



Decoupling the Complementarity Effect and the Selection Effect on the Overyielding of Fine Root Production Along a Tree Species Richness Gradient in Subtropical Forests

Cong Liu,^{1,2} Wenhua Xiang,^{2,3*} Binggeng Xie,^{1*} Shuai Ouyang,^{2,3}
Yelin Zeng,^{2,3} Pifeng Lei,^{2,3} and Changhui Peng^{3,4}

¹College of Resources and Environmental Sciences, Hunan Normal University, Changsha 410081, Hunan, China; ²Faculty of Life Science and Technology, Central South University of Forestry and Technology, Changsha 410004, Hunan, China; ³Huitong National Station for Scientific Observation and Research of Chinese Fir Plantation Ecosystems in Hunan Province, Huitong 438107, Hunan, China; ⁴Department of Biological Sciences, Institute of Environment Sciences, University of Quebec at Montreal, Montreal, Quebec H3C 3P8, Canada

ABSTRACT

The mechanism whereby tree species richness and identity affect the production of fine roots (≤ 2 mm) in forests remains controversial. Complementarity effects (via resource partitioning and facilitation, CEs) and selection effects (that is, dominant of species with particular traits, SEs) are the two hypotheses to explain biodiversity effects on ecosystem functions. This study aimed to (1) examine how tree species diversity affects fine root production and (2) disentangle the complementarity effect and the selection effect on the rela-

tionship between biodiversity and fine root production. A total of 60 tree clusters with 15 combinations of diversity gradients consisting of 1–4 tree species (*Pinus massoniana*, *Choerospondias axillaris*, *Cyclobalanopsis glauca* and *Lithocarpus glaber*) were established in subtropical forests. The sequential soil core and ingrowth core methods were used in each cluster to measure fine root biomass and productivity. Fine root production increased with increase in tree species richness. The biodiversity effects on fine root production mostly resulted from CEs. In the nongrowing season, in most cases, the CE on biomass was positive and became stronger as richness increased, but the opposite situation was observed in the growing season. The strong positive and negative effects of the proportions of *C. glauca* and *L. glaber* in the tree clusters on fine root biomass, CEs and SEs, suggest the coordinated action of species diversity and identity in modulating biodiversity effects on belowground processes.

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*Corresponding author; e-mail: xiangwh2005@163.com; xbgby1961@163.com

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INTRODUCTION

In the past two decades, many studies have shown that biodiversity improves ecosystem functions, including productivity, carbon (C) sequestration, nutrient cycling and hydrological processes (Loreau and others 2001; Cardinale 2012), stability (Leuschner and others 2009; Isbell and others 2011) and other ecosystem services (Gamfeldt and others 2013). In forests, fine roots (≤ 2 mm in diameter) are an important belowground C pool accounting for 2–15% of stand biomass C (Lukac and Godbold 2010; Finér and others 2011) and 33–67% of terrestrial net primary productivity (NPP) at a global scale (Abramoff and Finzi 2014). As soil nutrients and water are supplied in multiple dimensions and characterized by spatial heterogeneity in forests, fine roots show greater niche segregation than aboveground plant parts (Pärtel and others 2012). Revealing the mechanism of biodiversity effects on fine root production is crucial for advancing the understanding of forest belowground dynamics in the face of global biodiversity loss and climate change.

The existing studies on the effects of tree species richness on belowground production show contrasting results. Higher fine root productivity in species-rich than species-poor stands or monocultures has been found in plantations and temperate broad-leaved forests (Brassard and others 2011, 2013; Lei and others 2012). In contrast, studies have shown no significant influence of diversity on fine root productivity (Bauhus and others 2000; Meinen and others 2009a, c; Jacob and others 2013, 2014) or even a negative effect (McKay and Malcolm 1988; Bolte and Villanueva 2006). These controversial results in forests may be shaped by site conditions (for example, climate, water availability and soil fertility) (Steudel and others 2012; Forrester and others 2013) and stand age (for example, positive biodiversity effects on fine root production increase with stand development) (Ma and Chen 2017). It has been shown that the species composition (Xiang and others 2015), such as the proportions of conifers (Finér and others 2017) and evergreens (Archambault and others 2019), explains fine root production to a greater extent than tree species diversity and site factors. Additionally, it has been proposed that the positive role of

diversity on fine root production only operates in plantations of certain combinations of tree species with diverse functional traits or low-yield natural forests (Jacob and others 2013).

The biodiversity effect on production can be quantitatively described as the extent to which the yield of a mixed community exceeds the mean yield of monocultures of the species it contains (Schmid and others 2008). Typically, two main mechanisms have been proposed to explain biodiversity effects. The complementarity effect assumes that communities with a greater number of species can achieve greater production ('overyielding') via niche partitioning and facilitation. Interspecific trait differences are a prerequisite for achieving complementary resource utilization (Loreau and others 2001). Resource niche partitioning can be implemented via different forms of nutrient utilization [that is, various forms of nitrogen (NO_3^- , NH_4^+ and organic nitrogen)] and at different temporal (for example, leaf or root phenology) and spatial scales (for example, canopy architecture) in species-rich communities (Cardinale and others 2007; Roscher and others 2012; Tilman and others 2012; Zhao and others 2017). Different species can achieve mutual benefits via facilitation and positive feedback (for example, nitrogen fixation, mycorrhizal colonization and root secretion) through the expansion of available resource pools and acceleration of the nutrient cycle (Barry and others 2019). Remarkably, antagonistic interactions between plants (caused by physical and chemical factors) can lead to negative complementarity and lower productivity in mixtures than expected from monocultures (Loreau and others 2001). When evaluating belowground resource complementarity, a classical alternative index is the root distribution pattern (that is, vertical niche differentiation) (Parrish and Bazzaz 1976; Fitter 1986). Indeed, numerous studies have confirmed that differences in rooting depth between species can lead to more stable coexistence and reduced interspecific competition (Canadell and others 1996; Fargione and Tilman 2005). The selection effect assumes that overyielding in a species-rich community is due to high-yielding dominant species with particular traits (Špačková and Lepš 2001; Schmid and others 2008). In natural habitats and manipulated experiments, the two mechanisms are not mutually exclusive in communities and likely work together. Clear decoupling of the two effects is necessary for the interpretation of results and elucidation of mechanisms. The mathematical 'additive partitioning method' proposed by Loreau and Hector (2001) has been successfully applied for the

division of biodiversity effects in many biodiversity–productivity relationship studies.

Several studies aimed at disentangling the two dimensions (complementarity vs. selection) of the effects of biodiversity on community productivity have demonstrated that overyielding in some grasslands is attributed to both complementarity and positive selection effects (Tilman and others 2001; Cardinale and others 2007; Fargione and others 2007). The complementarity effect usually explains more of the variance with the advance of experimental time (Cardinale and others 2011; Tobner and others 2016). A field-based biodiversity experiment showed that the belowground selection effect decreased with increase in plant species richness (Oram and others 2018). Nevertheless, the proportion of the most productive species had a significant positive explanatory effect on belowground production, confirming the remarkable selection effect (Mommer and others 2015; Archambault and others 2019).

Subtropical areas in China with a monsoon climate are ecologically sensitive areas of global change. As one of the most typically biodiverse regions in the world, the secondary forests in these areas have reached a stable stage involving abundant tree species, which is very favorable for the study of biodiversity–productivity relationships (Bruehlheide and others 2014). Compared with the homogeneous soil conditions of artificial plantations, plant–soil feedback in natural forest soils with spatial heterogeneity significantly affects root interactions and interspecific competition (Hendriks and others 2015). Our study was carried out in a natural secondary forest in the absence of interference, where all possible tree species combinations are available, and the study benefitted from a replicated gradient of species richness. This provides a platform for examining biodiversity effects on belowground production. Previous studies in the same forests indicated that fine root biomass and productivity increased with tree species diversity (Liu and others 2014; Zeng and others 2019), but the positive effects of tree species diversity were dependent on the species identity of neighborhoods (Xiang and others 2015). However, how fine root production responds to various species compositions and the decoupling of biodiversity effects (complementarity vs. selection effect) have not been thoroughly investigated.

In this study, we investigated fine root biomass and productivity in tree clusters with different combinations of one to four tree species to (1) examine how tree species richness and identity affect fine root biomass and productivity; (2) dis-

entangle the relative importance of the complementarity effect and the selection effect for the relationship between biodiversity and fine root production; and (3) reveal the underlying mechanisms of the biodiversity effects on belowground production.

MATERIALS AND METHODS

Description and Tree Cluster Selection

The study site was located at Dashanchong Forest Park (latitude 28° 23′ 58″–28° 24′ 58″ N, longitude 113° 17′ 46″–113° 19′ 08″ E), Changsha County, Hunan, China. The area presents a typical low hilly topography with an elevation between 55 and 260 m. The climate is a mid-subtropical monsoon climate. The mean annual air temperature is 17.3°C. The annual precipitation ranges from 936.4 to 1954.2 mm, with an average of 1416.4 mm. The soil is a well-drained clay loam red soil developed from slate and shale parent rock, classified as an Alliti-Udic Ferrosol, corresponding to an Acrisol in the World Reference Base for Soil Resource (IUSS Working Group WRB 2006).

There are three secondary forests in the Park: a *Pinus massoniana* (PM)—*Lithocarpus glaber* (LG) coniferous and broad-leaved mixed forest; a *Chorospodias axillaris* (CA) deciduous broad-leaved forest; and a *L. glaber* (LG)—*Cyclobalanopsis glauca* (CG) evergreen broad-leaved forest. The stand characteristics of the three forests were reported by Liu and others (2014). To investigate how tree species diversity affects fine root biomass and productivity, we selected a total of 60 tree clusters consisting of one to four tree species (PM, CA, CG and LG) combinations in the forests. For each tree cluster, four target stems formed a microsite or ‘tree quadrilateral,’ and all possible species compositions involving the four species were represented (Jacob and others 2013; Xiang and others 2015). There were 15 possible compositions: 4 involving a single tree species, 6 combinations of two tree species, 4 combinations of three tree species and 1 combination of the four tree species (Figure S1). Each combination had four replicates. The 60 tree clusters included 1, 2, 3 or 4 tree species and presented low, medium and high functional diversity gradients based on the aboveground life forms linked to leaf light resource-use strategies (Figure S1). The mean distance between the plots was c. 60 m, which is sufficient to exclude fine root system overlap between neighboring plots in most cases. The aboveground stand structure characteristics (cumulative basal area, diameter at breast height,

tree height, canopy and distance between the tree clusters) and edaphic properties did not show significant differences between the four species richness levels (4 replicates \times 4 combinations of 1-species, 4 replicates \times 6 combinations of 2-species, 4 replicates \times 3 combinations of 3-species and 4 replicates \times 1 combination of 4-species clusters) (Table S1).

Root Sampling and Preliminary Processing

Sequential Coring

Fine root sampling was carried out in July 2015 and January 2016 when the relative maximum and minimum fine root biomass appeared in the forests (Liu and others 2014). To minimize interference between the two sampling events, we randomly selected two locations with a minimum distance of 60 cm in each of 60 clusters. Fine root samples were obtained using a steel auger (10 cm in diameter and 10 cm in length) at soil depths of 0–10 cm, 10–20 cm and 20–30 cm. Soil samples were removed from the auger and placed into polyethylene bags, then transported to the laboratory for further processing. The samples were stored under refrigeration at 4°C in the dark within 3 weeks until fine root separation.

Root Ingrowth Cores

The root ingrowth core method was used to measure fine root productivity. Although the values measured are usually lower than those obtained via the sequential coring method (Meinen and others 2009b; Brassard and others 2011), this approach is a simple, widely used method for fine root productivity estimation (Brassard and others 2013; Lei and others 2012). In May 2015, 60 ingrowth cores (one per cluster) were installed at the geometric center of each cluster, which were retrieved after 14 months in July 2016.

To set up the ingrowth cores, three soil cores were continuously extracted from the topsoil (0–30 cm) using a steel soil auger (10 cm in diameter and 10 cm in length) in each tree cluster. The extracted soils were sieved through a 2.5 mm mesh sieve, and roots were removed using a pair of tweezers. Subsequently, the sieved root-free soils were placed in 1.5 mm \times 1.5 mm mesh fiberglass cylindrical bags (10 cm in diameter and 30 cm high) and compressed to approximate the original soil structure and density as much as possible (Uselman and others 2007). The bags containing the root-free original soil were reinserted back into

the hole and marked with PVC sticks at the core edges. There is often a lag period before the initiation of root growth into the soils of ingrowth cores in temperate ecosystems (Vogt and others 1998; Lukac and Godbold 2001), and fine root regrowth was estimated to start after a 2 month interval (Jacob and others 2014; Liu and others 2014). Based on the pre-experiment study of ingrowth method in the same forest, few fine root growth (0–9.63 g m⁻²) was found during the first 2 months after ingrowth cores installment. Thus, fine root growth in the bulk of the ingrowth cores started after a 2-month lag period (July 2015). Upon harvest in July 2016, the installed ingrowth cores were carefully collected by using a spade and transported to and stored in the laboratory until fine root extraction. Each mesh bag from a soil ingrowth core was cut into three equal soil columns (representing 0–10 cm, 10–20 cm and 20–30 cm soil depths, respectively). Roots with diameters larger than 2 mm were rarely present in all the ingrowth cores because of mesh bag aperture limitation.

Annual fine root productivity based on the ingrowth core method was calculated for each tree cluster by summing the dry weight of the fine root biomass and necromass in each ingrowth core segment. Fine root productivity (g m⁻² y⁻¹) was expressed for the virtual 12-month period.

Fine Root Separation and Weighing

The soil coring samples were soaked in water and placed in 0.25 mm mesh sieves to separate fine roots (\leq 2 mm diameter). Coarse tree roots ($>$ 2 mm diameter) and roots of herbs and grasses were discarded. Fine roots were manually picked out from the soil using tweezers and rinsed with distilled water. The fine root fragments were separated into living and dead roots based on resilience, elasticity, and periderm color (Brassard and others 2011). At the experimental site, the density of herbaceous roots was very low, and they were discarded. Then, the living fine roots were sorted into different species under a stereomicroscope (4–40 \times) (Olympus Corporation SZX12, Tokyo, Japan) according to morphological criteria (branching patterns, color and surface structure of the periderm, size and shape of root tips, diameter of fine and finest roots). After separation, the sorted live biomass and necromass root samples were oven-dried at 80°C for 48 h to constant weight and then weighed to 0.0001 g. The root mass data were expressed as the dry mass per square meter of the ground area (g m⁻²).

Soil Chemical Analysis

Soil samples at depth of 0–30 cm were taken from each plot using a steel auger (5 cm in diameter and 30 cm in length) and transported to the laboratory. For each sample, 500 g of fresh soil was air-dried and sieved through 0.25 mm mesh. The pH values were measured at a soil-to-water (deionized) ratio of 1:2.5 using an FE20 pH meter (Mettler Toledo, Shanghai, China). Soil organic carbon (SOC) was determined by the $K_2Cr_2O_7/H_2SO_4$ oxidation method. Total nitrogen (N) was measured with the Semimicro-Kjeldahl method determined by Kjeltec K9840 automatic azotometer. Total phosphorus (P) was measured by using sodium hydroxide (NaOH) fusion and the Mo-Sb colorimetric method through spectrophotometry (Carter and Gregorich 2006).

Data Analysis

Relative Production Calculations

To reduce the influence of aboveground tree size on the fine root production data and facilitate comparisons between the four tree species richness levels, the fine root production (biomass and productivity) of specific species was adjusted to a single unit of its total basal area in the tree clusters. The relative adjusted fine root production (that is, the ratio between the adjusted fine root production values (because the amount of necromass was relatively low, we consider only live biomass here) of a species in the mixed and monoculture clusters) provides a representation of the fine roots of the species in the mixture (Schmid and Kazda 2002; Bolte and Villanueva 2006):

$$AP_{i,mon} = \frac{M_i}{BA_{i,mon}} \quad (1)$$

$$AP_{i,mix} = \frac{Y_{Oi}}{BA_{i,mix}} \quad (2)$$

$$APT_{mix} = \sum_{i=1}^N \frac{Y_{Oi}}{BA_{i,mix}} \quad (3)$$

$$rAP_{i,mix} = \frac{AP_{i,mix}}{AP_{i,mon}} = \frac{Y_{Oi}}{BA_{i,mix}} : \frac{M_i}{BA_{i,mon}} \quad (4)$$

where M_i is fine root production of species i in monoculture; Y_{Oi} is the observed production of species i in the mixture; N is the number of species present in the cluster ($i = 1, 2, \dots, N$); BA_i (m^2) is the total basal area of species i in each cluster (mix: mixed clusters, mon: pure clusters); AP is fine root production adjusted to the same basal area ($1 m^2$)

(mix: mixed clusters, mon: pure clusters); APT_{mix} is total fine root production in mixed clusters; and $rAP_{i,mix}$ is the relative adjusted fine root production of species i in mixed clusters.

$rAP_{i,mix} < 1$ indicates that the fine root production of the particular species in the mixed clusters is underrepresented compared to that in the monoculture clusters (1-species clusters = 1.0). Conversely, $rAP_{i,mix} > 1$ indicates that fine root production is overrepresented in the mixed clusters. The comparison of $rAP_{i,mix}$ among the four species is used to evaluate the fine root suppression or promotion of the species by interspecific competition (Bolte and Villanueva 2006; Xiang and others 2015).

Biodiversity Effect Partitioning

Several metrics are used to partition the effects of diversity on ecosystem production. The net biodiversity effects (NEs) are defined as the deviation between the observed (Y_O) and expected (from monocultures) yields (Y_E). NEs can be mathematically partitioned into complementarity effects (CEs) and selection effects (SEs) through additive bipartite partitioning according to Loreau and Hector (2001):

$$NE = Y_O - Y_E = CE + SE \\ = N \times \overline{\Delta RY} \bar{M} + N \times cov(\Delta RY, M) \quad (5)$$

where Y_O is the total observed yield of the mixture; Y_E is the total expected yield of the mixture; N is the number of species present in the cluster; \bar{M} is the average monoculture yield across all species present in the cluster; RY_{Oi} is the observed relative fine root yield of species i in the mixture (that is, $RY_{Oi} = \frac{Y_{Oi}}{M_i}$); RY_{Ei} is the expected relative yield of species i in the mixture; instead of the proportion seeded or planted, as used in some young plantations (Loreau and Hector 2001; Sun and others 2017), in natural forests, the proportion of the basal area is usually considered as RY_{Ei} (that is, $RY_{Ei} = \frac{BA_{i,mix}}{BAT_{mix}}$, where BAT_{mix} (m^2) is the total basal area in the mixed cluster) (Ma and others 2019); ΔRY is the deviation between the observed and expected relative yields (that is, $\Delta RY = RY_O - RY_E$); and $\overline{\Delta RY}$ is the average ΔRY across all component species in a cluster.

A positive CE occurs when the species in a mixture produce higher observed yields than expected, indicating niche partitioning or facilitation (Loreau and Hector 2001). The SE is positive when more-productive species with high monoculture yields dominate the mixture and negative when

species with lower-than-average monoculture yields perform better in mixtures (Loreau and Hector 2001; Tobner and others 2016).

Statistical Analyses

All data were tested for a normal (Gaussian) distribution by the Shapiro–Wilk test ($p < 0.05$). The results indicated that the data on fine root biomass and productivity fit a normal distribution. Linear regression was used to detect the relationship between species richness (SR) and fine root production. The effects of the presence/absence of each species (as fixed effects) on fine root biomass, net biodiversity effects on biomass (NE_b), complementarity effects on biomass (CE_b), selection effects on biomass (SE_b), fine root productivity, net biodiversity effects on productivity (NE_p), complementarity effects on biomass (CE_p) and selection effects on biomass (SE_p) were tested with linear mixed-effects models (LME) using species combinations and sampling times as random effects to test the significant effects of particular species. We tested the effects of SR and soil nutrient (C, N and P) concentrations with multivariate analysis of variance (MANOVA) on fine root production for the whole soil core (0–30 cm). The vertical heterogeneity index (VHI) was calculated as the standard deviation of the biomass percentage among the three layers within a single soil core. VHI implies the vertical distribution patterns of fine roots and indicates how fully and evenly the belowground space is utilized (Brassard and others 2011, 2013). The mean rooting depth of a given species (that is, the root vertical center of gravity) was calculated as the sum of its fine root mass in soil layer i multiplied by the mean depth of layer i and then divided by the total fine root mass of all layers (Mommer and others 2010). All statistical analyses were carried out using the statistical software R 3.5.1 (R Development Core Team, 2017). The linear mixed-effect analysis was performed using restricted maximum likelihood estimation with the *lme4* package (Bates and others 2017).

RESULTS

Effects of Tree Species Richness and Identity on Fine Root Production

Tree species richness (SR) significantly increased ($p < 0.01$) fine root biomass and productivity upon adjustment for tree size interference (Figure 1). The same pattern was found for each soil layer ($p < 0.01$) except the middle layer ($p = 0.4571$ for 10–20 cm) in July (Figure S8A).

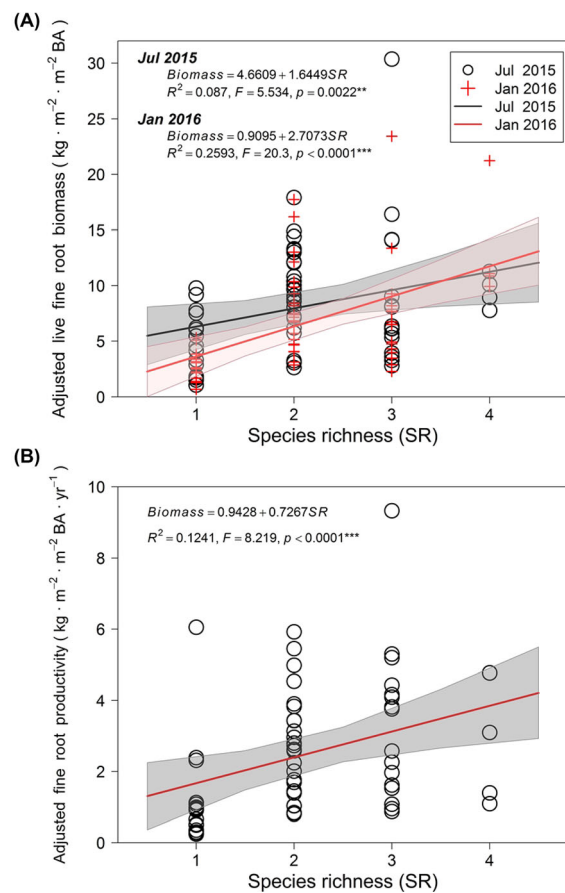


Figure 1. The relationship between aboveground tree species richness (SR), adjusted living fine root biomass (A) and productivity (B). The fitted line shows a significant relationship at $p \leq 0.05$ (*), $p < 0.01$ (**) and $p < 0.001$ (***). Gray and red shading indicate the 95% credible intervals.

However, significance was weakened in the unadjusted dataset (Figure S2). The mean fine root biomass was higher in July than in January at the same SR level, except in the 4-species plot, which presented a significantly higher value in January (Figure S3). The fine root growth rate into the in-growth cores in the 0–30 cm soil depth was significantly different between the clusters with differences in SR, with means increasing from 2.61 to 13.28 kg m⁻² m⁻² BA yr⁻¹ (Figure 1). The regression slope of the relationship between fine root productivity and SR was the highest in the topsoil layer (0–10 cm) and decreased across the sampled depths (Figure S8B).

At the species level, fine root biomass in the monospecific clusters was significantly different. The fine root biomass of CG was almost two times higher than those of CA and LG, while intermediate values were recorded for PM ($p < 0.05$).

Table 1. Fine Root Biomass and Relative Adjusted Fine Root Biomass (0–30 cm Profile) of the Four Tree Species at the Four Species Richness (SR) Levels

Species richness level	CA	CG	LG	PM	Mean for the four species
Fine root biomass (g m^{-2})					
1-species	184.20 aA* (3.81)	341.78 a***B (54.66)	180.31 a**A (34.02)	244.53 a***AB (11.58)	237.70 a*** (22.33)
2-species	137.83 abAB (27.27)	177.56 bA (35.32)	93.86 bB (14.66)	101.10 bB (16.33)	127.59 b (12.97)
3-species	97.45 bA (9.89)	82.26 bA (14.54)	68.34 bA (13.64)	92.73 bA (15.09)	85.20 c (6.71)
4-species	150.47 abA (27.12)	87.93 bAB (20.29)	44.82 bB (9.96)	83.47 bAB (32.72)	91.68 bc (14.54)
Mean for the four species richness	130.06 AB* (12.17)	151.15 A (21.53)	88.97 B (10.75)	113.69 AB (12.66)	
Relative adjusted fine root biomass					
1-species	1.00 abA (0.00)	1.00 ab*A (0.00)	1.00 aA (0.00)	1.00 aA (0.00)	1.00 ab** (0.00)
2-species	1.54 aAB (0.36)	1.67 aA (0.21)	1.07 aAB (0.15)	0.95 aB (0.21)	1.31 a (0.13)
3-species	0.75 bA (0.14)	1.03 bA (0.21)	0.66 aA (0.15)	0.63 aA (0.13)	0.77 b (0.08)
4-species	1.53 abA* (0.18)	0.70 bB (0.04)	0.94 aAB (0.36)	0.72 aB (0.09)	0.97 ab (0.13)
Mean for the four species richness	1.18 AB* (0.16)	1.23 A (0.13)	0.89 BC (0.09)	0.81 C (0.10)	

The means are provided with the errors in brackets. Different lowercase letters indicate significant differences between SR levels for a given species; different capital letters indicate significant differences between the species within an SR level (Tukey's test, $p \leq 0.05$). CA *Choerospondias axillaris*, CG *Cyclobalanopsis glauca*, LG *Lithocarpus glaber*, PM *Pinus massoniana*. * $p \leq 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Adjusted fine root biomass is fine root biomass of specific species adjusted to the same basal area (1 m^2). Relative adjusted fine root biomass is the ratio of adjusted fine root biomass in the mixture to monoculture.

(Table 1). In the monospecific clusters, the absolute fine root growth rate of CA was three or four times as high as that of CG or PM, respectively (Table 2). The relative adjusted fine root biomass (rAP_b) and productivity (rAP_p) of specific species in mixed clusters were calculated. On average, CA and CG produced markedly more fine root biomass in 2-species clusters relative to their monospecific clusters (54% and 67% overrepresentation, respectively), while PM tended to be underrepresented (Table 1). In mixed clusters, the mean rAP_p of CA and CG were overrepresented (mean of 1.91 and 2.57, respectively). Moreover, the fine root biomass and productivity of CG tended to be significantly higher in 2-species ($rAP_b = 1.67$) and 4-species ($rAP_p = 4.33$) clusters than in the respective 1-species clusters (Tables 1, 2). The differences in rAP between species were much more pronounced in the 4-species clusters, which suggested greater

species-specific differences in the species-rich plots (Tables 1, 2).

Partitioning of Biodiversity Effects on Fine Root Production

The partitioning of the net biodiversity effects (NEs) showed that negative NEs occurred in nine out of eleven mixtures for fine root biomass in July 2015, while nine positive NEs were observed for fine root biomass in January 2016 and for productivity (Figure 2A). The NEs on biomass ranged from -157.45 g m^{-2} for the LG-PM cluster in July 2015 to $+214.92 \text{ g m}^{-2}$ for the CA-CG-LG-PM cluster in January 2016 (Figure 2A). The NE values were largely due to significant complementarity effects (CEs) ($p < 0.05$), and contrasting patterns appeared for the CEs on fine root biomass in the growing season and nongrowing season (Figure 2A). The selection effects (SEs) on fine root

Table 2. Fine Root Productivity and Relative Adjusted Fine Root Productivity (0–30 cm Profile) at the Four Tree Species in the Four Species Richness (SR) Levels

Species richness level	CA	CG	LG	PM	Mean for the four species
Fine root productivity ($\text{g m}^{-2} \text{ yr}^{-1}$)					
1-species	126.69 a*A* (21.24)	47.30 abB (15.44)	75.92 a*AB (23.38)	38.38 aB (10.70)	72.07 a** (12.11)
2-species	51.58 bA (12.95)	57.57 abA (10.91)	51.11 abA (13.22)	30.68 aA (6.69)	47.74 ab (5.64)
3-species	59.44 abA* (15.25)	32.30 aAB (5.37)	27.54 bAB (3.76)	22.75 aB (4.91)	35.51 b (4.67)
4-species	38.24 abAB* (17.53)	70.09 bA (17.97)	19.79 bAB (3.46)	11.18 aB (3.57)	34.83 b (8.17)
Mean for the four species richness	62.25 A** (9.11)	48.38 AB (5.70)	41.46 AB (6.48)	26.23 B (3.55)	
Relative adjusted fine root productivity					
1-species	1.00 aA (0.00)	1.00 a*A (0.00)	1.00 aA (0.00)	1.00 aA (0.00)	1.00 a (0.00)
2-species	1.83 aA (0.69)	1.58 aA (0.40)	0.70aA (0.17)	1.23 aA (0.34)	1.34 a (0.22)
3-species	1.39 aAB (0.45)	1.79 aA (0.51)	0.86 aAB (0.19)	0.67 aB (0.15)	1.18 a (0.19)
4-species	2.52 aAB** (0.71)	4.33 bA (1.10)	0.61 aB (0.24)	0.40 aB (0.10)	1.96 a (0.51)
Mean for the four species richness	1.65 AB** (0.32)	1.93 A (0.32)	0.78 B (0.10)	0.89 B (0.15)	

The means are provided with the errors in brackets. Different lowercase letters indicate significant differences between SR levels for a given species; different capital letters indicate significant differences between the species within an SR level (Tukey's test, $p \leq 0.05$). CA *Choerospondias axillaris*, CG *Cyclobalanopsis glauca*, LG *Lithocarpus glaber*, PM *Pinus massoniana*.

Adjusted fine root productivity is fine root productivity of specific species adjusted to the same basal area (1 m^2). Relative adjusted fine root productivity is the ratio of adjusted fine root productivity in the mixture to monoculture.

* $p \leq 0.05$; ** $p < 0.01$; *** $p < 0.001$.

productivity were all negative except in the CA–PM and CA–CG–LG–PM clusters, and the SE values were significant only for the productivity of the CG–LG–PM cluster (Figure 2B). The values of NE on fine root production were the highest at the surface soil layer (0–10 cm) (Figure S9). Higher occurrence probabilities of positive NE values were observed in the deep (20–30 cm) than top (0–10 cm) depth for fine root production, and the significance of CEs on fine root biomass increased with soil depth in the nongrowing season (Figure S9).

When using the presence of particular species as the explanatory variables, most of the total variability in the fine root biomass, NE_b and CE_b , was significantly explained by the presence of CG ($p < 0.01$) (Table 3). The presence of LG significantly influenced SE_b , NE_p and CE_p ($p < 0.05$) and marginally significantly influenced fine root pro-

duction ($p < 0.1$) (Table 3). Linear regression analysis showed a strong and significant positive correlation between the proportion of CG in the mixture and fine root biomass, NE_b and CE_b ($p < 0.05$) (Figure 3A), while a significant negative relationship was found for the proportion of LG ($p < 0.05$) (Figure 3B). This contrasting pattern was also observed for productivity (Figure S4). The presence and proportion of CA and PM in the clusters had no significant effects on the above indexes.

Effects of Soil Nutrient Concentrations and Species Richness

The concentrations of soil nutrients (C, N and P) significantly affected fine root biomass ($p < 0.05$), but the effects on fine root productivity were not significant except for N ($p < 0.05$) (Table 4). The

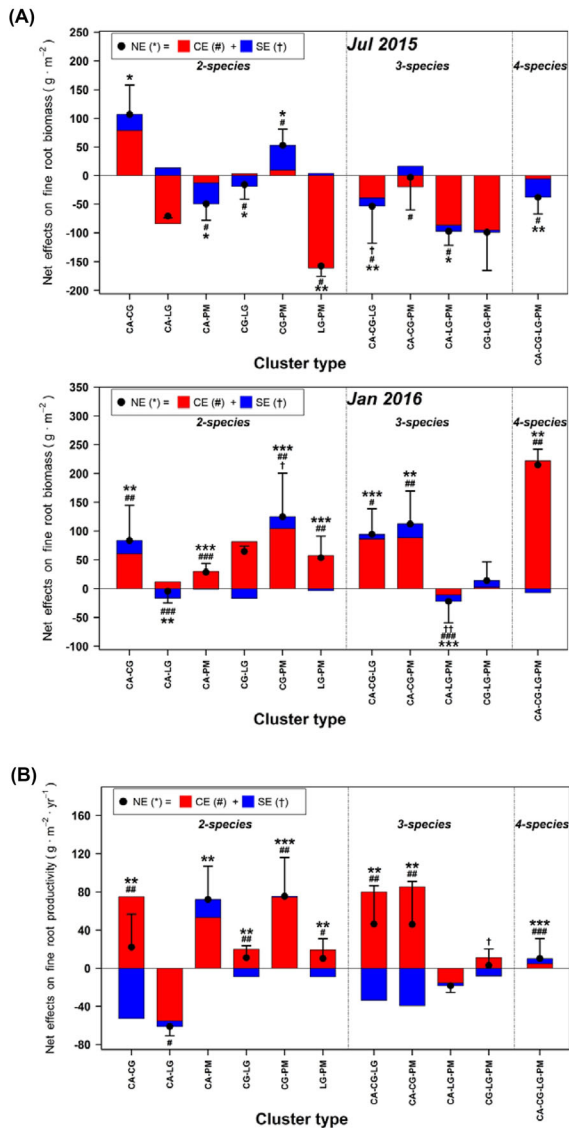


Figure 2. Biodiversity effects on fine root biomass **(A)** and productivity **(B)**. Net effects (NEs, filled circles) (mean \pm SE) and their two components: complementarity effects (CEs, red bars) and selection effects (SEs, blue bars). Combinations with significant NEs are annotated with *, whereas significant complementarity and selection effects are indicated using # and †, respectively ($p \leq 0.05$). CA—*Choerospondias axillaris*, CG—*Cyclobalanopsis glauca*, LG—*Lithocarpus glaber*, PM—*Pinus massoniana*. Significant relationships are indicated: * (#, †), $p \leq 0.05$; ** (##, ††), $p < 0.01$; *** (###, †††), $p < 0.001$.

interactive effects of SR \times C concentration \times P concentration on fine root biomass and SR \times C concentration \times N concentration on the productivity were significant ($p < 0.05$), respectively (Table 4).

DISCUSSION

Effects of Tree Species Diversity and Species Identity on Fine Root Production

This study investigated the diversity—belowground production relationship in a mature natural forest and distinguished the effects of species richness (SR) and species identity (defined as the presence or proportion of a given species in a plot). Our data showed that aboveground SR presented a positive linear relationship with fine root biomass and annual production. This result was in accord with the findings of a previous two-year study conducted a stand level four nearby large-scale (100 \times 100 m and 50 \times 50 m) plots with low to high species diversity gradients, where significant biodiversity effects on fine root biomass could be detected (Liu and others 2014). The positive effect of SR on fine root biomass and productivity has been observed in many studies, including studies addressing experimentally planted stands of uniform-aged trees (Lei and others 2012; Domisch and others 2015; Sun and others 2017) and mature forests (Schmid and Kazda 2002; Meinen and others 2009a, b; Brassard and others 2011, 2013; Ma and others 2019). The increase in fine root productivity with SR indicated in our study was in line with research results reported by Meinen and others (2009b) and Lei and others (2012), who also performed measurements using the ingrowth coring method and indicated that the ability to resist disturbance and regenerate was greater in species-rich forests. Our findings are in accord with a plantation diversity experiment carried out by Sun and others (2017) to detect a significant positive effect between SR and the ratio of fine root standing biomass to the basal area (defined here as adjusted fine root biomass and productivity), which revealed that biomass allocation shifts from above- to belowground with increase in SR (Sun and others 2017).

Globally, SR may not be the only factor influencing fine root production in forests. High variation in growth patterns and rooting strategies among symbiotic species can cause fine root overyielding (Jacob and others 2013). Our results are in accord with studies showing that species identity and interspecific interactions have important effects on fine root production (Cavard and others 2011; Brassard and others 2013). We found that different species respond differently to a given diversity level (Tables 1, 2). The species' relative belowground performance, which we expressed as the observed deviation from the expected fine root

Table 3. Summary of the Effects on Fine Root Biomass, Net Biodiversity Effects on Biomass (NE_b), Complementarity Effects on Biomass (CE_b), Selection Effects on Biomass (SE_b), Fine Root Productivity, Net Biodiversity Effects on Productivity (NE_p), Complementarity Effects on Productivity (CE_p) and Selection Effects on Productivity (SE_p) Determined Using Linear Mixed-Effect Models

	Fine root biomass (g m ⁻²)	NE _b (g m ⁻²)	CE _b (g m ⁻²)	SE _b (g m ⁻²)	Fine root productivity (g m ⁻² yr ⁻¹)	NE _p (g m ⁻² yr ⁻¹)	CE _p (g m ⁻² yr ⁻¹)	SE _p (g m ⁻² yr ⁻¹)
p-CA	F _{1,16} = 3.00	F _{1,16} = 0.51	F _{1,16} = 0.89	F _{1,16} = 0.52	F _{1,6} = 0.72	F _{1,6} = 0.17	F _{1,6} = 0.00	F _{1,6} = 0.60
p-CG	F _{1,16} = 36.05 ***	F _{1,16} = 15.02 **	F _{1,16} = 10.69 **	F _{1,16} = 2.68	F _{1,6} = 3.06	F _{1,6} = 2.06	F _{1,6} = 5.90 †	F _{1,6} = 3.08
p-LG	F _{1,16} = 3.72 †	F _{1,16} = 3.57 †	F _{1,16} = 0.98	F _{1,16} = 6.89 *	F _{1,6} = 4.98 †	F _{1,6} = 6.42 *	F _{1,6} = 6.63 *	F _{1,6} = 0.05
p-PM	F _{1,16} = 0.56	F _{1,16} = 0.06	F _{1,16} = 0.01	F _{1,16} = 0.24	F _{1,6} = 0.10	F _{1,6} = 0.64	F _{1,6} = 0.00	F _{1,6} = 1.67

Bold indicates significant effect.

The abbreviations p-CA, p-CG, p-LG and p-PM indicate the presence of the four tree species in the clusters. CA Choerospondias axillaris, CG Cyclobalanopsis glauca, LG Lithocarpus glaber, PM Pinus massoniana.

p ≤ 0.05; **p < 0.01; *p < 0.001; †0.05 < p < 0.1.*

biomass/basal area ratio in mixed plots compared to monospecific plots (rAP), showed an obvious overrepresentation of *C. glauca* fine root relative productivity in 2- and 3-species clusters (Figure S7B). In both the growing season and non-growing season, the proportions of *C. glauca* and *L. glaber* in the plots presented strong positive and negative relationships with fine root biomass, respectively (Figure 3). A previous study indicated that there were negative interactions between *C. glauca* and *L. glaber* that resulted in different mixture effects on fine root biomass in different species combinations (Xiang and others 2015). Our results further demonstrated that *C. glauca* presents an advantage in competition between these two evergreen broad-leaved species belonging to the same family. Interestingly, the presence of another deciduous (*C. axillaris*) and coniferous (*P. massoniana*) species exerted no influence on fine root production or biodiversity effects (Table 3). This observation implies that the difference in fine root production between different tree species combinations is the result of the interaction and coordination between diversity and species identity. To date, only a handful of studies comparing relatively few tree species have compared fine root production between tree species of different leaf phenologies growing in similar conditions, and their conclusions have varied. Finér and others (2017) investigated the effects of tree species diversity, evergreen species proportions, stand basal area and soil properties on fine root biomass across several major European forest types and found that fine root biomass in the soil organic layer is positively associated with the proportion of evergreen species. A recent paper by Archambault and others (2019) indicated a distinct positive effect of the proportion of evergreen species on root productivity, which

played a more important role than the biodiversity effect.

Soil nutrients, probably together with SR, were important factors to influence fine root biomass (Table 4). High SR has positive impact on soil biota diversity through which to increase the availability of soil nutrients, especially when the soil conditions are limiting (Spehn and others 2000; Stephan and others 2000). In diverse forests, soil nutrients, N foraging and niche complementarity were main ecological forces regulating fine root production (Loiola and others 2015). A recent study in the same forests showed that tree species richness had significant positive effects on soil organic carbon accumulation and availability of soil P, confirming that soil nutrients influenced fine root production (Wu and others 2019).

Partitioning of Biodiversity Effects on Fine Root Production

Recent studies that have aimed to provide a comprehensive generalization of positive net biodiversity effects (NE) showed that complementarity effects (CEs) and selection effects (SEs) explain 50% of the biodiversity–productivity relationship (Cardinale and others 2011). In some stands, in the early stages of forest development, SEs dominate NEs on forest production (Tobner and others 2016). However, with the development of the community, CEs become the principal mechanism (Montès and others 2008; Marquard and others 2009), and their dominance increases with time (Allan and others 2011; Reich and others 2012). This pattern that has frequently been shown for aboveground biomass in biodiversity experiments (for example, Cardinale and others 2007; Marquard and others 2009) has rarely been shown for belowground biomass in a field biodiversity experiment (Oram and others

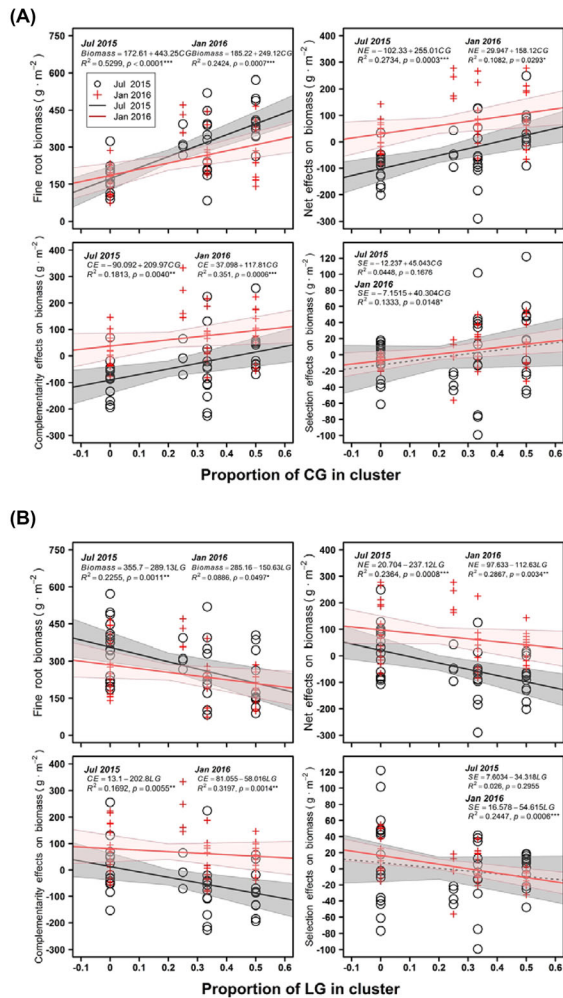


Figure 3. The relationships of the proportion of CG **(A)** and LG **(B)** in the mixed clusters with fine root biomass and biodiversity effects. A significant relationship is shown with a straight line at $p \leq 0.05$ (*), $p < 0.01$ (**), and $p < 0.001$ (***). Gray and red shading indicate the 95% credible intervals. A nonsignificant relationship is shown with a dotted line.

2018). Our study partitioned the mechanisms underlying biodiversity effects on fine root production in natural forests. Similar to most of the previous literature, we found that the CE presented the dominant effect and that the positive NE on fine root biomass was generally driven by CE (Oram and others 2018). In other words, fine root overyielding in mixed forests mainly benefits from interspecies mutual promotion niche complementarity.

In plant communities, resource allocation occurs in both temporal (for example, phenology of nutrient absorption) and spatial (for example, rooting depth divergence) dimensions. Normally, greater phenological complementarity among the

species in the community (for example, if early- and late-season species are present) may correspond to stronger ecosystem functioning (Barry and others 2019) and is likely to be responsible for the overyielding of diverse forests (Fargione and Tilman 2002, 2005). We observed that most of the complementary effects on fine root biomass were positive in the nongrowing season (Figure 2A), which suggested that species occupy different, nonoverlapping niches and/or facilitate another in the mixture. The interspecies competition for water and nutrient resources is usually more intense during the growing season. In contrast, the complementarity profit is more obvious in the nongrowing season (Mueller and others 2013). In forests with higher species diversity, as a strategy for responding to the interannual variation in nutrient supplies and climate, differences in belowground phenological rhythms among tree species can contribute to higher nutrient use efficiency and greater interannual flexibility of fine root production (Radvile and others 2016). We found that the vertical heterogeneity index (VHI) of fine root biomass was significantly negatively correlated with SR, indicating that the soil volume was more completely occupied in more diverse clusters at local neighborhood (Figure S5) (Brassard and others 2011, 2013). In the most diverse cluster, the higher proportion of fine root biomass in deeper soil layers in January than in July appears to suggest that the soil space was more completely utilized in January (Figure S3). Rooting space per se can be considered a soil resource (McConaughay and Bazzaz 1991). These phenomena verify that fine root foraging behaviors in species-rich clusters can be coordinated both spatially and temporally. This is one of the fundamental elements maintaining diversity and high productivity in natural forests (Brassard and others 2013).

In our 2-species mixed clusters, four species combinations showed significant differences in mean rooting depth between their component species; accordingly, overyielding was observed for all constituent species in these combinations (Figure S6A, S7A). This confirms that the belowground complementarity effect and overyielding are associated with the spatial separation of rooting patterns among component members at local neighborhood. Indeed, interspecific interactions can drive plants to change their root distribution in mixtures in response to neighboring species. For instance, *L. glaber* tends to occupy deeper soil spaces when grown with *P. massoniana*, while the roots of *C. glauca* can reach deeper soil layers when grown with *P. massoniana* or *L. glaber* (Figure S6A).

Table 4. Effects of Species Richness (SR), Main Soil Nutrients Parameter (C, N and P) and Their Interactions on the Fine Root Biomass ($n = 120$) and Fine Root Productivity ($n = 60$) (0–30 cm Profile)

Source	DF	Fine root biomass (g m^{-2})			Fine root productivity ($\text{g m}^{-2} \text{yr}^{-1}$)		
		Sum Sq	F value	p value	Sum Sq	F value	p value
SR	1	46,456	3.76	0.055 [†]	1937	0.64	0.427
C	1	117,747	9.52	0.003 **	4734	1.57	0.216
N	1	52,970	4.28	0.041 *	16,105	5.36	0.025 *
P	1	80,085	6.48	0.012 *	710	0.24	0.629
SR : C	1	14,145	1.14	0.287	127	0.04	0.838
SR : N	1	9594	0.78	0.380	6	0.00	0.964
SR : P	1	1293	0.11	0.747	617	0.21	0.653
C: N	1	5986	0.48	0.488	1544	0.51	0.478
C: P	1	180	0.02	0.904	5624	1.87	0.178
N: P	1	6989	0.57	0.454	3762	1.25	0.270
SR: C: N	1	1178	0.10	0.758	19,703	6.55	0.014 *
SR: C: P	1	56,385	4.56	0.035 *	1991	0.66	0.420
SR: N: P	1	19	0.00	0.968	2508	0.83	0.367
C: N: P	1	273	0.02	0.882	311	0.10	0.749
SR: C: N: P	1	8290	0.67	0.415	182	0.06	0.807
		$R^2 = 0.24$	$p = 0.012$ **		$R^2 = 0.31$	$p = 0.228$	

Bold indicates significant effect.

DF represents the degrees of freedom, and Sum Sq represents the sum of squares. Variance explained by R^2 of entire model. * $p \leq 0.05$; ** $p < 0.01$; *** $p < 0.001$; [†]0.05 < $p < 0.1$.

Moreover, we found that the presence of *C. glauca* explained most of the variance in the NE and CE on fine root biomass in the mixtures (Table 3). In the two sampling seasons, the proportion of *C. glauca* in the plots presented a strong positive relationship with the NE and CE on fine root biomass, while opposite tendencies were observed for *L. glaber* (Figure 3). These results suggest that *C. glauca* may undergo changes in its fine root functional traits (for example, morphology and rooting depth) to improve its competitive ability to obtain more soil resources. Accompanied by the expansion of the resource niche owing to exploration by *C. glauca*, complementarity effects in the communities are promoted.

We noticed that the proportions of two evergreen broad-leaved species had a significant impact on the SE in the nongrowing season (Figure 3). The likely explanation for this finding might be that evergreen trees typically invest more in leaf construction than deciduous trees during this time, causing the functional traits of fine roots to implement a more acquisitive resource strategy and thereby dominate the SE. In this study, we found that the SEs on fine root productivity in most clusters were negative (Figure 2B). Several experiments have indicated that positive biodiversity effects only become apparent after the second

growing season (for example, Tilman and others 2001; Fargione and others 2007; Marquard and others 2009). An SE appears to be an indicator of inherent species differences rather than their strength (Turnbull and others 2013). The growth core approach can detect the regeneration of fine roots after disturbance (Meinen and others 2009b). When environmental stability is disturbed, species require resources for regeneration, which leads to interspecific competition coupled with weak or negative SEs. This phenomenon is particularly evident in species-rich forests.

CONCLUSIONS

Our study revealed positive effects of aboveground species richness (SR) on fine root production in a natural subtropical forest. The most statistically significant net biodiversity effects (NEs) on fine root production were mainly driven by complementarity effects (CEs). In the nongrowing season, in most cases, the CEs on fine root biomass were positive and became stronger when richness increased, but the opposite situation was observed in the growing season. The fine root production and effects of biodiversity on production were strongly influenced by the identity of the tree species; for example, the presence and proportion of *C. glauca*

in the tree clusters significantly promoted the fine root biomass and had obviously positive effects on NEs and CEs. Our study showed that the mechanism of the CE on fine roots in mixtures is multifaceted, involving phenomena such as temporal niche partitioning to avoid interspecies competition for soil nutrient resources and spatial root system segregation among co-occurring species. There are limitations to the current study. For example, soil microbial and pathogen diversity were not measured but may influence the competition between individual trees (Hantsch and others 2014). In addition, soil fertility factors should be considered to better understand the role of biotic interactions with tree roots. Further research will be needed because this investigation is only a starting point for interpreting the patterns of fine root production in subtropical mixed forests.

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Compliance with Ethical Standards

Conflict of interest All authors declare that they have no conflict of interest.

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