selection and sample size. This could impact the reliability of inferred causal pathways. Future studies should address these limitations by incorporating more extensive sampling designs and advanced analytical approaches, such as non-linear structural equation modeling, to validate and extend our findings.

3. Results

3.1. Evaluation of the Ecological Function Indices

Table 1 summarizes the stand structure factors and functional indices of the study area's sample plots, including six secondary indices: *SD*, *CD*, *DBH*, *TH*, *W*, *M*, and *U*, with mean values of 1483, 0.714, 13.076, 11.919, 0.551, 0.362, and 0.438, and coefficients of variation (VCs) ranging from 0.079 to 0.629. The water-holding function was evaluated using seven indicators: soil capillary water-holding capacity, maximum water-holding

capacity, soil moisture, bulk density, deadfall water-holding capacity, thickness, and cover, with mean values of 321.024, 426.227, 11.883, 1.404, 4.65, 6.25, and 95.83, and VCs from 0.031 to 0.351. Forest carbon sequestration was quantified by carbon density and soil organic carbon content, with mean values of 84.18 and 15.942 and VCs of 0.308 and 0.421, respectively. Soil improvement function was assessed through total nitrogen, ammonium nitrogen, total phosphorus, and AP, with mean values of 1.137, 21.453, 0.24, and 0.832, and VCs ranging from 0.240 to 0.430.

Table 1. Characteristics of SSTFs and EFFIs in the *S. superba* forest.

Category	Grade I Index	Grade II Index	Max	Min	Mean	VC
SSTFs	Stand Structure Factors	Stand Density (plants·hm ⁻²)	3000	75	1483	0.493
		Canopy density	0.803	0.577	0.714	0.079
		Diameter at breast height (cm)	34.1	1.2	13.076	0.629
		Tree height (m)	27.2	1.1	11.919	0.547
		Uniform angle index	1	0	0.551	0.454
		Mixing degree	1	0	0.362	0.691
		Neighborhood comparison	1	0	0.438	0.571
EFFIs	WF	Capillary water holding capacity (g/kg)	402.984	214.286	321.024	0.147
		Maximum water holding capacity (g/kg)	586.784	285.714	426.227	0.177
		Soil moisture (%)	18.7	5.7	11.883	0.273
		Bulk Density(g/cm ³)	1.6	1.1	1.404	0.089
		Litter water holding capacity (%)	8.51	1.98	4.65	0.351
		Litter thickness (cm)	8.4	4.1	6.25	0.172
		Litter coverage (%)	100	88	95.83	0.031
	CS	Carbon Density (t·hm ⁻²)	141.381	37.575	84.18	0.308
		Organic Carbon (g/kg)	33.551	6.711	15.942	0.421
	SF	Total nitrogen (g/kg)	2.068	0.812	1.137	0.276
		Ammonia-nitrogen (mg/lg)	41.068	5.372	21.453	0.416
		Total phosphorus (g/kg)	0.386	0.156	0.24	0.240
		Available phosphorus (mg/kg)	1.758	0.326	0.832	0.430

According to the evaluation results of the ecological functions of *S. superba* at the sample site, the weights of the ecological function indices (EFFIs) ranged from 0.191 to 0.487 (Table 2). The weights of each functional index were ranked as follows: WF = 0.487, SF = 0.322, and CS = 0.191. The CS of the *S. superba* forest had the lowest weight, at 0.191. Additionally, the influence of stand structure on the ecological function indices was mainly observed in WF and SF, with WF showing a slightly higher level of significance. The weights of the sub-functional indices ranged from 0.047 to 0.093. Among these, the highest weights were observed for organic carbon content (0.109), maximum water-holding capacity (0.093), litter thickness (0.092), and total phosphorus content (0.091).

Table 2. Weight values of the EFFIs for the *S. superba* forest.

Grade I Index	Weight	Grade II Index	Weight
WF	0.487	Capillary water holding capacity	0.054
		Maximum water holding capacity	0.093
		Soil moisture	0.079
		Bulk Density	0.058
		Litter water-holding capacity	0.064
		Litter thickness	0.092
		Litter coverage	0.047
SF	0.322	Total nitrogen	0.074
		Ammonia-nitrogen	0.087
		Total phosphorus	0.091
		Available phosphorus	0.070
CS	0.191	Carbon Density	0.082
		Organic Carbon	0.109

Abbreviations: *EFFIs*, ecological function indices; *WF*, water-holding function; *SF*, soil improvement function; *CS*, carbon sequestration.

3.2. Influence of Stand Structure on Ecological Function Indices

The analysis described above enabled us to ascertain that there were differences in the *EFFIs* under different stands of the *S. superba* forest. Therefore, we used the RDA to study the effect of stand structure factors on the functional indices of the *EFFIs*. (Figure 2). The results showed that the total explanatory rate was 65.2% ($p < 0.01$, Table 3). Among the *SSTFs*, stand density had the highest explanatory power, accounting for 37.6%, as determined by the Mont% of the stand structure factors to functional indices of the *EFFIs*, which indicated that the stand structure effectively explained the difference of the *EFFIs* under different stands Carlo permutation tests, followed by canopy density at 10.5% and tree height at 5.1%. In the RDA plot, the first axis primarily captures the variation in stand structure, with *SD*, *CD*, and *TH* exhibiting strong positive correlations with *WF* and carbon *CS* indices. The second axis mainly reflects variation in ecosystem functions, where *SF* and *U* are negatively correlated with *WF*. The smaller the angle between *SD*, *TH*, and *CD*, the stronger their association, indicating shared environmental drivers, while the larger angle between *DBH* and *M* suggests that these factors exert more independent influences. These findings emphasize the complex interplay between stand structure and ecosystem functions, where specific structural factors are closely linked to particular functional attributes, while others show more independent effects.

In order to visualize the relationships between *SSTFs* and *EFFIs*, we plotted a Pearson's correlation analysis (Figure 3). Pearson's correlation analysis revealed that the *WF* was positively correlated with both *SD* and *CD* ($p < 0.05$). The *SF* exhibited a positive correlation with *SD*, *TH*, and *U*, and a negative correlation with *M* ($p < 0.05$). *CS* showed positive correlations with *SD*, *CD*, and *TH* while exhibiting a negative correlation with *M* ($p < 0.05$). Denser stands (higher *SD* and *CD*) generally enhance *CS* and *WF*, while *TH* and *DBH* also contribute to some extent. However, factors such as *M* and *DBH* appear to have more complex, often negative, relationships with ecosystem functions. These findings emphasize the multifaceted role of *SSTFs* in shaping *EFFIs*, particularly in terms of *CS* and *WF*.

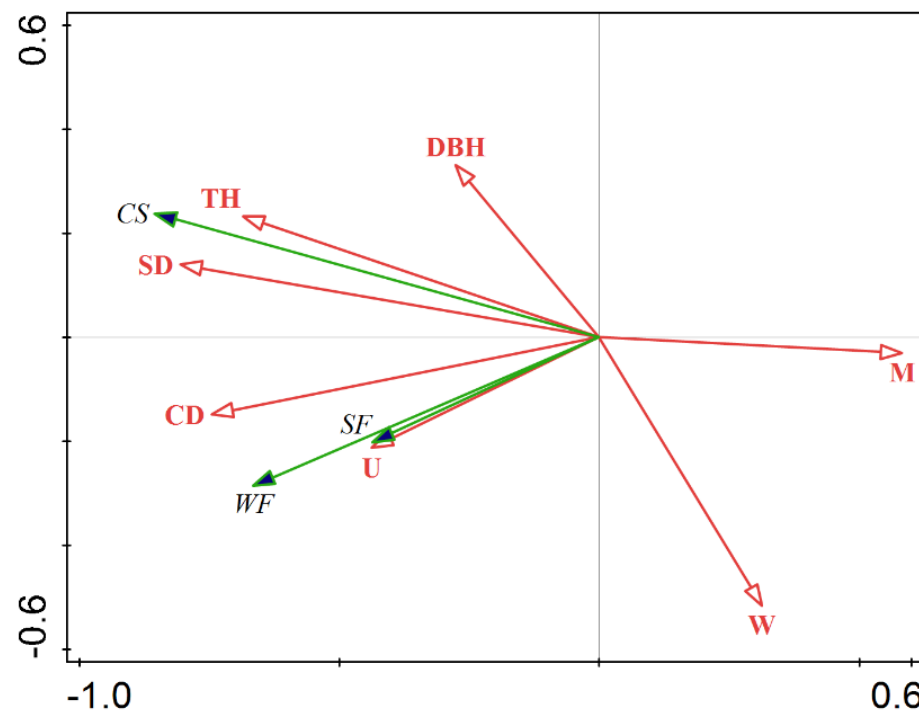
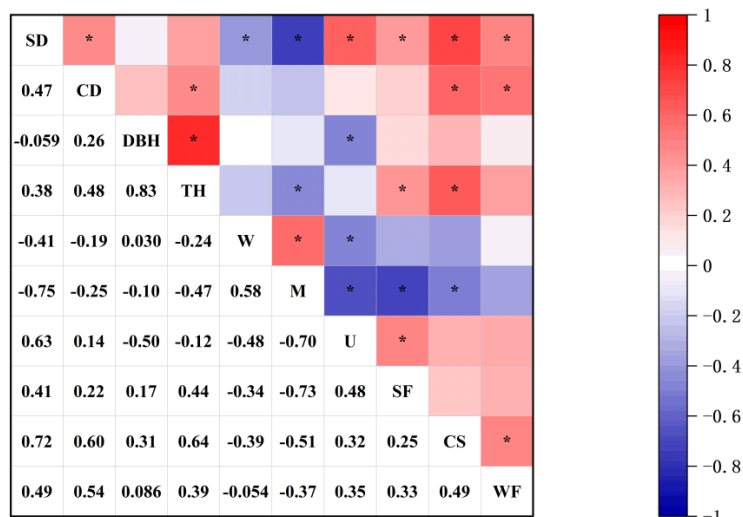


Figure 2. Coordination diagram for redundancy analysis of *SSTFs* and *EFFIs*. In the diagram, arrows represent *SSTFs* or *EFFIs*; the length of the arrows reflects the strength of the relationship between *SSTFs* and *EFFIs*. The angle between the arrows indicates the correlation: angles less than 90° represent a positive correlation, while angles greater than 90° indicate a negative correlation. The smaller the angle, the stronger the correlation; the larger the angle, the weaker the correlation. *WF*, water-holding function; *SF*, soil improvement function; *CS*, carbon sequestration; *SD*, stand density; *W*, uniform angle index; *TH*, tree height; *CD*, canopy density; *DBH*, diameter at breast height; *U*, neighborhood comparison; *M*, mixing degree.

Table 3. The *SSTF*-explained variance of the *EFFIs* in the *S. superb* forest.

<i>SSTFs</i>	Explains %	Contribution %	Pseudo-F	<i>p</i>
<i>SD</i>	37.6	57.6	13.3	0.002
<i>CD</i>	10.5	16.1	4.3	0.026
<i>TH</i>	5.1	7.8	2.2	0.102
<i>M</i>	4.6	7.1	2.1	0.16
<i>W</i>	3.8	5.8	1.8	0.214
<i>U</i>	2.3	3.6	1	0.384
<i>DBH</i>	1.3	2	0.6	0.566

Based on the two analysis results and practical operability, we selected *SD*, *CD*, *W*, and *M* as optimization indicators, and brought them into SEM to check the influence path of *SSTFs* and *EFFIs*.



* $p < 0.05$

Figure 3. Correlation between *SSTFs* and *EFFIs*, with colors of varying saturation levels indicating the strength of the correlations. Red indicates a positive correlation, while blue represents a negative correlation. The darker the color, the stronger the correlation between the variables. *WF*, water-holding function; *SF*, soil improvement function; *CS*, carbon sequestration; *SD*, stand density; *W*, uniform angle index; *TH*, tree height; *CD*, canopy density; *DBH*, diameter at breast height; *U*, neighborhood comparison; *M*, mixing degree.

3.3. Analysis of the Pathway of Action and Its Impact on SEM

To evaluate the combined effects of multiple stand structural factors on the functional indicators of *EFFIs*, SEM was used to develop models that link the stand structural factors of the *S. superba* forest with the functional indicators of *EFFIs* (Figure 4). After data testing and model modification, the revised model parameters accept the nihilistic hypothesis, and the test indices of the fitness statistics are $p > 0.7$, which indicates that the model is a good fit for the observed data (Figure 4). This indicates that the theoretical assumptions of the experiment, along with the data obtained from actual observations, are credible and applicable.

The SEM indicated that the stand structure factors had a positive effect on the *WF* with a path coefficient of 0.54 ($p < 0.01$). *SD*, *CD*, and *W* had positive effects with path coefficients of 0.27, 0.51, and 0.01, respectively. *M* had a negative effect with a path coefficient of -0.14 . The stand structure factors had a positive effect on the *SF* with a path coefficient of 0.61 ($p < 0.01$). *SD* and *M* had negative effects with path coefficients of -0.43 and -1.08 , respectively. *CD* and *W* had positive effects with path coefficients of 0.17 and 0.13, respectively. The stand structure factors had a positive effect on the *CS* with a path coefficient of 0.62 ($p < 0.01$). *SD*, *CD*, and *M* had positive effects with path coefficients of 0.58, 0.33, and 0.09 respectively. *W* had a negative effect with a path coefficient of -0.14 .

The stand structure factors showed varying degrees of response to each other. The strongest relationship was observed between *SD* and *M*, with a flux coefficient of -0.75 . The flux coefficients for *W* on *M*, *CD*, and *SD* were -0.43 , -0.19 , and 0.61, respectively. The flux coefficient for *M* on *CD* was -0.25 , while the flux coefficient between *CD* and *SD* was 0.47.

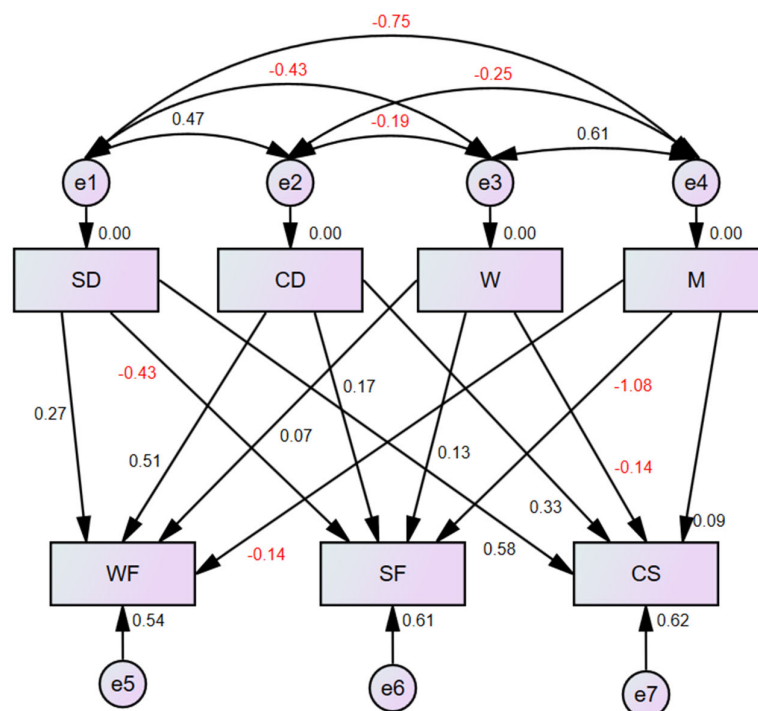


Figure 4. Coupling relationship model of the SSTFs and EFFIs. $p = 0.859$; RMSEA = 0.000; CFI = 1.000; GFI = 0.991; AGFI = 0.912; NFI = 0.992; IFI = 1.025. Black numbers denote positive effects, and red numbers denote negative effects. WF, water-holding function; SF, soil improvement function; CS, carbon sequestration; SD, stand density; W, uniform angle index; CD, canopy density; M, mixing degree.

3.4. Optimization and Adjustment of Forest Stand Structure

In order to improve the EFFIs of the *S. superba* forest, SD, CD, W, and M were selected as optimization indexes, and three multivariate optimization equations were established (Figure 5). With SF improvement as the main purpose, the optimal stand structure configuration was determined to be $SD = 1532$, $CD = 0.71465$, $W = 0.57360$, and $M = 0.41523$. According to model predictions, the optimized SF value was 5.37, representing a 9.16% reduction from the current mean SF of 5.92. To enhance the WF of the *S. superba* forest, additional optimization equations were developed (Figure 6). The optimal stand structure configuration was found to be $SD = 1228$, $CD = 0.74459$, $W = 0.50567$, and $M = 0.39493$. According to the model, the optimized WF value was 134.05, which is 8.64% higher than the current mean WF of 123.38. For optimizing CS in the *S. superba* forest, another multivariate model was created (Figure 7). The optimal stand structure configuration was $SD = 1675$, $CD = 0.71011$, $W = 0.55094$, and $M = 0.49377$. The model predicted an optimized CS value of 48.04, representing a 4.04% decrease from the current mean CS of 50.06. The optimized SF and CS values derived from the model were 5.37 and 48.04, respectively, both lower than the original data's mean values. This discrepancy arises because the optimization process prioritizes minimizing prediction errors, whereas the original data may display some skewness in its distribution. To validate the model's accuracy, an error analysis was conducted, revealing mean square errors of 0.828 and 0.986, respectively, which indicates a strong fit of the model to the overall trend. Therefore, although the optimized values are lower than the means, the results are reasonable, given the model's optimization objective and the characteristics of the original data.

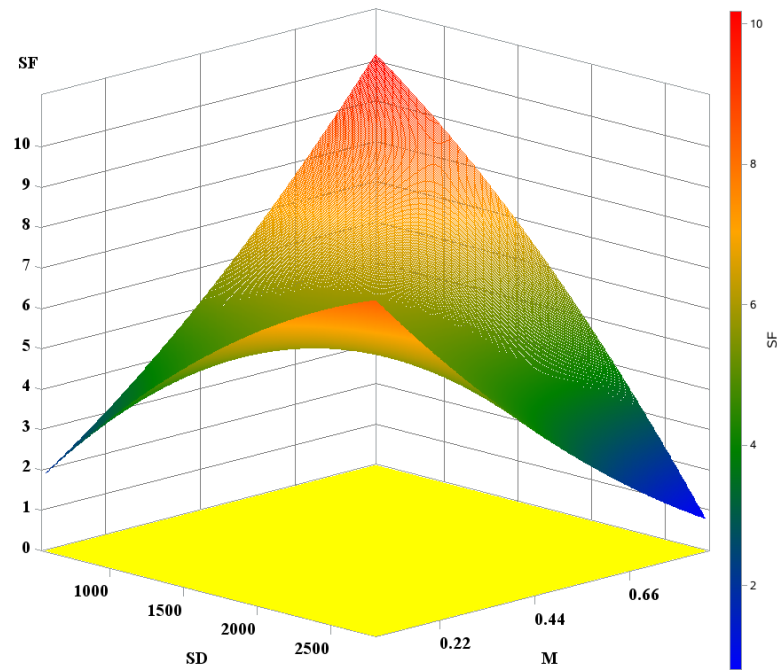


Figure 5. Optimization model of stand structure based on the improvement of SF . $SF = -0.017909 - 0.097999 \times SD - 0.04751 \times CD - 0.291592 \times W + 0.142754 \times M - 0.089562 \times SD^2 - 0.011856 \times CD \times SD - 0.085423 \times CD^2 - 0.079252 \times W \times SD + 0.029264 \times W \times CD + 0.128406 \times W^2 \times CD + 0.128406 \times W^2$. $SD = 1532$, $CD = 0.71465$, $W = 0.57360$, $M = 0.41523$.

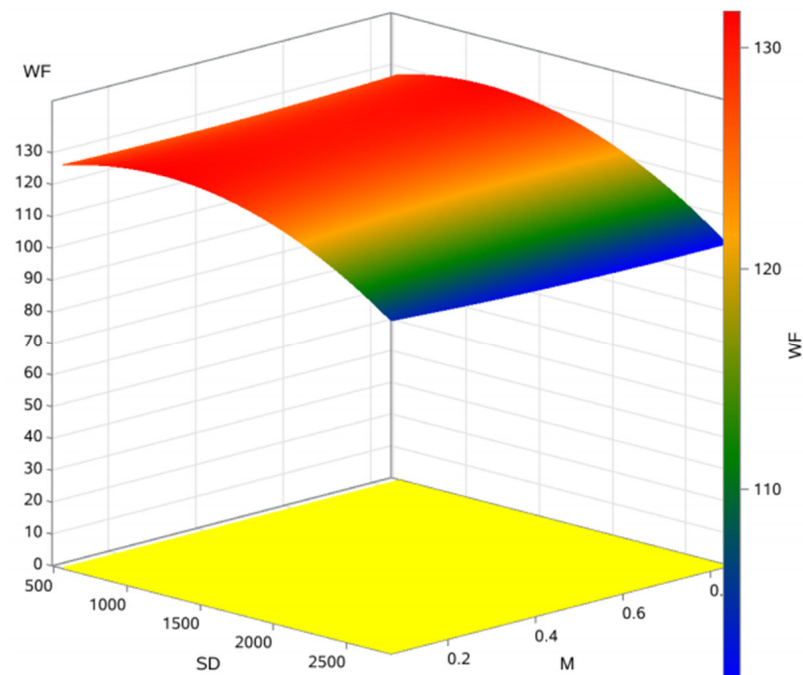


Figure 6. Optimization model of stand structure based on the improvement of WF . $WF = 0.491793 - 0.178684 \times SD + 0.078271 \times CD - 0.06825 \times W - 0.038328 \times M - 0.302165 \times SD^2 + 0.077447 \times CD \times SD - 0.170848 \times CD^2 + 0.197029 \times W \times SD - 0.096612 \times W \times CD - 0.055496 \times W^2 - 0.023271 \times M \times SD - 0.216957 \times M \times CD - 0.107602 \times M \times W + 0.02068 \times M^2$. $SD = 1228$, $CD = 0.74459$, $W = 0.50567$, $M = 0.39493$.

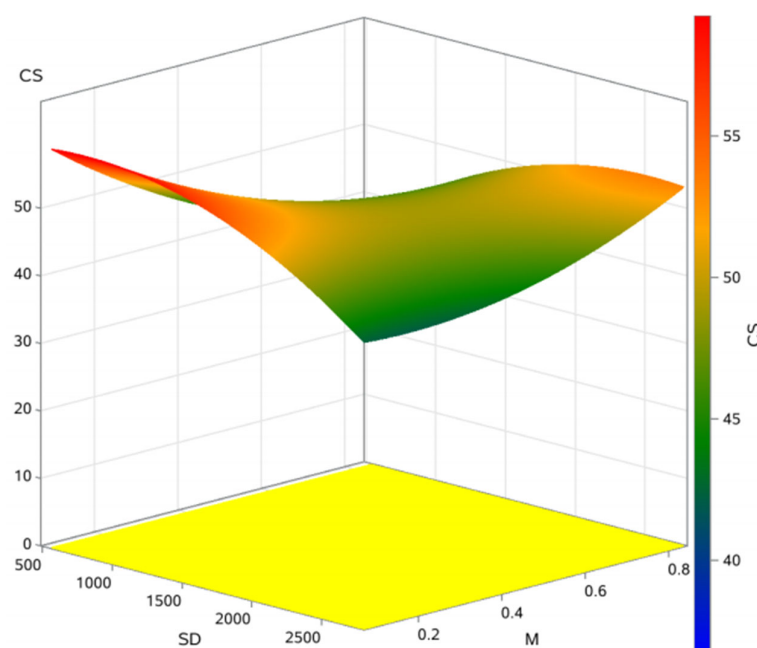


Figure 7. Optimization model of stand structure based on the improvement of CS. $CS = -0.111417 + 0.075627 \times SD + 0.123978 \times CD + 0.06192 \times W - 0.14167 \times M - 0.111047 \times SD^2 + 0.065036 \times CD \times SD + 0.266041 \times CD^2 - 0.07748 \times W \times SD + 0.133511 \times W \times CD - 0.126561 \times W^2 + 0.174012 \times M \times SD + 0.124901 \times M \times CD - 0.052847 \times M \times W + 0.076165 \times M^2$. $SD = 1675$, $CD = 0.71011$, $W = 0.55094$, $M = 0.49377$.

4. Discussion

4.1. Evaluation of the Ecological Functions of the *S. superba* Forest

Achieving forest ecosystem functions, such as soil and water conservation and carbon sequestration, requires a comprehensive and effective quantification of these functions. Enhancing these functions, while preserving the original afforestation area, is crucial for the high-quality forestry development of Dongbai Mountain. In the past, various methods have been employed to optimize stand structure, including tending management [31], forestry planning [32], and altering microtopography [33]. The current plot-based survey of the *S. superba* forest revealed that stand structure significantly influences local ecosystem functions. Among the sub-indices of the *S. superba* EFFIs, organic carbon content, maximum water retention capacity, litter water-holding capacity, total phosphorus, total nitrogen, and carbon density were the most prominent. This indicates that stand structure directly affects the forest's carbon sequestration capacity while also indirectly influencing WF and SF. Fluctuations in SF are likely due to variations in stand structure, which alter the amount, coverage, and decomposition rates of forest litter. These factors, in turn, impact nutrient absorption and replenishment in the soil, indirectly affecting SF. To optimize these ecological functions, appropriate forestry management techniques, such as thinning, selective felling, replanting, irrigation, and fertilization, should be employed [34–36].

4.2. Impact of Key Stand Structure on Ecosystem Functions in *S. superba* Forest

SD plays a crucial role in shaping forest ecosystem functions by influencing tree growth space, light availability, and competition for belowground resources such as nutrients and water [37]. In addition to its direct effects, SD interacts with other structural attributes, including tree size diversity and species richness, which together influence carbon storage dynamics [38–40]. Consistent with previous studies, our findings reveal that with increasing SD, WF and CS significantly improve. This relationship can be attributed to the increased accumulation of organic matter, such as litter and roots, under optimal canopy

conditions, which enhances soil organic carbon (SOC) content and promotes soil moisture retention [41–43]. These organic inputs stimulate root growth, improve soil structure, and enhance water-holding capacity, thereby supporting microbial activity and enhancing overall carbon storage. This process is closely linked to the “priming effect”, where microbial consumption of fresh organic carbon (FOC) regulates the mineralization and storage of SOC, further highlighting the importance of biodiversity-driven interactions in ecosystem functions [44,45].

Structural equation modeling (SEM) further revealed a positive direct effect of *SD* on *WF* and *CS*, while showing a negative impact on *SF* (Figure 4). These results highlight the complex and non-linear relationship between *SD* and ecosystem functions in subtropical *S. superba* forests. At lower *SD*, increased canopy cover promotes photosynthesis and carbon fixation, thereby enhancing carbon storage. However, when *SD* exceeds a critical threshold, competition for light, water, and soil nutrients intensifies, suppressing individual tree growth and reducing the forest’s overall carbon assimilation capacity [46]. Furthermore, high-density stands are characterized by limited root expansion, reduced nutrient uptake efficiency, and weakened rhizosphere microbial activity, all of which impair the supply of soil nutrients and the decomposition of organic matter [45,46]. In contrast to subtropical forests, studies in temperate forests generally suggest that higher stand densities are beneficial for carbon storage [3,15,41]. This discrepancy may be attributed to differences in climate conditions and ecological characteristics. In subtropical forests, although the warm and humid climate supports rapid tree growth, high stand densities limit the efficient utilization of water and nutrients due to increased evapotranspiration and intensified root competition. In temperate forests, slower growth rates and lower competition intensity allow for more efficient resource use under higher densities. This further underscores the importance of carefully managing *SD* to balance resource competition in subtropical forests. Moderate stand densities enhance light penetration and reduce competition for soil nutrients, promoting lower vegetation growth, optimizing resource allocation, and increasing carbon storage capacity [35,47]. In contrast, excessively high stand densities exacerbate resource competition, restrict root expansion, inhibit photosynthesis and soil microbial activity, ultimately reducing carbon storage and degrading forest health. On the other hand, sparse stands fail to fully exploit available resources, with excessive spacing between trees leading to lower utilization of water, light, and nutrients, and greater evaporation losses of soil moisture and nutrients, thereby impacting forest productivity and ecosystem function [48].

Thinning, as an important forest management practice, alleviates resource competition by removing highly competitive trees, and improving light penetration and ventilation within the forest [49]. Thinning also regulates soil moisture and temperature dynamics, reducing *CD* and thus decreasing rainfall interception and transpiration, which enhances soil moisture retention [49]. Additionally, thinning promotes soil microbial activity and accelerates organic matter decomposition rates [50,51]. This study determined the optimal stand densities for different ecosystem functions: 1532 plants·hm^{−2} for *SF*, 1228 plants·hm^{−2} for *WF*, and 1675 plants·hm^{−2} for *CS*. These optimal density values suggest that targeted adjustments based on specific functional objectives are essential for optimizing ecosystem functions. Dynamic adjustments of *SD* based on ecological and management priorities can maximize ecosystem benefits and support the long-term sustainable management of forests.

The degree of solar radiation penetration through the canopy, determined by its density, impacts a range of ecological processes, including understory plant diversity, litter decomposition, soil microbial community dynamics, and soil elemental composition, which collectively affect forest structure and ecosystem functionality [52–55]. In this study,

optimal *CD* was associated with increased resource availability—specifically light, water, and nutrients—resulting in enhanced soil water retention and nutrient accumulation [56,57]. Higher *CD* enhances tree growth and biomass accumulation by improving light interception in the upper canopy, which reduces soil temperature fluctuations and increases moisture retention. These conditions support greater photosynthetic efficiency, particularly in the understory, where plants benefit from increased light availability. This promotes nutrient uptake by roots, particularly in deeper soil layers, and facilitates carbon fixation through enhanced photosynthesis, ultimately boosting carbon storage capacity [58]. However, in temperate forests, the influence of *CD* on ecological functions is less pronounced compared to subtropical forests [3,15,41]. This disparity can be attributed to the relatively high climatic stability, simplified vegetation stratification, strong adaptability of shade-tolerant species, and reduced dependency of carbon balance mechanisms on *CD* in temperate forests. These factors collectively weaken the regulatory role of *CD* on resource distribution and ecological functions.

In contrast, studies in subtropical forests have shown that increased *CD* reduces ground-level radiation and soil moisture evaporation, thereby enhancing soil water retention [59,60]. Structural equation modeling (SEM) in the present study revealed that as *CD* increased, *CS* exhibited a significant upward trend, while *SF* and *WF* showed positive, albeit non-significant, trends. These relationships are primarily driven by the accumulation of understory litter and reduced decomposition rates under optimal canopy conditions. The buildup of organic matter, including deadwood, enriches *SOC*, promotes root development, improves soil structure, and enhances water-holding capacity [61,62]. Consequently, *WF* and *CS* are strengthened through the effective retention of organic material. Moreover, appropriate *CD* facilitates increased interception of precipitation by the canopy and forest litter, enhancing soil water infiltration and further improving *WF* [55]. This ability to regulate water dynamics is crucial for maintaining ecosystem functionality, especially in regions with variable precipitation patterns. These findings underscore the critical role of rational *CD* management in optimizing ecological functions. In subtropical regions, the adjustment of *CD* can be achieved through several key measures, including selective thinning to reduce *SD* and enhance light penetration, optimizing species composition by introducing a mix of species with complementary crown structures, and regulating spatial arrangement to improve light distribution and canopy coverage. Additionally, fertilization can be applied to promote growth in areas with insufficient canopy development, while pest and disease management helps prevent tree mortality and maintain canopy stability. By maintaining optimal *CD*, forest managers can enhance ecosystem services, including carbon sequestration, water retention, and biodiversity conservation, while ensuring the synergistic relationship between forest structure and ecosystem functionality is sustained.

The uniform angle index (*W*) is a key indicator for assessing forest spatial structure [63]. Forest spatial distribution, whether random, uniform, or clustered, affects stand structure and tree distribution, consistent with our findings [64]. This study, using structural equation modeling and correlation analysis, reveals that *W* negatively impacts *SF* and *CS*. Higher *W* values indicate a more clustered spatial pattern and higher tree density, intensifying competition for resources, thereby reducing ecosystem productivity, biomass, carbon sequestration, and soil protection capacity [65]. Our findings contrast with previous studies, where *W* showed a significant effect on *SF* or *WF*. This discrepancy may arise from differences in environmental and ecological conditions. For instance, Wang et al.'s study in the semi-arid Loess Plateau, with sparse vegetation, found that increased *W* altered canopy structure, reducing runoff and enhancing soil permeability, thus improving water retention [64]. In contrast, subtropical forests, with high precipitation and dense vegetation, may have soils close to saturation, where *W*'s influence on water dynamics is less pro-

nounced compared to other factors, such as soil texture, root distribution, and microclimate. Although W does not significantly influence WF or SF , its impact on CS is mediated through CD . CD alters resource allocation and light conditions, which are crucial for carbon fixation and storage, while promoting understory growth and water retention [66]. However, dense shrubs and grasses may deplete soil nutrients, requiring a balanced approach to managing plant diversity and nutrient conservation. These interactions highlight the complexity of forest spatial structure in shaping ecosystem processes. Mature forests tend to adopt a random distribution, reducing interspecies competition and stabilizing the ecosystem [67–69]. In this study, the optimal W values for three ecological function indicators were 0.57360, 0.50567, and 0.55094, all corresponding to a random spatial distribution. To improve the uniform angle index in subtropical forests, specific measures include selective thinning to reduce stand density and promote a more even spatial distribution of trees, adjusting tree spacing to ensure a more uniform arrangement, and introducing species with varied growth patterns to enhance spatial heterogeneity. Additionally, pruning dominant trees can help reduce clustering and improve the angular distribution of remaining trees, thereby enhancing the W . These findings underscore the importance of spatial pattern management for sustainability, resilience, and enhancing services like CS and SF .

The degree of mixing reflects species diversity and interspecies spatial distribution and influences species' ability to acquire light, water, and nutrients [70–72]. While previous studies suggest that species richness, rather than abundance, is a key driver of $EFFIs$ [73], our study found a significant negative correlation between M , SD , and $EFFIs$ (e.g., SF , WF , and CS) in *S. superba*-dominated stands. Lan et al. also showed that although *Castanopsis echidnocarpa* populations increased with higher M , its contribution to $EFFIs$ was minimal [41]. This suggests that few dominant species cannot maintain high levels of multiple $EFFIs$, emphasizing the importance of species richness for multifunctionality [74]. In contrast, in *S. superba*-dominated stands, the dominance of this species may further diminish the positive effects of species richness on $EFFIs$. This may result from the structural complexity of mixed stands and inappropriate species composition, which alter soil microbial communities, reduce nutrient use efficiency, intensify competition, and lead to nutrient depletion and decreased ecosystem productivity [75–77]. Additionally, differences in light requirements between species can hinder the growth of light-demanding species, reducing net primary productivity and CS [78,79]. In our study, the dominant species, *S. superba*, exhibited accelerated growth and increased competitiveness, slowing the growth of other species, creating resource acquisition pressure, and leading to nutrient imbalances, reduced SF , and decreased WF [80,81].

This complex dynamic relationship is crucial for understanding how mixing degree influences ecosystem functions. To balance forest ecosystem stability and multifunctionality, we recommend: (1) optimizing M and species composition, planning species arrangements to avoid resource monopolization by a single dominant species; (2) alleviating interspecific competition by regulating dominant species density, promoting secondary species recovery, and enhancing diversity's role in ecosystem functions; (3) improving resource use efficiency by introducing functionally complementary tree species combinations to increase $EFFIs$ [82–84]. These measures offer both theoretical and practical support for optimizing subtropical forest ecological function services.

The results indicate that SD plays a critical and positive role in forest ecosystem function enhancement, specifically in WF and SF . However, in some cases, excessively high density may lead to intense competition, which suppresses CS . This may be due to the high density limiting tree growth, reducing light availability, and increasing water competition, thus impacting the forest's carbon fixation capacity [11]. While species diversity typically enhances forest ecosystem functions, in this study, higher species mixing actually had a

negative effect on certain ecological functions, particularly CS. This phenomenon may be related to interspecies resource competition and niche overlap [7]. This insight fills a significant gap in the existing literature, suggesting that the relationship between species diversity and ecosystem functionality may not always be linear, particularly in subtropical forests. The study also found that *CD* and *W* have significant impacts on ecological functions, suggesting that the spatial distribution and stratification of stand structure play an important role in influencing forest ecosystem services. Therefore, reasonable adjustments to stand structure can significantly enhance the core ecological functions of forest ecosystems, providing valuable insights for sustainable forest management [15,16]. This research not only provides essential data for ecosystem studies in the Dongbai region but also offers a theoretical basis for the implementation of stand structure optimization strategies in subtropical regions. These findings provide practical guidance for maximizing ecological functions in stand management in the future.

4.3. Optimization Strategy of the Stand Structure of the *S. superba* Forest in Dongbai Mountain

The results of this study indicate that stand density, canopy density, uniform angle index, and mixing degree significantly affect the ecological functions of *S. superba* stands in Dongbai Mountain. To optimize the stand structure and improve ecological functionality, the following strategies are recommended:

- (1) By investigating stand structure factors such as stand density, *DBH*, stand height, canopy density, stand mixing degree, the neighborhood comparison and the uniform angle index, we gain insights into the characteristics of the stand structure and its ecological functions. This allows us to determine the optimization and regulation targets. Afterward, through a quantitative analysis of the forest stand's ecological functions (including *WF*, *SF*, and *CS*), we select specific functional indices as optimization targets. The degree of optimization for these indices is then clarified to identify the key factors influencing forest stand structure. These optimization targets are incorporated into the corresponding stand structure optimization model to determine the regulation direction and range for stand structure factors, along with specific stand control measures.
- (2) In this study, stand density regulation can be achieved by adjusting tree density through replanting or transplanting. The goal of regulating the uniform angle index is to balance the spatial distribution of clustered, random, and uniformly distributed structural units within the forest stand. To increase the uniform angle index, species with a more open canopy structure should be replanted or transplanted. Conversely, to decrease the uniform angle index, species with a denser canopy structure should be used. For *S. superba*, optimal canopy density can be achieved by selectively thinning dominant trees to reduce excessive shading, coupled with underplanting shade-tolerant species such as *Castanopsis fargesii* Franch. and *Lithocarpus glaber* (Thunb.) Nakai, which enhance soil fertility through leaf litter decomposition. To improve the mixing degree, integrating nitrogen-fixing species like *Ormosia pinnata* (L.) Merr. or drought-resistant species such as *Cyclobalanopsis glauca* (Thunb.) Oerst. can diversify functional traits, mitigate interspecies competition, and enhance carbon sequestration and water retention efficiency.
- (3) The optimal stand structure model, determined through the response surface equation in this study, can serve as a valuable reference for pre-planning afforestation objectives in forested areas. Additionally, the optimization targets for stand structure factors derived in this study are based on the ecological functions of the forest stands in Dongbai Mountain that require improvement. While these findings may not be directly applicable to optimizing the ecological functions of forest stands in other

regions, the research methodology and corresponding regulatory strategies can be applied to other regions or countries aiming to enhance their ecological environment and improve the quality of forest stands through stand structure optimization.

Additionally, the study's limited time span and small sample size may affect the generalizability of the results. Since the research was conducted in a specific region and during a particular time frame, the findings may only be applicable to similar environments or regions. Therefore, the study has certain limitations, particularly regarding the potential influence of environmental gradients and regional differences on the relationship between stand structure and ecological functions. A more thorough consideration of these factors is needed. Future research should address these limitations by exploring the impact of environmental variations and regional differences to enhance the broader applicability and scientific value of the findings.

5. Conclusions

This study systematically analyzes the coupling relationships between *SSTFs* and *EFFIs* and proposes strategies for optimizing the *S. superba* forest structure to enhance ecological functions in Dongbai Mountain. The results indicate that variations in stand structure significantly influence the ecological functions of *S. superba* forests, particularly in *WF*, *SF*, and *CS*. Among stand structure factors, *SD* exhibits the most significant effect on *EFFIs*, with optimal *SD* values for *WF*, *SF*, and *CS* being 1228 plants·hm⁻², 1532 plants·hm⁻², and 1675 plants·hm⁻², respectively. This deviates from the linear relationships observed in temperate forests. In subtropical forests, the study recommends employing reasonable intercropping and mixed planting strategies to optimize stand density and spatial structure based on specific ecological functions and practical conditions. These measures aim to maintain random spatial distributions, enrich stand structure, and standardize stand characteristics, avoiding excessive dominance by a single species. Additionally, appropriate species composition should be selected to prevent resource monopolization by a single dominant species. Adjusting the density of dominant species, promoting the recovery of secondary species, and introducing complementary functional species combinations are key strategies to enhance ecological functions and establish function-oriented stand structures. These strategies provide theoretical support for improving the ecological environment of Dongbai Mountain and offer valuable insights for optimizing stand structures and managing ecosystems in similar subtropical regions, particularly forests dominated by *Castanopsis eyrei* and *S. superba* in northern monsoonal subtropical climates. The structural and functional characteristics of such forests make them highly relevant for applying and testing the findings of this study. However, future research should further explore the role of interspecies interactions in promoting multifunctionality, validate the applicability of key regulatory factors across different habitats, including other forest types within monsoonal subtropical climates, and evaluate the feasibility and long-term ecological impacts of these management strategies. This will help refine and expand their applicability, ultimately achieving sustainable management objectives for subtropical forests.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/f16010048/s1>, Table S1: Biomass equations for forest sample plots.

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