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Effects of stand age, richness and density on productivity in subtropical forests in China

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Abstract

1. Forest productivity may be determined not only by biodiversity but also by environmental factors and stand structure attributes. However, the relative importance of these factors in determining productivity is still controversial for subtropical forests.
2. Based on a large dataset from 600 permanent forest inventory plots across subtropical China, we examined the relationship between biodiversity and forest productivity and tested whether stand structural attributes (stand density in terms of trees per ha, age and tree size) and environmental factors (climate and site conditions) had larger effects on productivity. Furthermore, we quantified the relative importance of environmental factors, stand structure and diversity in determining forest productivity.
3. Diversity, together with stand structure and site conditions, regulated the variability in forest productivity. The relationship between diversity and forest productivity did not vary along environmental gradients. Stand density and age were more important modulators of forest productivity than diversity.
4. *Synthesis.* Diversity had significant and positive effects on productivity in species-rich subtropical forests, but the effects of stand density and age were also important. Our work highlights that while biodiversity conservation is often important, the regulation of stand structure can be even more important to maintain high productivity in subtropical forests.

KEYWORDS

biodiversity and ecosystem functioning, complementarity effect, environmental conditions, functional diversity, phylogenetic diversity, selection effect, subtropical forests

1 | INTRODUCTION

The effects of biodiversity loss on ecosystem functioning and services have received increasing attention and concern by ecologists in the past decades (Barry et al., 2018; Huang et al., 2018; Liang et al., 2016). Forests play an important role in global carbon (C) sequestration through the absorption of 35% of CO₂ emissions from fossil fuel and account for nearly 25% of global terrestrial ecosystem C sinks of (King et al., 2012). Hence, a better understanding of the relationship between biodiversity and ecosystem functioning is critical to sustain forest ecosystem functions, such as C storage, productivity, nutrient cycling and climate change mitigation (Huang et al., 2018; Liang et al., 2016; Liu et al., 2018). The spatial distribution of forest productivity across landscapes has been well reported (e.g. Guo & Ren, 2014; Hlásny et al., 2017); however, the underlying mechanisms driving productivity are still not well understood in forest ecosystems at landscape scales.

Most studies have reported positive relationships between species richness and forest productivity (Baruffol et al., 2013; Liang et al., 2016; Poorter et al., 2015; Ruiz-Benito et al., 2014), although non-significant (Seidel et al., 2013; Vilà, Vayreda, Gracia, & Ibáñez, 2003) and even negative relationships (Cavard, Bergeron, Chen, & Pare, 2010; Forrester & Bauhus, 2016) have also been reported. Two hypotheses used to explain the positive effects of biodiversity on forest productivity are the niche complementarity effect and the selection probability effect. The niche complementarity effect assumes that increasing diversity enhances forest productivity through niche differentiation and facilitation (Tilman et al., 1997). In contrast, the selection probability effect proposes that higher species richness increases community productivity through an increased chance of possessing highly productive species (Hooper et al., 2005). The selection probability effect and niche complementarity effect may contribute to the positive effects of diversity on ecosystem functioning simultaneously (Chiang et al., 2016; Hooper et al., 2005; Sullivan et al., 2017); however, their relative importance is still controversial (Chiang et al., 2016; Fotis et al., 2018).

In addition to diversity, forest structure (such as stand density, age and tree size) affects biomass or productivity in natural forests (Baruffol et al., 2013; Forrester & Bauhus, 2016; Forrester, Kohnle, Albrecht, & Bauhus, 2013; Zhang & Chen, 2015). For example, higher stand densities increased forest C storage and wood production through higher canopy packing, which could capture more light (Forrester et al., 2018; Morin, 2015). Stand age is also an important driver for biomass and productivity (Liu et al., 2018; Michaletz, Cheng, Kerkhoff, & Enquist, 2014). Stand age can enhance biomass and productivity via the increase in tree size (Barry et al., 2018; Becknell & Powers, 2014) and size variation (Poorter et al., 2015; Zhang & Chen, 2015). Mean sizes of the largest trees have been used as a predictor of above-ground biomass variation across the pan-tropics (Bastin et al., 2018; Slik et al., 2013) or world-wide (Lutz et al., 2018). The variability in stem diameter, also referred to as size inequality, can also reduce or increase productivity, partly due to changes in the partitioning of light between individual trees (Binkley, Stape, Bauerle, & Ryan, 2010; Soares et al., 2016; Zhang & Chen, 2015).

The strength of the relationship between diversity and productivity can also be strongly confounded by environmental factors (e.g. climate, site conditions) in forests (Baruffol et al., 2013; Forrester & Bauhus, 2016; Liu et al., 2018; Mina, Huber, Forrester, Thürig, & Rohner, 2018). Environmental conditions may affect tree growth by influencing resource availability (water and soil fertility; Poorter et al., 2015; Sullivan et al., 2017). For example, forests in poor soil quality sites have been shown to exhibit stronger positive diversity effects on productivity than stands on high soil fertility sites (Pretzsch et al., 2013; Toïgo et al., 2015). Mean annual precipitation, mean annual temperature and potential evapotranspiration are also potential drivers of forest biomass at large scales (Fang et al., 2012; Schuur, 2003; Wu, Wang, Tang, et al., 2015). Therefore, it is important to consider these factors when testing multivariate and indirect relationships between diversity and productivity in forest ecosystems.

Most studies to date were conducted in relatively species-poor forest ecosystems (i.e. temperate and boreal forests; Fotis et al., 2018; Paquette & Messier, 2011; Yuan et al., 2018), with fewer studies in the subtropical natural forests (i.e. Baruffol et al., 2013; Wu, Wang, Tang, et al., 2015; Li et al., 2019; Liu et al., 2018). Subtropical forests are rich with tree species and characterized by complex stand structure and various environmental conditions (Liu et al., 2018; Xiang et al., 2016). Whether and to what degree biodiversity and other factors (environmental conditions and stand characteristics) influence productivity in diverse subtropical forests is not well understood, although non-significant (Wu, Wang, Tang, et al., 2015), relatively weak positive (Ouyang et al., 2016; Li et al., 2019) and moderate to strong effects (Baruffol et al., 2013; Liu et al., 2018) of species richness on biomass or C storage have been observed in these forests. These inconsistent patterns may result if relationships between productivity and biodiversity are masked by other confounding factors in these forests.

In this study, we analysed a large dataset from 600 permanent forest inventory plots across Hunan Province. We addressed the two major questions: (a) Is forest productivity significantly correlated with diversity in subtropical forests? (b) What are the main driving factors determining stand productivity of subtropical forests? In order to answer these two questions, we examined the correlations between biodiversity and forest productivity and further quantified the relative importance of diversity, stand structure and environmental conditions in determining productivity of subtropical forests. Specifically, we hypothesized that: (a) diversity is positively correlated with forest productivity after controlling for the effects of stand structure and environmental factors; (b) the relationship between diversity and productivity varies with environmental conditions; and (c) stand density, age and stem diameter have strong positive effects on forest productivity in addition to diversity.

2 | MATERIALS AND METHODS

2.1 | Study area

The study was conducted in Hunan Province (latitude 108°47'E–114°15'E, longitude 24°38'N–30°08'N) situated in the

mid-subtropical area of China (Figure 1). Hunan Province is located in the transition zone from the Yunnan–Guizhou plateau to the lower mountains and hills on the southern side of the Yangtze River and has an elevation of 21–2,122 m above sea level. A typical humid mid-subtropical monsoon covers this region. The average annual air temperature is 16–18°C. The annual precipitation is about of 1,200–1,700 mm, occurring primarily between April and October (Huang, Sun, Xue, & Zhang, 2014). The soils are red-yellow podzolic soils, which developed mostly from slate and shale parent material, and are classified as Plinthudults, according to the US Soil Taxonomy. The forest areas of Hunan Province have increased rapidly to 56% of total land area in the past several decades due to afforestation and natural forest restoration projects. Most forests are coniferous, deciduous broadleaved and evergreen broadleaved forests (Jiao, Xiang, & Tian, 2005).

2.2 | Data collection

Forest stand data came from the permanent sample plots with the size of 25.82 m × 25.82 m (according to the protocols of the National Forest Inventory standards issued by the Chinese Ministry of Forestry) across Hunan Province (Figure 1), which were surveyed in both the sixth (2009) and seventh National Forest Inventory of

China (2014). For each forest plot, geographic location (latitude, longitude), topographic variables (altitude, slope, aspect, slope position) and soil variables (depth, texture, type and gravel content) were collected. Tree species name and diameter at breast height (DBH, 1.3 m) of each individual stem with DBH ≥ 5 cm were recorded.

2.3 | Productivity calculations

All individuals with a DBH ≥ 5 cm were used in the analysis. Firstly, the total stock volume for each plot was calculated. Secondly, the total biomass of each plot was estimated using the biomass expansion factor method (Fang, Chen, Peng, Zhao, & Ci, 2001), which is an accurate way for forest biomass estimation at large scales (Fang et al., 2014; Wang, Fang, Tang, & Zhu, 2006). Finally, the forest productivity of each plot was determined as biomass increments from 2009 to 2014. For more detailed information on the productivity calculations, see the Appendix S1.

2.4 | Biodiversity indices and functional traits

We calculated species diversity, functional diversity and phylogenetic diversity to examine their effects on forest productivity. Species diversity was quantified as species richness (species

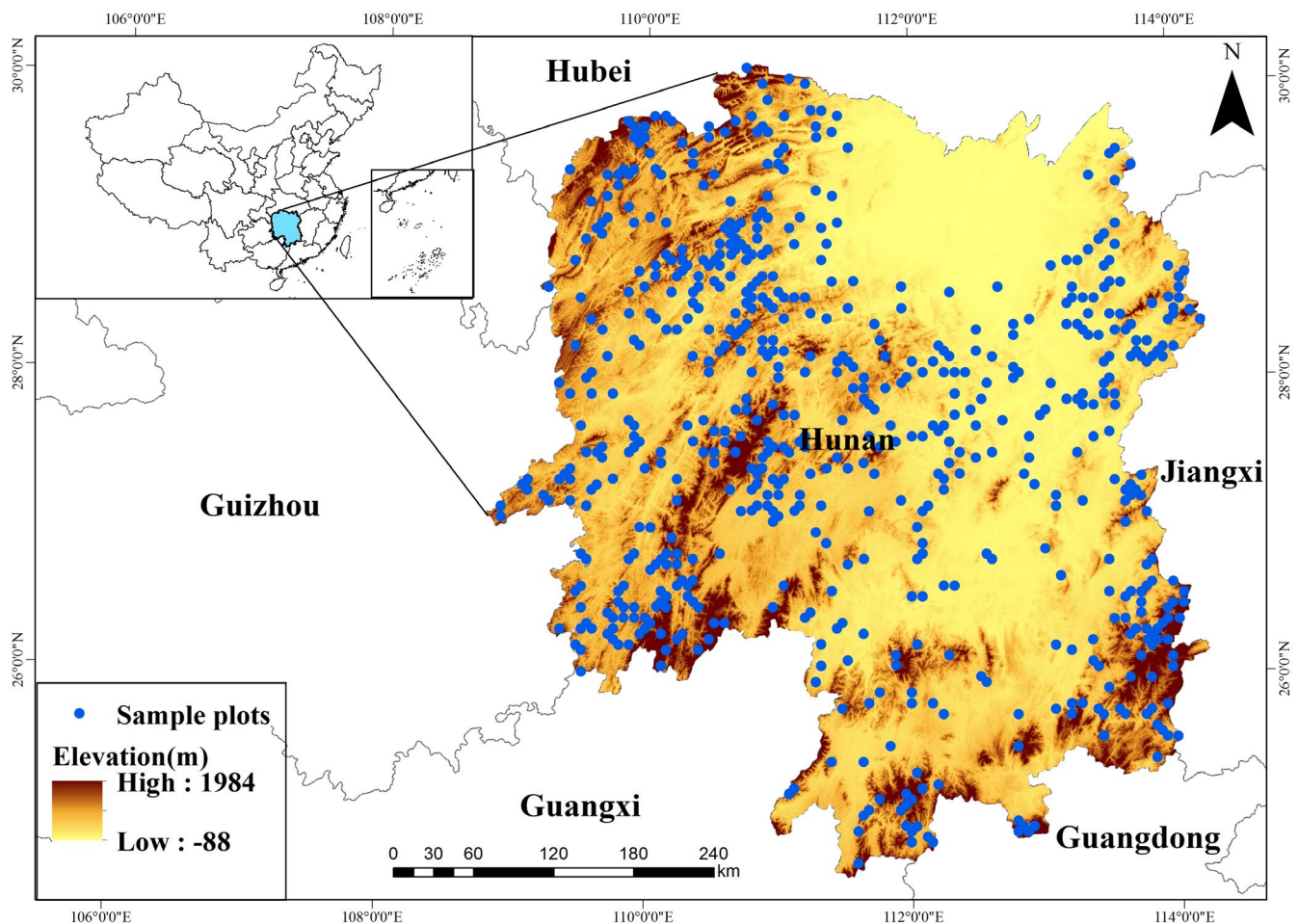


FIGURE 1 Spatial distribution of the forest plots in southern China [Colour figure can be viewed at wileyonlinelibrary.com]

number in a per plot). For functional diversity, we used the functional dispersion which describes the variability of functions or characteristics of the species in a community. Functional dispersion was calculated as the dispersion of functional traits of each plot using species wood density, maximum tree height and life-form (deciduous or evergreen) using the dbFD function of the R package 'FD' (Huang et al., 2018; Laliberté & Shipley, 2011). These traits are not only important and commonly used functional traits

but are also closely related to forest productivity (Ruiz-Benito et al., 2014; Wu, Wang, Wu, Xia, & Fang, 2015). Functional traits for 268 tree species that occurred in our plots were compiled from the literature. Wood density data for major tree species were extracted from the literature (Zhang, Slik, Zhang, & Cao, 2011) and the database of global wood density (<http://datadryad.org/repo/handle/10255/dryad.235>). Maximum height for each species was compiled from Flora of China (Editorial Committee of Flora of

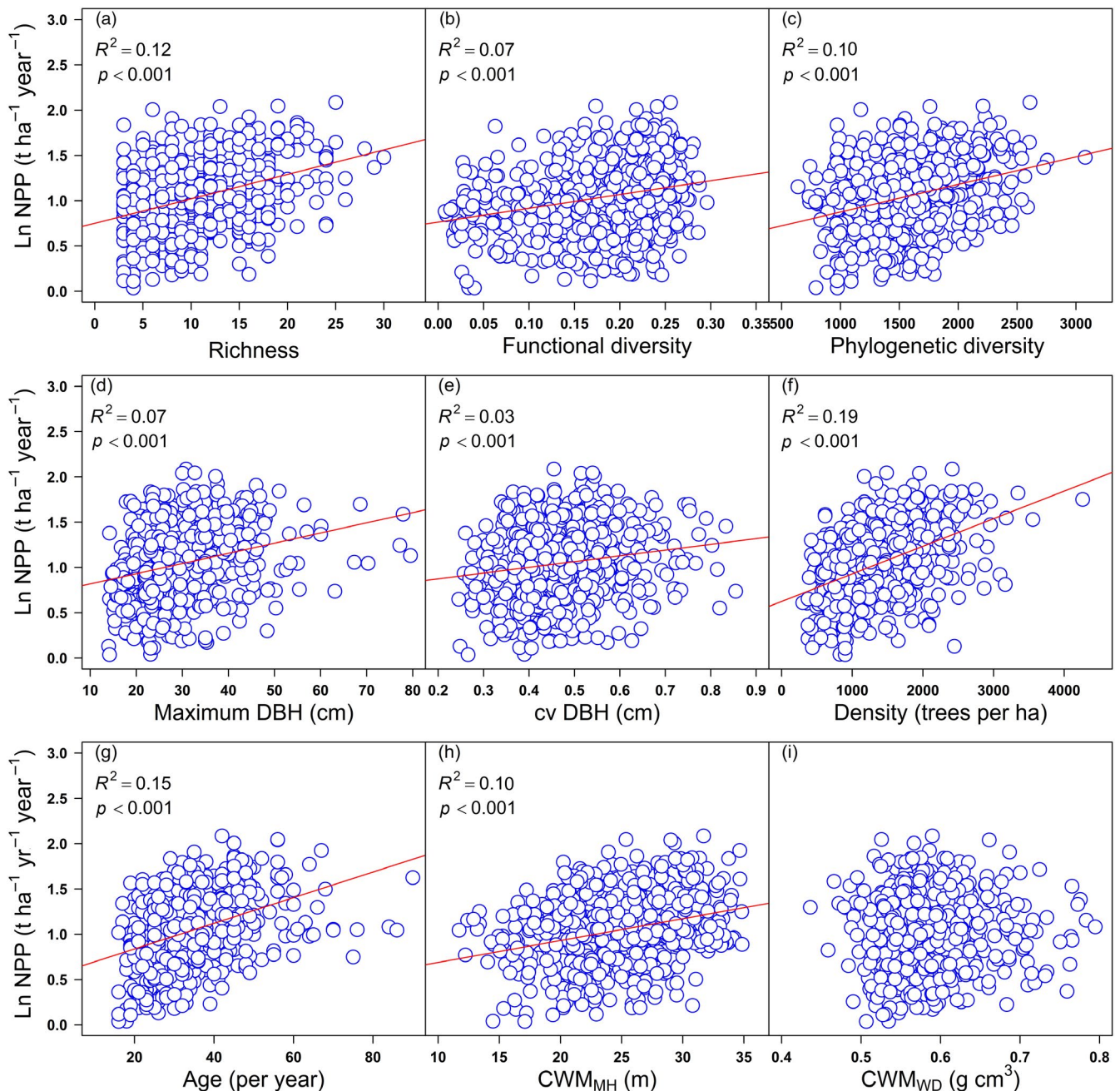


FIGURE 2 Bivariate relationships between forest productivity (ln-transformed) and biodiversity [(a) species richness, (b) functional diversity and (c) phylogenetic diversity], stand structure [(d) maximum diameter at breast height (DBH), (e) DBH variation (cv DBH), (f) stand density and (g) stand age] and (h) community-weighted mean trait value of tree maximum height (CWM_{MH}) and (i) wood density (CWM_{WD}) in southern China ($N = 600$) [Colour figure can be viewed at wileyonlinelibrary.com]

China, 2004). Community-weighted means (CWM) of each trait, weighted by the density of each species for each plot, were also calculated using the R package 'FD'.

Phylogenetic diversity index was used to quantify another aspect of biodiversity, which is based on species' evolutionary distances (Faith, 1992). A phylogenetic tree for the 268 species was constructed using the online software of Phylomatic version 3 (Webb, Ackerly, & Kembel, 2008, <http://phylodiversity.net/phyloomatic/>; Figure S1, Appendix S2). The tree with branch lengths generated by Zanne et al. (2014), which combined the DNA marker data with a molecular phylogeny (32,223 species) for land plants, was more accurate than using the tree APG III system (Angiosperm Phylogeny Angiosperm-Phylogeny-Group, 2009). The phylogenetic diversity was calculated as the total branch length of a phylogeny representing the species in a community. The phylogenetic analysis was implemented in Phylocom version 4.2 (Webb et al., 2008).

2.5 | Stand structural variables

Stand structural factors used in this study included maximum DBH, variation in DBH and stand density (trees per ha) and stand age. DBH variation was quantified as the coefficient of variation, which is the ratio of the standard deviation of all DBH measurements to the mean DBH, in a given plot. Five of the largest trees outside each plot were selected to sample stem cores and the ring counts of these five-tree samples were averaged to estimate stand age.

2.6 | Environmental variables

The environmental variables included climate and site conditions. Climate variables included mean annual precipitation, a good indicator of water availability (O'Brien, 1993) and potential evapotranspiration, an index of energy availability (Wu, Wang, Tang, et al., 2015). These are generally recognized to be the major climatic factors determining spatial patterns of forest productivity and biomass (e.g. Luo, 1996; Wu, Wang, Tang, et al., 2015). Mean annual precipitation and potential evapotranspiration of each plot were estimated

with the geographic coordination (latitude, longitude and altitude) of the plot, using the well-established method described in Fang et al. (2012).

The site conditions of each plot, an index of the soil quality, was determined using several topographical factors (altitude, slope, aspect and slope position) and soil factors (texture, depth, gravel content, bedrocks, bulk density) by cluster analysis and discriminant analysis (Courtin, Klinka, Feller, & Demaerschalk, 1988; Zhang & Chen, 2015). As a result, site conditions were quantitatively classified into three categories (poor, medium and good) according to national forest resource inventory standards established by the Chinese Forestry Administration.

2.7 | Statistical analysis

Forest productivity was ln-transformed prior to all analyses. We first used Pearson's correlation coefficients to examine bivariate relationships between forest productivity and the individual predictor variables. One-way analysis of variance (ANOVA), followed by the least significant difference (LSD), was used to test the differences in productivity among the three site conditions (poor, medium and good). We also used standardized major axis (SMA) regressions (Warton, Duursma, Falster, & Taskinen, 2012) to determine whether the relationships between the diversity and forest productivity vary with site conditions. These analyses were performed using the R package 'smatr' (Warton et al., 2012).

We used ordinary least squares (OLS) multiple regression models to examine the effects of diversity on forest productivity, in addition to those of covarying environmental and stand structural factors. All environmental variables, forest structure variables, diversity indices and forest productivity were standardized (average = 0 and SD = 1). To remove the multicollinear variables (Table S1, Appendix S2), the variance inflation factor (VIF) <3 was used to identify any multicollinear variables in the multiple regression models (Chen et al., 2019; Yang et al., 2017). The VIF was calculated using the R package 'CAR'. Consequently, the full model included two environmental factors (potential evapotranspiration and site

TABLE 1 Summary of the best ordinary least squares (OLS) multiple regression model for the effects of site conditions, forest structural factors (stand age, stand density and maximum DBH) and species richness on forest productivity in southern China ($N = 600$)

Variable	Estimate	CI	SE	t-value	p-value	VIF
Site conditions	0.150	0.085–0.214	0.033	4.535	<0.001	1.069
Age	0.232	0.163–0.301	0.035	6.596	<0.001	1.212
Density	0.380	0.311–0.449	0.035	10.830	<0.001	1.231
Maximum DBH	0.159	0.086–0.233	0.038	4.252	<0.001	1.406
Species richness	0.133	0.062–0.204	0.036	3.684	<0.001	1.748
	DF	R²	SE_{resid}	F-value	p-value	
Model statistics	594	0.384	0.788	74.12	<0.001	1.748

Abbreviations: CI, 95% confidence interval for the regression coefficients; DBH, diameter at breast height; DF, degree of freedom; SE, standard error; SE_{resid}, residual standard error; VIF, variance inflation factor.

The model selection is provided in Table S2 (Appendix S2).

conditions), three forest structure factors (stand age, stand density and maximum DBH) and one diversity index (species richness). The best model was selected using corrected Akaike information criterion (AIC_c) by considering the lowest AIC_c and number of predictors (Bartoń, 2016; Burnham & Anderson, 2002; Table S2, Appendix S2), as implemented in the R package 'MuMIn' (Bartoń, 2016). Shuffling the position of the predictor variables in the multiple regression models did not change their effects on forest productivity and showed that stand age, species richness and density had higher percentage of total explained variance (see the Table S3, Appendix S2). The relative influence of each predictor in the final multiple regression model was quantified by hierarchical partitioning analysis using the R package 'hier.part' (Walsh & Nally, 2013). Hierarchical partitioning evaluates the average independent and joint contribution of each regressor to the variability of the response variable by comparing all possible models in a multiple regression context (Chevan & Sutherland, 1991). As long as the number of tested factors does not exceed nine, hierarchical partitioning provides reliable results (Olea, Mateo-Tomás, & de Frutos, 2010).

Structural equation modelling (SEM) was used to examine the effects of all predictor variables on forest productivity. Nonparametric Bollen–Stine bootstrapping procedures were used to address the potential issues from nonlinear and remaining univariate non-normality after transformations as suggested by Zhang and Chen (2015). To examine whether stand structural factors simultaneously impact diversity and forest productivity, we also fitted a model with the opposite path direction between stand structural factors and diversity. Furthermore, we determined the total effects (direct plus indirect effects) of each factor on forest productivity. The SEM model was performed using the R package 'lavaan' (Rosseel, 2012). All the statistical analyses were implemented in R version 3.4.1 (R Development Core Team, 2016).

3 | RESULTS

3.1 | Relationship between diversity and forest productivity

When bivariate relationships between diversity and forest productivity were examined, forest productivity was positively correlated with all diversity indices. Species richness (Figure 2a; slope = 0.027 [CI: 0.021–0.033], $F_{1,598} = 84.97$, $R^2 = 0.12$, $p < 0.001$) explained the most variation in forest productivity, followed by phylogenetic diversity (Figure 2c; slope = 0.0003 [CI: 0.0002–0.0004], $F_{1,598} = 66.40$, $R^2 = 0.10$, $p < 0.001$) and functional diversity (Figure 2b; slope = 1.518 [CI: 1.061–1.975], $F_{1,598} = 42.53$, $R^2 = 0.07$, $p < 0.001$). There was also a significantly positive relationship between species richness and forest productivity ($F_{5,594} = 74.12$, $p < 0.001$) when site conditions, stand density, stand age and maximum DBH were included in the final multiple regression model (Table 1).

For the functional traits, a relatively strong positive correlation was found between forest productivity and CWM_{MH}

(Figure 2h; slope = 0.027 [CI: 0.020–0.034], $F_{1,598} = 64.31$, $R^2 = 0.10$, $p < 0.001$), but CWM_{WD} was not significantly correlated with forest productivity ($R^2 = 0.002$, $p > 0.05$; Figure 2i). CWM_{MH} had a stronger effect on forest productivity than functional diversity (Figure 2b,h).

3.2 | Environmental effects on the relationship between diversity and forest productivity

Climatic factors had weak effects on forest productivity, even though they were significant (slope = -0.001 [CI: -0.0014–0.0005], $F_{1,598} = 18.18$, $R^2 = 0.03$, $p < 0.001$; Table S1, Appendix S2). Site

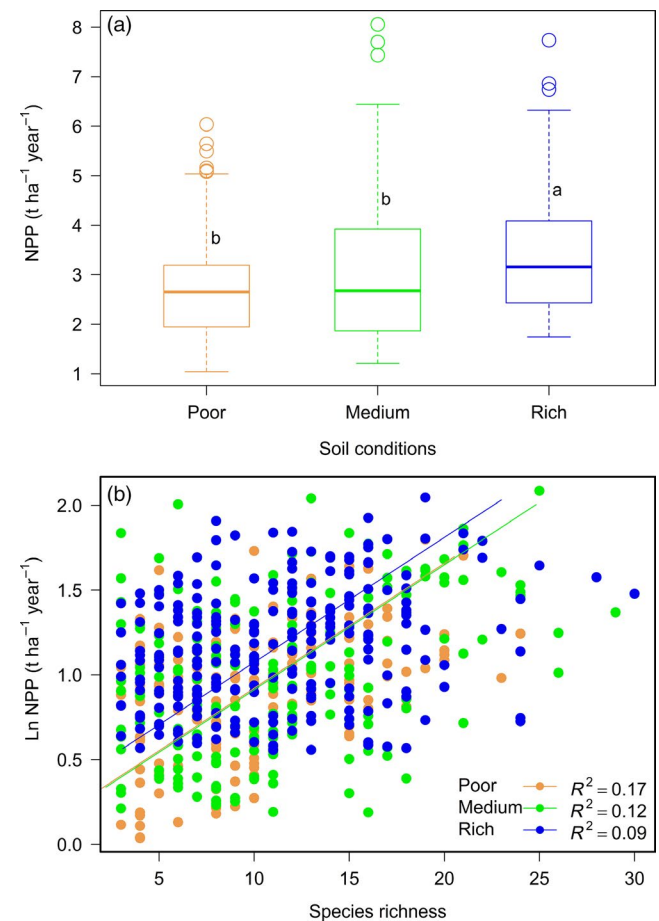


FIGURE 3 (a) Forest productivity at poor, medium and good site conditions. Boxes with different letters indicate significant differences at $p < 0.05$; (b) the relationship between species richness and forest productivity (ln-transformed) at the poor (orange circles), medium (green circles) and good (blue circles) soil sites. The best fitted models are: $\ln NPP = 0.074 \times \text{richness} + 0.184$ (orange line) at the poor sites ($r^2 = 0.17$, 95% CI for slope = 0.068–0.0795, 95% CI for intercept = 0.102–0.264, $p < 0.001$), $\ln NPP = 0.074 \times \text{richness} + 0.175$ (green line) at the medium sites ($r^2 = 0.13$, 95% CI for slope = 0.068–0.080, 95% CI for intercept = 0.080–0.270, $p < 0.001$) and $\ln NPP = 0.074 \times \text{richness} + 0.337$ (blue line) at the good sites ($r^2 = 0.09$, 95% CI for slope = 0.068–0.080, 95% CI for intercept = 0.254–0.420, $p < 0.001$) [Colour figure can be viewed at wileyonlinelibrary.com]

conditions did significantly affect forest productivity (Figure 3a; $F_{2,597} = 17.53$, $p < 0.001$), with forest productivity increasing with site conditions.

The relationship between species richness and productivity did not vary with site conditions (Figure 3b). This was indicated by no significant differences in slopes of the standardized major axis (SMA) regressions among site conditions (Figure 3b; likelihood ratio statistic = 5.582, $df = 2$, $p = 0.061$, SMA test). The regression intercepts were significantly different among site conditions (Figure 3b; Wald statistic = 18.6, $df = 2$, $p < 0.001$, SMA test).

3.3 | The relative importance of stand structure factors and diversity in determining stand productivity

The relative importance in determining productivity according to the hierarchical partitioning method, ranked in decreasing order of importance, was stand density (40.25%), age (22.62%), species richness (17.04%), maximum DBH (10.49%) and site conditions (9.60%; Figure 4). Stand density (Figure 2f; slope = 0.003 [CI: 0.002–0.004], $F_{1,598} = 145.8$, $R^2 = 0.19$, $p < 0.001$) and age (Figure 2g; slope = 0.014 [CI: 0.011–0.017], $F_{1,598} = 102.6$, $R^2 = 0.15$, $p < 0.001$) had the highest effects on forest productivity, while the effects of maximum DBH (Figure 2e; slope = 0.011 [CI: 0.008–0.014], $F_{1,598} = 46.12$, $R^2 = 0.07$, $p < 0.001$) and DBH variation (Figure 2f; slope = 0.634 [CI: 0.336–0.933], $F_{1,598} = 17.46$, $R^2 = 0.03$, $p < 0.001$) were significant but relatively weak.

The SEM model showed that all predictor variables together accounted for 37% of the variation in forest productivity (Figure 5a). Stand density, age, maximum DBH, species richness and site conditions all had significant positive effects on forest productivity (Figure 5a, Table S3). Site conditions also had a positive indirect effect via stand density, maximum DBH. Stand age had a positive indirect effect via stand density, maximum DBH and species richness. Stand density had a negative indirect effect via maximum DBH. Species richness also had a positive indirect effect via stand density and maximum DBH on forest productivity (Table S4, Appendix S2). More detailed information about the

direct and indirect effects of the predictors is presented in Table S4 (Appendix S2).

The alternative model with altered direction paths between species richness and stand density and maximum DBH also accounted for 37% of the variation in forest productivity (Figure 5b). Similar to the model in Figure 5a, site conditions and stand age had significant effects on stand density and maximum DBH. Both stand density and maximum DBH had positive effects on not only forest productivity but also species richness (Figure 5b).

4 | DISCUSSION

4.1 | Positive effects of biodiversity on forest productivity in subtropical China

Forest productivity increased with diversity, whether the effects of environmental and stand structural variables were accounted for or not (Figure 2, Table 1). This supports our hypothesis and is consistent with other studies that greater diversity enhances biomass and productivity in forests (Baruffol et al., 2013; Liang et al., 2016; Liu et al., 2018; Yuan et al., 2018). However, non-significant effects of species richness on biomass were also observed in temperate (Paquette & Messier, 2011) and subtropical forests (Wu, Wang, Tang, et al., 2015). The variable patterns may result because relationships between diversity and forest productivity can vary with the spatial scales (plots of 0.06 ha in this study) used in the analyses. For example, productivity and biomass were usually positively related to species richness at a relatively small spatial scale (plots of 0.04 ha), but became neutral or even negative at larger scales (0.25 or 1 ha; Chisholm et al., 2013; Wu, Wang, Tang, et al., 2015). How the diversity effects on forest productivity vary with plot size should be considered in the future studies.

Both the niche complementarity effect and the selection probability effect explained the positive effects (Hooper et al., 2005; Li et al., 2019). A strong positive relationship between functional diversity and forest productivity verifies the notion that niche complementarity plays a significant role in enhancing forest productivity in subtropical forests. CWM trait value of tree maximum height was

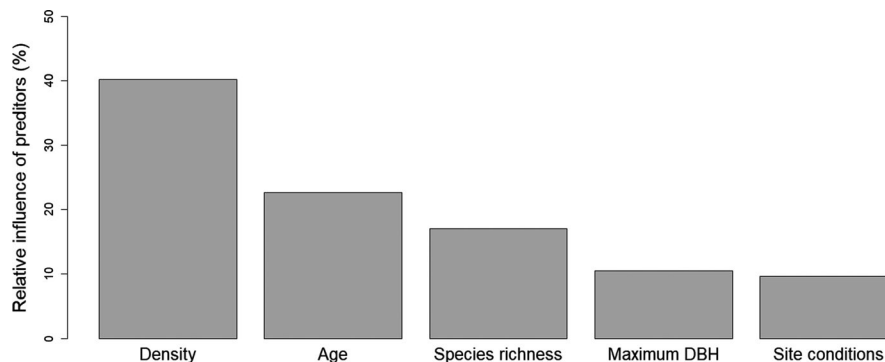


FIGURE 4 Relative percentage variation in forest productivity explained by site conditions, stand age, stand density, maximum diameter at breast height and species richness in the hierarchical partitioning analysis

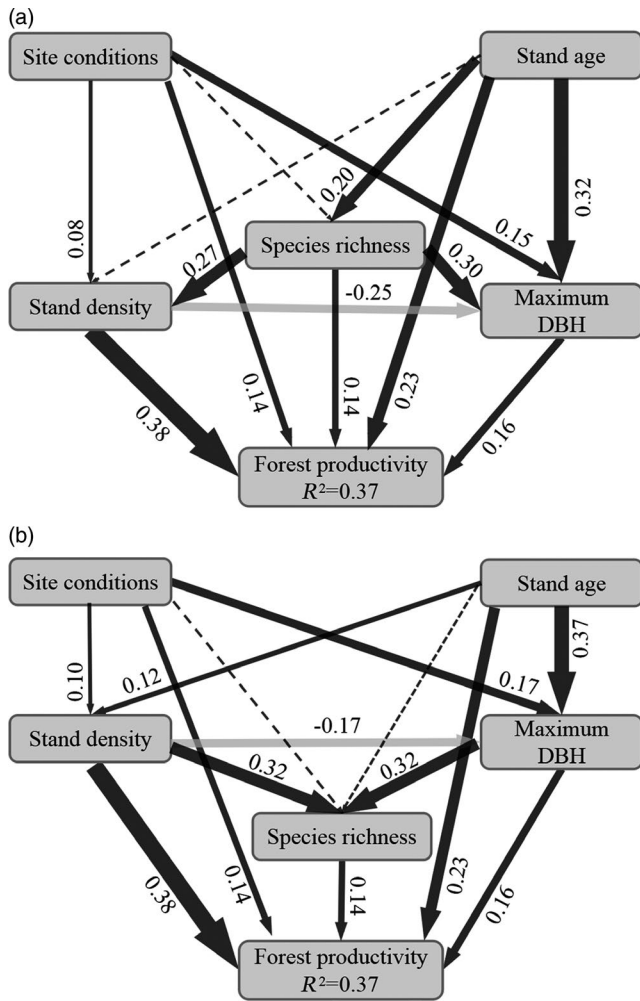


FIGURE 5 Structural equation model relating productivity to site conditions, stand age, stand density, maximum diameter at breast height (DBH) and species richness in subtropical forests. (a) Species richness had an effect on stand density and maximum DBH. (b) The alternative model with stand density and maximum DBH had an effect on species richness. The coefficients are standardized prediction coefficients for each causal path. Solid lines represent significant paths ($p \leq 0.05$; black: positive; grey: negative) and dashed lines indicate non-significant paths ($p > 0.05$). The thickness of the solid arrows reflects the magnitude of the standardized prediction coefficients. R^2 denotes the proportion of variance explained

positively related to forest productivity, indicating that the selection probability effect was also causing the positive relationship between diversity and productivity in our forests. Similar results were reported for above-ground biomass or productivity in temperate (Fotis et al., 2018; Yuan et al., 2018), subtropical (Chiang et al., 2016) and tropical forests (Finegan et al., 2015; Sullivan et al., 2017). Our results show that positive biodiversity effects on ecosystem functioning found by experimental studies (Hooper et al., 2005; Huang et al., 2018) and in boreal (Zhang & Chen, 2015) and temperate forests (Paquette & Messier, 2011; Ruiz-Benito et al., 2014) can also occur in these hyper-diverse subtropical forests, in line with the results of studies showing that biodiversity has significant positive effects on

forest productivity (Baruffol et al., 2013) and C storage (Liu et al., 2018).

4.2 | Environmental effects on forest productivity

In this study, site conditions had significant and positive effects on forest productivity, but the relationship between diversity and forest productivity did not vary significantly with site conditions (Figure 3). The highest forest productivity at good site conditions indicated that favourable resource supply (e.g. soil fertility and water availability) increased forest productivity (Forrester & Bauhus, 2016; Pretzsch et al., 2013; Toigo et al., 2015). The coefficient of determination of the relationship between species richness and forest productivity decreased from poor sites to good sites. This is consistent with the evidence that relationships between diversity and productivity can become stronger when environmental conditions are less favourable for tree growth (Toigo et al., 2015; Wu, Wang, Tang, et al., 2015). In addition, site conditions affected forest productivity indirectly through forest structural attributes, consistent with previous studies (Becknell & Powers, 2014; Zhang & Chen et al., 2015). Mean annual temperature and mean annual precipitation are major drivers of forest productivity at large spatial scales (Schoor, 2003; Wu, Wang, Tang, et al., 2015). However, no significant effects of climatic factors on forest productivity were found in this study (Table 1). This may result from the favourable climatic conditions of our study region, with a mean annual precipitation of 1,200–1,700 mm and an average annual air temperature is 16–18°C (Huang et al., 2014). In fact, tree growth in this region is probably not often limited by climatic conditions. Moreover, the magnitude of variation in climatic factors was not large enough to lead to significant changes in forest productivity in our study region.

4.3 | Stand structural factors more important than diversity in determining forest productivity

Stand density and stand age had larger effects on forest productivity than diversity (Figures 4 and 5). At low stand densities, the interactions among trees do not occur or will be weak so that niche complementarity effects are not significant (Forrester & Bauhus, 2016). As stand density increases, the interactions will be more intensive, trees occupy more space and utilize more resources (such as light, water, and nutrients; Morin, 2015), possibly leading to an increase in complementarity (Boyden, Binkley, & Senock, 2005; Forrester et al., 2013). Recent studies show that stand density has stronger effects on forest productivity than diversity based on large inventory datasets (Forrester & Bauhus, 2016; Guo & Ren, 2014; Paquette & Messier, 2011). At the same time, species richness affected stand density and thus had indirect effects on forest productivity (Figure 5a). These results indicate the importance of considering stand density, and the effects of diversity on stand density, when analysing the relationship between diversity and forest productivity (Baruffol et al., 2013).

In addition, we found that the increase in tree size with species richness and stand age had a significantly positive effect on forest productivity. This agrees with previous studies where large-diameter trees could enhance forest productivity in these forests because large-diameter trees have the ability to capture more light and compete against neighbours (Ligot et al., 2018; Xu et al., 2016). Stand age may affect biomass and productivity via changes in stand structure (i.e. density) and via increasing species richness as forests develop (Becknell & Powers, 2014; Liu et al., 2018; Zhang & Chen, 2015). Previous studies have shown that positive relationships between diversity and productivity were only found before canopy closure, or for early successional forests, and that the relationship declines at late successional stages and after canopy closure and competition (i.e. Vilà et al., 2003; Guo & Ren, 2014). Similar relationships between forest C stocks and diversity for different stand ages (e.g. 20–100 years) were found in subtropical forests in China (Liu et al., 2018). Notably most of the forests in our study are still young (age <45 years), and a positive relationship between diversity and forest productivity was found, indicating that these forests also have the potential to sequester greater amounts of C through forest growth in the future. In China, subtropical forests are a major potential C sink because of the development and implementation of large-scale afforestation programmes during the last four decades (Liu et al., 2018). Thus, future studies about the role of diversity on productivity and other ecosystem functions could benefit from accounting for these important stand structural attributes.

5 | CONCLUSIONS AND IMPLICATIONS

Much controversy has centred on the relationship between diversity and ecosystem functioning over the past two decades (Fotis et al., 2018; Liang et al., 2016). Our findings show that biodiversity, stand structure (i.e. stand density, age and maximum DBH) and environmental factors all contribute to the geographic variation in productivity in species-rich subtropical forests. Community-weighted means of traits had larger effects on forest productivity than functional diversity. Diversity significantly affected forest productivity directly and indirectly through their effects on the stand structure. However, the effects of stand density and age were stronger than diversity. Our results suggest that biodiversity and stand structures should be considered simultaneously when analysing the effects of biodiversity on forest ecosystem functions, such as productivity and C sequestration ability.

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AUTHORS' CONTRIBUTIONS

S.O.Y., W.H.X. and X.P.W. designed the research; W.H.X., W.F.X., S.G.L., D.I.F., L.X.Z., X.D.L. and C.H.P. conceived ideas; S.O.Y., L.C., H.S., X.W.D. and P.F.L. compiled and analysed the data; S.O.Y. and W.H.X. led the writing of the manuscript. All authors revised the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data were compiled by members of Huitong National Station for Scientific Observation and Research of Chinese Fir Plantation Ecosystems in Hunan Province. Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.s4r94b0> (Ouyang et al., 2019).

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SUPPORTING INFORMATION

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