RESEARCH ARTICLE

Tree species diversity promotes litterfall productivity through crown complementarity in subtropical forests

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Abstract

1. The role of niche complementarity for driving the positive biodiversity–ecosystem productivity relationship has been widely recognized, but there is scant evidence regarding the role of tree canopy structure on this relationship. Litterfall productivity is proportional to forest net primary productivity in natural forests, and we hypothesized that litterfall productivity would increase with tree species diversity via increased tree crown complementarity.

2. We investigated annual litterfall productivity, species diversity, tree crown architecture, soil moisture content, soil carbon content and stand age across 28 subtropical forest plots in eastern Zhejiang province, China. Simple linear regression was used to examine bivariate relationships among rarified species richness, crown complementarity, total crown volume, soil moisture content, soil carbon content, stand age and litterfall productivity. Structural equation modelling was employed to quantify the direct and indirect effects of species richness on litterfall productivity through tree crown complementarity.

3. Litterfall productivity increased with rarefied species richness via increasing crown complementarity rather than total crown volume. Species richness, crown complementarity and litterfall productivity increased with soil moisture content, while crown complementarity and litterfall productivity increased with soil carbon content. Neither species richness nor crown complementarity increased with stand age, even though litterfall productivity increased with stand age.

4. *Synthesis*. Our study provides evidence for the strong role of tree crown assembly in shaping ecosystem functions in complex natural forests. Our findings suggest that crown spatial complementarity among trees operates mechanistically to drive the positive tree species diversity–litterfall productivity relationship in subtropical forests. We argue that community and/or ecosystem ecology would benefit from more attention to crown variability among coexisting tree species.

KEYWORDS
biodiversity–productivity relationships, crown spatial complementarity, natural forest, niche partition, stand age, stand condition, structural equation model

1 | INTRODUCTION

Understanding the ecological processes underlying the relationship between biodiversity and ecosystem productivity has been a central pursuit of ecological research for the past three decades (Hooper et al., 2005; Zhang, Chen, & Reich, 2012). Among the many processes that contribute to the positive effects of species diversity on ecosystem productivity, niche complementarity is one of the central hypotheses being extensively tested across grassland and forest ecosystems (Grime, 1997; Loreau & Hector, 2001; Zhang & Chen, 2015). The niche complementarity hypothesis assumes that relative to communities with few species, species-diverse communities use available resources more efficiently through niche differentiation, thereby increasing ecosystem productivity (Cardinale et al., 2011; Tilman et al., 1997). The knowledge gained from this hypothesis has improved the theoretical and empirical foundation for the understanding of how increased species diversity enhances ecosystem functions such as productivity (Hardiman, Bohrer, Gough, Vogel, & Curtisi, 2011; Huang et al., 2018; Montgomery & Chazdon, 2001).

Niche differentiation can be measured among species or interactive individuals (Clark, 2010). However, in many experimental and theoretical studies of the relationship between species diversity and ecosystem productivity, niche differentiation has often been inferred rather than directly demonstrated (Brassard et al., 2013; Ruiz-Benito et al., 2014). For example, the role of niche differentiation in positive biodiversity–productivity relationships has been assessed indirectly from either difference of trait values or speculated from the importance of residual species (Mensah, Veldtman, Assogbadjo, & Seifert, 2016; Zhang & Chen, 2015). Therefore, finding a suitable way to quantify niche differentiation among species intuitively is an important step in revealing the mechanisms underlying the relationship between biodiversity and ecosystem function.

Quantifying niche differentiation is challenging in natural forests because of the complex nature of community structure and the large variability in tree form and function (Morin, Fahse, Scherer-Lorenzen, & Bugmann, 2011; Zuppinger-Dingley et al., 2014). Interspecific and intraspecific variations in tree architecture create niche differences in light resources among individuals (Yachi & Loreau, 2007). Crown architecture is linked to individual tree light interception and light is one of the major resources limiting tree growth (Pacala et al., 1996). Accordingly, the position and size of the tree crown strongly correlate with light capture, reflecting the niche partition of the light resource and the space among coexisting tree species (Ishii, Azuma, & Nabeshima, 2013). Therefore, the difference between tree crowns among coexisting individuals or species, here defined as the crown complementarity, is a direct and intuitive measurement of their niche complementarity.

Crown complementarity of tree species can help us understand community assembly and ecosystem functioning. A recent study has revealed that spatial complementarity in tree crowns increases stem production in species mixtures in high-density young plantations in Canada (Williams, Paquette, Cavender-Bares, Messier,

& Reich, 2017). This is a great step towards testing the direct effect of niche complementarity on ecosystem productivity based on crown differentiation across tree species. However, the relationships between crown complementarity and plant productivity remain unclear in structurally complex natural forests, due to the difficulties of measuring spatial complementarity of tall trees and the less available long-term data of tree production for long-lived trees in natural forests. Litterfall productivity represents forest net primary production to a certain extent because it accounts for a major component of forest net primary production (Chen, Brant, Seedre, Brassard, & Taylor, 2017; Clark et al., 2001). In particular, it contributes to 41% of net primary production across a wide range of tropical forest conditions (Campo & Merino, 2016; Kutsch, Liu, Hörmann, & Herbst, 2005; Vitousek, 1984). Litterfall productivity is associated with the spatial configuration of the crown structure in forests (Bray & Gorham, 1964). In species-diverse forests, the "multilayered" structure of tree crowns (e.g. canopy packing) increases community-level light capture and light use efficiency (Parker & Brown, 2000; Zhu, van der Werf, Anten, Vos, & Evers, 2015). The forests with different species of varying crown architectures and functional strategies can utilize different canopy positions in space, resulting in more efficient partitioning of space and light resources (Anten & Hirose, 1999; Ishii et al., 2013; Sapijanskas, Paquette, Potvin, Kunert, & Loreau, 2014) and the improvement of ecosystem productivity such as litterfall (Scherer-Lorenzen, Bonilla, & Potvin, 2010). Therefore, we hypothesized that tree species diversity would increase crown complementarity, thereby enhancing litterfall productivity.

To test this hypothesis, we investigated the crown architecture of individual trees and litterfall productivity across 28 secondary subtropical forest plots with varying tree species diversity in eastern Zhejiang Province, China. However, ample evidence has shown that environmental conditions and the developmental stage of natural forests influence species diversity, stand structure and forest biomass and productivity (Ali et al., 2016; Zhang & Chen, 2015). Therefore, we expected that stand age and site condition would simultaneously influence tree species diversity, litterfall productivity and crown complementarity, as well as total crown volume (Figure S1). Since tree crown volume is positively related to tree stem volume and biomass (Popescu, Wynne, & Nelson, 2003), total crown volume per unit area would approximate the standing volume or biomass per unit area. We used structural equation models (SEMs) to examine the multivariate relationships among tree species diversity, tree crown complementarity, total crown volume, litterfall productivity, stand age and site condition, with special reference to the causal path from species diversity to litterfall productivity (Figure S1). Specifically, we were interested in understanding: (a) whether tree crown complementarity plays a significant role in mediating the positive relationship between species diversity and litterfall productivity in complex natural forests, and (b) how site condition and stand age affect the relationships among species diversity, crown complementarity and litterfall productivity.

2 | MATERIALS AND METHODS

2.1 | Study areas and forest plots

This study was carried out in the Ningbo and Zhoushan region (29°13′–30°02′N, 121°15′–122°27′E), located in eastern Zhejiang Province, China. The region is a typical sea-land transition zone with a mixture of hills, plains and islands. This region features a subtropical monsoon climate characterized by hot, humid summers and dry, cold winters. The mean annual temperature and precipitation are 17°C and 1,600 mm respectively (National Meteorological Information Center, China Meteorological Administration; http://data.cma.cn). The vegetation is characterized by the subtropical evergreen broadleaf forests, which have been well protected from human disturbances for the past 40 years (Yan et al., 2009).

The plots selected for this study are located in four areas with varying stand ages and stand characteristics, including the vegetation types of evergreen broadleaf forests, deciduous broadleaf forests, evergreen and deciduous mixed broadleaf forests, and coniferous forests. Moreover, crown architecture across tree species varies widely due to stand age and site condition. Since these vegetation types are not fully available across the four areas, the number of the plots established in each area varied. Our study used 17 plots in Tiantong, 3 plots in Shuangfeng, 6 plots in Putuo and 2 plots in Logar for a total of 28 plots (Figure S2). The plot size ranged from 10 m × 10 m for forests at the early stage of development to 25 m × 50 m for mature forests, with most being 20 m × 20 m (see details in Table S1). Given that site condition may change with terrain and microclimate, the sampled plots also represent topography- and microclimate-mediated soil moisture and fertility gradients in the region (Figure S2). Previous studies have revealed that soil moisture is strongly associated with climate variables (e.g. wind speed and precipitation) and site topography (Humphries, 1996; Seneviratne et al., 2010). In this study, we selected soil moisture and carbon contents as the proxy to characterize variation in site condition across studied plots.

2.2 | Community and soil property survey

In each plot, woody individuals with a diameter at breast height ≥1 cm and taller than 1.50 m were taxonomically identified, marked and measured (GB/T 33027-2016: "Observation Methodology for Long-term Forest Ecosystem Research" of National Standards of the People's Republic of China, http://www.sac.gov.cn/). Due to the differences in plot size and stand density, we used rarefied species richness as the measure of species diversity. Rarefied species richness is less dependent on plot size and rarefaction removes the confounding effects of tree density and plot size on species richness (Poorter et al., 2015). Rarefied species richness was calculated by using the *vegan* package (Oksanen et al., 2013). Stand age of each plot was determined according to the number of years since the last stand-replacing disturbance (i.e. clearcutting) or by the official records of the forest development in the region (Yan et al., 2009, 2018).

Soil moisture content in the 0–20 cm soil layer was measured using Soil Moisture Smart Sensors (HOBO, Bourne, MA, USA) at five randomly chosen locations in each plot in October 2014. In addition, we collected a topsoil sample (0–20 cm) at each sample position to determine soil carbon content. Soil samples were air-dried for 30 days and passed through a 2-mm sieve. Soil total organic carbon content (TOC) of each sample was determined using the oil bath-K_2CrO_7 titration method. The average of soil moisture content and TOC from five locations were used for each plot.

2.3 | Litterfall collection and productivity estimation

Within each of the 28 plots, 9 randomly located circular litter traps with a diameter of 60 cm were installed at 1 m above the soil surface. The number of litter traps and the area covered in this study were greater than the recommended standard for forest ecosystems (Kaspari et al., 2010). Litterfall traps were made from plastic nets, which allowed throughfall but retained litter particles. The litterfall collection was conducted monthly from September 2013 to January 2016. In each month, samples collected from each trap were transported to the laboratory and transferred from plastic bags to paper bags, where they were then dried at 70°C until a constant mass was achieved (72 hr), at which point dry biomass was weighed. The annual litterfall productivity of each plot was calculated by summing dry litterfall biomass collected for the period of one full calendar year (Mg ha^{-1} year^{-1}) (Feng, Wang, Ma, Fu, & Chen, 2019). Although the litterfall collection was conducted from different years in our study (from September 2013 to September 2014 in Tiantong, Shuangfeng and Nanshan; from February 2015 to January 2016 in Putuo and Logar), we found that the interyear variation in annual litterfall productivity did not significantly differ in the plots (Putuo and Logar) that were repeatedly sampled over 3 years (Figure S3). Similarly, a study conducted from 2012 to 2016 in the same region also showed insignificant interyear variation in litterfall (Aqing, 2017).

2.4 | Tree crown measurement

We used a Vertex meter (Vertex-IV, Haglöf Haglof, Dalarna, Sweden) to measure tree height (H, m) and the height of the lowest leaf on the first living branch (H$_{leaf}$, m). The measure was conducted in August when leaves were fully flushed. The maximum radii of the east–west (C$_a$) and north–south (C$_b$) cross sections of the crown were determined using a meter stick. Crown depth (CD) was calculated by subtracting the height of the lowest leaf from the tree height (Yang, Yan, Chang, Liang-Jun, & Xi-Hua, 2015). As recommended (Jucker, Bouriaud, & Coomes, 2015), we viewed crown volume as a parabolic cone, and discriminated the shape of the crown into the spherical crown for broadleaf species (e.g. *Schima superba* and *Dalbergia hupeana*) and the conical crown for conifer species (e.g. *Pinus thunbergii*, *Pinus massoniana* and *Cunninghamia lanceolate*).

In line with the geometry of a parabolic cone, crown volume (CV; in m^3) of the spherical and conical crown of each tree was calculated according to Equations 1 and 2 respectively.

$$CV_{con} = \frac{1}{3}\pi \frac{C_a}{2} \frac{C_b}{2} CD \tag{1}$$

$$CV_{sph} = \frac{4}{3}\pi \frac{C_a}{2} \frac{C_b}{2} \frac{CD}{2} \tag{2}$$

where CV_{con} and CV_{sph} are the crown volume of the conical crown and the spherical crown, respectively, C_a and C_b are the maximum crown radius from the east–west direction and the north–south direction, respectively, and CD is crown depth.

2.5 | Quantification of total crown volume and crown complementarity at the stand level

We summed the crown volumes of all individual trees in a plot as the total crown volume, scaled to per ha at the stand level to account for the difference in plot size among sample stands. Similar to Williams et al. (2017), the crown complementarity for a pair of trees was based on the difference between two trees (i and j) along the height axis (Figure 1), and expressed as a proportion of the total volume of the pair of trees, as per Equation 3.

$$CC_{ij} = \frac{|V_{io} - V_{jo}| + V_{in} + V_{jn}}{V_i + V_j} \tag{3}$$

where V_{io} and V_{jo} are the crown volumes of tree i and tree j within the overlapping section along the vertical axis respectively. These two variables differ between two trees because the extent of vertical overlapping in the crown volume is dependent on the crown radii of individual trees. V_{in} and V_{jn} are the crown volume of tree i and tree j within the non-overlapping section along the height axis respectively. V_i and V_j are the total crown volume of tree i and tree j.

We estimated crown complementarity index (CCI) at the plot level by averaging all possible pairs of trees with respect to the differences in volume size with Equation 4. This estimation reflects canopy vertical stratification and crown size differentiation across individual trees within a community (Williams et al., 2017).

$$CCI = \frac{\sum (CC_{ij})}{n} \tag{4}$$

where n is the number of all possible pairs of the measured trees in a given plot.

2.6 | Statistical analysis

We used simple linear regression to examine bivariate relationships between litterfall productivity and species diversity, CCI, total crown volume, stand age, soil moisture and soil carbon content. Variables were transformed by natural logarithm to better achieve normality and linearity (Grace et al., 2016; Zhang & Chen, 2015).

Based on our conceptual framework (Figure S1), we fitted the full SEM model with our data. We quantified site condition using a latent variable representing soil moisture and soil carbon content. As the estimated probabilities associated with chi-square can be influenced by multivariate normality (Grace, 2006), we used Mardia's multivariate normality test, and the test confirmed the multivariate normality of our data ($K = 47.60$, $p = 0.08$). We assessed the fit of the full model using a chi-square test ($p > 0.05$), goodness-of-fit index (GFI),
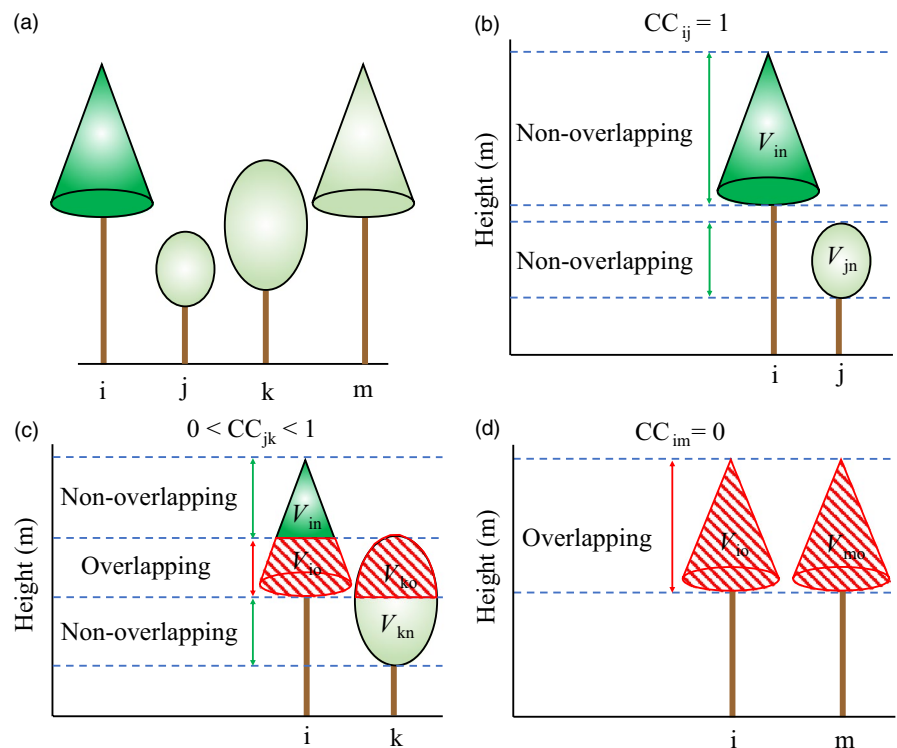

FIGURE 1 Conceptual diagram of crown complementarity (CC) calculations for a pair of trees. (a) Overview of several trees within a plot. (b–d) Three cases for calculating the crown complementarity index with respect to a focal tree i. (b) When the crowns of tree i and tree j are totally non-overlapping along the height axis, $CC_{ij} = 1$. (c) When the crowns of tree i and tree k are partly overlapping along the height axis, $0 < CC_{ik} < 1$. (d) When the crowns of tree i and tree m are equally overlapping along the height axis, $CC_{im} = 0$ [Colour figure can be viewed at wileyonlinelibrary.com]

comparative fit index and standardized root mean square residual (SRMR). The full model, however, did not confirm our data (Figure S4). As recommended (Grace, 2006), we subsequently performed a principal component analysis (PCA) of stand age, soil moisture content and soil carbon content, and extracted the first principal component (representing 73% of total inertia) (Figure S5) as a composite variable in the SEM. Moreover, using the Akaike information criterion (AIC), we selected the model with the lowest AIC value among alternative models.

The standardized coefficients were used to compare direct effects across paths. We added the standardized direct and indirect effects from all the given exogenous variables to calculate their total effects on litterfall productivity (Grace et al., 2016). The SEMs were fitted using the *lavaan* package (Rosseel, 2012). All analysis was conducted in R (version 3.5.0).

3 | RESULTS

The linear regression analyses showed that rarefied species richness, CCI and litterfall productivity increased with soil moisture content, but not total crown volume (Figure 2a–d). CCI and litterfall productivity increased in response to increasing soil carbon content, but rarefied species richness and total crown volume did not (Figure 2e–h). Litterfall productivity increased, CCI increased marginally ($p = 0.06$) and rarefied species richness had a positive trend ($p = 0.20$) with stand age, but not total crown volume (Figure 2i–l). Furthermore, litterfall productivity and tree crown complementarity increased significantly with rarefied species richness (Figure 3a,b). Crown complementarity was positively related to litterfall productivity (Figure 3c), but there were no significant relationships between rarefied species richness and total
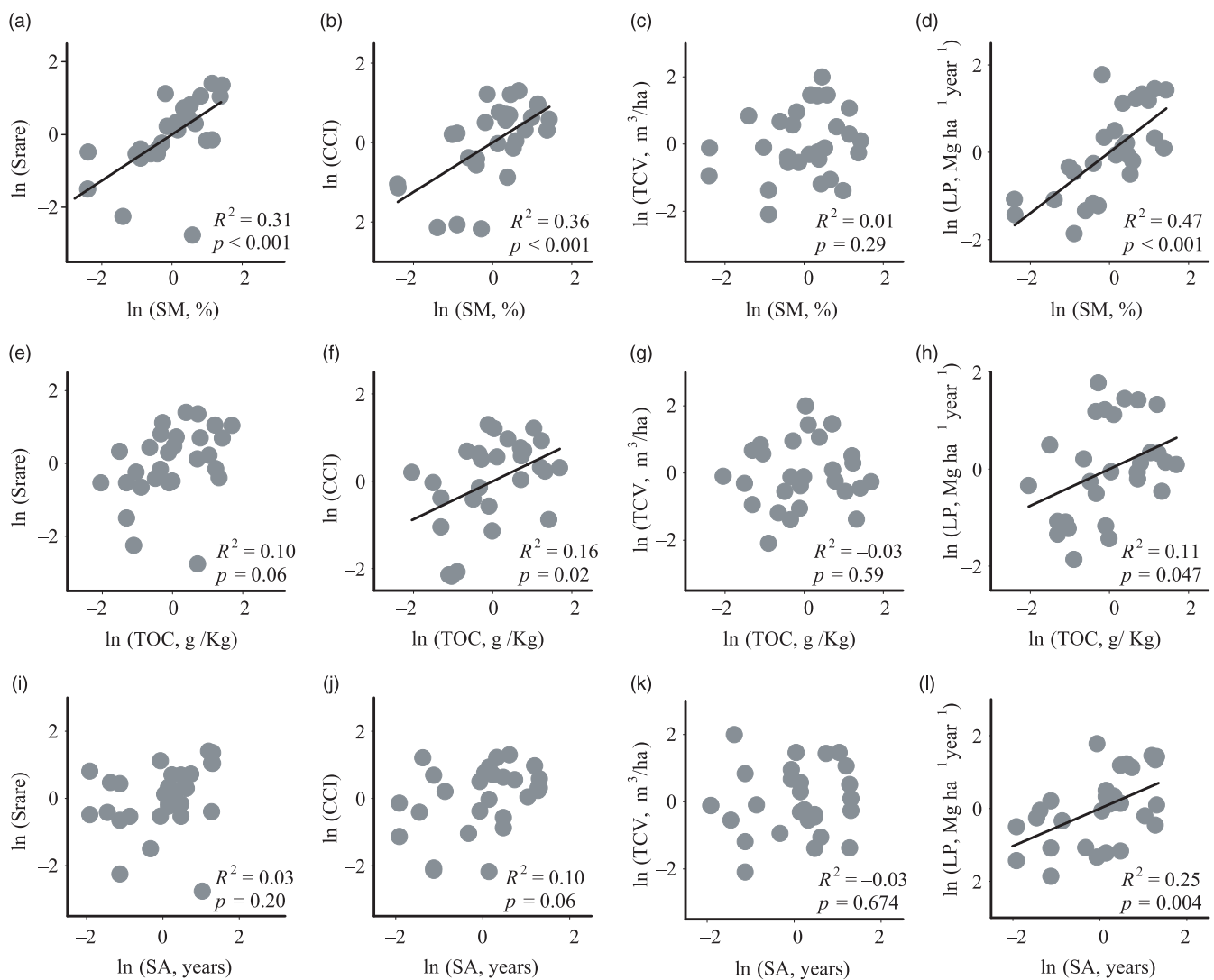

FIGURE 2 Bivariate relationships between endogenous (dependent) and exogenous (independent) variables ($n = 28$). (a–d) Soil moisture content (SM) versus rarefied species richness (Srare), crown complementarity index (CCI), total crown volume (TCV) and litterfall productivity (LP) respectively. (e–h) Soil total organic carbon content (TOC) versus rarefied species richness (Srare), CCI, total crown volume (TCV) and litterfall productivity (LP) respectively. (i–l) Stand age (SA) versus rarefied species richness (Srare), crown complementarity (CCI), total crown volume (TCV) and litterfall productivity (LP) respectively. Coefficients of determination (adjusted R^2) and p-values are shown. All numerical variables were natural log-transformed
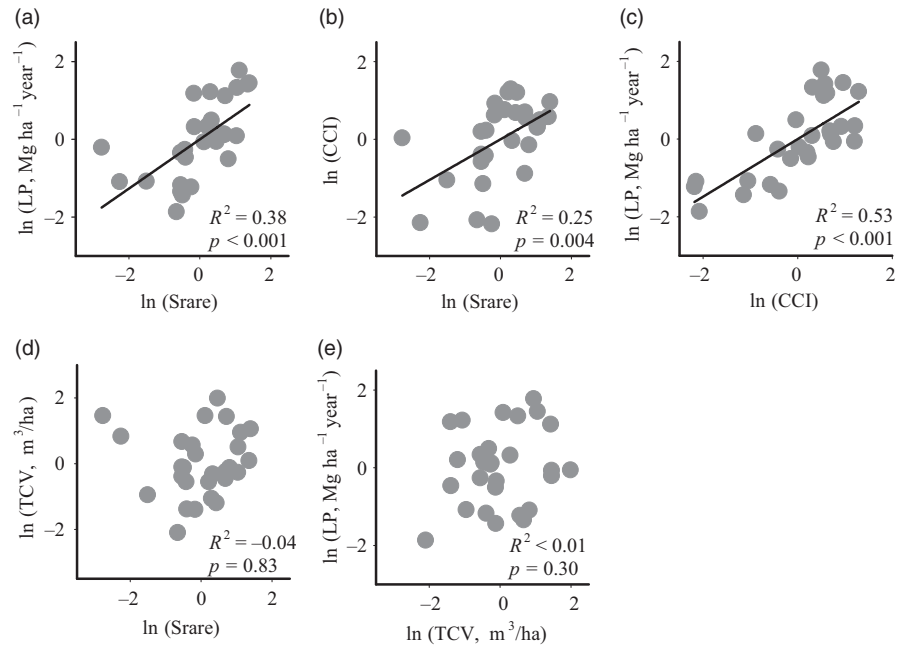
FIGURE 3 Bivariate relationships between endogenous (dependent) and exogenous (independent) variables (n = 28). (a, b) Rarefied species richness (Srare) versus litterfall productivity (LP) and crown complementarity index (CCI), respectively. (c) CCI versus litterfall productivity (LP). (d) Rarefied species richness (Srare) versus total crown volume (TCV); (e) total crown volume (TCV) versus litterfall productivity (LP). Coefficients of determination (adjusted R^2) and p-values are shown. All numerical variables were natural log-transformed

crown volume nor between litterfall productivity and total crown volume (Figure 3d,e).

The SEM model that used the composite environmental variable as the first principal component yielded a good fit to the data (AIC = 368.2, χ^2 = 0.710, df = 1, p = 0.399, SRMR = 0.035, GFI = 0.990), and accounted for 67% of the variation in litterfall productivity (Figure 4a, Table 1). The composite environmental variable (positively loaded by stand age, soil moisture and total carbon content) (Figure S5) had a significantly positive total effect on litterfall productivity (standardized coefficient, r = 0.53, p = 0.001) via its direct effect (r = 0.21) and indirect effects via rarefied species richness (r = 0.14), crown complementarity (r = 0.17) and total crown volume (r = 0.01). Rarefied species richness had a significantly positive effect on litterfall productivity (r = 0.45, p = 0.048) by its direct effect (r = 0.29) and indirect effects via crown complementarity (r = 0.16) and total crown volume (r < 0.01). Crown complementarity had a significant direct effect on litterfall productivity (r = 0.47, p = 0.001), but total crown volume did not (Figure 4a, Table 1).

By removing the site condition and stand age, the model yielded a good fit to the data and a substantially lower AIC value (AIC = 294.2, χ^2 = 1.091, df = 1, p = 0.296, SRMR = 0.060, GFI = 0.979). The model accounted for 63% of the variation of litterfall productivity. Nevertheless, similar to the model in Figure 4a, rarefied species richness had a strongly positive total effect on litterfall productivity (r = 0.64, p = 0.003) directly (r = 0.35) and indirectly via increasing crown complementarity (r = 0.29) but little effect from increased total crown volume (Figure 4b). The direct effect of total crown volume on litterfall productivity was insignificant.

FIGURE 4 Effects of rarefied species richness, crown complementarity and total crown volume on litterfall productivity, with (a) and without (b) considering stand age and site condition in the structural equation model. For each path, the standardized regression coefficient is shown. Black solid lines represent significant paths (p < 0.05), grey solid lines represent marginal significant paths (0.05 ≤ p < 0.1) and grey dash lines are for non-significant paths (p ≥ 0.1). R^2 indicates the total variation in an endogenous (dependent) explained by all exogenous (independent) variables

4 | DISCUSSION

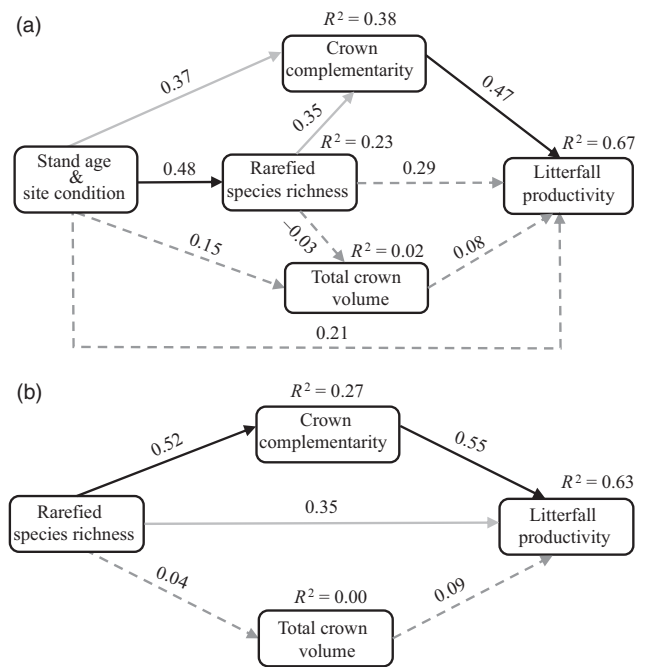This study used tree crown complementarity and litterfall productivity as a proxy for niche complementarity and stand productivity, respectively, and found positive relationships between rarefied species diversity, crown spatial complementarity and litterfall production in natural forests. As previously hypothesized, we showed that

TABLE 1 The direct, indirect and total standardized effects on litterfall productivity based on structural equation models (SEMs)

Predictor	Pathway to litterfall productivity	Model in Figure 4a		Model in Figure 4b	
		Effect	*p*-value	Effect	*p*-value
PCA1 of site condition and stand age	Direct effect	0.21	0.214	–	–
	Indirect effect through rarefied species richness	0.14	0.282	–	–
	Indirect effect through crown complementarity	0.17	0.085	–	–
	Indirect effect through total crown volume	0.01	0.788	–	–
	Total effect	0.53	0.001	–	–
Rarefied species richness	Direct effect	0.29	0.190	0.35	0.073
	Indirect effect through crown complementarity	0.16	0.072	0.29	0.010
	Indirect effect through total crown volume	<0.01	0.970	<0.01	0.930
	Total effect	0.45	0.048	0.64	0.003
Crown complementarity	Direct effect	0.47	0.001	0.55	<0.001
Total crown volume	Direct effect	0.08	0.555	0.08	0.594

rarified species richness had a positive effect on litterfall productivity via crown complementarity. Our results suggest that crown spatial complementarity could be an important mechanism for explaining the trend of species diversity enhancing productivity from experimental mixtures (Williams et al., 2017) to natural forests with varied forest types.

We found a positive bivariate relationship between species diversity and litterfall productivity, and our SEM showed that species diversity increased litterfall productivity via tree crown complementarity. This finding reinforces the importance of tree crown traits in shaping forest dynamics and functionality in complex natural forests (Forrester et al., 2017; Iida et al., 2014). The variations in tree crown size and crown deployment in the forest canopy space have profound implications for niche partitioning and resource use at the community level (Parker & Brown, 2000; Sterck, Martinéz-Ramos, Dyer-Leal, Rodríguez-Velazquez, & Poorter, 2003; Williams et al., 2017). Mixed forests consisting of species-specific crown architectures result in more complex, multilayered canopy structures compared to monocultures (Morin et al., 2011; Sapijanskas et al., 2014). As a result, resource use can become more efficient in mixtures due to the complementary use of canopy space and reduced competition (Forrester et al., 2017). Therefore, species-rich forests with varied tree crown architectures have higher productivity at the community level (Hardiman et al., 2011; Montgomery & Chazdon, 2001; Williams et al., 2017). On the other hand, we did not find a significant relationship between total crown volume and litterfall productivity. Total crown volume is expected to be positively correlated with stand biomass (Popescu et al., 2003). The lack of a relationship between litterfall productivity and total crown volume appears to be consistent with the finding of a study in boreal forests, where litterfall productivity changes little with standing biomass among the stands that have reached full canopy closure (Chen et al., 2017).

Although our SEM with the principal component that positively loaded stand age, soil moisture content and soil carbon content as an exogenous variable tended to over-fit our data, the model suggested that site condition and stand age contributed to the triangle relationships among species diversity, crown complementarity and litterfall productivity. The positive associations among soil moisture content, species richness and crown complementarity suggest that the effect of species diversity may be linked to diverse hydraulic strategies among constituent species. Several studies have shown that tree height and crown architecture are strongly correlated with hydraulic strategies (Dawson, 2010), and a wide range of hydraulic strategies tend to occur with more water availability (Anderegg et al., 2018; Choat, Sack, & Holbrook, 2007). The wide variation in hydraulic strategies might help to promote crown complementarity and contribute to the positive species richness–litterfall productivity relationship (Moreno-Gutiérrez, Dawson, Nicolás, & Querejeta, 2012; Poorter et al., 2015). Furthermore, in natural forests, soil water, carbon and nutrients are highly coupled as they are simultaneously controlled by topographical positions in a landscape with similar parent materials (Chen, Klinka, & Kabzems, 1998). As soil water and nutrient availability increases, competition for light intensifies and the fast growth of plants accelerates competition for light (Gower, Mcmurtrie, & Murty, 1996; Tilman, 1985), which forces crown differentiation, increasing crown complementarity (Seidel et al., 2013) and ecosystem productivity (Grace et al., 2016).

Our bivariate analysis showed that litterfall productivity and crown complementarity were positively associated with stand age and—to a much lesser extent—species richness. Our SEM also indicated a positive contribution of stand age to the triangle relationships among species diversity, crown complementary and litterfall productivity. This finding corroborates the previous studies that demonstrate that relationships between ecosystem productivity, species and functional diversity are considered to be largely dependent on stand age (Ali et al., 2016; Zhang & Chen, 2015; Zhang et al., 2012). The weak or nonexistent effect of stand age on species richness in our study might be attributable to the minute change in species diversity between early successional stages and late stages. In our studied area, even though species composition shifts substantially across successional forests (Figure S6), species richness can be balanced by different trajectories of species replacement between

climax forests and early successional forests (Yan, Wang, & Huang, 2006). The minimal variation in species numbers among successional stages could occur as a result of the various strengths of the colonization of pioneer species shortly after natural or anthropological disturbances and species replacement or competitive exclusion in later stages (Batalha, Pipenbaher, Bakan, Kaligarič, & Škornik, 2015).

In conclusion, we showed a positive relationship between tree species diversity and litterfall productivity in natural subtropical forests. We also showed crown spatial complementarity mediates the positive diversity effect on litterfall productivity. Crown spatial complementarity links tightly with species niche partition for light, water and nutrient availability across communities. This study advances our understanding of how niche complementarity operates to drive the positive biodiversity–ecosystem productivity relationships in complex natural forests. Lastly, we acknowledge that niche complementarity was assessed only based on tree crowns in this study. The role of niche partitioning—including below-ground complementarity—(Brassard et al., 2013) could also have contributed to the species diversity and litterfall productivity relationship.

AUTHORS' CONTRIBUTIONS

L.-T.Z. and E.-R.Y. designed the research; L.-T.Z. and H.Y.H.C. analysed data; L.-T.Z. drafted manuscript; and H.Y.H.C. and E.-R.Y. contributed to writing via multiple rounds of revision.

DATA ACCESSIBILITY

The data containing sample locations and variables used in the analyses are available from Dryad Digital Repository https://doi.org/10.5061/dryad.jq41758 (Zheng, Chen, & Yan, 2019).

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