

Short-term effects of management intensity on the spatial structure and biodiversity of *Camptotheca acuminata*-*Liquidambar formosana* mixed plantations

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Abstract

Aim of study: We aimed to 1) analyze the initial responses of stand spatial structure and understory biodiversity in *Camptotheca acuminata* Decne and *Liquidambar formosana* Hance mixed plantations to crop tree release (CTR) under varying thinning intensities, and 2) further explore the structural mechanisms driving biodiversity changes, intended to provide a theoretical basis for formulating effective CTR strategies to adjust spatial structure and modify biodiversity in the plantation.

Area of study: Beishan Forest Farm, Tongshan County, Hubei Province, China.

Material and methods: Twenty-five permanent plots were subjected to five thinning treatments: CK (control), WT (low-intensity), MT (moderate-intensity), HT (high-intensity), and ST (very high-intensity). Six spatial structure indices —uniform angle index (W), size ratio (U), mingling (M), openness (O), competition index (CI), and stand layer index (S)— were evaluated before, immediately after, and three years following CTR. Herbaceous and shrub layer biodiversity changes were also analyzed using redundancy analysis (RDA) and path analysis to identify key structural drivers.

Main results: Three years following CTR, W increased from 0.462 to 0.472, M from 0.593 to 0.640, and S from 0.429 to 0.569, while CI decreased from 0.689 to 0.589 but slightly increased by the end of the third year. Structural score rankings shifted over time. WT and HT improved herb layer diversity, while WT also enhanced the shrub layer's Shannon-Wiener index. Mingling promoted herb diversity, while competition intensity negatively affected it.

Research highlights: M and CI were key determinants of understory biodiversity. WT and HT treatments effectively improved diversity, offering practical guidance for sustainable mixed plantation management.

Keywords: *Camptotheca acuminata*-*Liquidambar formosana* plantation; crop tree release (CTR); species diversity; stand spatial structure; thinning intensity.

Efectos a corto plazo de la intensidad de manejo sobre la estructura espacial y la biodiversidad en plantaciones mixtas de *Camptotheca acuminata* y *Liquidambar formosana*

Resumen

Objetivo del estudio: Este trabajo tuvo como objetivos: 1) analizar las respuestas iniciales de la estructura espacial del rodal y de la biodiversidad del sotobosque en plantaciones mixtas de *Camptotheca acuminata* Decne., y *Liquidambar formosana* Hance sometidas a liberación de árboles de cultivo (CTR) con diferentes intensidades de aclareo, y 2) explorar los mecanismos estructurales que determinan los cambios en la biodiversidad, con el

propósito de aportar una base teórica para diseñar estrategias de CTR eficaces orientadas a optimizar la estructura espacial y mejorar la biodiversidad en las plantaciones.

Área de estudio: Finca Forestal Beishan, condado de Tongshan, provincia de Hubei, República Popular China.

Material y métodos: Se establecieron veinticinco parcelas permanentes en las que se aplicaron cinco intensidades de aclareo: CK (control), WT (baja), MT (moderada), HT (alta) y ST (muy alta). Se evaluaron seis índices de estructura espacial — índice de ángulo uniforme (W), relación de tamaño (U), mezcla (M), apertura (O), índice de competencia (CI) e índice de estratificación del rodal (S)— antes del CTR, inmediatamente después y tres años más tarde. Los cambios en la biodiversidad de las capas herbácea y arbustiva se analizaron mediante análisis de redundancia (RDA) y análisis de trayectorias para identificar los principales impulsores estructurales.

Resultados principales: A lo largo de los tres años posteriores al CTR, los valores de W aumentaron de 0.462 a 0.472, los de M de 0.593 a 0.640 y los de S de 0.429 a 0.569, mientras que el CI disminuyó de 0.689 a 0.589, aunque presentó un ligero repunte al final del tercer año. Las puntuaciones estructurales mostraron variaciones temporales. Los tratamientos WT y HT mejoraron la diversidad de la capa herbácea; además, WT incrementó el índice de Shannon–Wiener en la capa arbustiva. La mezcla tuvo un efecto positivo sobre la diversidad herbácea, mientras que la intensidad de competencia la afectó negativamente.

Aspectos destacados: Los índices M y CI fueron los principales factores que determinaron la biodiversidad del sotobosque. Los tratamientos WT y HT promovieron de manera efectiva la diversidad, proporcionando orientaciones prácticas para la gestión sostenible de plantaciones mixtas.

Palabras clave: *Camptotheca acuminata*–*Liquidambar formosana*; liberación de árboles de cultivo (CTR); diversidad de especies; estructura espacial del rodal; intensidad de aclareo.

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Introduction

Crop tree release (CTR) closely adheres to the principles of close-to-nature forestry, providing a pivotal method for advancing sustainable forest management within this framework (Lü, 2006). At its core, CTR is founded on the principles of natural succession (Li et al., 2022), utilizing selective thinning to optimize stand spatial structure and align natural processes with management objectives. This practice promotes species diversity and facilitates natural regeneration (Vogel et al., 2022). Furthermore, CTR accelerates natural succession, enhances forest productivity and ecological functions (Chen et al., 2022), increases carbon sequestration (Zou et al., 2023), and ultimately achieves sustainable development by integrating ecological, economic, and social benefits (Zhang et al., 2020).

Stand spatial structure is a crucial metric for evaluating spatial relationships among trees, competition dynamics, and growth conditions. It is commonly assessed by quantifying multi-objective structural parameters, including uniform angle scale, size ratio, mingling, and openness (Wu et al., 2013), which are highly controllable (Hui et al., 2016). Selective thinning, a fundamental aspect of CTR (Pang et al., 2023), plays a pivotal role in positively affecting stand spatial structure by regulating stand density and mitigating competition pressure (Li et al., 2021). For instance, selective thinning of interfering trees has been shown to significantly alter stand spatial structure and increase understory light availability in *Pinus massoniana* Lamb. mixed plantations (Zhang et al., 2023). Thinning typically increases openness and reduces competition, while its impact on mingling varies depending on whether tree removal targets multiple species or is species-selective (Vogel et al., 2022). Given this variability, a clearer understanding of the ecological importance of mingling is essential. Studies have shown that the positive effects of tree species richness on ecosystem

functions are closely linked to functional and phylogenetic diversity. Enhancing species richness can increase productivity, carbon storage, and ecosystem resilience (Huang et al., 2018). However, species diversity indices do not account for spatial segregation among species. In contrast, the mingling index reflects both species composition and spatial relationships within a stand, providing a more accurate assessment of structural diversity (Tang et al., 2012). Studies have demonstrated that CTR effectively modifies spatial structure and influence ecological processes across diverse forest types. In natural secondary forests of *Quercus mongolica* Fisch. ex Ledeb., CTR increases vertical stratification complexity and facilitates community succession toward greater structural stability (Feng et al., 2018). In *Cunninghamia lanceolata* (Lamb.) Hook. mixed plantations, CTR significantly increases openness, alleviates competition pressure (Huang et al., 2022), further modifies spatial distribution patterns, and promotes the development of healthy and resilient stands (Wu et al., 2015; Zhao et al., 2021; Chang et al., 2022). As a result, CTR has been widely implemented in forest management practices, demonstrating its effectiveness in enhancing forest ecosystem stability and significantly improving ecological benefits (Huang et al., 2022).

Crop tree release (CTR) has been reported to adjust stand spatial structure and, in some cases, to increase species richness in the understory shrub and herbaceous layers, contributing to overall biodiversity (Zhang et al., 2017). By modifying structural conditions, CTR may create more favorable growth conditions for understory vegetation, thereby increasing the diversity of shrubs and herbs (Wei et al., 2019), but further studies are needed to verify the general applicability of its effects on biodiversity. Studies indicate that the uniform angle index of the tree layer is strongly correlated with species evenness and richness in both the shrub and herbaceous layers (Zhang ZX et al., 2024). Understory openness is primarily influenced by stand density (Royo & Carson, 2006), while tree spatial patterns—such as those captured by the uniform angle index—may also contribute to micro-scale heterogeneity in light and space conditions (Pommerening, 2002). For instance, in *P. massoniana* mixed plantations, shrub species diversity tends to be higher in stands where the uniform angle index indicates a more random spatial distribution pattern (Zhang et al., 2021), promoting the growth of shrubs and herbaceous plants under the canopy of broadcast-sown stands (Li et al., 2016). Furthermore, areas with higher tree species richness tend to exhibit higher mingling index values in the tree layer and higher species richness in the shrub layers (Wang et al., 2024). For example, in *Abies fabri* (Mast.) Craib mixed plantations, a higher mingling index achieved through selective thinning has been shown to contribute to the long-term stability of species diversity (Liu et al., 2022). Although the neighborhood comparison (size ratio) has a limited direct effect on species diversity, it may indirectly influence herbaceous layer diversity by shaping spatial patterns of canopy coverage and micro-site competition (Ma & Zhang, 2023). Selective thinning, through adjustments to neighborhood comparison, creates more favorable growth environments for understory vegetation, thereby promoting species richness (Zhu et al., 2018).

In mixed plantations, low-density stands demonstrate significantly higher understory species diversity compared to high-density stands, primarily due to their random uniform angle index and greater openness (Mao et al., 2021). Adjusting stand density not only enhances openness but also significantly increases Simpson and Pielou's evenness indices, further fostering biodiversity (Zhang et al., 2022).

Although CTR has proven effective in optimizing stand spatial structure and enhancing biodiversity, previous studies have largely overlooked the dynamic effects of different thinning intensities on stand spatial structure and understory diversity in shrub and herbaceous layers, and only limited research has focused on the temporal dynamics of spatial structure-diversity relationships, particularly over short-to-medium time frames such as the three years examined in this study.

This study investigates *Camptotheca acuminata*-*Liquidambar formosana* mixed plantations, applying CTR under varying thinning intensities to address the following key scientific questions:

- (1) Which thinning intensity leads to the greatest changes in key stand spatial structure indicators three years after CTR?
- (2) Which thinning intensity maximally enhances shrub and herb layer biodiversity three years after CTR?
- (3) What are the key spatial structure factors driving shrub and herbaceous layer biodiversity? By addressing these questions, this study aims to determine the most appropriate thinning intensity and identify the key spatial structure factors influencing biodiversity. The findings are expected to provide a scientific foundation for developing effective CTR strategies to optimize the spatial structure of *Camptotheca acuminata*-*Liquidambar formosana* mixed plantations and enhance their biodiversity.

Materials and methods

Study area

The study was conducted in the Beishan Forest Farm, located in Tongshan County, southeastern Hubei Province, China (114°26'E, 29°31'N). The area is characterized by low hills and ridges, with red soils (pH 5.0–6.0) as the dominant soil type. It lies within a subtropical monsoon climate zone, featuring abundant sunlight, ample heat, a long frost-free period, and synchronized rainfall and heat conditions. The annual mean temperature is 16.3 °C, with an average annual precipitation of 1,577.0 mm, concentrated mainly between April and August. The average annual evaporation is 1,363.0 mm, and the mean relative humidity is 80.0%.

The forest farm is dominated by mixed plantations. The main tree species include *C. acuminata*, *L. formosana*, *Liriodendron chinense* (Hemsl.) Sarg., *Eucommia ulmoides* Oliv., and *Cunninghamia lanceolata* (Lamb.) Hook. The shrub layer primarily consists of *Rosa cymosa* Tratt., *Lindera glauca* (Siebold & Zucc.) Blume, *Elaeagnus argyi* H. Lév., *Smilax china* L., and *Rubus adenophorus* Rolfé. The herbaceous layer includes *Ophiopogon bodinieri* H. Lév., *Semiaquilegia adoxoides* (DC.) Makino, *Dryopteris championii* (Benth.) C. Chr., *Oplismenus undulatifolius* (Ard.) Roemer & Schuit., and *Aster ageratoides* Turcz.

Plot design and survey

In October 2020, a *Camptotheca acuminata*-*Liquidambar formosana* mixed plantation with consistent site conditions was selected as the experimental forest in the Beishan Forest Farm, Tongshan County. The study area was situated at an elevation of 268–303 m, with a slope gradient of 8°–15° in middle-slope positions. The plantation was established in 2002 and 2003 on clear-cut *C. lanceolata* sites, with an initial planting density of 2 m × 3 m. By the time of the study, *C. lanceolata* had regenerated as coppice forests.

The experiment followed a completely randomized block design with 25 standard plots (20 m × 20 m; 400 m² each). Geographic coordinates, elevation, aspect, and slope gradient of each plot were recorded using RTK devices. Within each plot, one 5 m × 5 m shrub subplot and one 1 m × 1 m herbaceous subplot were established at the four corners and the center. All trees with a diameter at breast height (DBH) ≥ 5 cm were tagged and numbered, and their coordinates, species, DBH, tree height, and crown width were recorded.

Five management treatments were implemented: CK (control, no thinning), WT (low-intensity thinning), MT (moderate-intensity thinning), HT (high-intensity thinning), and ST (super high-intensity thinning), each replicated five times. In November 2020, thinning operations were performed to remove interfering, defective, and suppressed trees. The thinning intensities corresponded to stand volume reductions of 0% (CK), 16.3% (WT), 25.6% (MT), 31.1% (HT), and 41.8% (ST).

All experimental plots were established within stands of uniform site conditions. Prior to thinning, the average stand density was approximately 1850 trees·ha⁻¹. The stand was dominated by *C. acuminata* (34.24%) and *L. formosana* (18.58%) based on the number of trees, with several other species present in smaller proportions and evenly distributed (Xu et al., 2023). Although their relative abundance was lower, these additional species may still influence stand dynamics, particularly through their contributions to vertical structure and understory conditions. Thinning was conducted within crop tree spatial units following near-natural management principles: “remove large, retain small; remove similar, retain different; and retain vertical stratification”. These principles were applied consistently across all species, without preference for *C. acuminata* or *L. formosana*, ensuring that the observed treatment effects were not influenced by species-specific bias.

In November 2023, a resurvey was conducted in all 25 plots. Tree-layer variables were measured using the same protocol as in the initial 2020 survey, and additional records of boundary trees and dead trees were included (Table 1). The shrub and herbaceous layers were reassessed, collecting data on species names, stem (or clump) counts, coverage and height. Data on natural regeneration were collected for documentation purposes but were not included in the analysis of understory diversity.

Table 1. Basic information of *Camptotheca acuminata*–*Liquidambar formosana* mixed plantations under different thinning intensities at Beishan Forest Farm, Tongshan County, Hubei Province, China.

Plot code	Thinning intensity	Immediately after CTR				Three years after CTR					
		Mean DBH/cm	Mean tree height/m	Stand Density /plant·hm ⁻²	Canopy density	Mean DBH/cm	Mean tree height/m	Stand Density /plant·hm ⁻²	Canopy density	Ingrowth tree/plant	Mortality tree/plant
15	ST	11.0	8.1	900	0.50	13.3	9.1	800.0	0.80	2	6
5		12.5	9.0	825	0.55	14.0	10.1	800.0	0.82	5	3
10		12.2	9.6	950	0.55	14.3	10.5	850.0	0.80	2	6
24		13.7	12.4	700	0.45	15.6	13.1	625.0	0.79	2	5
16		12.0	10.1	1050	0.50	15.0	11.8	875.0	0.80	6	9
20	HT	11.8	9.8	1000	0.55	13.6	10.8	900.0	0.80	2	6
3		10.6	9.7	1450	0.60	12.4	10.9	1175.0	0.85	4	13
23		11.2	11.9	1200	0.60	13.4	12.9	975.0	0.80	3	11
2		9.7	9.3	1550	0.65	11.0	10.1	1500.0	0.88	2	4
6		9.3	9.0	1875	0.75	10.2	9.5	1825.0	0.95	5	4
9	MT	11.1	9.5	1575	0.65	12.7	10.1	1475.0	0.88	4	6
1		8.8	8.1	2025	0.80	9.6	8.5	1975.0	0.92	5	4
4		10.2	9.2	1775	0.70	11.3	10.1	1475.0	0.90	3	14
14		10.1	10.2	1825	0.70	11.4	10.8	1800.0	0.92	7	3
11		10.1	10.7	1800	0.70	11.4	11.8	1650.0	0.90	5	8
22	WT	12.4	9.3	1375	0.55	14.5	10.6	1125.0	0.85	3	12
21		12.9	11.9	1400	0.65	14.1	12.2	1375.0	0.91	3	3
25		11.2	10.1	1700	0.70	12.6	10.7	1450.0	0.90	3	12
18		10.4	9.1	1750	0.70	10.9	11.6	1400.0	0.92	3	16
12		10.5	10.1	1800	0.75	11.8	10.7	1475.0	0.90	3	15
17	CK	10.4	9.6	2050	0.85	10.8	10.2	1725.0	0.92	3	15
8		13.1	12.4	1500	0.65	14.0	13.2	1150.0	0.87	1	16
19		12.4	12.4	2325	0.80	13.4	13.1	1975.0	0.95	3	16
7		9.3	9.4	2575	0.95	10.1	9.9	2375.0	0.94	3	10
13		12.4	13.8	2325	0.95	13.8	14.5	2125.0	0.95	1	10

CK: control; WT: weak thinning; MT: moderate thinning; HT: high thinning; ST: super high thinning. CTR: crop tree release; DBH: diameter at breast height

Stand spatial structure evaluation model

The uniform angle index (W), neighborhood comparison index (U), mingling index (M), stand layer index (S), openness index (O), and Hegyi competition index (CI) were selected as key indicators to evaluate forest spatial structure (Hui et al. 2016). W_i ranges from 0 to 1, with values of 0.00, 0.25, 0.50, 0.75, and 1.00 corresponding to absolutely uniform, uniform, random, uneven, and clumped tree distributions, respectively; U_i ranges from 0.00 to 1.00, with values of 0.00, 0.25, 0.50, 0.75, and 1.00, indicating tree dominance levels from dominant, subdominant, intermediate, suppressed, to completely suppressed; M_i also ranges from 0.00, 0.25, 0.50, 0.75 to 1.00, reflecting species mingling degrees from none, weak, moderate, strong, to complete (Hui et al. 2016). S_i ranges within (0, 1], where higher values represent greater complexity in vertical stratification. O_i ranges within (0, ∞) and is classified into five intervals —(0, 0.2], (0.2, 0.3], (0.3, 0.4], (0.4, 0.5], and (0.5, ∞)— indicating growing space from severely limited to very sufficient (Cao et al. 2015). CI is a dimensionless index of competition intensity; higher values indicate stronger competitive pressure experienced by individual trees (Hui et al. 2016).

To better quantify the deviation from spatial randomness, we transformed the original uniform angle index W ($0 < W \leq 1$) to $W' = |W - 0.5|$, where smaller W_i indicates a distribution closer to spatial randomness. For this purpose, only values in the range $W' \in (0, 0.5]$ were considered, with smaller values indicating less deviation from random spatial distribution (Cao et al., 2015). To eliminate edge effects, a 2 m buffer zone was established inward from the plot boundaries during the calculation of spatial structure indices. The stand spatial structure score was determined using a multi-objective comprehensive evaluation method (Cao et al. 2015).

$$Q_i = \frac{\frac{1 + M_i}{\sigma_{M_i}} \cdot \frac{1 + O_i}{\sigma_{O_i}} \cdot \frac{1 + S_i}{\sigma_{S_i}}}{\frac{1 + CI_i}{\sigma_{CI_i}} \cdot \frac{1 + W'_i}{\sigma_{W'_i}} \cdot \frac{1 + U_i}{\sigma_{U_i}}}$$

where Q_i is the stand spatial structure score of the i -th reference tree; M_i , O_i , S_i , CI_i , W'_i , and U_i represent the mingling index, openness index, stand layer index, competition index, transformed uniform angle index, and neighborhood comparison index of the i -th reference tree, respectively; and σ denotes the standard deviation of each indicator.

The stand spatial structure was evaluated using the mean values of the stand spatial structure indices (Zhao et al., 2021):

$$\bar{Q} = \frac{1}{N} \sum_{i=1}^N Q_i$$

where the overbar ($\bar{Q}$) represents the mean stand spatial structure score of all N reference trees in the plot.

Calculation of species diversity

Margalef index (MI), Shannon-Wiener index (H), Simpson index (D), and Pielou evenness index (J) were selected as indicators of species diversity for the shrub and herbaceous layers.

To compare diversity changes, we calculated the rates of change (R_x) for Margalef index (MI), Shannon index (H), Simpson index (D), and Pielou's evenness index (J) between pre-treatment and three years after CTR as:

$$R_x(\%) = \frac{X_t - X_0}{X_0} \times 100\%$$

where X_0 and X_t are the diversity index values before and after thinning, respectively. Positive values of R_x indicate an increase in diversity, negative values indicate a decrease, and zero indicates no change.

Data processing

Data collation and basic statistical analyses were conducted using Excel 2021 and SPSS 22. One-way ANOVA with Duncan's post-hoc tests ($P < 0.05$) was used to assess differences in stand structure indices and biodiversity among thinning treatments, and the results were expressed as mean $\pm$ standard deviation. To explore how stand spatial structure influences understory biodiversity, we employed redundancy analysis (RDA) using Canoco 5.0. RDA is appropriate when multiple response variables are assumed to respond linearly to continuous predictor variables. In our study, species diversity indices of the herbaceous and shrub layers (Hh , Dh , Jh and Mh for the Shannon-Wiener index, Simpson index, Pielou index and Margalef index of herbs, and Hs , Ds , Js and Ms for the Shannon-Wiener index, Simpson index, Pielou index and Margalef index of shrubs) were used as response variables, while six stand spatial structure indicators — W , U , M , O , S and CI — served as explanatory variables. This analysis was based on the hypothesis that spatial structural attributes shaped by thinning influence species diversity patterns in a linear fashion. Forward selection based on RDA was also performed in Canoco 5 to identify the most influential structure indices, with the significance of both RDA axes and selected variables tested using 999 Monte Carlo permutations. To further clarify the direct and indirect influences of stand spatial structure components on biodiversity, path analysis was conducted using the lavaan package in R 4.4.0. This method was chosen to test our hypothesized causal pathways. The model structure was informed by ecological theory and preliminary RDA results, and aimed to disentangle complex interactions among structure indices and their impact on biodiversity. Figures 1–3 were produced using Origin 2021.

Results

Changes in stand spatial structure before, immediately after, and three year post-thinning

To assess the temporal dynamics of stand spatial structure in response to CTR, changes in structural indices were examined at three time points—pre-treatment, immediately post-treatment, and three years after CTR—within each thinning intensity. Control plots (CK) were not included in this analysis, as the objective was not to compare among treatments but to evaluate changes over time within each treatment group.

Figure 1 illustrates the dynamic changes in stand spatial structure indices before management, immediately after management, and three years following CTR (excluding CK). Before management, the median value of W was 0.462. This increased to 0.474 immediately after management, approaching the random distribution range of [0.475, 0.517] (Hui et al., 2016). Three years following CTR, W remained relatively stable at 0.472. For U , the median value was 0.487 before management, and it decreased slightly to 0.485 both immediately after and three years following CTR. Regarding M , the median value increased from 0.593 before management to 0.619 immediately after, and further to 0.640 at three years following CTR, indicating an increased level of tree species segregation. For S , the median value rose from 0.429 before management to 0.478 immediately after, and further to 0.569 at three years following CTR, reflecting a progressive shift of vertical stand structure. O increased from 0.226 before management to 0.269 immediately after, and further to 0.293 at three years following CTR, demonstrating improved vertical space in the stand. As for CI , the median value decreased significantly from 0.689 before management to 0.589 immediately after. By three years following CTR, CI slightly increased to 0.612 but remained lower than the pre-management level. This suggests that competition among trees was significantly reduced following management. Although competition pressure began to rebound over time, it remained at a relatively low level in the short term.

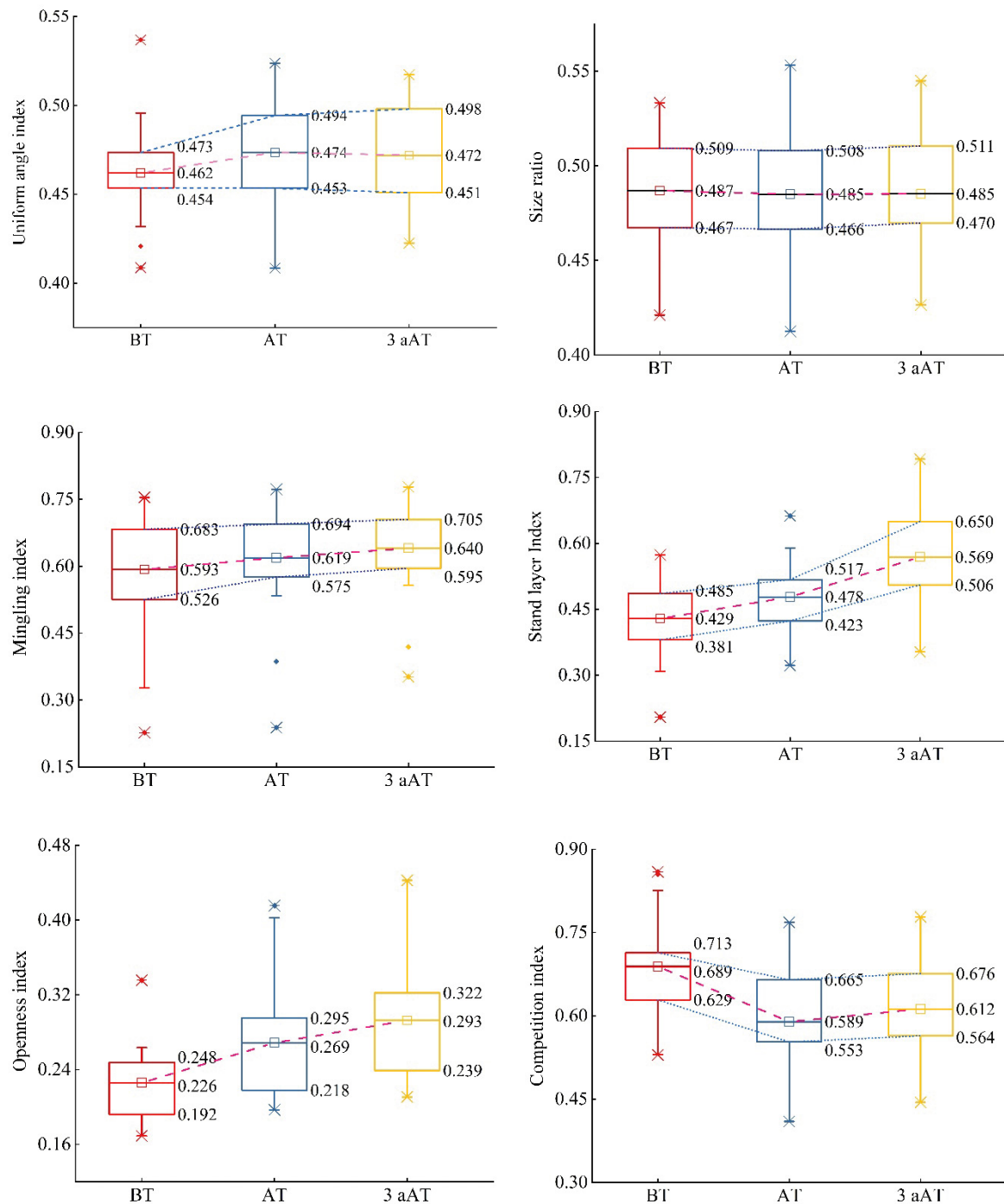


Figure 1. Dynamics of stand spatial structure index before, immediately after and three years after CTR under different thinning intensities in *Camptotheca acuminata*–*Liquidambar formosana* mixed plantations at Beishan Forest Farm, Tongshan County, Hubei Province, China. BT: Before thinning; AT: After thinning; 3aAT: Three years after CTR.

Note: The CK (control) treatment is not included in this figure.

Evaluation of stand spatial structure across thinning intensities before, immediately after, and three years after CTR

To evaluate the integrated spatial response to thinning, we used the mean stand spatial structure score ($\bar{Q}$), which aggregates multiple structural indices and serves as the response variable in this section.

Table 2 presents the changes and differences in stand spatial structure scores before CTR, immediately after CTR, and three years after CTR. Before CTR, no significant differences were observed among the treatment scores ($F = 0.471$, $P = 0.756$). After CTR, the scores increased significantly with thinning intensity ($F = 9.288$, $P = 0.000$), with the rankings as follows: ST (0.248) > HT (0.221) > MT (0.215) > WT (0.206) > CK (0.143). Three years after CTR, the stand spatial structure scores remained significantly different ($F = 9.258$, $P < 0.001$), with the following rankings: ST (0.189) > MT (0.161) > WT (0.156) > HT (0.153) > CK (0.132).

Table 2. Stand spatial structure score ($\bar{Q}$) of *Camptotheca acuminata*–*Liquidambar formosana* mixed plantations before, immediately after, and three years after CTR under different thinning intensities in Beishan Forest Farm, Tongshan County, Hubei Province, China.

Thinning intensity	QB	QA	Q3a
ST	0.154±0.037a	0.248±0.056a	0.189±0.024a
HT	0.150±0.015a	0.221±0.018ab	0.153±0.007b
MT	0.159±0.011a	0.215±0.018ab	0.161±0.011b
WT	0.155±0.010a	0.206±0.004b	0.156±0.010b
CK	0.143±0.018a	0.143±0.018c	0.132±0.016c
<i>F</i>	0.471	9.288	9.258
<i>P</i>	0.756	0.000	0.000

QB, QA, and Q3a represent the stand spatial structure scores before, immediately after, and three years after crop tree release (CTR), respectively. The values are presented as mean ± standard deviation, with different letters indicating significant differences ($P < 0.05$, Duncan). CK: control; WT: weak thinning; MT: moderate thinning; HT: high thinning; ST: super high thinning

Changes in species diversity before and three years after CTR

Before CTR, no significant differences were observed in the species diversity indices of the herbaceous layer across the thinning treatments. However, three years following CTR, both Dh and Hh exhibited notable changes across treatments. For Dh , all treatments showed higher values than the CK treatment, with MT significantly differing from CK. The rates of change (RDh) were ranked as follows: HT (39.42%) > WT (34.73%) > ST (25.27%) > MT (19.23%) > CK (10.95%).

For Hh , all treatments had higher values than CK, although the differences were not statistically significant. The rates of change (RHh) were ranked as: HT (64.50%) > WT (63.23%) > ST (34.78%) > MT (33.38%) > CK (19.85%).

Three years following CTR, Jh for all treatments exceeded that of CK, although the differences were not statistically significant. The rates of change (RJh) were ranked as follows: ST (10.55%) > HT (1.68%) > WT (-1.00%) > MT (-2.70%) > CK (-4.57%).

Although Mh for all treatments three years following CTR was higher than that of CK, it was lower than the pre-management values for each treatment, with no significant differences observed among treatments. The rates of change (RMh) were ranked as: WT (-2.37%) > HT (-3.78%) > MT (-8.49%) > CK (-11.96%) > ST (-22.03%).

Overall, HT and WT treatments exhibited the strongest increase on Dh and Hh (Figure 2).

Before the CTR intervention, Hs was generally higher in the treated plots than in CK, with a significant difference observed only between the HT and CK treatments. No significant differences were detected for other diversity indices across treatments.

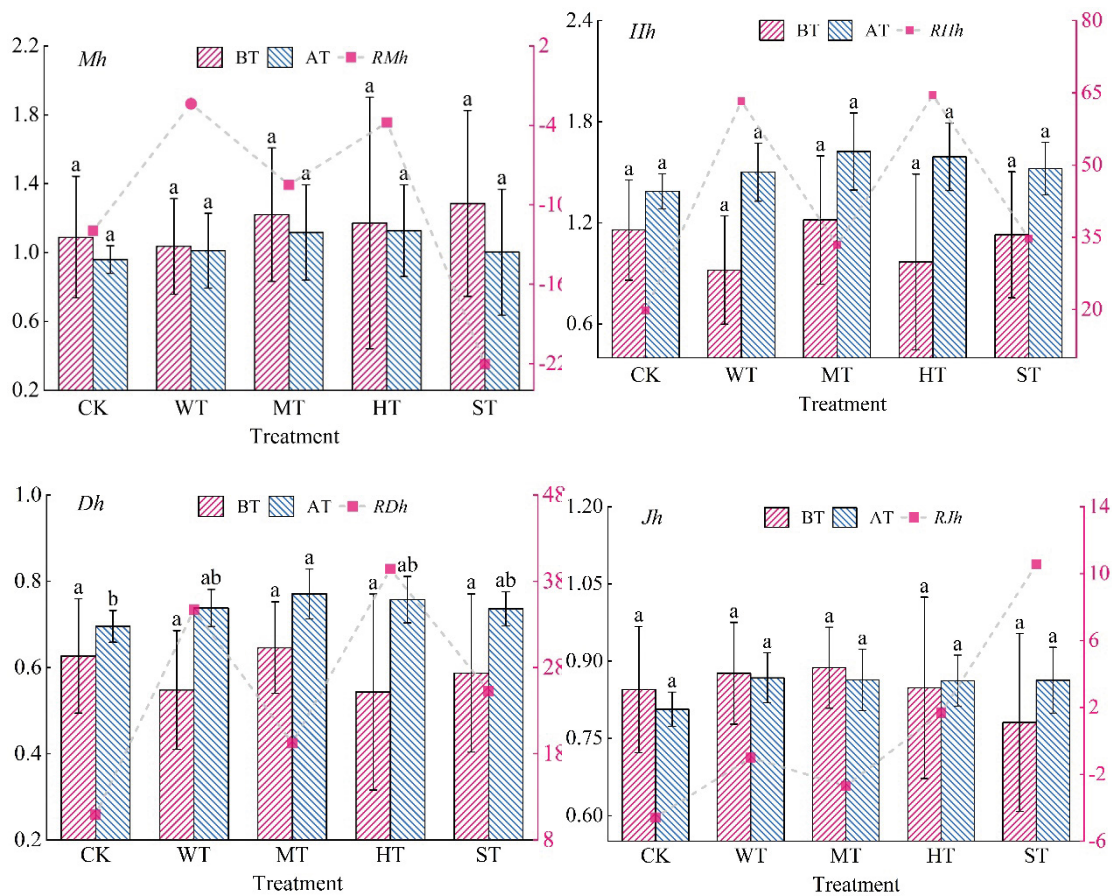


Figure 2. Changes and rates of change in herbaceous layer species diversity before and three years after crop tree release (CTR) under different thinning intensities in *Camptotheca acuminata*–*Liquidambar formosana* mixed plantations at Beishan Forest Farm, Tongshan County, Hubei Province, China. Different lowercase letters indicate significant differences at $P < 0.05$ based on Duncan's test. CK: control; WT: weak thinning; MT: moderate thinning; HT: high thinning; ST: super high thinning. BT: Before thinning; AT: After thinning. RDs: Rates of change.

Three years following CTR, D_s for all treatments exceeded that of CK, with the WT (0.840) and HT (0.817) treatments showing significant differences compared to CK (0.703). The rates of change (RD_s) were ranked as follows: WT (19.52%) > ST (4.82%) > CK (0.44%) > HT (0.02%) > MT (-3.06%). WT treatment demonstrated the most significant improvement in D_s , while MT treatment showed a slight decline.

For H_s , all treatments also had higher values than CK three years following CTR, with WT (2.043) significantly differing from CK. The rates of change (RH_s) were ranked as: WT (33.53%) > CK (10.10%) > ST (9.16%) > HT (3.71%) > MT (-4.38%). WT treatment had the most pronounced positive effect on H_s , while MT treatment showed a slight decline.

Three years following CTR, J_s under WT treatment (0.873) was significantly higher than CK (0.738) and ST (0.757). The rates of change (RJ_s) were ranked as: WT (10.74%) > HT (-0.77%) > ST (-1.26%) > MT (-5.79%) > CK (-6.40%). WT treatment significantly improved species evenness, while other treatments showed varying degrees of decline.

For M_s , all treatments had higher values than CK three years following CTR, although the differences were not significant. The rates of change (RM_s) were ranked as: CK (42.27%) > WT (40.90%) > ST (35.20%) > HT (27.01%) > MT (21.31%). Both CK and WT treatments exhibited the most notable increases in species richness.

Overall, the HT and WT treatments demonstrated substantial improvements across multiple diversity indices, while the MT treatment exhibited slight declines in most indices (Figure 3).

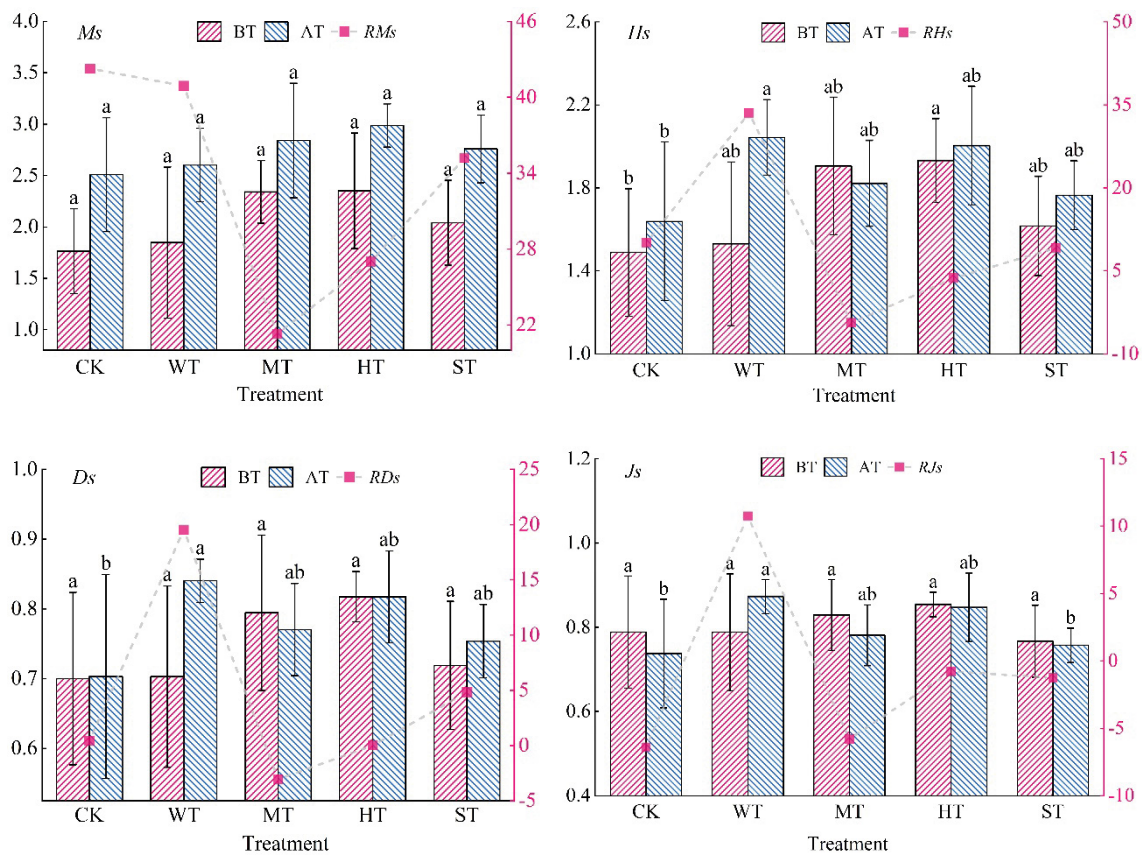


Figure 3. Changes and rates of change in shrub layer species diversity before and three years after crop tree release (CTR) under different thinning intensities in *Camptotheca acuminata*–*Liquidambar formosana* mixed plantations at Beishan Forest Farm, Tongshan County, Hubei Province, China. Different lowercase letters indicate significant differences at $P < 0.05$ based on Duncan's test. CK: control; WT: weak thinning; MT: moderate thinning; HT: high thinning; ST: super high thinning. BT: Before thinning; AT: After thinning; RDs: Rates of change.

Relationships between stand spatial structure and understory species diversity

As shown in Figure 4 and Table 3, significant differences in several stand spatial structure indices were observed among treatments three years following CTR, particularly under moderate to high thinning intensities. However, Redundancy analysis (RDA) revealed that the explanatory variables accounted for 59.0% of the variance in herbaceous layer diversity indices. *Mh*, *Hh*, and *Dh* showed positive correlations with *M*, while *Dh* and *Mh* were negatively correlated with *S* and *CI*. Among these, *M* exhibited the strongest explanatory power for herbaceous diversity. Additionally, the near-orthogonality of *M* and *Mh* in the ordination space suggests that these two variables may contribute independently to variation in herb layer composition. Shrub layer diversity indices—including the *Ms*, *Ds*, *Hs* and *Js*—showed varying relationships with stand spatial structure factors. *Ds* and *Js* were moderately associated with *CI* and *S*, whereas *Hs* and *Js* appeared nearly orthogonal to these variables in the ordination space, indicating weak or negligible correlation. *Ms* was negatively correlated with *CI* and *S*, suggesting contrasting responses among diversity metrics. These results indicate that structural factors such as *CI* and *S* may influence certain aspects of shrub layer diversity, though their effects vary across diversity indices.

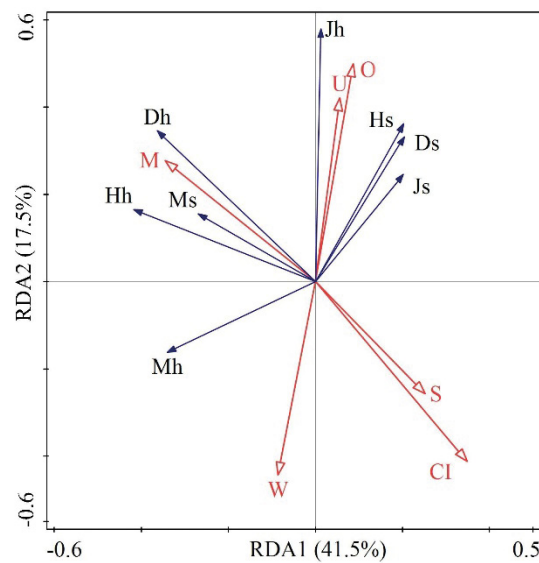


Figure 4. Redundancy analysis (RDA) ordination showing relationships between stand spatial structure variables and diversity indices of herbaceous and shrub layers in *Camptotheca acuminata*–*Liquidambar formosana* mixed plantations under different thinning intensities at Beishan Forest Farm, Tongshan County, Hubei Province, China. Red arrows represent explanatory variables while blue arrows represent response variables.

Table 3. Forward selection and Monte Carlo test results identifying key stand spatial structure factors influencing species diversity in *Camptotheca acuminata*–*Liquidambar formosana* mixed plantations under different thinning intensities at Beishan Forest Farm, Tongshan County, Hubei Province, China.

Indicator	Simple effect			Conditional effect		
	Explained %	F	P	Explained %	F	P
M	34.69	2.6	0.066	24.52	2.6	0.09
CI	21.77	1.6	0.206	26.20	3	0.042
O	19.05	1.4	0.242	2.64	0.3	0.81
U	6.8	0.5	0.672	13.22	1.6	0.208
S	9.86	0.2	0.864	16.83	0.9	0.426
W	7.82	0.5	0.622	16.59	2.1	0.134

M: Mingling index; CI: Competition index; O: Openness index; U: Neighborhood comparison; S: Stand layer index; W: Uniform angle index.

Forward selection and Monte Carlo test of stand spatial structure indices

The results of forward selection and Monte Carlo tests for stand spatial structure indices are summarized in Table 3. Comparisons between the simple and conditional effects of the indices revealed the following:

Simple effects: Three indices demonstrated explanatory powers greater than 10.0%, namely *M*, *CI*, and *O*. Conditional effects: Five indices surpassed the 10.0% explanatory threshold, including *M*, *CI*, *U*, *S* and *W*.

Overall, *M* and *CI* exhibited the highest and most stable explanatory capacities, with their contributions exceeding 20.0%. These indices were identified as having significant impacts on the diversity of understory shrub and herbaceous layers.

Path analysis of stand spatial structure on species diversity

The path analysis results indicate that different stand spatial structure indices have varying effects on the species diversity of the herbaceous and shrub layers (Table 4). To clarify the causal relationships, we distinguished between direct and indirect path effects. For example, *M* exhibited significant direct effects on several diversity indices (e.g., *Mh* and *Hh*), whereas other indices, such as *O* and *W*, contributed primarily through indirect paths with relatively smaller coefficients. Detailed values of direct and indirect effects are provided in Table 4. Overall, the effects of stand spatial structure on species diversity were predominantly direct.

Table 4. Path analysis of the effects of stand spatial structure on the species diversity of herb and shrub layers in *Camptotheca acuminata*–*Liquidambar formosana* mixed plantations under different thinning intensities at Beishan Forest Farm, Tongshan County, Hubei Province, China.

IV	DV	DPC	CC	IPC	R^2	DV	DPC	CC	IPC	R^2
<i>M</i>	<i>Mh</i>	1.171*	0.514	0.006	0.473	<i>Ms</i>	1.178	0.323	0.006	0.426
<i>O</i>		-0.967	-0.270	-0.007			-0.837	-0.146	-0.007	
<i>W</i>		0.278	0.032	0.005			-2.372	-0.170	0.005	
<i>U</i>		-2.854	-0.360	-0.001			3.744	0.295	-0.001	
<i>S</i>		0.000	0.236	0.002			-0.001**	-0.785	0.002	
<i>CI</i>		-0.712	-0.339	0.003			0.396	0.118	0.003	
<i>M</i>	<i>Jh</i>	0.025	0.052	0.006	0.692	<i>Js</i>	0.213	0.255	0.006	0.668
<i>O</i>		0.475*	0.615	-0.007			-0.002	-0.002	-0.007	
<i>W</i>		0.337	0.179	0.005			-0.503	-0.157	0.005	
<i>U</i>		0.563	0.329	-0.001			-0.816	-0.280	-0.001	
<i>S</i>		0.000	0.096	0.002			0.000	-0.503	0.002	
<i>CI</i>		0.025	0.056	0.003			0.412*	0.535	0.003	
<i>M</i>	<i>Hh</i>	0.752	0.446	0.006	0.389	<i>Hs</i>	0.850	0.357	0.006	0.436
<i>O</i>		-0.207	-0.078	-0.007			-0.037	-0.010	-0.007	
<i>W</i>		0.922	0.143	0.005			-2.233	-0.245	0.005	
<i>U</i>		-1.117	-0.190	-0.001			-0.472	-0.057	-0.001	
<i>S</i>		0.000	0.388	0.002			0.000**	-0.729	0.002	
<i>CI</i>		-0.887*	-0.571	0.003			0.917	0.418	0.003	
<i>M</i>	<i>Dh</i>	0.171	0.370	0.006	0.530	<i>Ds</i>	0.318	0.367	0.006	0.561
<i>O</i>		0.027	0.038	-0.007			-0.076	-0.056	-0.007	
<i>W</i>		0.386	0.218	0.005			-0.700	-0.211	0.005	
<i>U</i>		0.098	0.061	-0.001			-0.679	-0.225	-0.001	
<i>S</i>		0.000	0.327	0.002			0.000*	-0.607	0.002	
<i>CI</i>		-0.219	-0.513	0.003			0.294	0.368	0.003	

IV: Independent variable; DV: Dependent variable; DPC: Direct path coefficient; CC: Correlation coefficient; IPC: Indirect path coefficient; *Mh*: Margalef richness index of herb layer; *Jh*: Pielou evenness index of herb layer; *Hh*: Shannon-Weiner index of herb layer; *Dh*: Simpson index of herb layer; *Ms*: Margalef richness index of shrub layer; *Js*: Pielou evenness index of shrub layer; *Hs*: Shannon-Weiner index of shrub layer; *Ds*: Simpson index of shrub layer. * indicates significance level at $P < 0.05$; ** indicates significance level at $P < 0.01$. *M*: Mingling index; *CI*: Competition index; *O*: Openness index; *U*: Neighborhood comparison; *S*: Stand layer index; *W*: Uniform angle index.

For the herbaceous layer, *M* had a significant direct path coefficient of 1.171 ($P < 0.05$) for the *Mh* and also exerted significant positive effects on *Hh* and *Dh*. *O* had a direct path coefficient of 0.475 ($P < 0.05$) for *Jh*, while *W* showed a significant positive effect on *Hh* with a path coefficient of 0.922. Conversely, an increase in *U* significantly suppressed species diversity in the herbaceous layer, and *CI* negatively affected *Hh* with a path coefficient of -0.887 ($P < 0.05$). The stand spatial structure indices collectively explained the highest variance for *Jh* ($R^2 = 0.692$).

For the shrub layer, *S* showed small but significant direct path coefficients for *Ms*, *Hs*, and *Ds*. *CI* had direct path coefficients of 0.412 and 0.917 for *Js* and *Hs*, respectively, indicating that moderate competition promotes shrub layer species diversity. Stand spatial structure indices explained a relatively high proportion of the variance for *Js* ($R^2 = 0.668$).

Discussion

Dynamic changes in stand spatial structure under different thinning intensities

Immediately after CTR, stand spatial structure indices—including *W*, *M*, *O* and *S*—showed significant changes across all thinning intensities, with values generally higher than those in CK. These effects were particularly pronounced under the ST and HT treatments. High-intensity thinning, such as ST and HT, shifted tree spatial distribution from a more uniform pattern to a more naturally random distribution, effectively alleviating competition among trees (Huang et al., 2015). Furthermore, the study revealed that thinning, to varying degrees, increased the mingling index, with the ST and HT treatments showing particularly notable improvements. This suggests that selective thinning, by 'removing similar, retaining dissimilar' trees, markedly increased mingling index in mixed plantations. This increases tree species segregation and optimizes the stand's spatial structure (Zhang et al., 2023). A higher *M* reflects increased spatial intermixing of tree species, which does not necessarily intensify competition. In our study, *M* increased after thinning due to species selection favoring dissimilar neighbors, while *CI* declined mainly because of reduced stand density. Although these changes arose from different processes, their co-occurrence suggests that thinning, by promoting spatial heterogeneity, may help improve stand spatial structure. Zhou et al. (2016) compared three forest communities and found that the spruce-fir near-pristine forest had the highest *M* and the lowest proportion of zero mingling, indicating low species aggregation and high structural stability. This implies that higher mingling can reduce intraspecific clustering and enhance spatial balance. Similarly, Huang et al. (2018) showed that species-rich forests improve productivity through niche complementarity, thereby alleviating competitive stress. These findings support the view that increasing mingling, when guided by appropriate thinning, may contribute to more stable and resilient stands.

However, some stand spatial structure indices exhibited a gradual rebound over time. For instance, *CI* progressively increased three years following CTR, indicating that while competition pressure among trees was significantly reduced in the early stages following thinning, it began to recover over time. This trend was particularly pronounced under the MT and WT treatments, where the rate of increase was faster than that observed under the HT and ST treatments.

This change can be attributed to the natural growth of trees following thinning, which suggests that competition pressure increases as trees continue to grow (Zhang ZX et al., 2024). While moderate and low intensity thinning (e.g., MT and WT treatments) effectively reduced competition in the short term, the limited release of growing space led to a faster rebound in competition pressure. As a result, the stand gradually returned to a higher level of competition (Wu et al., 2015).

Over time, the improvements in stand spatial structure diminished across all treatments. However, the effects of ST and HT treatments remained superior to those of the lower-intensity thinning treatments, indicating that higher-intensity thinning significantly enhances stand spatial structure. Furthermore, it effectively delays the resurgence of competition among trees in the short term, thus delaying the decline in spatial structure quality (Zhao et al., 2021).

Short-term response of species diversity to different thinning intensities

Species diversity in the shrub and herbaceous layers showed limited variation among treatments prior to management. However, noticeable increases in herbaceous diversity were observed three years after

thinning, particularly under moderate and high thinning intensities, suggesting a delayed positive response of understory vegetation to canopy disturbance. This indicates that moderate thinning effectively promotes herbaceous layer species diversity in the short term by improving understory light conditions and reducing competition pressure (Kern et al., 2013; Feng et al., 2018).

Although the ST treatment increased Jh , other treatments resulted in declines in Js . This suggests that while high-intensity thinning reduces competition among trees, it may enable dominant herbaceous species in the understory to acquire more resources, thereby reducing species evenness (Royo & Carson, 2006). Ares et al. (2010) reported that intense disturbances, such as thinning, could disrupt the survival conditions of certain plant species, potentially leading to declines in species diversity (Ares et al., 2010). This finding may explain the observed decline in Mh of the herbaceous layer across all treatments three years following CTR.

Although the ST treatment improved Dh and Hh in the herbaceous layer, the increases were smaller compared to the HT and WT treatments. Excessive disturbance may suppress the growth of species that depend on specific environmental conditions, thereby limiting further improvements in species diversity (Roberts, 2004).

Three years after CTR, Ms of the shrub layer increased significantly across all thinning treatments. The WT treatment demonstrated the most significant increases in Ds and Hs of the shrub layer, indicating that moderate thinning effectively enhances shrub layer species diversity by improving light availability and redistributing resources (Thibault et al., 2002; Zhao et al., 2021).

Additionally, the WT treatment significantly enhanced Js of the shrub layer, suggesting that low-intensity thinning fosters community evenness, balances resource distribution, and supports the coexistence of a greater number of species (Ares et al., 2010). In contrast, under the MT treatment, both Ds and Hs declined. Although competition pressure was reduced, insufficient light availability for heliophilous species limited their growth (Battles et al., 2001). Similarly, Js decreased under MT treatment, indicating that in competitive environments, dominant species tend to monopolize resources, suppressing other species and leading to a reduction in evenness (Royo & Carson, 2006).

Thinning and gap formation often induce microclimatic changes, including increased temperature, decreased humidity, and altered soil moisture and nutrient dynamics. These factors significantly affect plant growth conditions, particularly in larger gaps, where the effects are more pronounced (Gray et al., 2002). Excessive openness can reduce the litter layer, impair nutrient cycling within the soil, and lower soil moisture. Over time, this may limit the growth of species that are highly dependent on soil nutrients or moisture (Battles et al., 2001). This phenomenon likely explains why, although the ST treatment increased Ds and Hs in the shrub layer, the gains were smaller compared to the WT treatment.

Key spatial structure factors driving understory species diversity

Redundancy analysis and path analysis consistently identified M , CI , and O as the primary structural variables influencing species diversity in the understory shrub and herbaceous layers.

M had a significant positive effect on both Mh and Hh in the herbaceous layer, and also contributed to increased diversity in the shrub layer. A higher mingling index indicates greater spatial mixing among species, which may reduce species dominance and promote niche differentiation (Gray et al., 2002). This spatial heterogeneity facilitates resource partitioning, creating more favorable conditions for the establishment and coexistence of understory species (Sayer, 2006; Liu et al., 2022).

CI showed contrasting effects across layers. In the shrub layer, moderate competition was positively associated with Ds and Js , suggesting that controlled competition can limit species dominance and support diversity (Wu et al., 2015; Wang et al., 2021). This aligns with the view that excessive or minimal competition can both suppress diversity, whereas intermediate CI levels under thinning treatments (e.g., WT) may create more favorable conditions for diverse shrub communities (Lopes, 2023). In contrast, CI had a negative effect on herbaceous diversity, likely due to competitive suppression by shrub species, which more effectively occupy space and capture light and nutrients. Previous studies have shown that increased diversity in the shrub layer can suppress herbaceous layer diversity, as shrubs dominate access to these critical resources (Zhang HC et al., 2024).

O had a positive effect on Jh , highlighting the role of light availability in maintaining balanced species distributions. A more open canopy can enhance the penetration of light to the forest floor, reduce spatial light

heterogeneity, and enable co-occurrence of shade-tolerant and light-demanding herbaceous species (Wu et al., 2015).

Together, these findings indicate that light to moderate thinning treatments (WT and MT), which optimize mingling, reduce excessive competition, and improve canopy openness, are most beneficial for enhancing understory species diversity.

Conclusions

After CTR, the ST and HT treatments resulted in the highest recorded values in stand spatial structure, particularly in increasing *M* and *O*, while reducing *CI*. Three years after CTR, the ST treatment resulted in the highest improvement in stand spatial structure among all treatments. However, as tree growth progressed and competition pressure gradually resumed, the effects of the thinning treatments diminished. Therefore, timely implementation of subsequent thinning cycles is crucial for maintaining long-term stability in stand spatial structure.

Among all treatments, WT and HT generally enhanced species diversity, with WT showing significant improvements in both richness and evenness indices of the shrub layer. *M* and *CI* were identified as key factors influencing species diversity in both the shrub and herbaceous layers of *Camptotheca acuminata*–*Liquidambar formosana* mixed plantations. Increased mingling significantly enhanced species diversity in both layers, while moderate competition positively contributed to shrub layer species diversity. These findings provide empirical support for using moderate-intensity thinning (e.g., WT and HT) under crop tree release to optimize spatial structure and enhance understory biodiversity. Such practices can serve as effective strategies for improving the ecological stability and multifunctionality of mixed plantations in subtropical forest management.

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