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Herbaceous competition does not affect positive tree diversity effects on seedling crown complementarity

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ABSTRACT

Naturally regenerated herbaceous species play a significant role in shaping community structure and stand dynamics, particularly through their interactions with tree seedlings in early-successional stands. The seedling and grass competition can affect seedling crown complementarity, a key canopy process that enhances the productivity of tree mixtures compared to monocultures by optimizing light capture and resource use. However, little is known about how their competition advantages shift from "grass to seedling" or "seedling—grass—seedling" or just grass. We conducted a four-year tree diversity experiment involving weeded versus unweeded treatments, with eight functionally divergent woody species comprised of 17 functional combinations. We examined how crown complementarity, crown volume, and stem basal area of tree seedlings varied between weeded and unweeded treatments along the gradients of tree species richness and functional diversity over time. Crown complementarity and crown volume of tree seedlings were positively affected by tree species richness and functional diversity, and the positive tree diversity effects on seedling crown complementarity strengthened over time under both weeded and unweeded treatments. On average, seedling crown complementarity was greater in unweeded than weeded treatments. Herbaceous plants increased crown volume but decreased stem basal area after three years, and the tree diversity effects on stem basal area were not significant in both weeded and unweeded treatments. Overall, herbaceous plants did not change the tree diversity effects on seedling crown complementarity, but mediated biomass allocation trade-offs between crown expansion and horizontal growth of stem in tree seedlings during the early stage of stand development. Our results suggest that herbaceous plants can boost seedling crown complementarity but their competitive effects are not large enough for affecting the positive tree diversity effects on seedling crown complementarity in the early stage of stand development. This study provides mechanistic insight into the role of herbaceous plants in shaping tree diversity effects on canopy processes and stand structures through resource competition during the early successional period of forest communities.

1. Introduction

Unfolding stand dynamics through tree-crown patterns is pivotal for understanding the ecological processes that govern ecosystem structure and functioning (Seidel et al., 2011). Crown complementarity, increased crown engagements among interacting species, is a key mechanism that drives the positive diversity – productivity relationship by maximizing the use of canopy space among coexisting trees (Williams et al., 2017; Ali et al., 2019; Zheng et al., 2019; Kunz et al., 2019; Xu et al., 2022). In both natural and experimental forest stands, tree and herbaceous species are two main components of plant diversity that interactively shape community structure and dynamics (Germany et al., 2017). Herbaceous

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plants can influence the growth and crown complementarity of tree seedlings in contrasting directions. On the one hand, they may inhibit seedling growth by competing for limited resources, particularly during the early successional stage (Watt et al., 2003a; Gilliam, 2007), and on the other hand, herbaceous plants can promote seedling growth by increasing nutrient availability through their faster decomposition rates (D'Hervilly et al., 2021). Over the last decade, numerous tree diversity experiments have demonstrated that spatial complementarity in tree crowns contributes to the diversity effects on overyielding of tree mixtures (Williams et al., 2017) and underyielding of understory herbaceous biomass (Zheng et al., 2022). However, since these experiments often involve weed non-target species to prevent the immigration of herbaceous plants (Grossman et al., 2017; Williams et al., 2017; Huang et al., 2018), little is known about whether understory herbaceous plants play an interactive role with tree seedlings in structuring seedling crown complementarity.

The effects of tree diversity on seedling crown complementarity can be altered by the presence of understory herbaceous plants due to their significant influence on seedling growth through resource competition during the early stand development stage (Richardson et al., 1996; Watt et al., 2003a). The tree diversity-productivity relationship intricately ties to competition between tree seedlings and early colonizing herbaceous plants, which influences the biomass allocation of seedling crowns during stand development (Watt et al., 2003b). Tree seedlings tend to prioritize crown growth over stem and root growth when facing intensive herbaceous plant competition (Vandenberghe et al., 2006). Compared to small-stature herbaceous plants, fast-growing tree species can quickly outcompete herbaceous plants by developing large and broad crowns at the expense of stem growth (Kirongo et al., 2002; Fichtner et al., 2017; Van de Peer et al., 2018) and root development to optimize light capture (Watt et al., 2003a). As such, the biomass allocation patterns toward crown expansion in both width and depth increase the crown complementarity among functionally different tree seedlings under intensive competition between tree seedlings and herbaceous plants (Zheng et al., 2022). Therefore, we hypothesize that the presence of herbaceous plants strengthens tree diversity effects on seedling crown complementarity, in other words, competition advantages shift from grass to seedling, during the early stage of stand development.

However, the effects of herbaceous competition on seedling crown complementarity may depend on the functional characteristics of herbaceous species (Depauw et al., 2020). Competition from tall and fast-growing herbaceous species may impede the growth of tree seedlings by casting shade on their crowns (Watt et al., 2003a). Fast-growing herbaceous species can also outcompete tree seedlings by harming tree crowns (Roberts and Long, 1992). For instance, broadleaved (*Convolvulus arvensis* L.) and vining weeds (*Parthenocissus quinquefolia* L.) can exacerbate physical abrasion and shading of the surrounding tree crown (Llorens and Leishman, 2008). In contrast, small and slow-growing herbaceous species may exert less competition for light due to their low light compensation points (Givnish, 1988), but they may increase competition for belowground resources such as soil nutrients and water (Rey et al., 2003; Watt et al., 2015). Such intensive belowground competition can shift carbon allocation in tree seedlings towards root growth at the expense of crown development (Raison et al., 1992; Richardson et al., 1996; Reich et al., 2012), ultimately reducing crown area (Kirongo et al., 2002). For instance, herbaceous competition can substantially reduce stem growth by 64 % (Watt et al., 2003b) and crown growth by 95 % (Kirongo et al., 2002). In this context, we hypothesize further that the presence of herbaceous plants weakens or does not change the tree diversity effects on seedlings crown complementarity during the early stage of stand development.

Functional diversity is a main determinant of the effects of tree mixtures on the efficient utilization of aboveground space (Williams et al., 2017). Functionally diverse tree species may strengthen seedling crown complementarity by adjusting crowns in different heights across vertical canopy space (Zheng et al., 2022). In monoculture stands, tree seedlings increase height to pre-empt light and space (Lines et al., 2012), but with similar crown architecture, thereby decreasing seedling crown complementarity. In contrast, in functionally diverse stands, tree seedlings with divergent crown morphologies (i.e., vertical and horizontal crown extensions) enable them to make efficient use of available light resource and space, thereby promoting horizontal crown adjustments without overlapping (Dieler and Pretzsch, 2013; Tobner et al., 2016; Forrester et al., 2017; Grossman et al., 2017). Concurrently, variation in height of interacting species promotes the complementary vertical placement of tree crowns (Jucker et al., 2015). Overall, variations in vertical and horizontal crown extensions (crown plasticity) strengthen crown engagement in both directions (Purves et al., 2007; Seidel et al., 2011; Longuetaud et al., 2013). Therefore, crown complementarity is likely to be stronger in compositionally and functionally diverse stands than in monoculture stands (Williams et al., 2017; Kunz et al., 2019; Hildebrand et al., 2021; Zheng et al., 2022).

As tree seedlings grow to larger, the competition effects of herbaceous plants on seedling crown complementarity may weaken, because of intensifying interactions among tree species (Gilliam et al., 1995, Bongers et al., 2021) and increasing influence of their distinct architectural differences on alignments of their crowns (Williams et al., 2017). Both long-term and short-term experiments have demonstrated that complementarity effects tend to increase with stand age (Cardinale et al., 2007; Bongers et al., 2021; Trogisch et al., 2021). This suggests that tree species with varying crown architectures tend to optimize crown alignments for efficient resource usage (Jucker et al., 2015; Huang et al., 2018). Therefore, the influence of herbaceous on seedling crown complementarity is expected to weaken over time as tree stands tend to develop dense canopy cover, which can impede the growth of herbaceous plants by capturing resources, especially light (Zheng et al., 2022).

Here, we conducted a four-year tree diversity experiment in subtropical China by using eight functionally distinct tree species. The experiment included four diversity levels including 1, 2, 4, and 8 species and 17 functional combinations, and each diversity level had both weeded and unweeded treatments. Specifically, we aimed to answer two questions: i) do herbaceous plants increase or decrease seedling crown complementarity at the early stand development stages? ii) whether the temporal shifts of tree diversity effects on seedling crown complementarity as well as growth of tree stems and crown volume are consistent between weeded and unweeded treatments?

2. Methods

2.1. Study site and experimental design

We conducted a tree diversity experiment on Putu Island, Zhoushan Archipelago (29° 97´ N, 121° 38´ E), eastern China. Putu Island has featured a subtropical monsoon climate, with a mean annual temperature of 16 °C and mean annual precipitation of 1358 mm. The soil at this site is characterized by sandy clay laterite with 20–40 % sand and 10–15 % clay. The natural secondary vegetation around the experimental site is the broadleaved and coniferous mixed forests, with the dominant species being *Pinus massoniana, Liquidambar formosana, Cinnamomum camphora and Celtis sinensis* (Yan et al., 2018). The forest at this experimental site was transformed to cropland by local people in 1988, but agricultural activities stopped in 2016. In the 2017, all remaining crops, vegetables and weeds were removed, and the soil was plowed to a depth of 30–40 cm using a land preparation machine to establish the tree diversity experiment. To determine the effects of herbaceous plants on the tree diversity-ecosystem function relationship, we retained seed banks of herbaceous species by preventing the use of herbicide or other chemical agents in unweeded plots.

The tree diversity experiment was established in April 2018 and included 8 tree species located in various positions on the 'fast-slow' economic spectrum (Zheng et al., 2022). This species set included four light demanding fast growing species (*Sapindus mukorossi*, *Koelreuteria bipinnata*, *Liquidambar formosana* and *Sapium sebiferum*) and four shade tolerant species (*Machilus thunbergii*, *Neolitsea sericea*, *Cyclobalanopsis glauca*, *Schima superba*). The experiment included two treatments: weeding, with two levels (unweeded and weeded), and tree species richness, with four levels (combinations of 1, 2, 4, or 8 species). We manipulated 17 functional combinations: eight monocultures, four two-species mixtures, four four-species mixtures, and one mixture including all eight species. The functional characteristics of the species were dissimilar, ranging from the acquisitive to the conservative end of the plant functional spectrum (Table S1). The weeded and unweeded treatments were nested within functional diversity treatments, i.e., all 17 functional combinations were implemented under both weeded and unweeded treatments.

The experiment laid out four random blocks for each treatment to buffer random environmental variations, and the plots were randomized within each block. The plot size was $4.2 \times 4.2\ \mathrm{m}^2$ plots and 64 one-year-old tree seedlings of the selected species were planted on 8×8 grid with 0.6 m distance between individuals. Seedlings were grown in containers under standard nursery environment for one season and then transplanted into the field. The size of the transplanted seedlings in terms of diameter and height were detailed in Zheng et al. (2022). For a given species mixture plot, species were planted randomly in equal proportions but avoided having the eight nearest neighbors of each focal seedling belong to the same species. This approach ensures that diversity effects occur at the neighborhood level in tree mixtures, as neighboring tree individuals interact strongly and contribute to the diversity effects in forest communities (Grossman et al., 2017). The plots were spaced 1 m apart to allow movement and to minimize inter-plot interactions. In total, there were 136 plots (17 tree combinations × 2 treatments (weeded and unweeded) × 4 blocks) and 8704 tree individuals. After two months of the experiment establishment, dead tree seedlings were replanted to mitigate the shock of planting (Figure S1; Figure S2; Zheng et al., 2022).

In all weeded plots we clipped off the herbaceous plants at ground level by using sickles, which avoided the soil disturbance. Weeding was performed with one-month intervals in the first two years (2018–2019) and at three-month intervals through the third year after the establishment of experiment. In contrast, for the unweeded plots, weeding and any other human interference were banned to allow the plots to develop naturally. This management approach allowed us to test how herbaceous species and tree species interactively affect community structure and ecosystem processes over time. There were different types of herbaceous plants in our experiment plots, including grasses, forbs, fern and sedges (Table S2).

2.2. Measurements of seedling crown and stem

Tree crown measurements and stem basal area were recorded each September (end of the growing season) every year by using a meter stick and Vernier caliper; respectively. We measured the tree seedling height (H) from the base of the stem to the crown top, the height of the first branch (BH) from the ground, and the stem diameter (D) for each individual tree across 136 plots. For a given individual tree, we also measured crown radii (R) from two directions (east–west and north–south). The crown depth (CD) was calculated as the difference between plant height and the height of the first branch. As this experiment included all broadleaved tree species with spherical crown shapes, we calculated the crown volume (CV, m^3) for each tree according to Eq. (1).

$$\mathrm{CV} = \frac{4}{3}\pi \frac{\mathrm{C_a}}{2}\ \frac{\mathrm{C_b}}{2}\ \frac{\mathrm{CD}}{2} \tag{1}$$

Where $\mathrm{C_a}$ and $\mathrm{C_b}$ represent the maximum crown radius calculated from the east-west and north-south directions, respectively, while CD denotes the crown depth, as determined by Zheng et al. (2019). We calculated the stem basal area (BA, m^2) by following the Eq. (2).

$$BA = D^2 \times \frac{\pi}{4} \tag{2}$$

Where D is the stem diameter at the height of 5 cm from the ground surface (Oyebade and Anaba, 2018).

In our studied subtropical region with plenty availability of sunshine, temperature and precipitation, that is, superior thermal and water conditions, plants grow very fast. Often, as showed for the mean crown diameter, crown volume, basal diameter and height of each tree species across four experimental years in Table S3, tree seedlings especially those pioneer species can grow 0.6–1 m in the second year, and exceeded 1 m by the third year. The average plant height of each species was 2.5 m in second year and surpassed this height by the third year. As shown in Table S4, the plot-level average crown area coverage increased over time, reaching 28.10 %, 45.40 %, 73.40 %, and 275.32 % in the first, second, third, and fourth years, respectively. The rapid crown development and increase in seedling height ensured crown interaction from the early years of the experiment. Therefore, in our experimental plots, the crowns of tree seedlings not only horizontally overlap, influenced by the 0.6 m spacing between them, but also vertical overlap due to variations in crown depth between acquisitive and conservative tree species.

2.3. Estimation of crown complementarity of tree seedlings

We estimated the plot-level seedling crown complementarity (CC) by following the approach in Williams et al. (2017) and Zheng et al. (2019). We first calculated the crown complementarity for a pair of tree seedlings as the difference in crown size between two individuals along the height axis, according to Eq. (3):

$$\mathrm{CC_{ij}} = \frac{\left|\mathrm{V_{iO}} - \mathrm{V_{jO}}\right| + \mathrm{V_{in}} + \mathrm{V_{jn}}}{\mathrm{V_i} + \mathrm{V_j}} \tag{3}$$

Where $\mathrm{V_{io}}$ and $\mathrm{V_{jo}}$ represent the crown volume of individuals i and j, respectively, within the overlapping section along the vertical axis of canopy. $\mathrm{V_{in}}$ and $\mathrm{V_{jn}}$ are the crown volume of individuals i and j in the non-overlapping section along the height axis. $\mathrm{V_i}$ and $\mathrm{V_j}$ indicate the total crown volume of individual i and j, respectively.

The plot level CC was then calculated by averaging the $\mathrm{CC_{ij}}$ of all possible pairs of measured individuals according to Eq. (4).

$$\mathrm{CC} = \frac{\Sigma\left(\mathrm{CC_{ij}}\right)}{\mathrm{n}} \tag{4}$$

Where n is the number of all pairs of individuals in each plot.

To remove edge effects, we excluded data from the outer rows of seedlings in each plot by using a central area of 3 m × 3 m out of 4.2 m × 4.2 m. We included 36 seedling individuals for data analysis out of 64 individuals in each plot. This strategy was applied for calculating the plot-level seedling crown complementarity, total crown volume and basal diameter.

2.4. Calculation of the functional identity and diversity of the tree mixture

We used species richness to represent species diversity for each tree mixture. We estimated the functional identity of the tree mixtures by using the community-weighted mean values (CWM). These values of six traits recognized as important for resource capture and usage and key features of the plant leaf and wood economic spectra. The six traits were leaf longevity (LL, month), specific leaf area (SLA, $\mathrm{cm}^2\ \mathrm{g}^{-1}$), leaf area (LA, cm^2), leaf dry mass content (LDMC, %), leaf nitrogen content (LNC, $\mathrm{mg\ g}^{-1}$), and wood density (WD, $\mathrm{g\ cm}^{-3}$). These traits are known to determine key features of plant leaf and wood economic spectra, in relation to resource capture and usage (Reich, 2014). The functional trait measurements were detailed in Zheng et al. (2022). These CWM values were calculated as the average trait values of each species mixture. We conducted a principal component analysis (PCA) using the CWM values of six traits to derive a comprehensive predictor of the combination of each tree mixture. We then extracted the first principal component, $\mathrm{CWM_{PC1}}$, which accounted for 79.3 % of the total variability, to represent the functional identity of the tree mixtures ($\mathrm{CWM_{PC1}}$), with high value of $\mathrm{CWM_{PC1}}$ representing the acquisitive economic strategy of a tree mixture. The functional trait measurement and CWM calculation processes are detailed in Zheng et al. (2022).

The functional diversity of each tree mixture was quantified as the Rao's quadratic entropy index (RaoQ). RaoQ is a measure of trait dissimilarity weighted by species abundances according to Eq. (5).

$$\mathrm{RaoQ} \ = \Sigma_{i\ =1}^{s} \Sigma_{i=1}^{s} d_{ij}\ p_i\ p_j \tag{5}$$

Where S is the species number in a given tree mixture. p_i and p_j denote the relative abundance of species i and j, respectively, and d_{ij} is the functional dissimilarity of interacting species in a given tree mixture (Ricotta, 2005). The CWM values and RaoQ were determined using the FD package (Laliberte and Legendre, 2010).

2.5. Statistical analysis

We employed linear mixed effect models to examine how tree species richness (SR), functional diversity (RaoQ) and functional composition ($\mathrm{CWM_{PC1}}$) and treatment (i.e., weeded or unweeded) interactively impact CC, CV and BA of tree seedlings over time. SR was log2-transformed, BA and CV were natural logarithm-transformed to improve the normality of the residuals of the models. The first model (Eq. 6) tested the effects of SR, treatments, experimental years and their interactions on the CC, CV and BA. The second model (Eq. 7) was used to observe the effects of RaoQ, treatments, experimental years and their interactions on CC, CV and BA. The third model (Eq. 8) was used to examine the effects of $\mathrm{CWM_{PC1}}$, treatments, experimental years and their possible interactions on the CC, CV and BA.

$$y_i \sim \beta_{\circ} + \beta_1 \mathrm{SR} + \beta_2 \mathrm{Treatment} + \beta_3\ \mathrm{Year} + \beta_4(\mathrm{SR} \times \mathrm{Treatment}) + \beta_5(\mathrm{SR} \times \mathrm{Year}) + \beta_6(\mathrm{Treatment} \times \mathrm{Year})\ \beta_7(\mathrm{SR} \times \mathrm{Treatment} \times \mathrm{Year}) + \pi_{\mathrm{Block}}/\pi_{\mathrm{Plot.ID}} + \varepsilon \tag{6}$$

$$y_i \sim \beta_{\circ} + \beta_1 \mathrm{RaoQ} + \beta_2 \mathrm{Treatment} + \beta_3\ \mathrm{Year} + \beta_4(\mathrm{RaoQ} \times \mathrm{Treatment}) + \beta_5(\mathrm{RaoQ} \times \mathrm{Year}) + \beta_6(\mathrm{Treatment} \times \mathrm{Year}) + \beta_7(\mathrm{RaoQ} \times \mathrm{Treatment} \times \mathrm{Year}) + \pi_{\mathrm{Block}}/\pi_{\mathrm{Plot.ID}} + \varepsilon \tag{7}$$

$$y_i \sim \beta_{\circ} + \beta_1 \mathrm{CWMPC1} + \beta_2 \mathrm{Treatment} + \beta_3\ \mathrm{Year} + \beta_4(\mathrm{CWMPC1} \times \mathrm{Treatment}) + \beta_5(\mathrm{CWMPC1} \times \mathrm{Year}) + \beta_6(\mathrm{Treatment} \times \mathrm{Year}) + \beta_7(\mathrm{CWMPC1} \times \mathrm{Treatment} \times \mathrm{Year}) + \pi_{\mathrm{Block}}/\pi_{\mathrm{Plot.ID}} + \varepsilon \tag{8}$$

Where y_i symbolizes CC, CV, and BA of tree seedlings, respectively for three models (Eqs. 6–8). These variables are associated with partial regression coefficients, and β_i are partial regression cofficients to be estimated. The 'Treatments' represent weeded and unweeded treatments to indicate the influence of herbaceous plants; π_{Block} and $\pi_{\mathrm{Plot.ID}}$ are the random effect factors originating from 'Block' and 'Plot identity'; respectively; while ε are the sampling errors.

It was noted that crown volume can also directly affects CC. Even though there was a moderate positive correlation between CC and CV (Pearson correlation coefficient was 0.58 and 0.59 under weeded and unweeded treatments, respectively). The alternative model for CC considering CV as a covariate yielded similar AIC values compared with the models not including CV as a covariate. Therefore, we selected the simpler model (i.e., not including CV as a covariate) as our final model (Table S5).

We performed type III analysis of variance (ANOVA) to assess the effects of SR, RaoQ or $\mathrm{CWM_{PC1}}$, treatments, year and their interactions on CC, CV and BA of tree seedlings using the "effects" package in R. To test the differences in average CC, CV and BA between weeded and unweeded treatments within each year, we utilized the R package "emmeans" (Liepins et al., 2023). All of the above statistical analyses were performed using R version 4.3.1 (R Development Core Team, http://www.R-project.org).

3. Results

3.1. Differences in CC, CV and BA of tree seedlings between weeded and unweeded treatments across years

On average, seedling crown complementarity (CC) increased with the experimental year under both weeded and unweeded treatments, and was significantly lower in the weeded than the unweeded treatments after the first year (Fig. 1a). However, crown volume (CV) did not

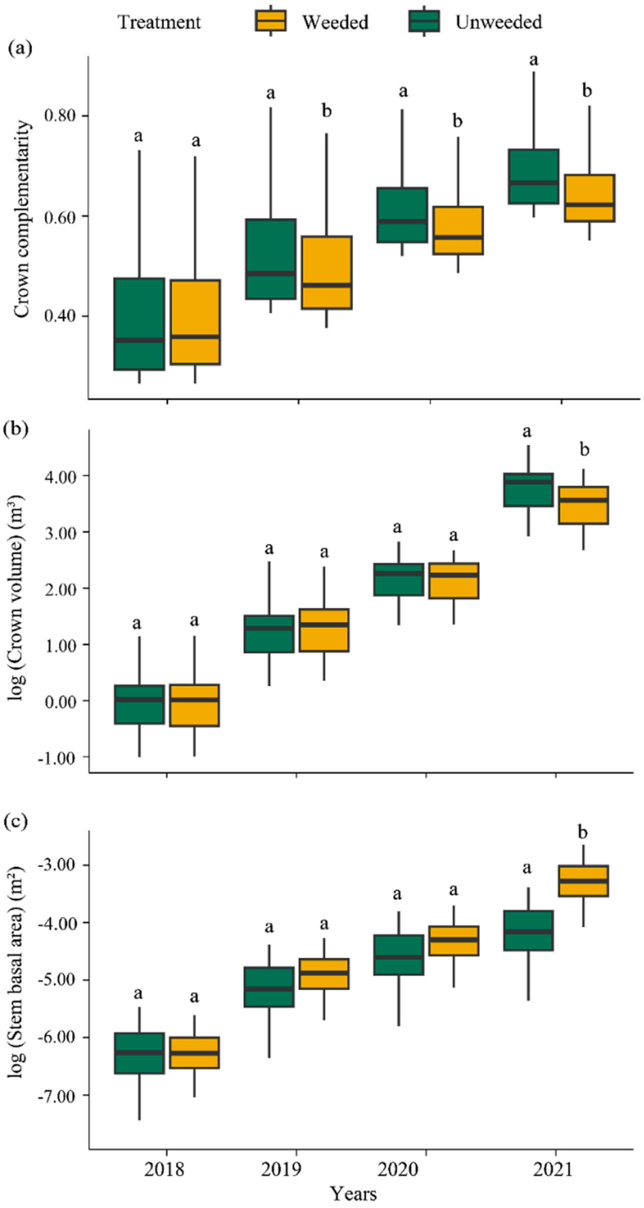

Fig. 1. Temporal changes in crown complementarity, crown volume and stem basal area between weeded and unweeded treatments. The letters “a” and “b” indicate significant differences between two treatments within a given year. Crown volume and stem basal area were natural log-transformed.

differ between weeded and unweeded treatments in the first three years, but was significantly higher in the unweeded than the weeded treatments in the fourth year (Fig. 1b). Tree basal area (BA) did not differ significantly in the first three years between weeded and unweeded treatments, but was significantly higher in the weeded than the unweeded treatments in the fourth year (Fig. 1c).

3.2. Effects of species richness on CC, CV and BA of tree seedlings between weeded and unweeded treatments over four years

The positive effects of tree species richness (SR) on tree CC increased with the experimental year in both weeded and unweeded treatments. However, herbaceous plants did not influence the effect of tree species richness on CC, and the temporal shifts of tree species richness effects on seedling crown complementarity were consistent between weeded and unweeded treatments (SR × Treatment and SR × Treatment × Year interactions were nonsignificant; Fig. 2a; Table 1).

The positive effects of tree SR on CV also strengthened over time in both weeded and unweeded treatments. On average, the CV in the unweeded treatment was higher than in the weeded treatment over time, whereas herbaceous plants did not influence the effect of tree species richness on CV over time (Fig. 2a; Table 1). The interactive effects among SR, treatment and experimental years on CV was also nonsignificant (Fig. 2b; Table 1).

Tree SR did not increase the BA in both weeded and unweeded treatments, but the BA was on average lower in the unweeded than the weeded treatments (Fig. 2c; Table 1). Tree SR and its interaction with treatment and experimental year did not affect BA (Fig. 2c; Table 1).

3.3. Effects of functional diversity on CC, CV and BA of tree seedlings between weeded and unweeded treatments over four years

Tree functional diversity (RaoQ) had significant positive effects on CC of tree seedlings and the effects strengthened over experimental years. The CC of tree seedlings was not influenced by treatment and its interaction with RaoQ, but was significantly impacted by the interaction between treatment and experimental year. There was none-significant interactive effect of tree RaoQ, treatments and experimental year on CC of tree seedlings (Fig. 3a; Table 2). Tree CV was also positively influenced by tree RaoQ, experimental year and their interaction. The temporal shifts of tree RaoQ effects on CV were also consistent between weeded and unweeded treatments. The three-way interaction among tree RaoQ, treatment and experimental year did not affect CV (Fig. 3b; Table 2). Similar to the effects of tree species richness, tree RaoQ did not increase the BA in weeded and unweeded treatments, but the BA was on average lower in the unweeded treatment than in the weeded treatment (Fig. 3c; Table 2). The interaction among tree RaoQ, experimental year and treatment did not affect BA (Fig. 3c; Table 2). In addition, tree functional composition ($\mathrm{CWM_{PC1}}$) did not influence CC and BA, but increased CV (Figure S3; Table S6).

4. Discussion

This experiment disclosed that crown complementarity and crown volume of tree seedlings increased with time and on average were greater in unweeded than in weeded treatments. This finding supports our first hypothesis that the presence of herbaceous plants promotes seedling crown complementarity through increasing canopy development during the early stage of stand development. Although seedling crown complementarity increased significantly with increasing in species richness and functional diversity in both weeded and unweeded treatments, the presence of herbaceous plants did not alter the tree diversity effects on seedling crown complementarity. These results support our second hypothesis that herbaceous plants competition does not affect the tree diversity effects on seedling crown complementarity during the early stage of stand development. Together, our findings contribute to understanding the role of herbaceous plants in mediating the tree diversity effects on canopy processes and growth of tree seedlings during the early stand development stage.

4.1. Influence of herbaceous plants on canopy processes of tree seedlings in early-successional stands

We found that seedling crown complementarity in unweeded plots exceeded that in weeded plots after one-year of stand development. This result suggests that tree seedlings experience high resource competition with herbaceous plants during the early stage of stand development. Logically, compared with herbaceous plants, tree seedlings have lesser ability to compete light aboveground and soil nutrients and water underground due to poor root establishment just after planting (Adams et al., 2003). For instance, fast-growing herbaceous plants hinder the crown growth of tree seedlings by casting shade (Roberts and Long, 1992) and exacerbating physical abrasion (Watt et al., 2003a), while

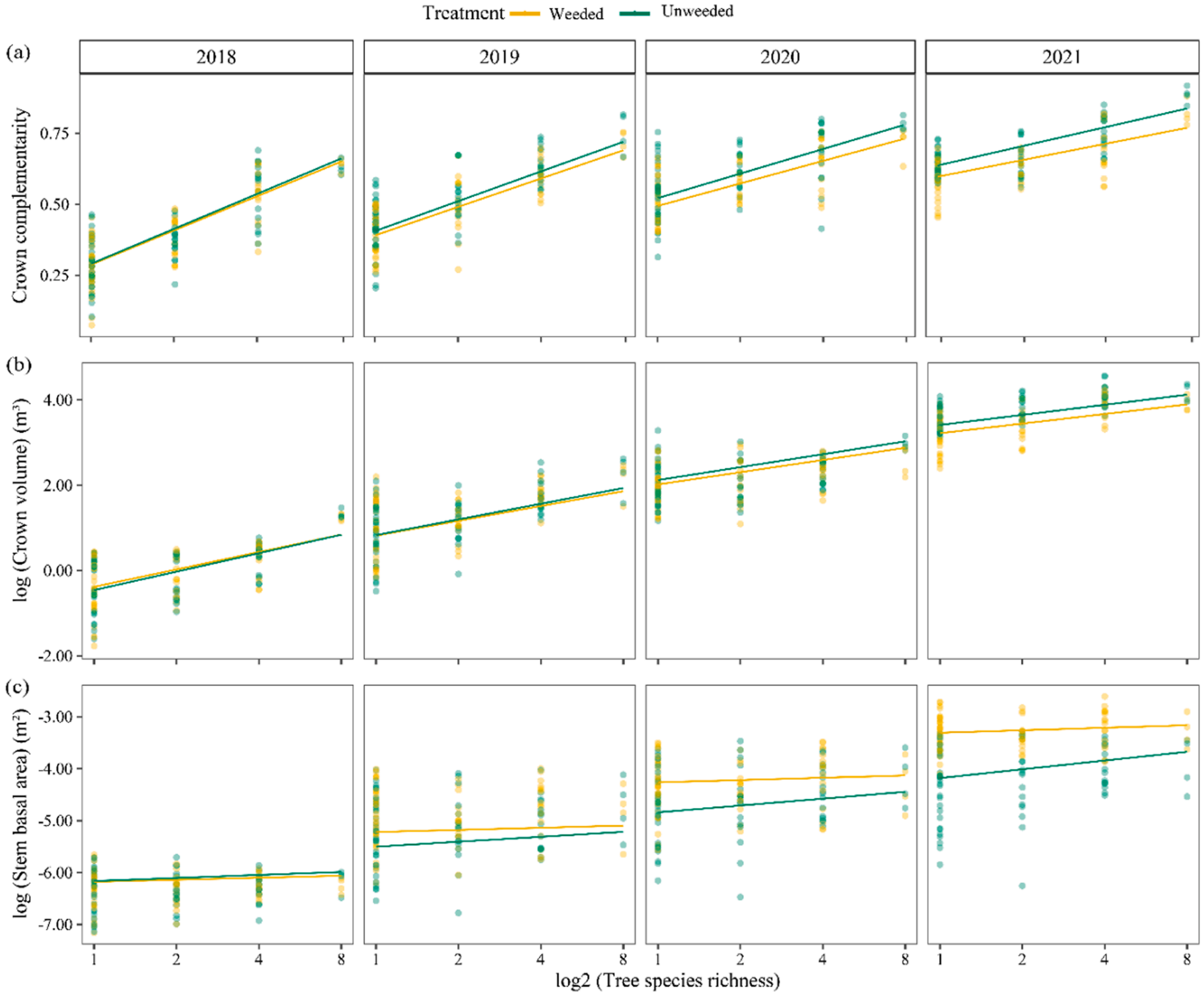

Fig. 2. Relationship of crown complementarity (a), crown volume (b) and stem basal area (c) with tree species richness between weeded and unweeded treatments across four years. Crown volume and stem basal area were natural log-transformed and tree species richness was log-2 transformed. Refer to Table 1 for the detailed statistical analyses.

slow-growing perennial grasses with their extensive root systems can deplete relatively more soil water and nutrients than tree seedlings (Moore, 1975; Remaury et al., 2019). However, when tree seedlings are successfully established during stand development (after one year in our experiment), they can overcome the growth of herbaceous plants through the rapid acquisition of both soil water and nutrients by installing root systems at variable soil depths (Liu et al., 2021), and light interception by extending crown volume and optimizing canopy packing (Jucker et al., 2015; Williams et al., 2017; Zheng et al., 2022). Altogether, this stand age-dependent variation in resource competition between herbaceous and tree seedlings suggests that herbaceous plant competition plays a crucial role in shaping stand dynamics, particularly in canopy processes and stem growth of tree seedlings.

Herbaceous plants can induce differences in crown development and stem growth in tree seedlings through altering available resources (e.g., light, water and nutrients) (Valladares et al., 2002; Watt et al., 2003a). Our result showed that herbaceous plants facilitated an increase in crown volume but hindered the horizontal growth of the stem (i.e., stem basal area) of tree seedlings in the early stage of stand development (Fig. 1b-c). The biomass allocation trade-off between crown expansion and horizontal growth of the stem of tree seedlings is relevant to resource competition by herbaceous plants (Watt et al., 2003a). To effectively intercept light, tree seedlings tend to invest greater biomass in stem growth vertically than horizontally (Falster and Westoby, 2003). Concurrently, intensive competition for light favors great biomass allocation toward crown development in tree seedlings (Watt et al., 2003b).

As a result, in response to herbaceous competition, tree seedlings improve their access to light through the efficient distribution of leaves and branches in both vertical and horizontal directions (Jucker et al., 2015). With a great ability to increase crown volume and vertical growth of stems, tree seedlings may benefit more from increasing leaf area, improving physiological activity and the photosynthetic rate (Mohammed et al., 1998; Adams et al., 2003), and expanding crown width and depth (Williams et al., 2017). In mixed stands, tree species with inherent divergence in growth rate and crown morphology enable them to fit limited space efficiently, regardless presence of understory herbaceous plants.

Table 1
Results of the linear mixed effect models for the effects of tree species richness (SR), treatments, year, and their interactions on crown complementarity, crown volume and stem basal area of tree seedlings. NumDF, numerator degrees of freedom; DenDF, denominator degrees of freedom; F and the P-value of the significance test, respectively.

Dependent variable	SOV	SumSq	NumDF	DenDF	F	P
Crown complementarity	SR	0.81	1	527.36	135.17	**< 0.001**
	Treatment	< 0.001	1	527.36	0.16	0.686
	Year	1.96	1	404.00	325.63	**< 0.001**
	SR × Treatment	< 0.001	1	527.36	< 0.001	0.988
	SR × Year	0.14	1	404.00	23.35	**< 0.001**
	Treatment × Year	0.01	1	404.00	2.27	0.132
	SR × Treatment × Year	< 0.001	1	404.00	0.14	0.708
Crown volume	SR	5.65	1	405.32	44.53	**< 0.001**
	Treatment	0.21	1	405.32	1.65	0.199
	Year	266.35	1	404.00	2100.67	**< 0.001**
	SR × Treatment	0.01	1	405.32	0.09	0.768
	SR × Year	1.17	1	404.00	9.23	**0.002**
	Treatment × Year	0.75	1	404.00	5.88	**0.015**
	SR × Treatment × Year	< 0.001	1	404.00	0.02	0.878
Stem basal area	SR	0.02	1	307.94	0.22	0.642
	Treatment	0.55	1	307.94	4.89	**0.027**
	Year	168.85	1	404.00	1490.91	**< 0.001**
	SR × Treatment	< 0.001	1	307.94	0.02	0.9
	SR × Year	< 0.001	1	404.00	0.03	0.865
	Treatment × Year	8.06	1	404.00	71.12	**< 0.001**
	SR × Treatment × Year	0.18	1	404.00	1.56	0.211

4.2. *Tree diversity effects on canopy processes are independent to herbaceous competition in early-successional stands*

We observed that seedling crown complementarity positively associated with both species and functional diversity. Tree seedlings in mixtures increase crown complementarity due to variant capabilities for crown development among functionally divergent species (Williams et al., 2017). Compared with those in monocultures, functionally diverse tree seedlings in mixed stands with variable growth rates can partition spatial space efficiently through optimizing canopy packing plastically (Jucker et al., 2015) and placing crown complementarity along the height profiles (Van de Peer et al., 2018). In other words, their variant crown morphologies (e.g., slim, wider or laterally expanded) can increase crown adjustments for efficient space usage (Dieler and Pretzsch, 2013; Forrester et al., 2017). Moreover, there are advantages to strengthen crown complementarity for functionally dissimilar tree seedlings due to different branching patterns and frequencies, distinct crown plasticity, variable crown repositioning tendency and contrasting leaf attributes (e.g., phenology and leaf size) (White, 1983; Valladares et al., 2002; Longuetaud et al., 2013). Concurrently, functionally different tree species in mixed stands may have variable rooting depths which enables them to use nutrients and water more efficiently (Com and Eissenstat, 2012; Liu et al., 2021), thus benefiting to canopy development and crown complementarity of tree seedlings.

Canopy processes of functionally divergent tree species with varying crown architectures and resource economics might be unaffected by small-stature herbaceous plants. Acquisitive species mainly extend their branches by investing greater biomass in foliage production (leaves) at the expense of branching frequency per unit crown area (morphological trade-off) (White, 1983). Acquisitive species also have great crown repositioning ability in both horizontal and vertical directions in order to enhance light capture and occupy more canopy space (Purves et al., 2007; Valladares et al., 2002, Holzwarth et al., 2015; Díaz et al., 2016). Simultaneously, tree seedlings can absorb large amount of water and nutrients through high fine root production and installing root system away from weed zone of influence (Costantini, 1989). In short, these competitive advantages may allow acquisitive tree species to outgrow herbaceous plants by rapidly developing their crowns (Depauw et al., 2020; Zheng et al., 2022).

In contrast, crown architectural plasticity (crown adaptive capacity) tends to be low in conservative species due to their high shade tolerance tendency (Valladares and Niinemets, 2008). Conservative tree species often invest heavily for inner crown development (White, 1983), which favour to high branching frequency per unit crown area for the shade tolerance. Generally, the shade that is exerted by overstory tree crowns can favour crown growth in conservative understory species (Hart and Chen, 2008; Bartels and Chen, 2010; Depauw et al., 2020). Therefore, in mixed stands, acquisitive and conservative tree species with varying crown architecture configuration strategies and great interspecific complementarity often lead to greater degree of crown complementarity due to more efficient space usage (Huang et al., 2018), regardless of the presence of herbaceous plants.

We also observed that the positive tree diversity effects on seedling crown complementarity increased over the experimental years (Figs. 2a-3a). The increase in tree diversity effects on seedling crown complementarity might be primarily attributable to the emergence of more variant crown architecture due to increased functional differences over time (Williams et al., 2017; Bongers et al., 2021; Zheng et al., 2022). Conversely, community functional composition (CWM_{PC1}) did not significantly impact seedling crown complementarity. This might be caused by the presence of relatively identical crown architectures when communities are dominated by tree species with similar economic strategies, i.e., acquisitive or conservative (Zheng et al., 2019).

Although herbaceous plants do not alter the tree diversity effects on crown complementarity and crown volume of tree seedlings in the early stage of stand development as observed in this study, from the long-term perspective, functional reorganization in herbaceous plants might significantly impact the tree diversity effects on stand structure and dynamics and even productivity (Depauw et al., 2020; Zheng et al., 2022). For example, the presence of large-statured herbaceous plants or vines may hinder tree growth by creating stressful limitations on light availability, as they overshadow the tree crown (Llorens and Leishman, 2008). Moreover, vines can create groves on tree stems and branches through twisting and winding, and their excessive growth can increase the loads on tree stems and crowns, potentially leading to stem breakage (Rowe and Speck, 2015). Future research should investigate how tree diversity interacts with large-statured herbaceous plants in shaping canopy processes over time.

5. Conclusion

Based on a tree diversity experiment that included the weeded *versus*

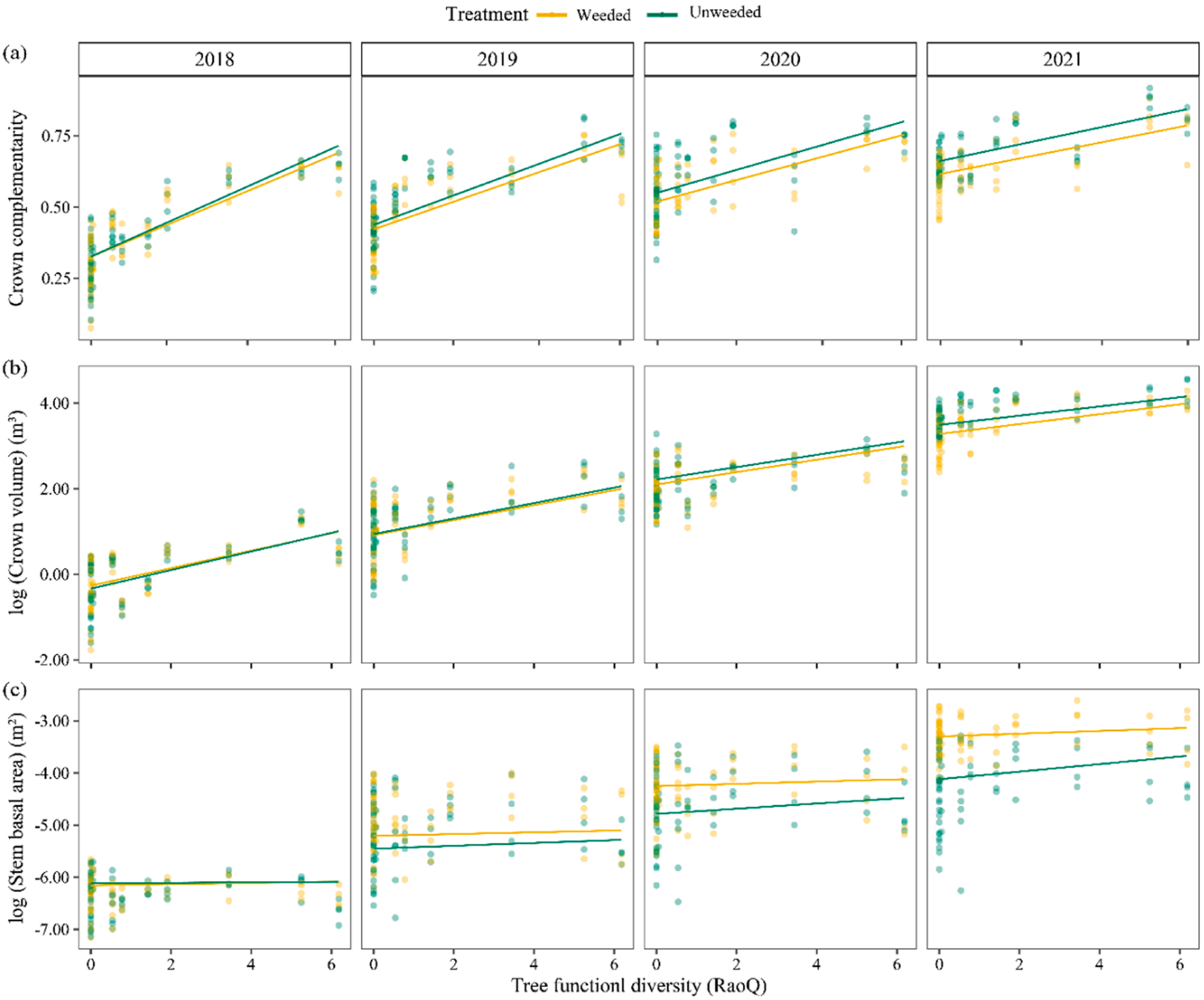

Fig. 3. Relationship of crown complementarity (a), crown volume (b) and stem basal area (c) with tree functional diversity between weeded and unweeded treatments across four years. Crown volume and stem basal area were natural log-transformed. Refer to Table 2 for detailed statistical analyses.

unweeded treatments, this study demonstrated that herbaceous plants increased seedling crown complementarity by enhancing crown volume at the expense of stem growth for better light capture and space coverage, during the early stage of stand development. However, herbaceous competition could not alter the tree diversity effects on seedling crown complementarity because tree species with contrasting functional strategies in the mixed stands are advantageous to light interaction and water and nutrients acquisition, thus outcompeting small stature herbaceous plants. These findings hence provide mechanistic insight into the functioning of herbaceous plants in shaping seedling crown complementarity through mediating biomass allocation trade-offs between crown expansion and horizontal growth of stem in tree seedlings during the early stage of stand development. Moreover, this study highlights the non-negligible role of naturally regenerated herbaceous plants in shaping canopy processes and stand structure and dynamics in the beginning of forest succession.

CRediT authorship contribution statement

Bao Di-Feng: Data curation. **Fang Xiao-Chen:** Conceptualization. **Yang Bai-Yu:** Formal analysis, Data curation. **Zhang Li:** Formal analysis, Data curation. **Zheng Li-Ting:** Writing – review & editing, Validation, Software, Project administration, Formal analysis, Data curation, Conceptualization. **Abdullah Muhammad:** Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Yan En-Rong:** Writing – review & editing, Validation, Supervision, Project administration, Investigation, Funding acquisition, Conceptualization. **Zhao Ci-Liang:** Project administration. **Samreen Ghulam Rasool:** Visualization, Validation, Software, Methodology, Formal analysis, Data curation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Table 2
Results of the linear mixed effect models for the effects of tree functional diversity, treatments, years and their interactions on crown complementarity, crown volume and stem basal area of tree seedlings. NumDF, numerator degrees of freedom; DenDF, denominator degrees of freedom; F and P-values of the significance test, respectively.

Dependent variable	SOV	SumSq	NumDF	DenDF	F	P
Crown complementarity	RaoQ	0.70	1	532.39	117.88	**< 0.001**
	Treatment	< 0.001	1	532.39	0.51	0.476
	Year	2.28	1	404.00	385.20	**< 0.001**
	RaoQ × Treatment	< 0.001	1	532.39	0.26	0.607
	RaoQ × Year	0.13	1	404.00	22.50	**< 0.001**
	Treatment × Year	0.03	1	404.00	4.64	**0.031**
	RaoQ × Treatment × Year	< 0.001	1	404.00	0.05	0.824
Crown volume	RaoQ	5.28	1	397.05	41.81	**< 0.001**
	Treatment	0.27	1	397.05	2.10	0.148
	Year	340.99	1	404.00	2697.91	**< 0.001**
	RaoQ × Treatment	0.02	1	397.05	0.16	0.69
	RaoQ × Year	1.06	1	404.00	8.36	**0.004**
	Treatment × Year	1.09	1	404.00	8.59	**0.003**
	RaoQ × Treatment × Year	0.03	1	404.00	0.24	0.626
Stem basal area	RaoQ	< 0.001	1	304.31	0.03	0.859
	Treatment	0.81	1	304.31	7.15	**0.007**
	Year	221.72	1	404.00	1967.14	**< 0.001**
	RaoQ × Treatment	0.02	1	304.31	0.20	0.651
	RaoQ × Year	0.03	1	404.00	0.26	0.609
	Treatment × Year	10.03	1	404.00	88.94	**< 0.001**
	RaoQ × Treatment × Year	0.19	1	404.00	1.67	0.196

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.122529.

Data Availability

Data available from the Dryad Digital Repository when manuscript is accepted.

References

Adams, P., Beadle, C., Mendham, N., Smethurst, P., 2003. The impact of timing and duration of grass control on growth of a young *Eucalyptus globulus* Labill. plantation. N. For. 26, 147–165. https://doi.org/10.1023/A:1024490707175.

Ali, A., Lin, S.L., He, J.K., Kong, F.M., Yu, J.H., Jiang, H.S., 2019. Tree crown complementarity links positive functional diversity and aboveground biomass along large-scale ecological gradients in tropical forests. Sci. Total Environ. 656, 45–54. https://doi.org/10.1016/j.scitotenv.2018.11.342.

Bartels, S.F., Chen, H.Y., 2010. Is understory plant species diversity driven by resource quantity or resource heterogeneity? Ecology 91 (7), 1931–1938. https://doi.org/10.1890/09-1376.1.

Bongers, F.J., Schmid, B., Bruelheide, H., Bongers, F., Li, S., von Oheimb, G., Li, Y., Cheng, A., Ma, K., Liu, X., 2021. Functional diversity effects on productivity increase with age in a forest biodiversity experiment. Nat. Ecol. Evol. 5 (12), 1594–1603. https://doi.org/10.1038/s41559-021-01564-3.

Cardinale, B.J., Wright, J.P., Cadotte, M.W., Carroll, I.T., Hector, A., Srivastava, D.S., Weis, J.J., 2007. Impacts of plant diversity on biomass production increase through time because of species complementarity. Proc. Natl. Acad. Sci. 104 (46), 18123–18128. https://doi.org/10.1073/pnas.0709069104.

Com, L.H., Eissenstat, D.M., 2012. Linking fine root traits to maximum potential growth rate among 11 mature temperate tree species. Funct. Ecol. 18, 388–397. https://doi.org/10.1111/j.0269-8463.2004.00835.x.

Costantini, A., 1989. Definition of a plant zone for weed management during the establishment of *Araucaria cunninghamii* plantations. For. Ecol. Manag. 29 (1-2), 15–27. https://doi.org/10.1016/0378-1127(89)90053-4.

D'Hervilly, C., Marsden, C., Capowiez, Y., Béral, C., Delapré-Cosset, L., Bertrand, I., 2021. Trees and herbaceous vegetation strips both contribute to changes in soil fertility and soil organism communities in an agroforestry system. Plant Soil 463, 537–553. https://doi.org/10.1007/s11104-021-04932-x.

Depauw, L., Perring, M.P., Landuyt, D., Maes, S.L., Blondeel, H., De Lombaerde, E., Brūmelis, G., Brunet, J., Closset-Kopp, D., Czerepko, J., 2020. Light availability and land-use history drive biodiversity and functional changes in forest herb layer communities. J. Ecol. 108 (4), 1411–1425. https://doi.org/10.1111/1365-2745.13339.

Díaz, S., Kattge, J., Cornelissen, J.H.C., Wright, I.J., Lavorel, S., Dray, S., Gorné, L.D., 2016. The global spectrum of plant form and function. Nature 529, 167–171. https://doi.org/10.1038/nature16489.

Dieler, J., Pretzsch, H., 2013. Morphological plasticity of European beech (*Fagus sylvatica* L.) in pure and mixed-species stands. For. Ecol. Manag. 295, 97–108. https://doi.org/10.1016/j.foreco.2012.12.049.

Falster, D.S., Westoby, M., 2003. Plant height and evolutionary games. Trends Ecol. Evol. 18 (7), 337–343. https://doi.org/10.1016/S0169-5347(03)00061-2.

Fichtner, A., Härdtle, W., Li, Y., Bruelheide, H., Kunz, M., von Oheimb, G., 2017. From competition to facilitation: How tree species respond to neighbourhood diversity. Ecol. Lett. 20, 892–900. https://doi.org/10.1111/ele.12786.

Forrester, D.I., Benneter, A., Bouriaud, O., Bauhus, J., 2017. Diversity and competition influence tree allometric relationships–developing functions for mixed-species forests. J. Ecol. 105 (3), 761–774. https://doi.org/10.1111/1365-2745.12704.

Germany, M.S., Bruelheide, H., Erfmeier, A., 2017. Limited tree richness effects on herb layer composition, richness and productivity in experimental forest stands. J. Plant Ecol. 10 (1), 190–200. https://doi.org/10.1093/jpe/rtw109.

Gilliam, F.S., 2007. The ecological significance of the herbaceous layer in temperate forest ecosystems. Bioscience 57 (10), 845–858 https://doi.10.1641/b571007.

Gilliam, F.S., Turrill, N.L., Adams, M.B., 1995. Herbaceous-layer and overstory species in clear-cut and mature central Appalachian hardwood forests. Ecol. Appl. 5 (4), 947–955. https://doi.org/10.2307/2269345.

Givnish, T.J., 1988. Adaptation to sun and shade: a whole-plant perspective. Aust. J. Plant Physiol. 15, 63–92. https://doi.org/10.1071/PP9880063.

Grossman, J.J., Cavender-Bares, J., Hobbie, S.E., Reich, P.B., Montgomery, R.A., 2017. Species richness and traits predict overyielding in stem growth in an early-successional tree diversity experiment. Ecology 98 (10), 2601–2614. https://doi.org/10.1002/ecy.1958.

Hart, S.A., Chen, H.Y., 2008. Fire, logging, and overstory affect understory abundance, diversity, and composition in boreal forest. Ecol. Monogr. 78 (1), 123–140. https://doi.org/10.1890/06-2140.1.

Hildebrand, M., Perles-Garcia, M.D., Kunz, M., Haerdtle, W., von Oheimb, G., Fichtner, A., 2021. Reprint of: tree-tree interactions and crown complementarity: the role of functional diversity and branch traits for canopy packing. Basic Appl. Ecol. 55, 53–63. https://doi.org/10.1016/j.baae.2021.01.010.

Holzwarth, F., Ruger, N., Wirth, C., 2015. Taking a closer look: Disentangling effects of functional diversity on ecosystem functions with a trait-based model across hierarchy and time. R. Soc. Open Sci. 2, 140541. https://doi.org/10.1098/rsos.140541.

Huang, Y., Chen, Y., Castro-Izaguirre, N., Baruffol, M., Brezzi, M., Lang, A., Li, Y., Härdtle, W., von Oheimb, G., Yang, X., 2018. Impacts of species richness on productivity in a large-scale subtropical forest experiment. Science 362 (6410), 80–83. https://doi.org/10.1126/science.aat6405.

Jucker, T., Bouriaud, O., Coomes, D.A., 2015. Crown plasticity enables trees to optimize canopy packing in mixed-species forests. Funct. Ecol. 29 (8), 1078–1086. https://doi.org/10.1111/1365-2435.12428.

Kirongo, B.B., Mason, E.G., Nugroho, P.A., 2002. Interference mechanisms of pasture on the growth and fascicle dynamics of 3-year-old radiata pine clones. For. Ecol. Manag. 159 (3), 159–172. https://doi.org/10.1016/S0378-1127(00)00726-X.

Kunz, M., Fichtner, A., Härdtle, W., Raumonen, P., Bruelheide, H., von Oheimb, G., 2019. Neighbour species richness and local structural variability modulate aboveground allocation patterns and crown morpdiazogy of individual trees. Ecol. Lett. 22 (12), 2130–2140. https://doi.org/10.1111/ele.13400.

Laliberte, E., Legendre, P., 2010. A distance-based framework for measuring functional diversity from multiple traits. Ecology 91 (1), 299–305. https://doi.org/10.1890/08-2244.1.

Liepins, J., Jaunslaviete, I., Liepins, K., Jansone, L., Matisons, R., Lazdins, A., Jansons, A., 2023. Effect of stem rot on wood basic density, carbon, and nitrogen content of living deciduous trees in hemiboreal forests. Silva Fenn. 57 (3). https://doi.org/10.14214/sf.23040.

Lines, E.R., Zavala, M.A., Purves, D.W., Coomes, D.A., 2012. Predictable changes in aboveground allometry of trees along gradients of temperature, aridity and competition. Glob. Ecol. Biogeogr. 21 (10), 1017–1028. https://doi.org/10.1111/j.1466-8238.2011.00746.x.

Liu, C., Xiang, W., Xie, B., Ouyang, S., Zeng, Y., Lei, P., Peng, C., 2021. Decoupling the complementarity effect and the selection effect on the overyielding of fine root production along a tree species richness gradient in subtropical forests. Ecosystems 24, 613–627. https://doi.org/10.1007/s10021-020-00538-z.

Llorens, A.M., Leishman, M.R., 2008. Climbing strategies determine light availability for both vines and associated structural hosts. Aust. J. Bot. 56 (6), 527–534. https://doi.org/10.1071/BT07019.

Longuetaud, F., Piboule, A., Wernsdörfer, H., Collet, C., 2013. Crown plasticity reduces inter-tree competition in a mixed broadleaved forest. Eur. J. For. Res. 132 (4), 621–634. https://doi.org/10.1007/s10342-013-0699-9.

Mohammed, G.H., Noland, T.L., Wagner, R.G., 1998. Physiological perturbation in jack pine (*Pinus banksiana* Lamb.) in the presence of competing herbaceous vegetation. For. Ecol. Manag. 103 (1), 77–85. https://doi.org/10.1016/S0378-1127(97)00178-3.

Moore, R.J., 1975. THE BIOLOGY OF CANADIAN WEEDS.: 13. *Cirsium arvense* (L.) Scop. Can. J. Plant Sci. 55 (4), 1033–1048. https://doi.org/10.4141/cjps75-163.

Oyebade, B.A., Anaba, J.C., 2018. Individual tree basal area equation for a young *Tectona grandis* (Teak) plantation in Choba, Port Harcourt, Rivers State, Nigeria. World N. Nat. Sci. 16, 130–140.

Purves, D.W., Lichstein, J.W., Pacala, S.W., 2007. Crown plasticity and competition for canopy space: a new spatially implicit model parameterized for 250 North American tree species. PloS One 2 (9), e870. https://doi.org/10.1371/journal.pone.0000870.

Raison, R., Myers, B., Benson, M., 1992. Dynamics of Pinus radiata foliage in relation to water and nitrogen stress: I. Needle production and properties. For. Ecol. Manag. 52 (1-4), 139–158. https://doi.org/10.1016/0378-1127(92)90499-Y.

Reich, P.B., 2014. The world-wide 'fast–slow'plant economics spectrum: a traits manifesto. J. Ecol. 102 (2), 275–301. https://doi.org/10.1111/1365-2745.12211.

Reich, P.B., Frelich, L.E., Voldseth, R.A., Bakken, P., Adair, E.C., 2012. Understorey diversity in southern boreal forests is regulated by productivity and its indirect impacts on resource availability and heterogeneity. J. Ecol. 100 (2), 539–545. https://doi.org/10.1111/j.1365-2745.2011.01922.x.

Remaury, A., Guittonny, M., Rickson, J., 2019. The effect of tree planting density on the relative development of weeds and hybrid poplars on revegetated mine slopes vulnerable to erosion. N. For. 50, 555–572. https://doi.org/10.1007/s11056-018-9678-9.

Rey, B., José, M., Espigares, T., Castro-Díez, P., 2003. Simulated effects of herb competition on planted *Quercus faginea* seedlings in Mediterranean abandoned cropland. Appl. Veg. Sci. 6 (2), 213–222. https://doi.org/10.1111/j.1654-109X.2003.tb00582.x.

Richardson, B., Vanner, A., Ray, J., Davenhill, N., Coker, G.Z.J., 1996. Mechanisms of Pinus radiata growth suppression by some common forest weed species. N. Z. J. For. Sci. 26 (3), 421–437.

Ricotta, C., 2005. A note on functional diversity measures. Basic Appl. Ecol. 6 (5), 479–486. https://doi.org/10.1016/j.baae.2005.02.008.

Roberts, S.D., Long, J.N., 1992. Production efficiency of *Abieslasiocarpa*: influence of vertical distribution of leaf area. Can. J. For. Res. 22 (9), 1230–1234. https://doi.org/10.1139/x92-164.

Rowe, N.P., Speck, T., 2015. Stem biomechanics, strength of attachment, and developmental plasticity of vines and lianas. Ecol. lianas 323–341. https://doi.org/10.1002/9781118392409.ch23.

Seidel, D., Leuschner, C., Müller, A., Krause, B., 2011. Crown plasticity in mixed forests—quantifying asymmetry as a measure of competition using terrestrial laser scanning. For. Ecol. Manag. 261 (11), 2123–2132. https://doi.org/10.1016/j.foreco.2011.03.008.

Tobner, C.M., Paquette, A., Gravel, D., Reich, P.B., Williams, L.J., Messier, C., 2016. Functional identity is the main driver of diversity effects in young tree communities. Ecol. Lett. 19 (6), 638–647. https://doi.org/10.1111/ele.12600.

Trogisch, S., Liu, X., Rutten, G., Xue, K., Bauhus, J., Brose, U., Bu, W., Cesarz, S., Chesters, D., Connolly, J., 2021. The significance of tree-tree interactions for forest ecosystem functioning. Basic Appl. Ecol. 55, 33–52. https://doi.org/10.1016/j.baae.2021.02.003.

Valladares, F., Niinemets, Ü., 2008. Shade tolerance, a key plant feature of complex nature and consequences. Annu. Rev. Ecol. Evol., Syst. 39, 237–257. https://doi.org/10.1146/annurev.ecolsys.39.110707.173506.

Valladares, F., Balaguer, L., Martinez-Ferri, E., Perez-Corona, E., Manrique, E., 2002. Plasticity, instability and canalization: is the phenotypic variation in seedlings of sclerophyll oaks consistent with the environmental unpredictability of Mediterranean ecosystems? N. Phytol. 156 (3), 457–467. https://doi.org/10.1046/j.1469-8137.2002.00525.x.

Van de Peer, T., Verheyen, K., Ponette, Q., Setiawan, N.N., Muys, B., 2018. Overyielding in young tree plantations is driven by local complementarity and selection effects related to shade tolerance. J. Ecol. 106 (3), 1096–1105. https://doi.org/10.1111/1365-2745.12839.

Vandenberghe, C., Freléchoux, F., Gadallah, F., Buttler, A., 2006. Competitive effects of herbaceous vegetation on tree seedling emergence, growth and survival: does gap size matter? J. Veg. Sci. 17 (4), 481–488. https://doi.org/10.1111/j.1654-1103.2006.tb02469.x.

Watt, M., Rolando, C., Kimberley, M., Coker, G., 2015. Using the age shift method to determine gains from weed management for *Pinus radiata* in New Zealand. Weed Res. 55 (5), 461–469. https://doi.org/10.1111/wre.12159.

Watt, M.S., Whitehead, D., Richardson, B., Mason, E.G., Leckie, A.C., 2003b. Modelling the influence of weed competition on the growth of young *Pinus radiata* at a dryland site. For. Ecol. Manag. 178 (3), 271–286. https://doi.org/10.1016/S0378-1127(02)00520-0.

Watt, M.S., Whitehead, D., Mason, E.G., Richardson, B., Kimberley, M.O., 2003a. The influence of weed competition for light and water on growth and dry matter partitioning of young *Pinus radiata*, at a dryland site. For. Ecol. Manag. 183 (1-3), 363–376. https://doi.org/10.1016/S0378-1127(03)00139-7.

White, P.S., 1983. Corner's rules in eastern deciduous trees: allometry and its implications for the adaptive architecture of trees. Bull. Torre Bot. Club 203–212. https://doi.org/10.2307/2996342.

Williams, L.J., Paquette, A., Cavender-Bares, J., Messier, C., Reich, P.B., 2017. Spatial complementarity in tree crowns explains overyielding in species mixtures. Nat. Ecol. Evol. 1 (4), 0063. https://doi.org/10.1038/s41559-016-0063.

Xu, Y., Chen, H.Y., Xiao, Z., Wan, D., Liu, F., Guo, Y., Qiao, X., Jiang, M., 2022. Species richness promotes productivity through tree crown spatial complementarity in a species-rich natural forest. Forests 13 (10), 1604. https://doi.org/10.3390/f13101604.

Yan, E.R., Zhao, C., Hu, J., Mao, H., Yu, Z., Ou, D., Liu, H., 2018. Vegetation in Putuo Island—Type, Structure, Function and Management. Science Press, *Beijing*.

Zheng, L.T., Chen, H.Y., Yan, E.R., 2019. Tree species diversity promotes litterfall productivity through crown complementarity in subtropical forests. J. Ecol. 107 (4), 1852–1861. https://doi.org/10.1111/1365-2745.13142.

Zheng, L.T., Chen, H.Y., Hautier, Y., Bao, D.F., Xu, M.S., Yang, B.Y., Zhao, Z., Zhang, L., Yan, E.R., 2022. Functionally diverse tree stands reduce herbaceous diversity and productivity via canopy packing. Funct. Ecol. 36 (4), 950–961. https://doi.org/10.1111/1365-2435.14009.