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Species Richness Promotes Productivity through Tree Crown Spatial Complementarity in a Species-Rich Natural Forest

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Abstract: Ecological theory suggests that species with complementary architectural and physiological traits can optimize crown packing to improve resource efficiency and promote ecosystem productivity in forest communities. However, empirical evidence of this prediction is rare in species-rich natural forests, as little is known about how crown spatial complementarity regulates community species richness-productivity relationship (SRPR). In this study, we measured tree architectural traits (stem diameter, height, crown depth and width) for 11,337 trees, and quantified species richness, functional diversity, crown spatial complementarity, soil fertility and forest productivity for 44 quadrats (20 m × 20 m per quadrat) in the Badagongshan 25 ha forest plot, central China. We tested bivariate correlations between species richness, crown complementarity, functional diversity and forest productivity. We employed linear mixed effects models to predict crown complementarity and examined its relationship with functional diversity. Finally, we applied structural equation modeling to quantify the mediation effects of crown complementarity on SRPRs. Species richness promoted crown complementarity and forest productivity. Crown complementarity varied across quadrats, with increases driven primarily by changes in tree height. Crown complementarity was positively related to functional diversity and forest productivity. Species richness increased with soil total phosphorus, while functional diversity decreased with soil bulk density. Forest productivity increased with soil organic carbon and total nitrogen, but decreased with bulk density. Crown complementarity partially mediated the positive effect of species richness on forest productivity, and the mediation effect was mainly through functional diversity. Our results suggest that the crown complementarity index accurately reflects the niche complementarity through light utilization and carbon reallocation. Our study emphasizes that species richness can promote crown complementarity, leading to greater forest productivity, which provides greater insight into the mechanical understanding of the SRPRs.

Keywords: forest productivity; functional diversity; species richness; crown architecture; niche complementarity; life-history trait; forest dynamic plot

1. Introduction

Explaining the underlying mechanisms of species richness-ecosystem functioning relationships is crucial for understanding the consequences of biodiversity loss and formulating sound policies for ecosystem management [1,2]. Over the past decade, the majority of long-term experiments in grasslands and forest plantations have found that productivity

increases with community diversity [3,4]. However, the positive effect of species richness on productivity in natural ecosystems, especially in natural regenerating forests, is still hotly debated [5–9]. The controversy possibly arises from our limited understanding of patterns and causes of species richness-productivity relationships (SRPRs) in natural ecosystems. Cotta [10] and Dănescu et al. [11] suggest that diverse and structurally complex forests provide better ecosystem services relative to pure and even-aged stands—a concept that may contribute to resolving the gap in the literature. However, empirical evidence of this hypothesis is rare. Improving our understanding of the ecological mechanisms behind SRPRs may help unravel the complex ecological processes that govern forest ecosystems.

In recent years, the role of canopy structure as a mechanism to explain ecosystem overyielding has attracted extensive attention [12,13]. Many indices have been introduced to quantify canopy structure, including, size inequality [14], structural complexity [15], structural diversity [11], crown variation [16], canopy roughness [17] and canopy packing [18]. However, results from studies that apply these indices in an effort to link species diversity with forest productivity have found positive, neutral and negative relationships [17,19,20]. It is possible that these papers may have explored different aspects of community canopy structure, and the correlation with niche complementarity is weak. Recently, the canopy complementarity index (CCI) was introduced to explain overyielding in species mixture ecosystems [13,21,22]. CCI calculates the canopy space occupied by crowns with different spatial positions, providing a direct measure of canopy space partitioning, similar to the concept of "realized niche". Nevertheless, how it relates to niche complementarity is still unknown.

Tree crown architecture is determined by species-specific growth strategies and actual growing conditions, which are critical for maximizing light capture and closely related to plant performance [23–25]. Moreover, plant performance is an important link between phenotype and ecological success, which makes tree architecture ecologically and evolutionary relevant [26]. For forest understory plants, light is one of the most limited resources. Thus, whether differentiation in tree architecture contributes to light gradient partitioning is important for population growth, survival and species coexistence in forest communities [23]. Studies find that larger stature species with a higher light requirement and lower wood density have slender trucks and larger but shallower crowns compared to small stature species, and vice versa, although differences can occur between early- and late-life stages [25,27,28]. Additionally, tree species can plastically respond to light environmental changes within the canopy by adjusting the expansion of leaves and branches or reallocating carbon between plant modules [15,18]. Therefore, if inter-specific variations in crown architecture can differentiate species' partitioning of light resources, this should be reflected in the relationships between crown architecture and the functional traits closely related to light interception and biomass allocation [25]. Species-specific adult stature, shade tolerance and wood density are closely related to species strategy of light capture and carbon allocation in forests. Tree species difference in adult stature (e.g., canopy, subcanopy, understory species) and shade tolerance reflect abilities of tree species to partition light at the vertical and horizontal gradient within a forest canopy [23,25,28]. Wood density is important in determining mechanical stability and whole plant carbon allocation [27,29]. Therefore, detecting the relationships between tree crown architecture and functional diversity will further our understanding of niche complementarity, one of the most important mechanisms in explaining the positive effect of species mixing on ecosystem functionality [1,30].

At both regional and local scales, abiotic and biotic environmental conditions influence species composition, canopy structure, forest productivity, and their interrelationships [16,24,31]. Communities with higher species diversity have more diversified ecological strategies, which reduce competition among adjacent trees, allowing them to obtain a higher proportion of available resources and growth space, resulting in greater forest productivity. However, tree species may compete for multiple resources and complement the utilization of one resource but not another [18]. In a resource-limited environment, trees may plastically change their biomass allocation to away from space that most limit

their growth, enabling them to forage for and fully utilize resources [32,33]. For example, if competition for light is critical for forest canopy structure and tree growth, trees will allocate more carbon to tree height growth and less to branch extensions. In infertile and water-limited soils, however, tree species compete for soil nutrients more fiercely, and allocate more biomass to leaves than roots, which leads to increases in above-ground space occupying and competition. Species-diverse communities with various life-history strategies in carbon allocation may alleviate inter-specific competition.

In this study, we examined how species richness can promote forest productivity through crown complementarity with a large dataset in a subtropical evergreen deciduous broad-leaved forest. The studied forest is located at the eastern Sichuan-western Hubei endemic plant genus distribution center (relic center), and has a high species diversity. It is also one of the most northern zones of the evergreen broad-leaved forest. Therefore, there is an urgent need to explore the mechanisms underlying the SRPR in this species-rich forest. To guide our work, we put forward the following three hypotheses: (1) crown spatial complementarity increases with species richness, and is higher in communities with more variation in crown structure; (2) greater crown complementarity comes from niche differentiation (greater diversity in shade tolerance, adult stature and wood density), and leads to greater utilization of above-ground sources and tree growth; and (3) crown complementarity mediates the species richness and forest productivity relationship.

2. Materials and Methods

2.1. Study Area

Our study was conducted in the Badagongshan 25 ha (500 m × 500 m) forest dynamics plot (hereafter BDGS plot) in Hunan Province, central China (29°46.041′ N, 110°5.248′ E). The BDGS 25 ha plot was developed in 2011. Forest type is a typical subtropical evergreen and deciduous broad-leaved mixed forest that has been well protected and without anthropogenic disturbance since the 1950s. The area has a monsoon humid subtropical climate with a mean annual temperature of 11.5 °C and an average annual precipitation of 2105 mm [34]. The dominant soil type is Hapludalfs. The BDGS plot was systematically divided into 625 20 m × 20 m quadrats. Within each quadrat, all free-standing woody stems ≥1 cm stem diameter (D; 1.3 m) were tagged, identified, measured and mapped [35]. Elevation in the plot ranges from 1369.6 m to 1470.9 m. According to the census in 2011, there were 232 tree species belonging to 114 genera and 53 families, and a total of 186,556 living stems were counted. The five most dominant species are *Fagus lucida*, *Cyclobalanopsis multinervis*, *Rhododendron stamineum*, *Cyclobalanopsis gracilis* and *Sassafras tzumu*.

2.2. Tree Architecture and Soil Properties Measurement

Between June–July 2017, we selected two subplots of the 25 ha BDGS plot (Figure S1) that are relatively flat to reduce the influence of complex topography. One subplot was 0.8 ha in size (80 × 100 m², that is including 20 quadrats) with an elevation range of 1411.42 to 1455.03 m a.s.l and the other was 0.96 ha (80 × 120 m², 44 quadrats) with an elevation range of 1399.75–1436.39 m a.s.l. In the two subplots, we measured tree diameter (D), total tree height (H), the height of the lowest foliage (F) and crown widths in four cardinal directions (east, west, north and south). We used a measuring pole to measure tree height for trees below 15 m, and a Vertex IV Hypsometer (Haglöf Sweden, http://www.haglofcg.com (accessed 1 May on 2017) for taller trees. Crown dimensions were measured as the length from the midpoint of the trunk to the edge of the crown in the four cardinal directions using a steel tape with centimeter precision. We calculated crown width in the east-west and north-south directions (represented by W_1 and W_2, where $W_1 > W_2$). A total of 11,337 individuals were measured in the two subplots.

We used soil characteristics as a proxy for the microenvironmental conditions [36]. We took soil samples in 0–10 cm soil layer for each quadrat (20 m × 20 m) in the two subplots in 2014, and then measured soil organic carbon (SOC), total nitrogen (TN), total phosphorus (TP) and bulk density (BD). All soil samples were air-dried, then passed through 2.0 and

0.15 mm sieves in the laboratory. We then measured soil total carbon, total nitrogen, total phosphorus, and bulk density for each soil sample. For detailed information on soil analyses, see Li et al. [36].

2.3. Quantification of Crown Spatial Complementarity

The volume of each tree crown can be estimated as the volume of an ellipsoid, which needs the lengths of the three principal semi-axes [13]. We measured crown width along the long- and short-axes and crown depth for each focal tree.

The crown volume of a tree was estimated as

$$V = \frac{\pi}{6}(W_1 \times W_2 \times CD)$$ (1)

where CD is the difference between tree height and height of the lowest foliage (in m), and W_1 and W_2 are the long and short width of the crown (in m).

To evaluate the partitioning of forest canopy space by trees, we used a crown complementarity index (*CCI*). The *CCI* was estimated based on the difference in volume size between two neighbor trees along the height axis of the forest canopy. We assumed that all trees within the quadrat overlap each other and share a proportion of crown volume. Thus, crown complementarity for a pair of neighbor trees is described as the ratio of non-overlapping parts to the sum of total crown volume [13]. The *CCI* for each quadrat was calculated by averaging the index for all possible pairs within the quadrat (Equation (2)). The *CCI* scores are within a range between 0 (fully overlapping) and 1 (non-overlapping)

$$CCI_q = \sum_1^n (\frac{|V_{io} - Vjo| + V_{in} + V_{jn}}{V_i + V_j})/n$$ (2)

where CCI_q is crown complementarity index for quadrat q, n is the number of all possible pairs of trees within quadrat q, and V_i and V_j are the crown volume of tree i and tree j, respectively. V_{io} and V_{jo} are the overlapping section of crown volume for tree i and tree j along the vertical axis of canopy, respectively, and V_{in} and V_{jn} are the non-overlapping section for tree i and tree j along the vertical axis of canopy, respectively [22].

2.4. Characterizations of Variation in Tree Height, Crown Size and Crown Shape

We developed a suite of crown structure features to represent the crown shape and crown size in order to quantify and compare their effects on crown spatial complementarity. Variables for crown size included crown volume, crown length, crown projection area, crown width, and the ratio of crown volume to D^2H (basal diameter square multiplied by tree height). Variables for crown shape included ratios of crown-width-to crown-length, crown-length to tree-height, crown-width to tree-height, and crown width of the East-West direction to the North-South direction. We then used a functional dispersion index to represent local variations in crown size and shape, respectively [37].

2.5. Calculation of Species Richness, Functional Diversity and Forest Productivity

Species richness was the number of species in each quadrat (20 m × 20 m). Functional diversity was calculated based on three functional traits—shade tolerance, adult stature, and wood density–which are closely related to biomass allocation and tree architecture. Shade tolerance was estimated via the Ellenberg light index for each species, an ordinal classification of plant species based on their positions along one or more environmental gradients [38,39]. We obtained the Ellenberg light index for the studied 139 species from Song et al. [39]. The Ellenberg light index ranges from 1 to 9, and a higher value indicates that the species has a higher light demand and lower shade tolerance for growth and regeneration. The adult stature of a tree species was estimated by the upper 95th percentile stem diameter for a subgroup of trees whose diameters are larger than 10% of the maximum stem diameter of the population [40]. The index was applied due to its stability, and should not be significantly affected by population size or tree size structure [40,41]. To

guarantee sufficient individuals for each species, the inventory data of the BDGS 25 ha in the 2016 plot was used to calculate adult stature. Wood density was obtained from previous tree sampling data close to the plot [34] and published wood density data [42]. We estimated functional richness (Fric), functional evenness (Feve), functional divergence (Fdiv), functional dispersion (Fdis) and Rao's quadratic entropy (RaoQ) at the quadrat level. A review of these indices of functional diversity can be found in [37]. For details about the studied 139 tree species please, see Table S1.

Annual net forest primary productivity (ANPP; Mg ha^{-1} year^{-1}) was estimated by changes in forest biomass between each quadrat during two censuses (2011–2017). Total biomass, including above-and below-ground biomass (AGB and BGB) of each individual with a diameter larger than 1 cm in each quadrat, was estimated using published site-specific allometric models.

The allometric biomass models used in this study were previously developed to estimate forest biomass for the BDGS plot [34]. Individual biomass was summed for all stems for each 20 m × 20 m quadrat. The allometric models were as follows

$$AGB = \exp(-1.823 + 2.411\ln(D) + 0.578\ln(\rho)); \ R^2 = 0.93; \tag{3}$$

$$BGB = exp(-2.803 + 2.0441\ln(D)); \ R^2 = 0.92 \tag{4}$$

where D is the stem diameter (cm) and ρ is wood specific gravity (g/cm^3).

A correction factor (1.022 in this study) was multiplied to the predicted biomass value for each tree as Xu et al.'s [34] biomass models are log-transformed.

Annual net productivity was calculated for the two subplots, as follows

$$ANPP = (G + R - De)/6 \tag{5}$$

where $ANPP$ is growth of forest biomass between 2011–2017; G is the annual growth in biomass of trees that were alive during 2011–2017; R is the annual growth in biomass of individuals recruited into the minimum diameter class (1 cm); and De is the net decreases in biomass of individuals dead between the two census dates. Litter fall was not included in this study.

2.6. Statistical Analysis

To examine how species richness affects crown spatial complementarity, we used simple linear regression to examine the relationship between species richness and crown spatial complementarity. Furthermore, we used linear mixed-effect models to examine the effects of tree height, crown size and crown shape on crown complementarity, and then partitioned the variances of each variable in the fixed-effect model. The subplot was random effect used to control for differences between the two subplots in the mixed-effect models.

In order to further explore the relationship between crown complementarity and niche partitioning, we first tested the relationship between functional diversity indices and crown complementarity at the quadrat level. Second, we tested the community-weighted mean value of three functional traits (light requirement, adult stature, and wood density) against variations in tree height, crown shape and crown size, respectively.

To examine the mediating effect of crown spatial complementarity on SRPR, we applied structural equation modeling (SEM), as it is particularly suited for analyzing multi-factor causal relationships [43]. We used principal component analysis (PCA) to assess soil fertility quality. Soil variables were exogenous variables, while species richness, functional diversity, crown complementarity and ANPP were endogenous variables in SEM. We complemented a SEM model containing only soil variables, species richness, CCI, functional diversity and ANPP to test the mediation effect of CCI and functional diversity on SRPR.

All analyses were conducted in environment R 3.5.1 [44]. The mixed-effect linear regression models, functional diversity and SEM were calculated using R packages '*lme4*' [45], '*FD*' [37] and '*piercewiseSEM*' [46], respectively.

3. Results

Species richness increased with crown complementarity in our subtropical forest ($R^2 = 0.18$, $p < 0.01$) (Figure 1). Species richness had a mean value of 41, and ranged from 28 to 57. CCI had a mean value of 0.78, and ranged from 0.77 to 0.89 at the quadrat level (Table 1). Variations in tree height, crown size, crown size, basal area and species richness explained 38% of the variation in CCI. Among these factors, tree height variation accounted for 46% of the total variation, followed by variation in crown shape and crown size, accounting for 27% and 16%, respectively (Figure 1, Table S2).
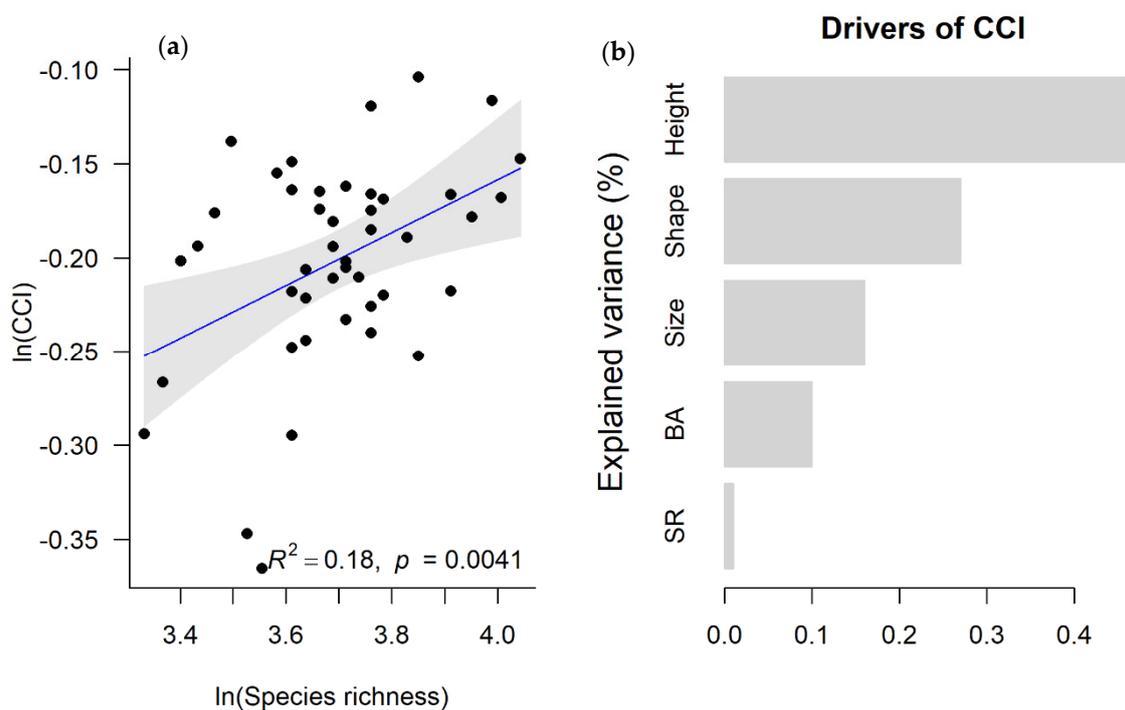
Figure 1. Species richness and crown spatial complementarity. (**a**) Bivariate relationship between species richness and crown spatial complementarity; and (**b**) relative contributions of drivers on crown spatial complementarity.

Table 1. Characteristic of stand variables in this subtropical forest. Values are mean value and its ranges for each variable.

Variables	Unit	Abbreviation	Values
Species richness	unitless	SR	40.80 [28.00, 57.00]
Crown complementarity index	unitless	CCI	0.82 [0.69, 0.90]
Annual forest productivity	Mg ha^{-1} yr^{-1}	ANNP	5.24 [2.27, 9.49]
Basal area	m^2 ha^{-1}	BA	1.64 [0.70, 3.03]
Shape variation	unitless	Fdis_shape	0.51 [0.41, 0.65]
Size variation	unitless	Fdis_size	0.89 [0.60, 1.20]
CWM. wood density	unitless	CWM.WD	0.56 [0.53, 0.60]
CWM. adult stature	unitless	CWM.d95k	18.67 [13.83, 24.29]
CWM. shade tolerance	unitless	CWM.ST	6.10 [5.89, 6.32]
Functional richness	unitless	FRic	21.83 [10.22, 32.40]
Functional divergence	unitless	FDiv	0.77 [0.66, 0.84]

Table 1. *Cont.*

Variables	Unit	Abbreviation	Values
Functional dispersion	unitless	FDis	1.32 [1.04, 1.66]
Rao's quadratic entropy	unitless	RaoQ	2.23 [1.41, 3.40]
Soil organic carbon content	g Kg^{-1}	TOC	8.25 [6.65, 9.98]
Soil nitrogen content	g Kg^{-1}	TN	0.62 [0.45, 0.74]
Soil phosphorus content	g Kg^{-1}	TP	5.05 [3.14, 6.55]
Bulk density	g cm^{-3}	BD	0.53 [0.41, 0.73]

There were positive relationships between CCI and functional richness (FRic: $p < 0.05$), functional dispersion (FDis: $p < 0.05$) and Rao's quadratic entropy (RaoQ: $p < 0.01$) (Figure 2a–c). Variations in tree height, crown size and crown shape increased with the community-weighted mean of shade tolerance, adult stature and wood density, except a neutral relationship between variation in crown shape and community-weighted mean of adult stature (Figure 2d–l).
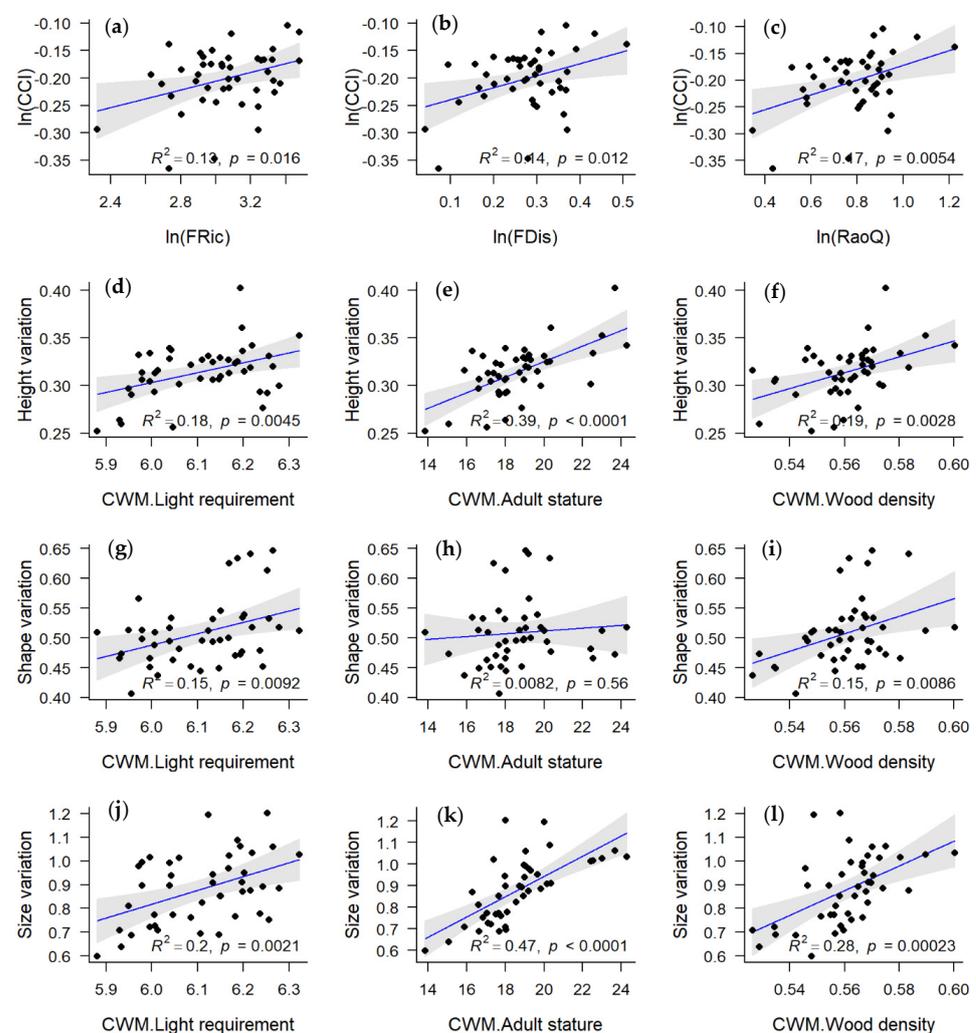
Figure 2. Bivariate relationships between crown spatial complementarity and functional diversity. The upper three scatter plots (**a–c**) capture crown complementarity index vs. (**a**) functional richness (FRic), (**b**) functional dispersion (FDis) and (**c**) the Rao's quadratic entropy (RaoQ). The 9 plots in the lower panel capture the regressions between variations in tree height (**d–f**), crown shape (**g–i**) and crown size (**j–l**) and community-weighted mean of shade tolerance, adult stature and wood density, respectively. The R^2 and *p*-values are shown.

ANPP increased with species richness, functional diversity and CCI (Figure 3). Among the four soil variables, species richness increases with soil organic carbon and total phosphorus, but not with soil nitrogen content or bulk density (Figure 4a–d). Functional diversity increased with soil organic carbon and decreased with bulk density, but not with the other two variables (Figure 4e–h). CCI was invariant across soil variables (Figure 4i–l). ANPP increased with soil organic carbon and total nitrogen content, but decreased with soil bulk density (Figure 4m–o).
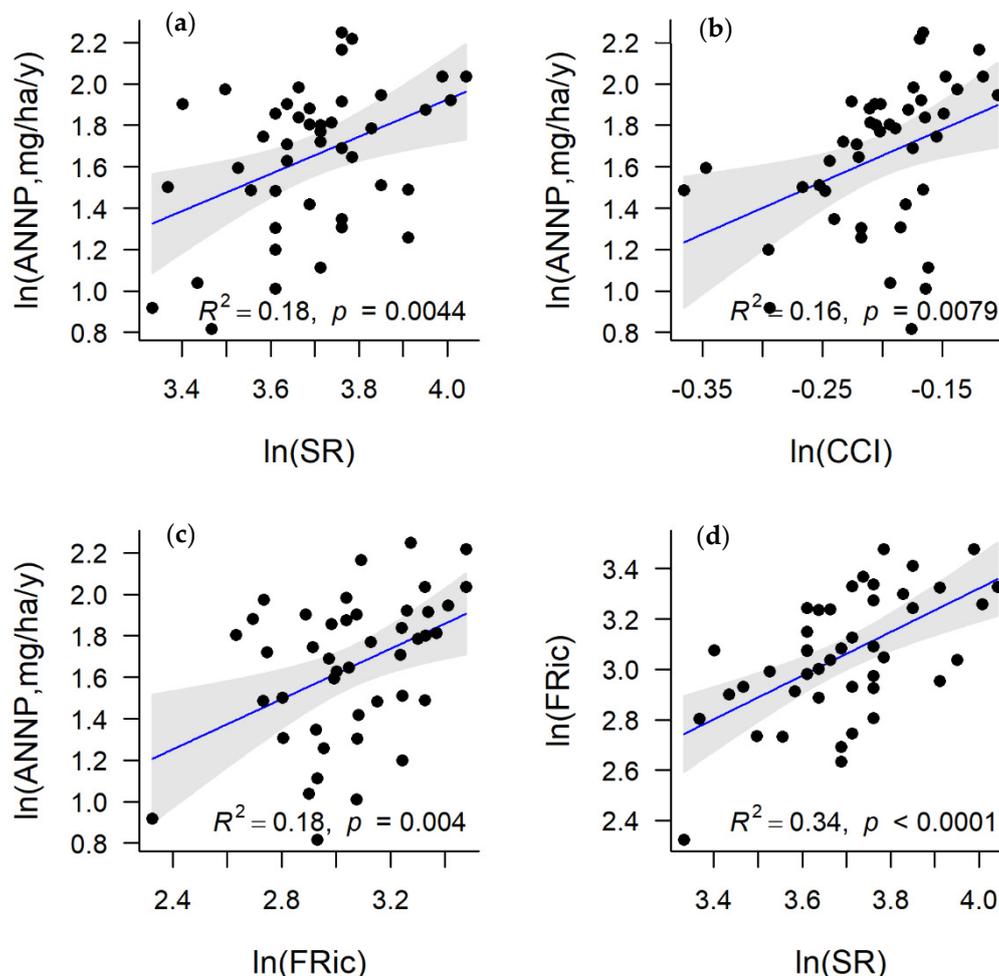
Figure 3. Linear relationships between endogenous and exogenous variables (n = 44 quadrats). The upper three scatter plots (**a**–**c**) capture annual forest productivity (ANPP) versus species richness (SR), crown complementarity index (CCI) and functional diversity (FD), respectively; and (**d**) measures functional diversity (FD) regressed on species richness (SR). The R^2 and *p*-values are shown. All numerical variables were natural log-transformed.

The PCA analysis showed that the first and second main axes explained almost 80% of the total variation in soil properties (Figure S2a,b; Table S3). The SEM model demonstrated positive species richness and forest productivity relationship (Figure 5b; Table 2). Overall, 45% of the variation in ANPP was explained by the direct and indirect paths from soil fertility, in which the direct effect of soil PCA1 and the paths through species richness, functional diversity and crown complementarity were the main drivers (Figure 5b; Table 2). However, the paths between soil fertility and the three endogenous variables were negative, except for the path from soil PCA2 to SR and CCI (Figure 5b). CCI partially mediated the effect of species richness on ANPP. Additionally, when functional diversity acted as a mediating variable between SR and CCI, the total explanation of ANPP variation was nearly unchanged, but the direct positive effect from SR to CCI disappeared (Figure 5b).
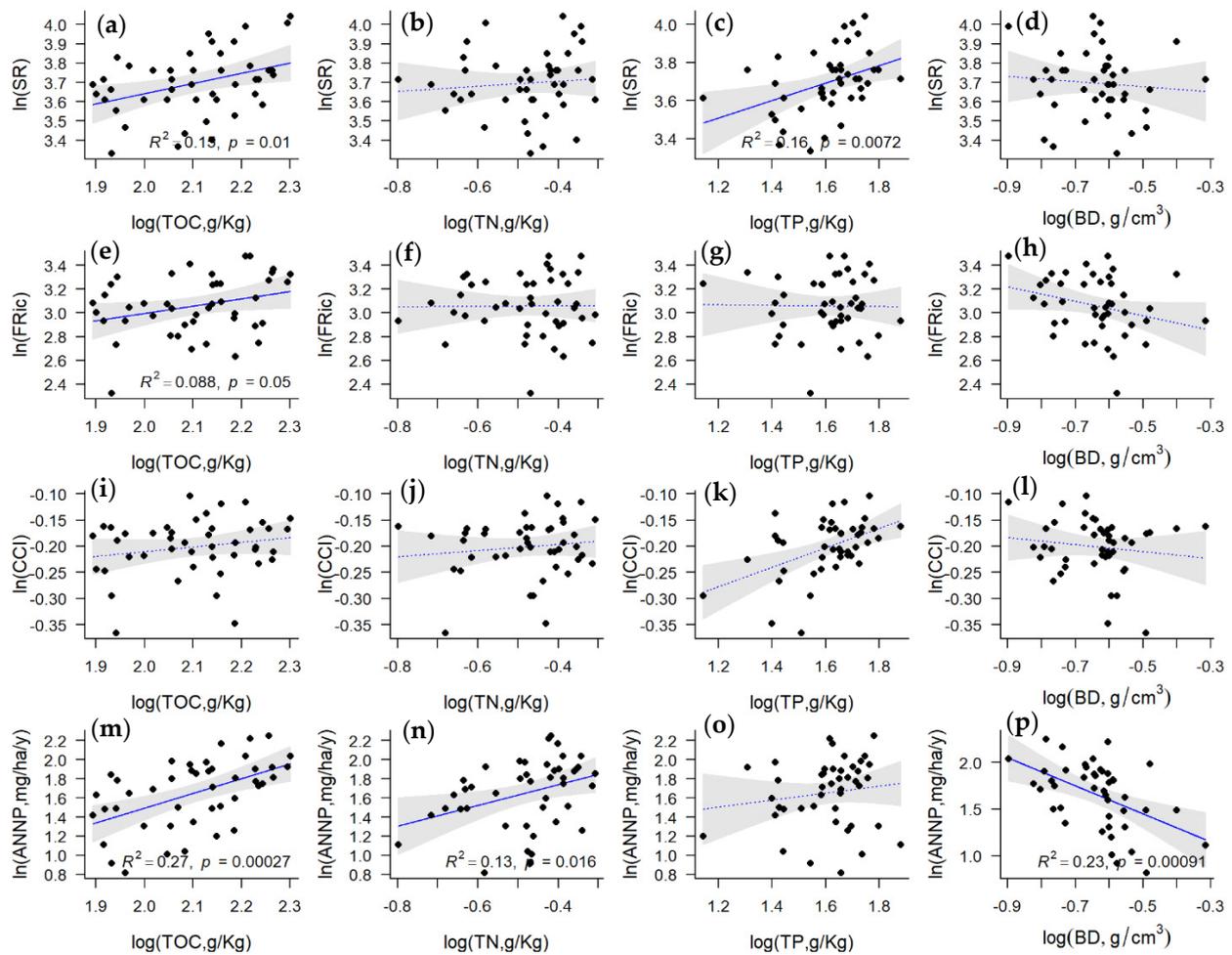
Figure 4. Bivariate relationships between endogenous and exogenous variables (n = 44). The scatter plots (**a**–**d**), (**e**–**h**), (**i**–**l**) and (**m**–**p**) capture the relationships between species richness (SR), functional diversity (FD), crown complementarity index (CCI), annual forest productivity (ANPP), soil organic carbon (TOC), total nitrogen content (TN), total phosphorus content (TP) and soil bulk density (BD). The R^2 and p-values are shown. All numerical variables are natural log-transformed.

Table 2. The direct, indirect and total standardized effects on ANPP based on structural equation models (SEMs).

Predictors	Pathway to ANPP	Effect	p-Value
Soil PCA1	Direct	-0.43	<0.001
	Through SR	-0.08	<0.001
	Through FD	-0.01	-
	Through CCI	-0.03	<0.001
	Total effect	-0.55	-
Soil PCA2	Direct	-0.09	<0.001
	Through SR	0.14	<0.001
	Through FD	-0.07	<0.001
	Through CCI	0.1	-
	Total effect	0.08	-

Table 2. *Cont.*

Predictors	Pathway to ANPP	Effect	*p*-Value
SR	Direct	0.18	<0.001
	Through FD	0.15	<0.001
	Through CCI	~0.00	<0.001
	Total effect	0.33	-
FD	Direct effect	0.14	<0.001
	Through CCI	0.08	<0.001
	Total effect	0.22	-
CCI	Direct effect	0.23	<0.001
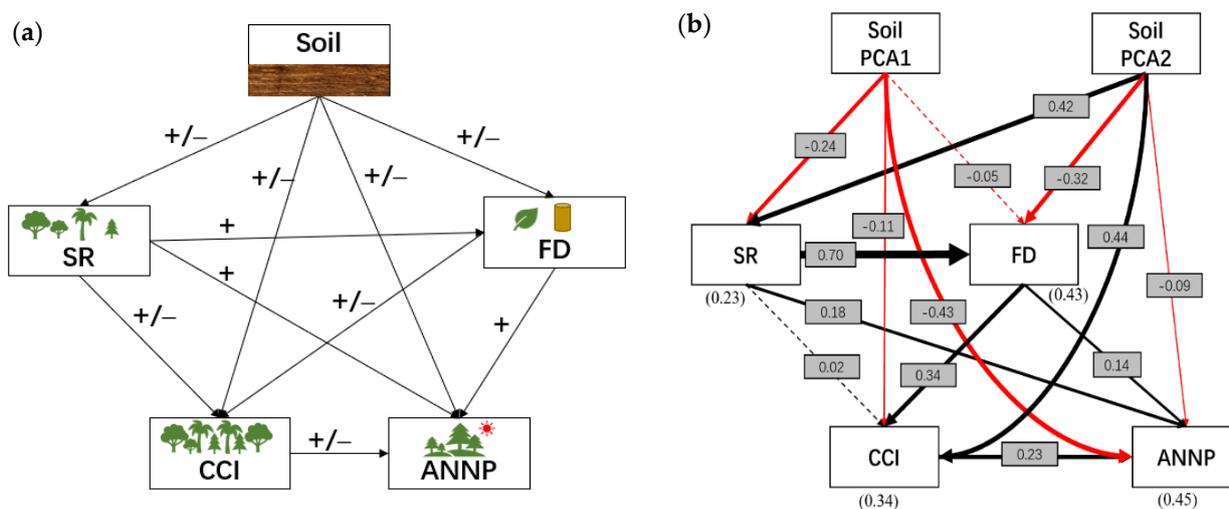
Figure 5. Structure equation models linking species richness and annual forest productivity. (**a**) Conceptional diagram for examining the SRPRs in a subtropical forest; (**b**) model consisting of soil variables, species richness, crown complementarity index, functional diversity, and annual forest productivity. Numbers on the arrows indicate standardized path coefficients. Solid lines and dotted lines indicate significant and non-significant path correlation, respectively. Black and red lines indicate positive and negative path correlations, respectively. R^2 indicates the total variation in an endogenous variable explained by the exogenous variables.

4. Discussion and Conclusions

In this study, we use a large data set to examine how tree species enhance forest productivity through crown complementarity in a natural forest community. This study provides evidence that crown spatial complementarity is an underlying mechanism in explaining the positive SRPR. Crown complementarity is positively related to functional diversity indices. Furthermore, variation in crown architecture is positively related to the community-weighted mean of adult stature, shade tolerance and wood density. Overall, these findings suggest that CCI can well capture spatial partitioning of space and resources within a canopy, which operates mechanistically to drive the positive biodiversity-productivity relationship in forest communities.

Tree crown spatial complementarity is determined by species-specific tree architecture and growth plasticity to local environmental conditions [18,32]. A previous study in this forest plot found that almost all tree species have distinct tree architectural allometry, such as tree height-stem diameter allometry and crown width- and crown depth-tree height allometric relationships [28]. Therefore, communities with higher species diversity have tree crowns that are packed more densely. In this study, variations in crown vertical stratification, crown size and crown shape strongly regulate the positive effect of species richness on crown complementarity. This result is consistent with studies that find that tree crowns in mixed-species plantations are packed more densely than single-species

plantations [32,47]. However, variation in tree height is the most important driver of CCI in this forest, but it is often neglected in studies of plantations [18,48]. An explanation for this phenomenon is that high individual density in natural forests may lead to intense species competition for limited resources, such as light [49,50]. Consequently, large-stature tree species allocate more photosynthetic products to tree height growth to intercept upper light and overtop neighbors in crowded environments in forest understory, which in turn lowers leaf mass fraction, and thus carbon gain [28]. Even so, crown size and shape are two important driving forces to obtain the maximum diffused light in the forest understory. Compared to plantations with simple community structures, natural forests develop crowns with complementary heights and individuals of various sizes, which complexifies forest canopies [18,48]. Furthermore, natural mature forests are older on the timescale than plantations, allowing enough time for crown vertical differentiation. Therefore, vertical stratification of tree crowns can reduce direct light competition in dense natural forests, which may help trees adjust the crown size and shape to maximize light interception [49,50].

Our bivariate analyses show that crown complementarity is positively correlated to species richness and functional diversity. Shade tolerance, adult stature and wood density are frequently used to link tree architecture and specific life history strategies [23,49,51]. Shade tolerance is an important feature of light resource partitioning, and is closely related to local complementarity and selection effects that drive SRPR in forests [30]. Variation in tree height, crown shape and crown size increase with community-weighted mean of shade tolerance, which suggests that communities with a higher diversity of shade-tolerance among coexisting species should have more variation in crown architecture. Adult stature and wood density refer to maximum potential growth and biomass reallocation strategies, respectively, and are good predictors of tree architecture [25,27,49]. The positive relationships between these two characteristics and crown size and shape variation (except for crown shape variation and adult stature) suggest that communities with larger maximum tree sizes and greater wood density should have higher crown complementarity. Larger-stature species extend the outer canopy and increase total canopy space, while species with a denser wood increase the mechanical stability of tree architecture [25,27]. Therefore, the strongly positive relationship between functional diversity and community-level crown architecture suggests that forest communities with higher species diversity improve resource utilization efficiency and carbon reallocation, which is reflected in the complexity of the canopy structure.

In this study, we provide evidence that species richness increases with forest productivity, and crown complementarity is a mediator affecting the positive SRPR in the species-rich and structurally complex forest. This result is consistent with studies from subtropical successional forests [22], temperate old-growth forest [17] and forest plantations [13]. This finding strengthens the importance of crown architecture and functional diversity in maintaining species diversity and promoting ecosystem functions in forest communities [3,13,22]. At the community level, variations in crown vertical stratification, crown size and crown shape have significantly positive effects on resources capture and utilization [23]. Natural forests consisting of high diversity of tree species with distinctive tree architectural allometry result in canopy space packed more efficiently and structures more complex compared to plantations [28]. At the individual level, trees growing in species-rich neighborhoods can increase volume both of trunks and branches, and the wood volume allocation will shift as neighborhood species diversity changes [21]. As a result, canopy growing space and resources are more fully and efficiently utilized due to the spatial complementarity of tree crowns. Besides, tree species with species-specific tree architecture can promote niches partitioning and reduce species competition. In a forest, trees are sessile and have similar resource requirements, making tree size a critical resource competition and acquisition ability, especially for morphologically flexible species [52]. In monoculture stands, most individuals are homogeneous in tree size to compete for growing space and resources in a similar manner, leading to them not being sufficient for all. Meanwhile, in mixed-species communities, trees have more canopy space to expand their

crown sizes and shapes without mechanical abrasion if they complement each other [32]. Soil C, N and P content has positive effects on species richness, and ANNP, which suggests that species-diverse communities in fertile soil can increase soil use efficiency and then allocate more biomass to above ground. Relationships between soil fertility and CCI are weak, but still positive, which is possible due to soil fertility affecting more in stem biomass and less in crown architecture [4,24].

In conclusion, understanding the mechanisms associated with the effect of biodiversity on ecosystem functioning is critical for predicting the consequences of biodiversity loss and guiding the future direction of human efforts. Nowhere is more demanding of evidence than natural forests. Our study demonstrates that crown spatial complementary and functional diversity is a key mechanism underlying the positive SRPRs in natural subtropical forests. A previous meta-analysis shows that the net species diversity effect tends to saturate when species richness is greater than 6 [8]. Surprisingly, however, we find the positive SRPRs in a species-rich forest where species richness ranges from 27 to 57 species per 20 m × 20 m quadrat. The positive relationship between crown spatial complementary and functional diversity demonstrates that species with diverse life-history strategies in light utilization and biomass allocation will fully use canopy space and resources. Additionally, our findings suggest that a more structurally complex canopy will enhance forest productivity above and below ground, which has significant implications for silviculture and regional carbon storage by making forests more structurally complex.

References

1. Loreau, M. Linking biodiversity and ecosystems: Towards a unifying ecological theory. *Philos. Trans. R. Soc. B Biol. Sci.* **2010**, *365*, 49–60. [CrossRef] [PubMed]
2. Fichtner, A.; Härdtle, W.; Bruelheide, H.; Kunz, M.; Li, Y.; Von Oheimb, G. Neighbourhood interactions drive overyielding in mixed-species tree communities. *Nat. Commun.* **2018**, *9*, 1144. [CrossRef] [PubMed]
3. Sapijanskas, J.; Paquette, A.; Potvin, C.; Kunert, N.; Loreau, M. Tropical tree diversity enhances light capture through crown plasticity and spatial and temporal niche differences. *Ecology* **2014**, *95*, 2479–2492. [CrossRef]
4. Ammer, C. Diversity and forest productivity in a changing climate. *New Phytol.* **2019**, *221*, 50–66. [CrossRef] [PubMed]
5. Chen, H.Y.; Klinka, K. Aboveground productivity of western hemlock and western redcedar mixed-species stands in southern coastal British Columbia. *For. Ecol. Manag.* **2003**, *184*, 55–64. [CrossRef]
6. Jiang, L.; Wan, S.; Li, L. Species diversity and productivity: Why do results of diversity-manipulation experiments differ from natural patterns? *J. Ecol.* **2009**, *97*, 603–608. [CrossRef]
7. Jacob, M.; Leuschner, C.; Thomas, F.M. Productivity of temperate broad-leaved forest stands differing in tree species diversity. *Ann. For. Sci.* **2010**, *67*, 503. [CrossRef]
8. Zhang, Y.; Chen, H.Y.; Reich, P.B. Forest productivity increases with evenness, species richness and trait variation: A global meta-analysis. *J. Ecol.* **2012**, *100*, 742–749. [CrossRef]
9. Sullivan, M.J.P.; Talbot, J.; Lewis, S.L.; Phillips, O.; Qie, L.; Begne, S.K.; Chave, J.; Cuni-Sanchez, A.; Hubau, W.; Lopez-Gonzalez, G.; et al. Diversity and carbon storage across the tropical forest biome. *Sci. Rep.* **2017**, *7*, 39102. [CrossRef]
10. Cotta, H. *Anweisung zum Waldbau*; Arnoldische Buchhandlung: Dresden, Germany, 1828.
11. Dănescu, A.; Albrecht, A.T.; Bauhus, J. Structural diversity promotes productivity of mixed, uneven-aged forests in southwestern Germany. *Oecologia* **2016**, *182*, 319–333. [CrossRef]
12. Taubert, F.; Jahn, M.; Dobner, H.; Wiegand, T.; Huth, A. The structure of tropical forests and sphere packings. *Proc. Natl. Acad. Sci. USA* **2015**, *112*, 15125–15129. [CrossRef] [PubMed]
13. Williams, L.J.; Paquette, A.; Cavenderbares, J.; Messier, C.; Reich, P.B. Spatial complementarity in tree crowns explains overyielding in species mixtures. *Nat. Ecol. Evol.* **2017**, *1*, 0063. [CrossRef] [PubMed]
14. Zhang, Y.; Chen, H.Y. Individual size inequality links forest diversity and above-ground biomass. *J. Ecol.* **2015**, *103*, 1245–1252. [CrossRef]
15. Fahey, R.T.; Fotis, A.T.; Woods, K.D. Quantifying canopy complexity and effects on productivity and resilience in late-successional hemlock-hardwood forests. *Ecol. Appl.* **2015**, *25*, 834–847. [CrossRef]
16. Ali, A.; Lin, S.L.; He, J.K.; Kong, F.M.; Yu, J.H.; Jiang, H.S. Tree crown complementarity links positive functional diversity and aboveground biomass along large-scale ecological gradients in tropical forests. *Sci. Total Environ.* **2019**, *656*, 45–54. [CrossRef]
17. Hardiman, B.S.; Bohrer, G.; Gough, C.M.; Vogel, C.S.; Curtis, P.S. The role of canopy structural complexity in wood net primary production of a maturing northern deciduous forest. *Ecology* **2011**, *92*, 1818–1827. [CrossRef]
18. Jucker, T.; Bouriaud, O.; Coomes, D.A. Crown plasticity enables trees to optimize canopy packing in mixed-species forests. *Funct. Ecol.* **2015**, *29*, 1078–1086. [CrossRef]
19. Seidel, D.; Leuschner, C.; Scherber, C.; Beyer, F.; Wommelsdorf, T.; Cashman, M.; Fehrmann, L. The relationship between tree species richness, canopy space exploration and productivity in a temperate broad-leaf mixed forest. *For. Ecol. Manag.* **2013**, *310*, 366–374. [CrossRef]
20. Bohn, F.J.; Huth, A. The importance of forest structure to biodiversity-productivity relationships. *R. Soc. Open Sci.* **2017**, *4*, 160521. [CrossRef]
21. Kunz, M.; Fichtner, A.; Härdtle, W.; Raumonen, P.; Bruelheide, H.; von Oheimb, G. Neighbour species richness and local structural variability modulate aboveground allocation patterns and crown morphology of individual trees. *Ecol. Lett.* **2019**, *22*, 2130–2140. [CrossRef]
22. Zheng, L.; Chen, H.Y.; Yan, E. Tree species diversity promotes litterfall productivity through crown complementarity in subtropical forests. *J. Ecol.* **2019**, *107*, 1852–1861. [CrossRef]
23. Poorter, L.; Bongers, L.; Bongers, F. Architecture of 54 moist-forest species: Traits, trade-off and functional groups. *Ecology* **2006**, *87*, 1289–1301. [CrossRef]
24. Heineman, K.D.; Jensen, E.; Shapland, A.; Bogenrief, B.; Tan, S.; Rebarber, R.; Russo, S. The effects of belowground resources on aboveground allometric growth in Bornean tree species. *For. Ecol. Manag.* **2011**, *261*, 1820–1832. [CrossRef]
25. Iida, Y.; Kohyama, T.; Kubo, T.; Kassim, A.R.; Poorter, L.; Sterck, F.J.; Potts, M.D. Tree architecture and life-history strategies across 200 co-occurring tropical tree species. *Funct. Ecol.* **2011**, *25*, 1260–1268. [CrossRef]
26. Valladares, F.; Sanchez-Gomez, D.A.V.I.D.; Zavala, M.A. Quantitative estimation of phenotypic plasticity: Bridging the gap between the evolutionary concept and its ecological applications. *J. Ecol.* **2006**, *94*, 1103–1116. [CrossRef]
27. Iida, Y.; Poorter, L.; Sterck, F.J.; Kassim, A.R.; Kubo, T.; Potts, M.D.; Kohyama, T.S. Wood density explains architectural differentiation across 145 co-occurring tropical tree species. *Funct. Ecol.* **2012**, *26*, 274–282. [CrossRef]
28. Xu, Y.; Iida, Y.; Huang, H.; Shi, Z.; Franklin, S.B.; Luo, Y.; Bao, D.; Qiao, X.; Lu, Z.; Jiang, M. Linkages between tree architectural designs and life-history strategies in a subtropical montane moist forest. *For. Ecol. Manag.* **2019**, *358*, 1–9. [CrossRef]
29. Chave, J.; Coomes, D.; Jansen, S.; Lewis, S.L.; Swenson, N.G.; Zanne, A.E. Towards a worldwide wood economicsspectrum. *Ecol. Lett.* **2009**, *12*, 351–366. [CrossRef]

30. Van de Peer, T.; Verheyen, K.; Ponette, Q.; Setiawan, N.N.; Muys, B. Overyielding in young tree plantations is driven by local complementarity and selection effects related to shade tolerance. *J. Ecol.* **2018**, *106*, 1096–1105. [CrossRef]
31. Liu, Y.; Ren, X.; Zhang, Q.; Li, Q.; Tao, J. Soil depth alters the effect of species diversity on productivity in an experimental karst herbaceous community. *Plant Soil* **2022**, *471*, 61–71. [CrossRef]
32. Pretzsch, H. Canopy space filling and tree crown morphology in mixed-species stands compared with monocultures. *For. Ecol. Manag.* **2014**, *327*, 251–264. [CrossRef]
33. Guillemot, J.; Kunz, M.; Schnabel, F.; Fichtner, A.; Madsen, C.P.; Gebauer, T.; Härdtle, W.; Von Oheimb, G.; Potvin, C. Neighbourhood-mediated shifts in tree biomass allocation drive overyielding in tropical species mixtures. *New Phytol.* **2020**, *228*, 1256–1268. [CrossRef] [PubMed]
34. Xu, Y.; Zhang, J.; Franklin, S.B.; Liang, J.; Ding, P.; Luo, Y.; Lu, Z.; Bao, D.; Jiang, M. Improving allometry models to estimate the above-and belowground biomass of subtropical forest, China. *Ecosphere* **2015**, *6*, 1–15. [CrossRef]
35. Condit, R. *Tropical Forest Census Plots: Methods and Results from Barro Colorado Island, Panama and a Comparison with Other Plots*; Springer Science and Business Media: Berlin, Germany, 1998; pp. 37–71.
36. Li, Q.; Wang, X.; Jiang, M.; Wu, Y.; Yang, X.; Liao, C.; Liu, F. How environmental and vegetation factors affect spatial patterns of soil carbon and nitrogen in a subtropical mixed forest in Central China. *J. Soils Sediments* **2017**, *17*, 2296–2304. [CrossRef]
37. Laliberté, E.; Legendre, P.; Shipley, B. *FD: Measuring Functional Diversity from Multiple Traits, and Other Tools for Functional Ecology*, R package version 1.0–12; R Core Team: Vienna, Austria, 2014.
38. Ellenberg, H. Indicator values of vascular plants in central Europe. *Scr. Geobot.* **1979**, *9*, 97.
39. Song, Y.; Yan, E.; Song, K. Synthetic comparison of 8 dynamics plots in the evergreen broad-leaved forests in China. *Biodivers. Sci.* **2015**, *23*, 139–148. (In Chinese) [CrossRef]
40. Thomas, S.C. Asymptotic height as a predictor of growth and allometric characteristics in Malaysian rain forest trees. *Am. J. Bot.* **1996**, *83*, 556–566. [CrossRef]
41. King, D.A.; Davies, S.J.; Noor, N.S.M. Growth and mortality are related to adult tree size in a Malaysian mixed dipterocarp forest. *For. Ecol. Manag.* **2006**, *223*, 152–158. [CrossRef]
42. Zhang, S.B.; Slik, J.F.; Zhang, J.L.; Cao, K.F. Spatial patterns of wood traits in China are controlled by phylogeny and the environment. *Glob. Ecol. Biogeogr.* **2011**, *20*, 241–250. [CrossRef]
43. Grace, J.B.; Anderson, T.M.; Seabloom, E.; Borer, E.; Adler, P.B.; Harpole, W.S.; Hautier, Y.; Hillebrand, H.; Lind, E.; Pärtel, M.; et al. Integrative modelling reveals mechanisms linking productivity and plant species richness. *Nature* **2016**, *529*, 390–393. [CrossRef]
44. R Core Team. *R: A Language and Environment for Statistical Computing*; R Foundation for Statistical Computing: Vienna, Austria. Available online: https://www.R-project.org/ (accessed on 1 September 2021).
45. Bates, D.; Mächler, M.; Bolker, B.; Walker, S. Fitting linear mixed-effects models using lme4. *arXiv* **2014**, arXiv:1406.1:133-199, arXiv:1406.1:133-199.
46. Lefcheck, J.S. PIECEWISESEM: Piecewise structural equation modeling in R for ecology, evolution, and systematics. *Methods Ecol. Evol.* **2016**, *7*, 573–579. [CrossRef]
47. Kelty, M.J. The role of species mixtures in plantation forestry. *For. Ecol. Manag.* **2006**, *233*, 195–204. [CrossRef]
48. Binkley, D.; Campoe, O.; Gspaltl, M.; Forrester, D.I. Light absorption and use efficiency in forests: Why patterns differ for trees and stands. *For. Ecol. Manag.* **2013**, *288*, 5–13. [CrossRef]
49. King, D.A.; Davies, S.J.; Nur Supardi, M.N.; Tan, S. Tree growth is related to light interception and wood density in two mixed dipterocarp forests of Malaysia. *Funct. Ecol.* **2005**, *19*, 445–453. [CrossRef]
50. Laurans, M.; Hérault, B.; Vieilledent, G.; Vincent, G. Vertical stratification reduces competition for light in dense tropical forests. *For. Ecol. Manag.* **2014**, *329*, 79–88. [CrossRef]
51. Aiba, M.; Nakashizuka, T. Architectural differences associated with adult stature and wood density in 30 temperate tree species. *Funct. Ecol.* **2009**, *23*, 265–273. [CrossRef]
52. Iida, Y.; Swenson, N.G. Towards linking species traits to demography and assembly in diverse tree communities: Revisiting the importance of size and allocation. *Ecol. Res.* **2020**, *35*, 947–966. [CrossRef]