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Thinning Effects on Aboveground Biomass Increments in Both the Overstory and Understory of Masson Pine Forests

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Abstract: Masson pine (*Pinus massoniana* Lamb.) is a tree species that is widely distributed throughout southern China and holds significant economic and ecological value. The main objective of our study was to assess the effects of thinning on aboveground biomass increments and tree diversity in both the overstory and understory. Additionally, the underlying factors and mechanisms responsible for driving changes in biomass increment were analyzed. Four different thinning treatments (control, light thinning, moderate thinning, and heavy thinning) were implemented in 214 plots (~1800 tree ha^{-1}) in three Masson pine forests in Hunan Province, China. A robustly designed experiment was used with over six years of repeated measurements. The differences in biomass increment and tree diversity among the different treatments were compared using repeated measures ANOVAs. The Mantel test was used to determine environmental metrics correlated with biomass increments across tree strata. Structural equation modeling was utilized to explore the multivariate relationships among site environment, tree diversity, and post-treatment biomass increment. The results indicated that thinning overall increased biomass increment, the Shannon index, and the Gini index, while decreasing the Dominance index over time. Moderate thinning (25%–35% of trees removed) was found to promote overstory biomass increment to 9.72 Mg·ha^{-1}·a^{-1} and understory biomass increment to 1.43 Mg·ha^{-1}·a^{-1} six years post-thinning, which is significantly higher than that of other treatments. Environmental metrics such as light intensity, soil organic matter, and other soil physiochemical properties were positively correlated with biomass increments, and their effects on the overstory and understory differed. Structural equation modeling revealed that thinning treatments, environmental metrics, tree diversity, and their interactions could be the main drivers for biomass increments across tree strata. Specifically, thinning treatments, light intensity, and tree size diversity (Gini index) had significant effects on overstory biomass increment, while understory species richness (Shannon index) and soil organic matter affected understory biomass increment. In conclusion, moderate thinning is an effective silvicultural treatment for stimulating biomass increments of both the overstory and understory in Masson pine forests in southern China if a middle period (e.g., six years) is considered. Some factors, such as species richness, tree size diversity, and environmental metrics (e.g., light and soil), are suggested for consideration to improve the efficiency of thinning.

Keywords: thinning; biomass increment; tree strata; environmental metrics; tree diversity; Masson pine forests

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1. Introduction

Masson pine (*Pinus massoniana* Lamb.) covers a total of 1.13 million hectares in China's subtropical zone, and it plays key roles in the development of the ecology and society due to its wide distribution and ability to grow and regenerate naturally [1,2]. Masson pine can form mixed conifer forests with companion species, which contributes to vegetation cover, soil and water conservation, and carbon balance [3]. Several national policies have been established to maintain the quality and stability of Masson pine forests [4]. However, most Masson pine forests at our study sites are middle-aged or nearly mature, and the protection (banning logging) strategy alone may not be sufficient for sustaining ecological service functions, biodiversity, and productivity, as well as enhancing resistance to disease and natural disturbances [5]; in such cases, thinning treatment might be warranted. Thinning is an important silvicultural activity that was initially used for commercial timber production but is now increasingly used for sustainable forest management [6]. Thinning improves tree growth and biomass productivity by regulating the growth space and microsite environment [7,8]. However, its effects in Masson pine forests are far from conclusive, particularly concerning thinning intensity, community response, and assessment methods [9].

Thinning intensity is an important factor in determining the effectiveness of thinning treatment. Some studies have reported that thinning tree cover to approximately 40%–60% can improve overstory biomass in Masson pine forests and other pine forests [2]. However, others have suggested that thinning intensities should be within 30%–40%, considering understory regeneration [10]. If thinning intensity is light, the benefits may be temporary and primarily affect the overstory rather than the understory. Conversely, excessive thinning can substantially alter environmental conditions, reduce seed sources, and suppress understory regeneration [11]. In some cases, although moderate thinning is potentially optimal, the observed effect may be weaker than expected, which can be due to various factors such as site-specific environmental conditions and follow-up treatments [12,13]. In light of these findings and the emerging situations regarding the increasing development potential of Masson pine forests, there is a need for ongoing observations and assessments of the effectiveness of various thinning intensities [14,15].

Some studies have reported that thinning reduces overstory trees, thus increasing sunlight availability and providing more water and mineral nutrients for the forest ecosystem [16,17]. These processes can promote the growth of tree height and DBH, alleviate interspecies competition, and stimulate the biomass increments of both the overstory and understory [18,19], although on occasions some authors have found that there was no such response [9,20]. For example, Liu et al. [21] reported that increased sunlight availability enhances aboveground biomass or productivity for the overstory in pine forests in southern China while simultaneously increasing underground biomass for the understory. Reports have indicated that snow disturbances significantly influence tree growth in managed forests with varying thinning intensities [22]. This influence is primarily reflected across different forest strata. While the overstory and understory are the most common strata in Masson pine forests, there is limited research on how their biomass increments relate to different site-specific environmental metrics.

Furthermore, tree species composition and forest structure are also important for post-treatment productivity or biomass increment [23,24]. Some studies have suggested that environmental metrics not only directly affect biomass increment but also indirectly influence it by shaping the diversity of tree composition and size [25]. This is a complex process, and we are still unclear about how environmental metrics, tree diversity, and their interactions affect biomass increment after thinning. The multivariate productivity–diversity hypothesis [26,27] provides us with insights, as biomass increment is a crucial component of productivity. This hypothesis has been validated at both the plot and landscape levels [28,29], but the majority of evidence comes from natural stands [30], with only a few empirical analyses of managed forests having been conducted to date. Thus, it is worthwhile to consider the effects of thinning on biomass increment within the context of this hypothesis when formulating forest management strategies.

Previous studies have utilized meta-analysis methods to assess the impact of thinning on forest biomass [6,9,16], but their findings varied due to several limitations. First, most of these meta-analyses have been conducted using data from a single research site, with little consideration given to situations across multiple sites, limiting their ability to provide a comprehensive assessment of the response patterns of post-treatment biomass change. Second, most studies directly analyze the relationship between site environment and biomass using sampled data, despite potential issues such as small sample sizes, non-normal distributions, and autocorrelation. Some studies have shown that utilizing the Mantel test with similarity matrices could improve the accuracy and interpretability of correlation analysis, avoiding result biases [28]. Third, most studies have considered the effects of factors such as thinning intensity, site environment, and species diversity on post-treatment recovery while ignoring how their interactions affect biomass increment. A simple emphasis on the effectiveness of a single observed variable may be biased, as it overlooks the causal relationships among variables, including direct and indirect effects. This approach fails to comprehensively reveal the underlying mechanisms. Therefore, it is necessary to conduct further studies on the effects of thinning on biomass increment using suitable assessment methods.

In this study, we asked the following questions: how does thinning treatment influence biomass increments of both the overstory and understory over time? What are the underlying mechanisms of these effects? Our hypotheses are detailed below. (1) The moderate thinning should have the greatest potential to promote biomass increments and tree diversity in both the overstory and understory over time. (2) The environmental metrics such as light availability and soil physiochemical properties would be correlated with biomass increments, and their effects on the overstory and understory would differ. (3) Thinning treatments, environmental metrics, tree diversity, and their interactions would be the main drivers of biomass increments, with the driving mechanisms potentially differing between the overstory and understory.

2. Materials and Methods

2.1. Site Description

This study utilized three Masson pine sites that were established in Pingjiang, Anhua, and Huitong in Hunan Province, China (Figure 1; Table 1). These sites experience a humid subtropical climate with a hot summer, and the average daily temperatures range from 4.2 °C in January to 30.5 °C in July. The mean annual precipitation is between 1300 and 1800 mm, and 60%–70% of the precipitation falls during the growing season (April to September). Average daily solar radiation in the growing season is between 14.5 and 16.5 MJ/m^2. The soils of the three sites are classified as a mountain yellow-red soil derived from granite parent material, with an average pH ranging from 4.7 to 5.9. The soil has a shallow A horizon (approximately 20 cm), but the soil profile extends from 100 cm to more than 150 cm in depth before reaching fractured granite bedrock.

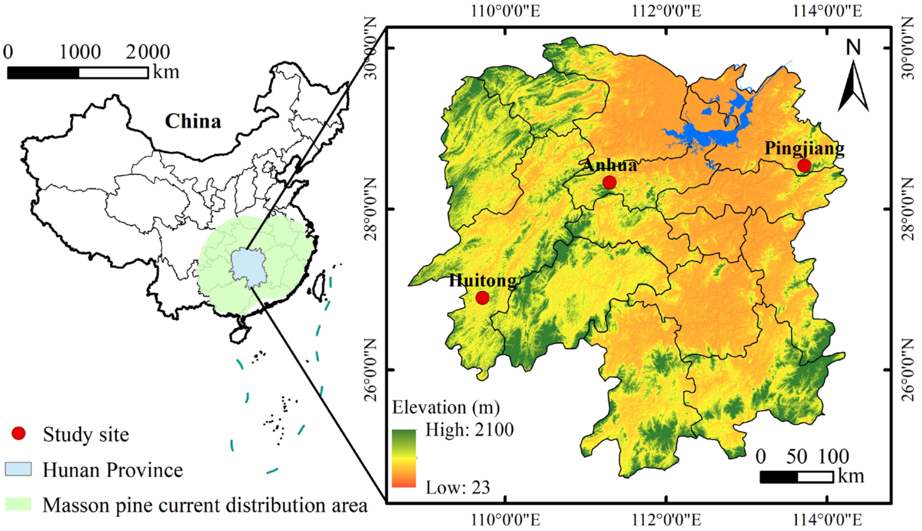

Figure 1. Locations of the three study sites in Hunan Province, China.

Table 1. Site description of the three Masson pine forests in Hunan Province, China.

Site	Pingjiang	Anhua	Huitong
Location	28°25′ N, 113°10′ E	27°44′ N, 111°58′ E	26°88′ N, 109°73′ E
Average annual temperature (°C)	16.8	16.2	17.1
Average annual precipitation (mm)	1450.8	1706.1	1361.2
Average daily solar radiation (MJ/m^2)	15.4	16.3	14.8
Soil organic matter content (g·kg^{-1})	21.61	24.09	23.74
Elevation (m, a.s.l.)	750	600	650
Aspect	SW	W	SW
Stand age	24	22	22
Overstory density (stems ha^{-1})	1750	1820	1860
Understory density (stems ha^{-1})	2280	2150	1975

All sites are artificially seeded Masson pine forests on timber-harvesting patches that were established in the 1990s. The forests were initially planted at a density of approximately 2300 stems ha^{-1}. Forest tending was conducted first in 2010 to improve the natural regeneration and growth of the remaining trees. The stand age ranged from 21 to 24 years (middle-aged). *P. massoniana* dominated the overstory (≥4 m tall and ≥5 cm diameter at breast height [DBH]) in the stand, and other tree species such as *Sassafras tzumu* (Hemsl.) Hemsl. and *S. superba* (*Schima superba* Gardn. et Champ.) were identified. Understory (<4 m tall) tree species mainly comprised Chinese fir (*Cunninghamia lanceolata* (Lamb.) Hook), *Cinnamomum camphora*, *Quercus glauca*, and *Castanopsis sclerophylla*. The overstory density ranged from 1750 to 1860 stems ha^{-1}, while the understory density ranged from 1975 to 2280 stems ha^{-1}. At the beginning of the experiment (2016), an initial field survey was conducted in these sites to determine homogeneity in composition, structure, and physiography.

2.2. Experimental Design

The experiment was conducted in a completely randomized block design with subsampling. Six blocks (replicates) were established adjacent to each other in reasonably uniform stand conditions in Pingjiang. Four blocks were established in Anhua and Huitong, respectively. Each block was repeatedly subdivided into four rows of rectangular subsampling units. Each subsampling unit was randomly assigned four treatment plots (20 m × 20 m): heavy thinning (HT, 35%–45% of the trees by number were removed), moderate thinning (MT, 25%–35% of the trees by number were removed), light thinning (LT, 10%–25% of the trees by number were removed), and control (CK). A total of 214 plots were established, including 93 in Pingjiang, 60 in Anhua, and 61 in Huitong. For instance, the schematic diagram of the experimental treatments in the Pingjiang field trial is shown in Figure 2.

The selective thinning strategy followed the nature-approximating management guidelines in the NFA [31], a national management publication aimed at converting even-aged pine forests into all-sized stands and enhancing forest vigor and quality. To determine which trees to cut, we first used Voronoi diagrams to partition the nearest-neighbor region of individual trees [32]; we then established the spatial relationship among trees within each plot. Trading off these structure indexes at the stand scale by marking individual trees with potential cutting requirements was an iterative process [33], in which the upper and lower limits of the residual basal area (according to the treatment assigned to that plot) were constraints [34]. In practice, priority for cutting was given to dominant trees that would be expected to damage their neighbors, suppressed trees with exceptionally poor form, trees with clumpy distributions, dead trees, or trees with minimal ecological potential. According to previous studies suggesting that the minimum residual basal area be approximately 15 to 22 m^2 ha^{-1} for pine forests [35], we determined the residual basal area for HT (15.17 m^2·ha^{-1}), MT (20.48 m^2·ha^{-1}), and LT (22.05 m^2·ha^{-1}). To reduce damage to understory individuals, trees were carefully felled using felling machinery so that they fell outside of the plots; the portions of the boles inside the perimeter of plots were removed manually.

Figure 2. A schematic diagram of the experimental treatments in Pingjiang. The experiment has four types of treatments as follows: 22 heavy thinning (HT), 24 moderate thinning (MT), 24 light thinning (LT), and 23 control (CK). Unmarked plots are unsuitable for thinning. The site was established in October 2016. Subsequent surveys were made in August 2017, July 2018, July 2020, and August 2022.

2.3. Field Investigation

In 214 plots, trees were identified, and the density, diameter at breast height, and basal area were tallied. A total of 189 sampled trees were allocated as evenly as possible among diameter classes in the four treatments (HT, MT, LT, and CK). After a sample tree was felled, diameter at breast height and height were measured, and the stem, branches, and foliage were collected. Materials were dried at 70 °C for at least 72 h or until a constant dry weight was obtained; they were then added together to obtain the total aboveground biomass of each tree. Tree metrics were collected one month before and after thinning (September 2016 and November 2016, respectively) to account for the stand characteristics of pre- and post-thinning treatments (Table 2). The subsequent surveys were conducted in August 2017, July 2018, July 2020, and August 2022, corresponding to the years following the thinning process (years 1, 2, 4, and 6, respectively). *F*-tests were also used to confirm the homogeneity of stand characteristics before thinning. We calculated the aboveground biomass and annual biomass increments using the following method:

$$\mathrm{OBI} = AGB_{o(T)} - AGB_{o(T-1)} \tag{1}$$

$$\mathrm{UBI} = AGB_{u(T)} - AGB_{u(T-1)} \tag{2}$$

$$\mathrm{AGB_o} = f(dbh, h) \times D \tag{3}$$

$$\mathrm{AGB_u} = f(d,h) \times D \tag{4}$$

where OBI and UBI are the annual biomass increments ($\mathrm{Mg{\cdot}ha^{-1}{\cdot}a^{-1}}$) in the overstory and understory, respectively. T is the current survey year and $T - 1$ is the previous survey year. $\mathrm{AGB_o}$ and $\mathrm{AGB_u}$ are the tree aboveground biomass in the overstory and understory, respectively. f is the tree allometric growth model (Table S1) used to calculate individual tree biomass (kg), dbh is tree diameter at breast height (cm), h is tree height (m), d is ground diameter (cm), and D is stand density ($\mathrm{N{\cdot}ha^{-1}}$).

Stand environment metrics were collected in July and August 2022 (post-thinning year 6). In each plot, the light intensity was measured using black thermopile-based pyranometers (LP02; Hukseflux, Delft, The Netherlands), and soil moisture was measured using thermistors (105T; Campbell, Logan, UT, USA). The light intensity was measured at 15 min intervals, and soil moisture was measured every 30 min, with hourly averages recorded, from 8:00 to 18:00 h under sunny conditions. After removing the upper litter and organic layer, soil samples (0–20 cm depth) were randomly collected with an auger at nine points within each plot. Soil samples were then processed through 2 mm mesh sieves, pooled as mixed samples, and stored in a refrigerator at 4 °C for each plot. Soil pH was determined in a 1:2.5 soil/water suspension. Soil organic matter was determined using the potassium dichromate volumetric method. Soil total nitrogen (TN) was measured using the Kjeldahl method, and total phosphorous (TP) and total potassium (TK) were measured using the nitrification method. Available nitrogen (AN) was extracted from 10 g of fresh soil sample using 50 mL of 2 M KCL solution by shaking at 200 rpm for 1 h; it was then quantified using colorimetric methods. Available phosphorous (AP) was extracted by 0.5 M $\mathrm{NaHCO_3}$ at pH 8.5 (Olsen method) and then was determined by spectrophotometry. Available potassium (AK) was determined using a flame photometer (FP6430; Inesa, Shanghai, China). More detailed information on the extraction procedures for measurements of soil physicochemical characteristics is provided in previous studies [36,37]. According to our field investigation and flora records, tree strata were analyzed in two height categories: overstory ($\geq$4 m tall and $\geq$5 cm diameter at breast height [DBH]) and understory (<4 m). Tree metrics and environmental metrics in both the overstory and understory were measured six years post-thinning (Table 3).

2.4. Data Analyses

2.4.1. Biomass Increment and Tree Diversity

Replicate (e.g., a thinned plot or reference area within a block) means were considered random subsamples within each block. Repeated measures ANOVA was used to test the effects of treatment intensity, survey year, and their interactions on the variables, including biomass increment, Shannon index, Dominance index, and Gini index across tree strata. The biomass increments of plots were the absolute difference of replicated biomass means between the post-thinning initial value and the value in subsequent survey years (years 1, 2, 4, and 6). Shannon–Wiener's index (hereafter referred to as the Shannon index) was used to measure species richness. The Baker–Parker dominance index (hereafter referred to as the Dominance index) was used to measure the ratio of the basal area of the most abundant species to the total basal area per hectare [38]. Tree size diversity was characterized using the Gini index, which was used to estimate the diameter distribution; it is usually conceptualized as the area between the Lorenz curve and the diagonal line of absolute equality [39]. These variables were log-transformed to meet requirements for the normalization of residuals and homogeneity of variances. Post hoc pairwise comparisons (Bonferroni-corrected) were made when group differences were detected. Simple main-effects analysis was used when a significant interaction between thinning intensity and survey year was detected. p-values < 0.05 were regarded as statistically significant. Statistical analyses were performed using R version 4.2.0 [40]. The R "nlme" package was used for ANOVAs, and the "emmeans" package [41] was used for post hoc and simple main-effects tests.

Table 2. The basic characteristics (means (standard error [se])) of the plots before and after thinning treatments in Masson pine forests in Hunan, China.

		Before Thinning					**After Thinning**					**Thinning Amount**			
	Plots (P/A/H)	**Density ($N \cdot ha^{-1}$)**	**Basal Area ($m^2 \cdot ha^{-1}$)**	**DBH (cm)**	**Height (m)**	**Biomass ($Mg \cdot ha^{-1}$)**	**Density ($N \cdot ha^{-1}$)**	**Basal Area ($m^2 \cdot ha^{-1}$)**	**DBH (cm)**	**Height (m)**	**Biomass ($Mg \cdot ha^{-1}$)**	**Tree ($N \cdot ha^{-1}$)**	**%**	**Biomass ($Mg \cdot ha^{-1}$)**	**%**
HT	51 (22/14/15)	1790 (32.12)	26.39 (0.67)	13.7 (0.28)	10.8 (0.24)	63.13 (1.26)	882 (15.67)	15.17 (0.25)	14.8 (0.23)	10.9 (0.19)	37.69 (0.63)	908 (13.09)	50.7	25.44 (0.38)	40.3
MT	55 (24/15/16)	1785 (35.82)	27.09 (0.64)	13.9 (0.26)	10.6 (0.23)	62.98 (1.21)	1207 (21.93)	20.48 (0.41)	14.7 (0.23)	11.1 (0.22)	43.58 (0.82)	578 (8.41)	32.4	19.4 (0.27)	30.8
LT	57 (24/16/17)	1750 (31.08)	25.05 (0.63)	13.5 (0.27)	10.4 (0.23)	61.54 (1.24)	1354 (22.40)	22.05 (0.39)	14.4 (0.22)	10.8 (0.18)	48.99 (0.83)	396 (5.88)	22.6	12.5 (0.21)	20.4
CK	51 (23/15/13)	1809 (30.24)	27.07 (0.58)	13.8 (0.25)	10.2 (0.24)	63.46 (1.23)									
	F *	0.40	0.94	1.05	0.88	0.96									

* Critical value, $F_{0.05}(3210) = 2.648$. Abbreviations: P, Pingjiang, A, Anhua, H, Huitong.

Table 3. Biomass, tree metrics of overstory and understory, and environment metrics (means (standard error [se])) in post-thinning year 6 in Masson pine forests in Hunan, China.

	HT		MT		LT		CK	
	Mean	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**
Overstory								
Aboveground biomass (Mg·ha^{-1})	74.79	1.57	91.18	1.48	93.59	1.51	107.48	1.49
Biomass increased (Mg·ha^{-1})	37.1	0.78	47.61	0.77	44.61	0.72	44.02	0.62
Biomass increment (Mg·ha^{-1}·a^{-1})	7.79	0.16	9.73	0.16	7.71	0.12	7.32	0.11
Shannon index	0.89	0.02	1.05	0.02	0.82	0.01	0.69	0.01
Dominance index	0.58	0.01	0.51	0.01	0.49	0.01	0.62	0.01
Gini index	0.55	0.01	0.57	0.01	0.43	0.01	0.36	0.01
Understory								
Aboveground biomass (Mg·ha^{-1})	6.87	0.13	7.31	0.12	5.12	0.09	4.51	0.07
Biomass increased (Mg·ha^{-1})	4.21	0.09	4.63	0.07	2.45	0.04	1.85	0.03
Biomass increment (Mg·ha^{-1}·a^{-1})	1.22	0.02	1.41	0.02	0.43	0.01	0.32	0.00
Shannon index	1.69	0.03	1.78	0.03	1.51	0.02	0.94	0.01
Dominance index	0.28	0.01	0.21	0.00	0.26	0.00	0.45	0.01
Gini index	0.44	0.01	0.45	0.01	0.43	0.01	0.42	0.01
Environment								
Light intensity (MJ·m^{-2}·d^{-1})	8.03	0.16	6.45	0.11	4.28	0.06	3.52	0.05
Soil moisture (%)	30.5	0.62	35.43	0.56	35.25	0.57	37.56	0.54
pH	5.03	0.11	5.18	0.09	5.15	0.09	5.06	0.07
Organic matter (g·kg^{-1})	40.43	0.82	37.83	0.62	28.87	0.47	22.58	0.32
Total N (g·kg^{-1})	2.32	0.06	2.48	0.03	1.97	0.03	1.57	0.02
Total P (g·kg^{-1})	0.37	0.01	0.33	0.01	0.36	0.01	0.36	0.01
Total K (g·kg^{-1})	7.31	0.15	7.01	0.11	9.87	0.15	8.05	0.12
Available N (mg·kg^{-1})	82.56	1.74	84.77	1.35	71.23	1.16	61.09	0.87
Available P (mg·kg^{-1})	3.19	0.07	3.24	0.05	3.96	0.07	2.06	0.03
Available K (mg·kg^{-1})	40.53	0.84	43.42	0.71	41.61	0.68	57.95	0.83

2.4.2. Relationships between Biomass Increment and Environmental Metrics

To assess relationships between post-thinning biomass increment and environmental metrics, two dissimilarity matrices (i.e., plot–biomass matrix and plot–environment matrix) were prepared and examined using Mantel tests [28]. In the plot–biomass matrix, overstory biomass increment (OBI) and understory biomass increment (UBI) were used as response variables to construct row vectors for each plot: $[OBI_{1i}, OBI_{2i}, OBI_{4i}, OBI_{6i}, UBI_{1i}, UBI_{2i}, UBI_{4i}, UBI_{6i}]$, where subscripts 1, 2, 4, and 6 indicate the first, second, fourth, and sixth years after thinning, and i indicates the ith plot. Similarly, the ten environmental metrics described in Table 3 were used as explanatory variables to form a plot–environment matrix with i rows and 10 columns. All variables were standardized using z-score normalization. The significance of the normalized Mantel coefficient was calculated using a two-tailed Monte Carlo permutation test with 10,000 permutations in the R "vegan" package [42]. A significant Mantel test ($p < 0.05$) indicates a linear correlation between the biomass dissimilarity matrix and the environment dissimilarity matrix, suggesting that the differences in the environment may be an important factor influencing the differences in biomass among different plots. Correlations between environmental metrics were calculated using Pearson's correlation coefficients.

2.4.3. Multivariate Statistical Analysis

Structural equation modeling (SEM) [43] was used to estimate the multivariate relationship in post-thinning forests and reveal the relative contributions of the explanatory variables to biomass increments across tree strata. The explanatory variables included thinning treatments, Shannon index, Dominance index, and Gini index for the overstory and understory, as well as significant environmental variables according to Mantel tests.

The initial multivariate model was established based on the productivity–diversity hypothesis [25,44]. An SEM path diagram was used to characterize the complex relationships among various explanatory variables and biomass increment. The path diagram was iteratively optimized, and pathways were added according to the residual correlations, or nonsignificant pathways were eliminated unless the pathways were biologically informative. Model fitting and evaluation were carried out based on the chi-square value (χ^2, $p > 0.05$), goodness-of-fit index (GFI > 0.9), and root square mean error of approximation (RMSEA < 0.05) [45]. The maximum likelihood method was used to estimate the coefficients of each edge in the path graph. The standardized path coefficients of the SEM reflect the direct, indirect, or total effects of explanatory variables on biomass increment. The SEM tests were performed in the R "lavaan" package [46].

3. Results

3.1. Effect of Thinning on Tree Biomass and Diversity

Thinning resulted in a lower aboveground biomass (AGB) of the overstory compared to the control plots (CK), but this difference gradually diminished with years after thinning (Figure 3a). Conversely, the understory AGB exhibited the opposite trend (Figure 3b). For example, in year 6, the mean overstory AGB in thinned plots was about 71%–87% of that in the CK, while the mean understory AGB was approximately 113%–162% higher in the CK.

Furthermore, tree growth changed significantly in biomass increment, Shannon index, Dominance index, and Gini index over time (Figure 4 and Table 4). The overstory biomass increment followed a temporal dynamic reflective of regeneration development, with the maximum mean value occurring in the CK during the early years and in thinned plots during the later years (Figure 4a and Table 4). For example, the maximum mean overstory biomass increment was observed in the CK at 7.03 $\mathrm{Mg{\cdot}ha^{-1}{\cdot}a^{-1}}$ in year 1, while it was observed under MT at 9.72 $\mathrm{Mg{\cdot}ha^{-1}{\cdot}a^{-1}}$ in year 6. The understory biomass increment consistently remained higher than those in the CK, with this advantage becoming increasingly apparent over time (Figure 4b). The Shannon index in the two strata showed similar biomass increment patterns over time, with thinned plots gradually exceeding the CK (Figure 4c,d). Furthermore, thinning generally reduces the Dominance index for both overstory and understory (Figure 4e,f) while also having a positive effect on the Gini index for the overstory (Figure 4g).

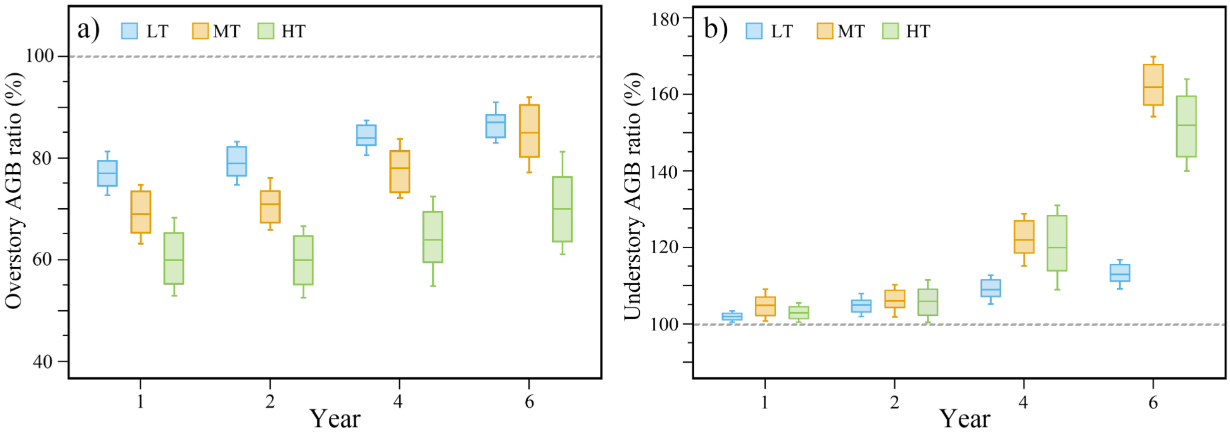

Figure 3. The relative ratios of aboveground biomass for both the (**a**) overstory and (**b**) understory during the post-thinning years compared to the CK (represented by the dashed line).

Table 4. p-values from full model analysis for biomass increment, Shannon index, Dominance index, and Gini index by strata class in Masson pine forests in Hunan, China. Significant values (<0.05) are in bold.

Strata Class	Effect	Biomass Increment	Shannon	Dominance	Gini
Overstory	Thinning	**<0.001**	**<0.001**	**0.002**	**<0.001**
	Year	**<0.001**	**<0.001**	**0.007**	**0.005**
	Thinning × Year	**<0.001**	**<0.001**	**<0.001**	**0.010**
Understory	Thinning	**<0.001**	**<0.001**	**<0.001**	0.320
	Year	**<0.001**	**<0.001**	**<0.001**	**<0.001**
	Thinning × Year	**<0.001**	**<0.001**	**0.003**	0.275

Because thinning and thinning × survey year were significant in most models of biomass increments and tree diversity for both the overstory and understory (Table 4), subsequent models were run by year to isolate the effects of thinning (Table 5). Thinning significantly increased biomass increments and the Shannon index for overstory and understory classes in later years (Figure 4 and Table 5). Specially, thinning initially reduced overstory biomass increment, but in later years, it exceeded that of the CK ($p \leq 0.001$ pairwise comparison). Similarly, understory biomass increment averaged 1.21 Mg·ha^{-1}·a^{-1} in HT and 1.43 Mg·ha^{-1}·a^{-1} in MT in year 6, both significantly higher than the 0.32 Mg·ha^{-1}·a^{-1} observed in the CK ($p \leq 0.001$ pairwise comparison). Thinning significantly increased the overstory Shannon index compared to the CK since year 4 ($p \leq 0.001$ pairwise comparison), peaking at a maximum mean value of 1.05 under MT in year 6, while their indices were similar in earlier years. The understory Shannon index was significantly different between various thinning treatments and the CK during post-thinning years ($p \leq 0.001$ pairwise comparison).

Thinning reduced the Dominance index for both the overstory and understory over time. For instance, the overstory Dominance index continued to decrease since the treatment, becoming significantly lower than the CK since year 4 ($p \leq 0.001$ pairwise comparison), reaching its minimum under LT (0.47) in year 6. Additionally, thinning significantly increased the Gini index for the overstory, with values notably higher than those of the CK during the post-thinning years ($p \leq 0.001$ pairwise comparison). No significant differences were observed in the understory Gini index.

Table 5. p-values from thinning intensity submodel analysis and overall means (standard error [se]) for biomass increment (Mg·ha^{-1}), Shannon index, Dominance index, and Gini index by survey year and stratum class in Masson pine forests in Hunan, China. Significant values (<0.05) are in bold.

Stratum Class	Year	Biomass Increment		Shannon		Dominance		Gini	
		p-Value	Mean (se)	p-Value	Mean (se)	p-Value	Mean (se)	p-Value	Mean (se)
Overstory	1	**0.001**	**5.46** (0.09)	0.255	0.63 (0.02)	0.424	0.68 (0.02)	**0.001**	**0.52** (0.02)
	2	**0.001**	**6.35** (0.13)	0.301	0.69 (0.01)	0.203	0.63 (0.01)	**0.001**	**0.49** (0.01)
	4	**0.001**	**7.92** (0.14)	**0.011**	**0.75** (0.02)	**0.001**	**0.57** (0.02)	**0.001**	**0.48** (0.01)
	6	**0.001**	8.09 (0.16)	**0.001**	**0.86** (0.02)	**0.001**	**0.54** (0.02)	**0.001**	**0.46** (0.01)

Table 5. *Cont.*

Stratum Class	Year	Biomass Increment		Shannon		Dominance		Gini	
		p-Value	Mean (se)	*p*-Value	Mean (se)	*p*-Value	Mean (se)	*p*-Value	Mean (se)
Understory	1	0.697	0.32 (0.01)	**0.001**	**1.05** (0.02)	0.085	0.46 (0.01)	0.834	0.33 (0.01)
	2	0.089	0.43 (0.01)	**0.001**	**1.21** (0.02)	0.001	0.36 (0.01)	0.06	0.35 (0.02)
	4	**0.001**	**0.52** (0.01)	**0.001**	**1.36** (0.03)	**0.001**	**0.32** (0.01)	0.068	0.39 (0.01)
	6	**0.001**	**0.84** (0.02)	**0.001**	**1.51** (0.03)	**0.001**	**0.29** (0.01)	0.726	0.43 (0.02)

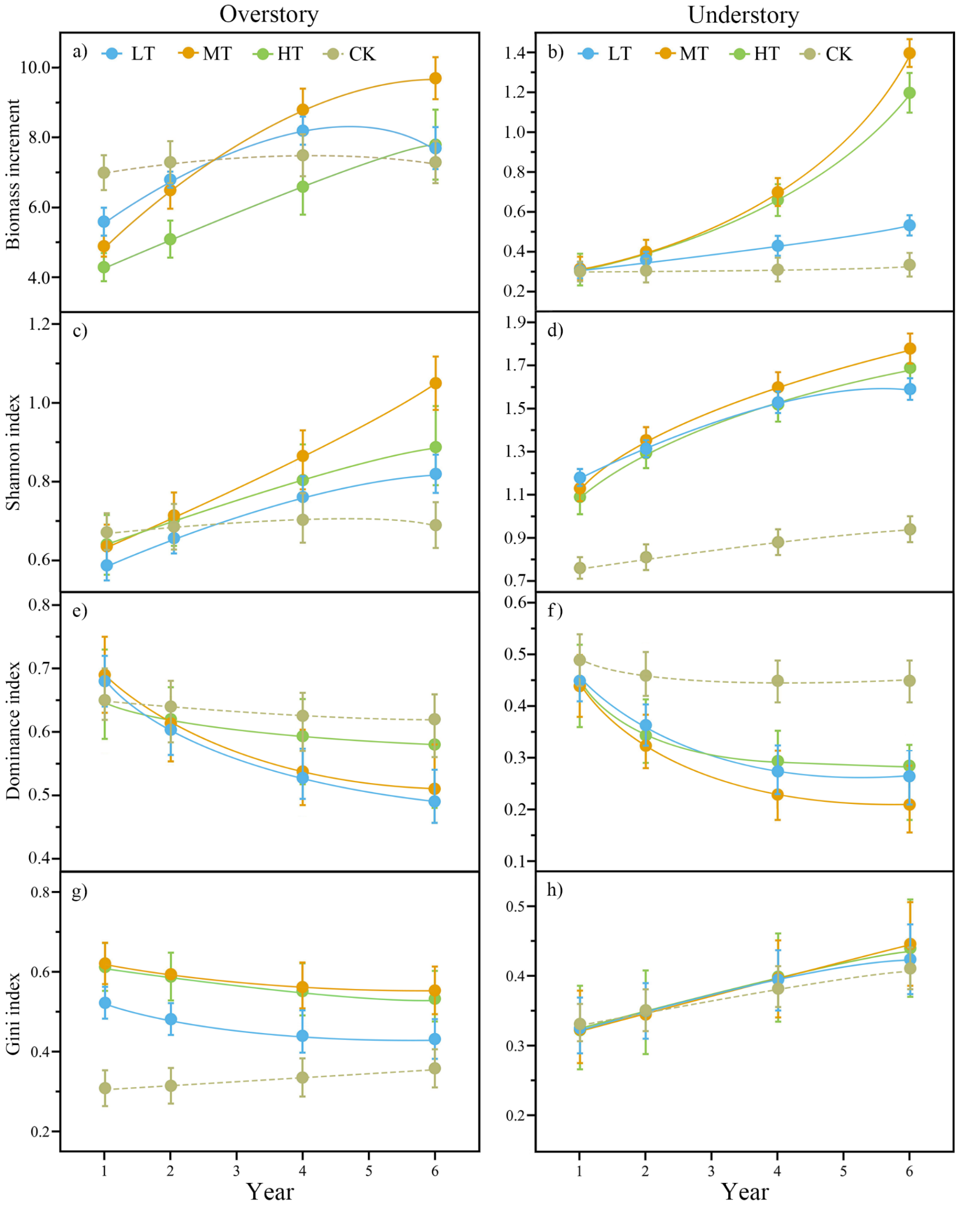

Figure 4. Mean biomass increment (**a**,**b**), Shannon index (**c**,**d**), Dominance index (**e**,**f**), and Gini index (**g**,**h**) during the post-thinning years in the overstory and understory of Masson pine forests in Hunan, China.

3.2. Correlation between Environmental Factors and Biomass Increment

We utilized the Mantel test to examine the correlations between distance-adjusted dissimilarities in biomass increments of both the overstory and understory with environmental metrics. Results showed that light intensity and soil physiochemical properties played distinct roles in driving biomass increments in the overstory and understory (Figure 5; Table 6). Specifically, light intensity (Mantel test; r = 0.502, $p < 0.05$) and soil organic matter (Mantel test; r = 0.355, $p < 0.05$) were positively correlated with overstory biomass increment. Soil moisture (Mantel test; r = −0.272, $p < 0.05$) was significantly negatively correlated with overstory biomass increment, and the correlation between soil moisture and overstory biomass increment was weaker than that between light intensity and soil organic matter. Soil organic matter (Mantel test; r = 0.424, $p < 0.05$), TN (Mantel test; r = 0.346, $p < 0.05$), and AP (Mantel test; r = 0.303, $p < 0.05$) were significantly correlated with understory biomass increment.

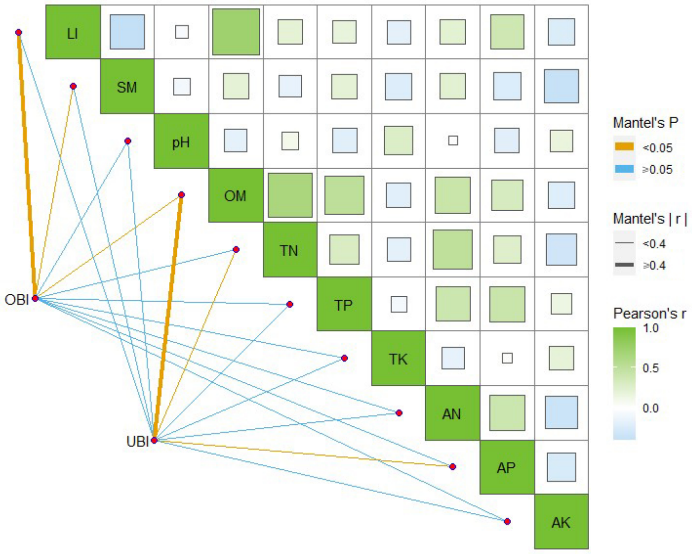

Figure 5. Biomass increments of overstory and understory were related to each factor by Mantel tests. Edge width corresponds to the Mantel's r statistic for the corresponding correlations, and edge color denotes the statistical significance based on 10,000 permutations. Pairwise comparisons of environmental factors are shown, with a color gradient denoting Pearson's correlation coefficients. Abbreviations: OBI, overstory biomass increment; UBI, understory biomass increment; LI, light intensity; SM, soil moisture; pH, soil pH; OM, soil organic matter; TN, total nitrogen; TP, total phosphorus; TK, total potassium; AN, available nitrogen; AP, available phosphorus; AK, available potassium.

Table 6. Effects of factors in the Mantel test analysis undertaken on biomass increments in the overstory and understory of Masson pine forests in Hunan, China. Significant values ($p < 0.05$) are in bold.

Factor	Overstory Biomass Increment ($\mathrm{Mg{\cdot}ha^{-1}{\cdot}a^{-1}}$)		Factor	Understory Biomass Increment ($\mathrm{Mg{\cdot}ha^{-1}{\cdot}a^{-1}}$)	
	p-Value	r-Value		*p*-Value	r-Value
LI	**0.001**	**0.502**	LI	0.064	0.232
SM	**0.046**	**−0.272**	SM	0.229	−0.146

Table 6. *Cont.*

Factor	**Overstory Biomass Increment (Mg·ha^{-1}·a^{-1})**		**Factor**	**Understory Biomass Increment (Mg·ha^{-1}·a^{-1})**	
	***p*-Value**	**r-Value**		***p*-Value**	**r-Value**
pH	0.169	−0.188	pH	0.612	−0.057
OM	**0.020**	**0.355**	OM	**0.001**	**0.424**
TN	0.072	0.209	TN	**0.022**	**0.346**
TP	0.053	0.243	TP	0.101	0.194
TK	0.413	−0.058	TK	0.062	−0.215
AN	0.066	0.211	AN	0.053	0.240
AP	0.153	0.189	AP	**0.041**	**0.303**
AK	0.212	−0.166	AK	0.275	−0.138

Furthermore, strong collinearity among environmental factors was observed (Figure 5). For example, decreases in soil moisture (Pearson's r = 0.37, $p < 0.05$) and increases in soil organic matter (Pearson's r = 0.73, $p < 0.05$) were accompanied by increases in light intensity. Soil moisture was negatively associated with AK (Pearson's r = 0.38, $p < 0.05$). A significant positive association was observed among soil organic matter, N, and P (Pearson's r = 0.32–0.54, $p < 0.05$).

3.3. Multivariate Statistical Analysis

We employed SEM to investigate how thinning treatments, environmental factors, tree diversity, and their interactions influence biomass increments in both the overstory and understory. The results indicated that SEM had a high level of goodness of fit for biomass increments in both the overstory (GFI = 0.932; RMSEA < 0.001) and understory (GFI = 0.978; RMSEA < 0.001), indicating a close match between the predicted and observed data. SEM accounted for 48% of the variation in overstory biomass increment (Figure 6a) and 57% of the variation in understory biomass increment (Figure 6b). Overall, the thinning treatments play an originative role in driving biomass increment via altering environmental conditions and tree diversity.

Specially, light intensity, which was directly affected by thinning treatments (standardized path coefficient, b = 0.32, $p < 0.05$), had a positive and direct effect on overstory biomass increment (b = 0.40, $p < 0.05$) (Figure 6a). Similarly, soil organic matter (b = 0.23, $p < 0.05$) and overstory Gini index (b = 0.42, $p < 0.05$), which were mainly affected by thinning, were positively correlated with overstory biomass increment. Soil moisture and overstory Shannon index had biological information for overstory biomass increment. Furthermore, soil organic matter, TN, and AP were mainly driven by thinning and positively affected (b = 0.22–0.34, $p < 0.05$) understory biomass increment (Figure 6b), which was consistent with the results of the Mantel tests (Table 6). Among tree diversity factors, the understory Shannon index (b = 0.47, $p < 0.05$) caused by thinning or environment had the strongest positive effect on understory biomass increment, followed by understory Dominance index and overstory Shannon index.

Standardized direct, indirect, and total effects (direct plus indirect effect) derived from SEM indicated that the effects of these factors on biomass increments in the overstory and understory were diverse (Figure 7); thus, the mechanisms underlying these effects might vary among tree strata. Thinning treatments (standardized total coefficient = 0.62) and the concomitant increase in light intensity (standardized total coefficient = 0.49) and overstory Gini (standardized total coefficient = 0.42) played key roles in shaping overstory biomass increment (Figure 7a). The tree diversity and environment, especially the understory Shannon and soil organic matter (standardized total coefficient = 0.47 and 0.35, respectively), induced by thinning were the main drivers of understory biomass increment (Figure 7b).

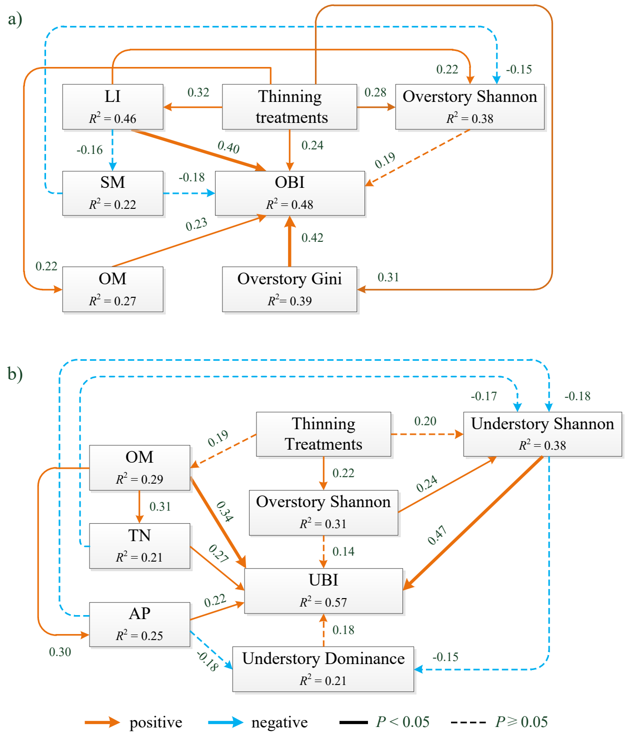

Figure 6. Structural equation model (SEM) showing the relationships among treatment, tree diversity, environment factors, and biomass increments in both the overstory (**a**) and understory (**b**). Red and blue arrows indicate positive and negative relationships, respectively. Arrow width corresponds to statistical significance. Numbers near the pathway arrow indicate the standard path coefficients. R^2 represents the proportion of variance explained for every dependent variable. Abbreviations: OBI, overstory biomass increment; UBI, understory biomass increment; LI, light intensity; SM, soil moisture; OM, soil organic matter; TN, total nitrogen; AP, available phosphorus.

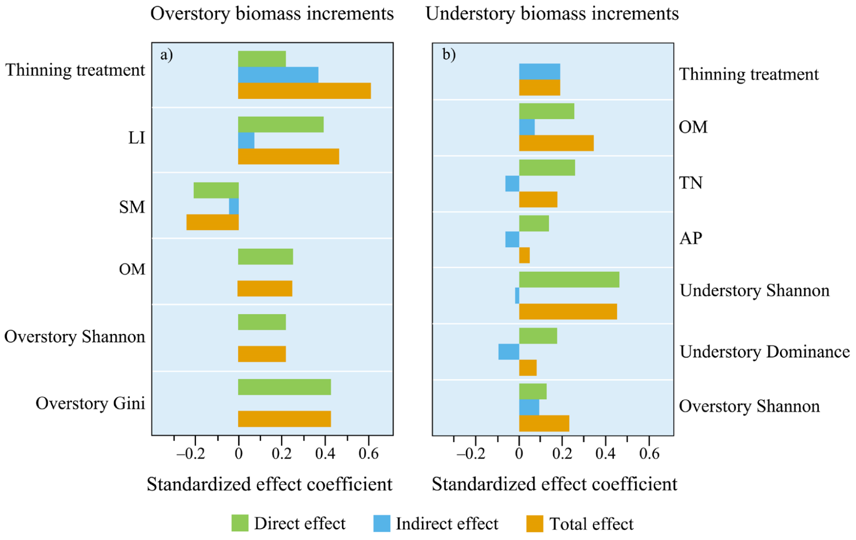

Figure 7. Standardized direct effect, indirect effect, and total effect (direct plus indirect effect) derived from SEM fitted to biomass increments in the overstory (**a**) and understory (**b**). The absolute of standardized total effect coefficient greater than 0.3 indicates that this is the key factor affecting biomass increment. Abbreviations: LI, light intensity; SM, soil moisture; OM, soil organic matter; TN, total nitrogen; AP, available phosphorus.

4. Discussion

Developing management approaches that can maintain ecosystem services and functions is crucial in the face of ongoing ecological change. Here, we tested the effect of thinning on biomass and diversity over six years in Masson pine forests in Hunan, China. The three sites exhibit similar climates, topographies, and stand conditions to ensure a stable and reliable thinning effect. In partial agreement with prediction 1, we found that MT is most effective in stimulating biomass increment and tree diversity, but this is evident in the later years. Prediction 2 was confirmed, as we found that environmental factors such as light intensity and soil physiochemical properties were not only correlated with biomass increments after thinning but also varied across tree strata. Moreover, thinning treatments, environmental factors, tree diversity, and their interactions had effects on biomass increments, and the mechanisms underlying these effects differed in the overstory and understory, which was consistent with prediction 3.

4.1. Effects of Thinning on Biomass of the Overstory and Understory

Thinning treatments can promote the growth and biomass of retained trees, but additional analysis is needed to understand their impact on the overall AGB of the stand. The short-term accumulation of retained tree biomass is not enough to make up for the biomass removed during thinning [16]. For example, in the first year, the post-treatment AGB of the overstory in the plots was noticeably lower than that of the CK, and the reduction expanded as the thinning intensity increased (Figure 3a). However, as thinning-induced biomass increment was released over time, the AGB difference between thinned plots and CK decreased. Thus, the positive effects of thinning treatments on biomass increment were evident in later years. In year 6, MT exhibited the highest average overstory biomass increment at 9.72 $Mg{\cdot}ha^{-1}{\cdot}a^{-1}$, significantly higher than both LT (7.71 $Mg{\cdot}ha^{-1}{\cdot}a^{-1}$) and HT (7.84 $Mg{\cdot}ha^{-1}{\cdot}a^{-1}$) (Figure 4a). Coupled with its moderate initial retained biomass, this resulted in the overstory AGB under MT exceeding that of other thinning treatments and approaching that of CK. Similarly, MT showed the highest average understory biomass increment at 1.43 $Mg{\cdot}ha^{-1}{\cdot}a^{-1}$ in year 6, followed by HT at 1.21 $Mg{\cdot}ha^{-1}{\cdot}a^{-1}$ and LT at 0.42 $Mg{\cdot}ha^{-1}{\cdot}a^{-1}$ (Figure 4b). The results indicated that while thinning initially reduced AGB in the overstory, it subsequently enhanced biomass increments in both the overstory and understory. MT provided the most significant benefits in later years.

In practice, the minimum stand density or residual basal area, which affects the retention biomass, might require consideration when establishing thinning strategies. Previous studies of middle-aged Masson pine forests have suggested that stand density should be maintained between 1000 and 1200 stem ha^{-1} [47,48]. The density-dependent stand-level optimization approach proposed by Bettinger, Graetz, and Sessions [34] suggested that the minimum residual basal area in pine forests should be approximately 16.0–20.5 $m^2{\cdot}ha^{-1}$. The range roughly coincides with the density and basal area of MT in the early years after thinning (Table 2). From this viewpoint, the MT (25%–35% tree removed) we examined could be considered as the optimal thinning intensity for the management of middle-aged Masson pine forests.

Our results indicated that overstory biomass increment from thinning treatments gradually exceeded those of the CK after year 4, suggesting that the benefits of thinning became apparent in the later years (Figure 4a). The understory biomass increment followed similar patterns over time (Figure 4b). The growth and regeneration of juvenile trees also exhibited a time lag effect in response to thinning treatments. Thus, determining the time scale at which positive responses are achieved may help explain the changes in post-processing time dynamics [9,34]. Previous studies indicated that an observation period consistent with the regeneration cycle of a forest should be adopted [23,49]. Ming [35] indicated that the post-treatment developmental pathway of a subtropical coniferous forest exhibited a unimodal pattern in which tree growth was most active for six to seven years and then gradually declined. While our study demonstrated the expected outcomes over the 6-year period, extending the observation duration remains a viable strategy for a more comprehensive analysis of forest recovery following thinning treatments.

4.2. Effects of Thinning on Diversity of the Overstory and Understory

Thinning releases growth space and increases light availability, which stimulates diverse responses by trees. Pioneer or shade-intolerant tree species exhibit stronger relative responses than other species to thinning. Wang and Liu [50] have also shown that overstory species richness increases less frequently in pine forest after cutting treatments, and emerging species are mostly saplings with a high demand for light. This also partially explains why the overstory accounted for the majority of the biomass but was not diverse in this study. Providing trees with enough space and time to grow, selectively retaining overstory species during thinning treatments, or planting trees might increase overstory species diversity [12].

Thinning had a more positive effect on understory species diversity than on overstory species diversity. Thinning can induce environmental heterogeneity and regulate understory habitat, facilitating the coexistence of different species. Some light-demanding species are likely to invade the understory after thinning, especially following MT and HT; however, such species were infrequently observed or absent in the CK. In addition, some native species do not require thinning to become established, but thinning often facilitates their establishment and expansion [11]. As shown in Figure 4d, the maximum mean Shannon index of the understory was obtained under MT within 6 years. The proportion of broadleaf and shade-tolerant species increases after thinning treatment. Although individuals of understory species are generally small, the number of species is relatively high. Furthermore, increases in understory species richness potentially induce the growth of a suite of mixed species, ranging from tree pests to disturbance-resistant species, and this can drive shifts to more stable and sustainable forest communities [21,51]. Therefore, the effective promotion of species coexistence to maintain forest resilience is a crucial consideration in implementing thinning treatments.

Tree size diversity in the stand was characterized using the Gini index, as has been conducted in several forest ecosystems [52]. Gini index values of 0, 0.5, and 1 correspond to even, uniform, and uneven forest structures, respectively [39]. In this study, MT and HT resulted in overstory Gini index values greater than 0.5; starting from a peaked reverse J, the success of natural regeneration and ingrowth can be indicated by a decreasing Gini index [39]. Under LT and the CK, the Gini index was less than 0.5, which indicates that self-thinning processes are dominant when stand development is determined by competition for light and space (Figure 4g). Tree size diversity can increase the complexity of stand structure in both the vertical and horizontal dimensions. Large trees usually occupy the canopy and are surrounded by smaller trees below, which can form a complementary growth space. A group of trees of different sizes can intercept rainfall and light according to their needs, which improves resource utilization and reduces competition among trees. In addition, large trees may provide shelter and shade for smaller trees [53], promoting their regeneration and growth. Therefore, tree size diversity should be considered when selecting MT to regulate the coexistence of trees of different sizes, reduce competition, and promote stand regeneration [23].

4.3. Correlation between Environmental Factors and Biomass Increments across Tree Strata

In this study, Mantel tests of environmental factors and biomass increment were conducted to test prediction 2, which proposes that light intensity and soil metrics were significantly correlated with biomass increments and that their effects on the overstory and understory differed. The environmental factors significantly correlated with overstory biomass in Masson pine forests were light intensity, soil organic matter, and soil moisture (Figure 5; Table 6). In a post-thinning forest, physiological regeneration niches are possessed by different species to cope with environment conditions. *P. massoniana*, which is the dominant overstory species, is the most light-demanding and thermophilic tree species, and optimum sites for this species include the upper canopy and canopy openings [21]. Under high light conditions, *P. massoniana* exhibits high photosynthetic activity and higher net CO_2 assimilation than other species over a growing period, which is consistent with the results of a previous study [54]. Carbon assimilation and xylem formation directly stimulate tree growth and regeneration, which promotes stand biomass accumulation. Furthermore, Huang et al. [55] showed that the duration of xylem formation in Masson pine forests in subtropical China was several months longer than expected due to photosynthetic activity, which indicates that the overstory might accumulate more biomass. Although the photosynthetic rate of trees increases as the amount of incident light increases, some physiological traits of trees cannot be ignored [56]. For example, under high irradiance and temperatures, native species in the understory such as *Castanopsis sclerophylla* may develop deep root systems to withstand adverse conditions or photoinhibition, and this results in the accumulation of underground biomass. In subtropical forests, intense irradiance accompanied by transpiration reduces the water potential of vegetation, leading to serious restrictions on understory trees. Thus, light has a significant positive effect on biomass increments of the overstory but not on the understory.

Mantel test results indicate that additional soil moisture over the growing season negatively affects biomass (Table 6). Most precipitation in subtropical China occurs during the growing season (April to September), which inevitably leads to increases in soil moisture. Previous studies indicate that the relationship between mean precipitation and biomass productivity in most coniferous forests is a nonlinear, concave-down function [57]. Increasing soil moisture in humid ecosystems may reduce tree biomass by reducing soil oxygen availability or increasing nutrient leaching. Therefore, Masson pine forests mostly grow well on the dry, xeric sides of mountains or ridges with high light [21,55]. This result also indicates that Masson pine forests would benefit from longer dry periods because they might result in better growth and greater biomass accumulation under continued climate warming.

Soil organic matter was strongly correlated with both overstory and understory biomass increments (Table 6), which suggests that thinning increased the content of soil organic matter and supplied more soil nutrients for tree growth [7]. In post-thinning forests, the main source of soil organic matter is litter, and this mainly stems from the remaining trees and logging residuals. Thinning enhances the abundance of understory plants (especially deciduous broadleaf species), which increases the accumulation of litterfall and enhances N storage [58]. Moreover, thinning increases solar radiation on the forest floor, soil temperature, and thus the decomposition of organic matter. The decomposition process is generally mediated by interactions between understory plants and microorganisms, which stimulate N mineralization and nitrification in forest soil [37]. The thinning-induced divergence in N demand favors an exploitative tree N-use strategy. For example, understory pioneer species had a greater demand for NO^{3-} than for NH^{4+} [59], which might promote N cycling and thus the biodiversity and structure of forests. Although the improvements to soil fertility associated with thinning are complex, organic matter and soil total N responded significantly and positively to understory biomass increments, suggesting that thinning enhances tree growth and maximizes forest production in warm regions [7].

Thinning also increased soil P availability, and this P was likely derived from organic matter, especially from logging residuals and roots [60]. As the P demand of understory plants and the number of remaining trees after thinning increased, the efficiency of P transformation from the subsoil increased, which enhanced understory biomass. However, the AP was relatively low (3.96–3.19 $mg \cdot kg^{-1}$), partly because the soil in southern China is acidic to strongly acidic, and the concentrations of free Fe^{3+} and Al^{3+} are high, which induces the precipitation of soil P [61]. In addition, thinning reduces forest canopy interception and increases surface erosion, which may increase soil eluviation and thus reduce concentrations of soil nutrients. Therefore, N and P should be supplemented to increase soil fertility during post-thinning years in Masson pine forests in southern China.

4.4. Relationships of Thinning, Environmental Factors, and Tree Diversity with Biomass Increments

We used SEM to show that thinning, tree diversity, environmental factors, and their interactions affected biomass increments (Figure 6), and the mechanisms underlying these effects differed in the overstory and understory (Figure 7); this was consistent with prediction 3. Thinning treatments, light intensity, and tree size diversity had significant effects on overstory biomass increment, and species richness and soil organic matter affected understory biomass.

Light inputs increase with thinning intensity. Liu, et al. [21] suggested that the average daily light intensity intercepted by the overstory in thinned subtropical forests is approximately 1.3 to 2.5 times higher than that of the understory. Trees with access to direct sunlight can generally respond better to thinning. In this study, dominant and codominant trees, such as *P. massoniana* and *Q. fabri*, are highly sensitive to light intensity and enhance their photosynthetic capacity under improved light environments. Previous reports indicated that thinning-induced light increase could have significant impacts on the CO_2 assimilation and nitrogen content of light-demanding trees, resulting in greater overstory biomass accumulation [35,55]. Therefore, the demand for light shapes overstory growth in a post-thinning Masson pine forest.

Although biomass generally increases exponentially with DBH, with large trees contributing most of the biomass, stands with trees of various sizes might be preferable [23]. Our results suggested that tree size diversity played an important role in driving overstory biomass increase (Figure 7a). The group selection strategy with thinning regulates the canopy tree size and stand structure and alleviates competition among neighboring trees, which may promote tree growth and biomass increments [62,63]. In this study, canopy trees of various sizes have complementary crown architectures and branch inclinations, especially under MT and HT, which might form a complex structure that intercepts resources at different points in space or at different times. But within the CK, even-sized trees invest heavily in height growth and less in branching to avoid shading from neighbors, thus inhibiting biomass increase. Jucker et al. [64] showed that competition for light and water was evident in monoculture stands, and mixing species with different sizes increased the amount of resources received and growth rates. These results suggest that both light intensity and tree size diversity could play prominent roles in mediating thinning-induced overstory biomass increase.

SEM showed that the standardized total coefficient of the understory Shannon index was larger than that of other factors, suggesting that species richness made the greatest contribution to understory biomass increment (Figure 7b). According to the diversity–productivity hypothesis, positive interactions among species improve the utilization of environmental resources when environmental conditions are favorable and different species are allowed to coexist, and this increases community biomass and productivity [65]. Complementarity and facilitation are the two primary mechanisms leading to productivity increments [66], and understory biomass gains after thinning exceeded yields in the CK stand. More diverse communities are more likely to include combinations of species that integrate resource patches by increasing niche complementarity with functionally dissimilar species [67]. Such facilitation could occur if certain species alter the environment in such a way that it enhances the fitness of other species. Seed availability is increased when the number of seed trees of different species in the overstory is higher, and this can enhance understory species richness [56]. A positive relationship between species richness and biomass increments for both the overstory and understory has also been observed in other recent studies [30,68]. Regulating the composition of species is essential for maintaining high community productivity and biomass. In practice, some native species, such as *Q. fabri* and *Castanopsis sclerophylla*, should be planted in the understory to stabilize understory tree diversity and improve productivity [35].

Although tree growth and community productivity theoretically increase with increasing soil fertility, the amplification of biomass gains in the understory post-thinning is usually pronounced in nutrient-poor soils in tropical and subtropical forests [69,70]. In this study, thinning increased soil organic matter inputs and soil N and P requirements, which can improve the fertility of soil and enhance tree growth. Our results suggest that the understory was affected to a greater degree by improvements in soil conditions compared with the overstory. When soil conditions are improved, conservative nutrient strategies might no longer be employed by some understory species, and their growth might be stimulated [36]. Therefore, understory biomass might be mainly driven by biotic interactions and improvements in soil conditions [37].

5. Conclusions and Management Implications

In conclusion, the findings of our study suggest that (1) moderate thinning (25%–35% of trees removed) was effective for biomass increment in middle-aged Masson pine forests in southern China, as well as for increasing tree diversity across tree strata; (2) diverse environmental factors were found to be correlated with biomass increment, including light intensity, soil organic matter, and other soil physiochemical properties; and (3) thinning increment, environmental factors, tree diversity, and their interactions might affect biomass increments, and the mechanisms underlying their effects might differ in the overstory and understory.

These results have implications for silvicultural practices when thinning treatments are used to regulate the regeneration and biomass of Masson pine forests. The excellent performance of moderate thinning in promoting diversity in the overstory and understory, as well as biomass increments, indicates that it could be considered the optimum treatment for maintaining Masson pine forest ecosystem services. Biomass increments are influenced by more factors than thinning increments alone, including tree diversity, light inputs, and soil physiochemical properties. Specifically, thinning increment, light intensity, tree size diversity, and their interactions had significant effects on overstory biomass increment, and species richness and soil organic matter affected understory biomass. In addition, thinning treatments should be dynamically programmed at specific intervals to improve light inputs and soil fertility, as this would enhance tree growth. Given that massive Masson pine forests have been established during the past decades in China, our findings are of significance for improving the ecosystem functions in sustainable forest management.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/f15071080/s1, Table S1: The main species and tree allometric growth model in Masson pine forests in Hunan, China.

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