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ARTICLE

Effects of tree functional diversity and environmental gradients on belowground biomass in a natural old-growth forest ecosystem

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Abstract: The positive effects of biodiversity on aboveground biomass in natural terrestrial ecosystems have been well documented, whereas the relationships between tree biodiversity and belowground biomass remain largely unexplored. Traditionally, two sets of hypotheses based on the functional trait approach, niche complementarity (NC) and mass ratio (MR), have been proposed to explain the positive effects of biodiversity. Whereas NC emphasizes that functional discrepancy enhances the collective functioning of a given ecosystem, MR states that ecosystem functioning is mainly regulated by the functional traits of dominant species. This study explored the relative importance of these two hypotheses and the effects of forest stand and environmental characteristics on belowground biomass in an old-growth broad-leaved evergreen forest. The mean coarse-root biomass, fine-root biomass, and fine-root necromass were 117.78 ± 54.000, 4.09 ± 0.85, and 0.60 ± 0.31 $\mathrm{Mg \cdot ha^{-1}}$, respectively. We found positive effects of functional diversity on belowground biomass; however, the community-weighted mean trait values were more relevant, indicating that MR exhibited more explanatory power than NC. The combination of informative environmental factors explained 62.0%, 53.2%, and 37.8% of the variation of coarse-root biomass, fine-root biomass, and fine-root necromass, respectively. Our results suggest that the functional identity of dominant tree species exerts more influence than functional diversity on the belowground biomass in old-growth forest ecosystems and that forest stand characteristics and topographic and edaphic factors also play important roles in shaping belowground biomass patterns in old-growth forest ecosystems.

Key words: coarse-root biomass, fine-root biomass, fine-root necromass, niche complementarity hypothesis, mass ratio hypothesis, environmental gradients.

Résumé : Les effets bénéfiques de la biodiversité sur la biomasse aérienne dans les écosystèmes terrestres naturels ont été bien documentés. Par contre, les relations entre la biodiversité arbustive et la biomasse souterraine sont encore largement inexplorées. Deux hypothèses fondées sur l'approche des caractères fonctionnels : la complémentarité de niche (CN) et le rapport de masses (RM), ont traditionnellement été proposées pour expliquer les effets bénéfiques de la biodiversité. Tandis que la CN soutient que la divergence fonctionnelle améliore le fonctionnement collectif d'un écosystème donné, le RM indique que le fonctionnement des écosystèmes est régulé principalement par les caractères fonctionnels des espèces dominantes. Cette étude explore l'importance relative de ces deux hypothèses ainsi que les effets des caractéristiques des peuplements forestiers et de l'environnement sur la biomasse souterraine dans une vieille forêt feuillue sempervirente. La biomasse des grosses racines, celle des racines fines et la nécromasse atteignaient en moyenne respectivement 117,78 ± 54,00, 4,09 ± 0,85 et 0,60 ± 0,31 $\mathrm{Mg \cdot ha^{-1}}$. Nous avons trouvé des effets bénéfiques de la diversité fonctionnelle sur la biomasse souterraine. Cependant, les valeurs moyennes pondérées des caractères de la communauté étaient plus pertinentes, indiquant que le RM démontre une plus grande capacité d'explication que la CN. La combinaison de facteurs environnementaux informatifs expliquait respectivement 62,0, 53,2 et 37,8 % de la variation de la biomasse des grosses racines, de celle des racines fines et de la nécromasse. Nos résultats indiquent que l'identité fonctionnelle de l'espèce arborescente dominante plutôt que la diversité fonctionnelle exerce plus d'influence sur la biomasse souterraine dans les écosystèmes de forêt ancienne et que les caractéristiques des peuplements forestiers ainsi que les facteurs topographiques et édaphiques jouent également un rôle important dans la définition des patrons de biomasse souterraine dans les écosystèmes de forêt ancienne. [Traduit par la Rédaction]

Mots-clés : biomasse des grosses racines, biomasse des racines fines, nécromasse des racines fines, hypothèse de la complémentarité de niche, hypothèse du rapport de masse, gradients environnementaux.

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Introduction

Over the past two decades, one of the most important developments in the field of plant ecosystem ecology is the recognition that biodiversity and ecosystem services are intimately linked (Hooper et al. 2005). Both experimental studies and observations of natural ecosystems have shown the positive effects of biodiversity on ecosystem functioning (Liang et al. 2016). Particularly, more diverse assemblages lead to enhanced community productivity, stability, invasibility resistance, and nutrient cycling (Bruelheide et al. 2014), and biodiversity has been identified as a major determinant of ecosystem processes and dynamics (Tilman et al. 2014). As one of the most important terrestrial ecosystems, forests sustain high levels of species diversity and provide crucial ecosystem services to human beings (Nadrowski et al. 2010), but there is less evidence of biodiversity effects on ecosystem functioning in forest ecosystems than in other ecosystems (e.g., aquatic and grassland ecosystems) (Cardinale et al. 2011). Moreover, in comparison with the well-documented relationships between biodiversity and aboveground biomass, belowground biomass has often been ignored in studies on biodiversity and ecosystem functioning (hereafter referred to as BEF) (Brassard et al. 2009; Cardinale et al. 2011; Domisch et al. 2015). Among available cases, the study of biodiversity effects on belowground biomass is usually limited to a comparison of the fine-root biomass of monocultures with that of two-species mixtures (Meinen et al. 2009; Jacob et al. 2013), and the results have been contentious: some of these studies confirmed "belowground overyielding" (Brassard et al. 2013; Ma and Chen, 2016), whereas others found no consistent effects of plant diversity on fine-root biomass (Gastine et al. 2003; Meinen et al. 2009; Jacob et al. 2013).

Traditionally, two sets of hypotheses based on the functional trait approach prevail in addressing the mechanisms of positive BEF relationships: the niche complementarity (NC) hypothesis and the mass ratio (MR) hypothesis. The NC hypothesis emphasizes that functional discrepancy represents a greater variety of resource uptake strategies among species and thus enhances the collective functioning of a given ecosystem (Finegan et al. 2015). In contrast, the MR hypothesis proposes that ecosystem functioning is mainly regulated by the functional traits of dominant species (Grime 1998), which can be measured by community-weighted mean trait values (Ruiz-Benito et al. 2014). Regarding relationships between biodiversity and belowground biomass, the high fine-root biomass of mixed forests compared with that of forests dominated by a single species was ascribed to belowground niche segregation and complementary soil exploration by coexisting tree species (Brassard et al. 2011*a*; Jacob et al. 2013). A system with high species diversity may generate an effective utilization of soil resources and reduce exploitative competition among individual trees, thus facilitating root growth (Brassard et al. 2013; Domisch et al. 2015). Despite the fact that most BEF studies use species richness as a proxy for biodiversity, it has been reported that functional diversity performs better in predicting aboveground biomass (Roscher et al. 2012; Ruiz-Benito et al. 2014) and functional identity of tree species exerts greater influence than species richness on belowground biomass (Domisch et al. 2015). Therefore, functional diversity should be included in the studies that explore biodiversity effects on belowground biomass.

Plant roots are highly dynamic systems and respond sensitively to environmental variability (de Kroon et al. 2012). At the local level, forest stand characteristics and environmental factors largely determine fine-root patterns and biomass (Yuan and Chen 2010; Finér et al. 2011*a*). Forest stands dominated by pioneer trees have deep root systems with fine roots aggregated around respective stems, whereas those dominated by late-successional species are characterized by shallow root systems with regularly distributed fine roots (Brassard et al. 2009; Yuan and Chen 2010). Furthermore, in previous studies, fine-root biomass changed with stand development and generally increased up to a certain time and declined thereafter (Yuan and Chen 2010), peaking in adult stands but not in mature stands (Claus and George 2005). Meanwhile, other forest stand characteristics, including life-form, basal area, and stem density, are also widely used to explain the variation in fine-root biomass (Finér et al. 2011*b*). With respect to environmental factors, fine-root biomass of broad-leaved forests increases with higher elevation and lower temperature (Leuschner and Hertel 2003). The physical conditions of soil constrain the movement of roots, and the chemical properties of soil determine vertical and horizontal rooting characteristics (Brassard et al. 2009). Soil nutritional and moisture statuses regulate fine-root biomass by controlling fine-root growth and mortality (Leuschner and Hertel 2003; Finér et al. 2011*a*). Furthermore, abiotic factors may simultaneously affect biodiversity and productivity in natural ecosystems (Ma et al. 2010). For example, the patterns between biodiversity and ecosystem functioning may partly depend on soil conditions such as fertility and water availability because of the effects of soil conditions on species coexistence and root production (de Kroon et al. 2012). Overall, particular emphasis should be placed on environmental factors given their enormous influence on fine-root biomass, production, and turnover rate (Yuan and Chen 2010).

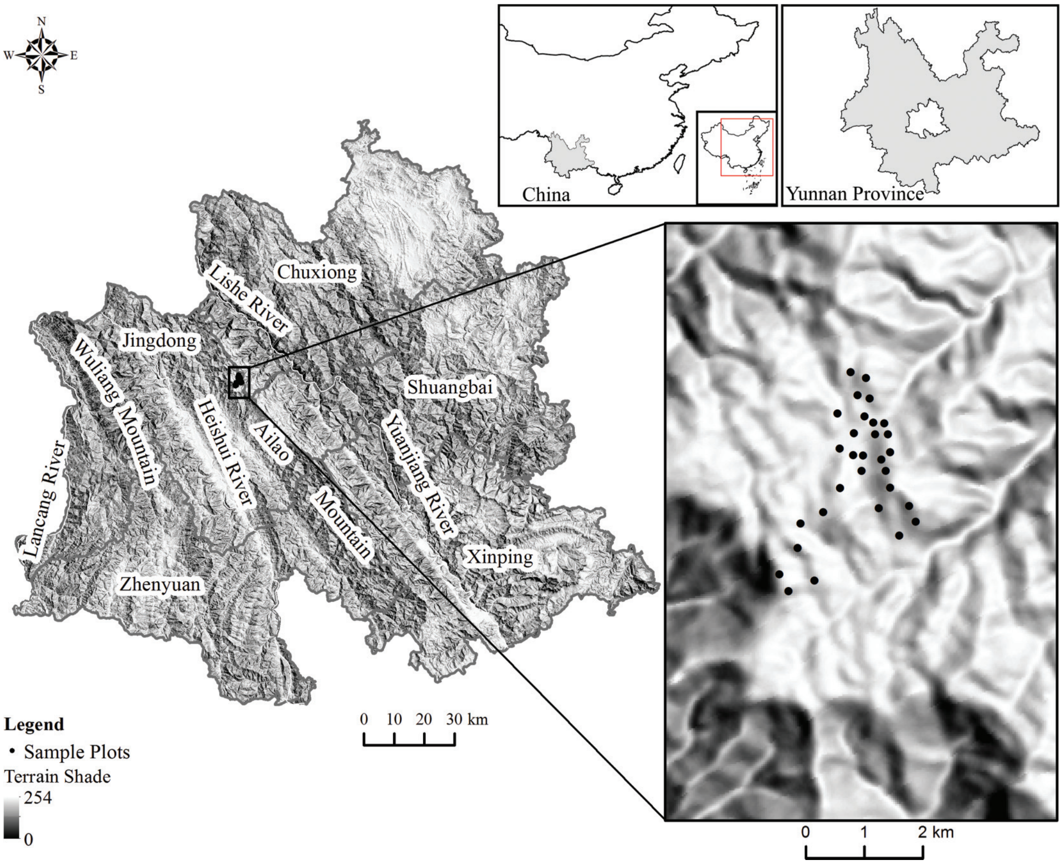
Understanding the underlying mechanism of biodiversity effects on belowground biomass is essential to the preservation of biodiversity and the maintenance of ecosystem services. Leaf traits and wood density are closely linked to carbon and nutrient investment strategies of tree species (Poorter and Bongers 2006), thus are widely used in BEF studies (Pla et al. 2012; Conti and Díaz 2013; Finegan et al. 2015). Through analysis of relevant functional traits, topographic and edaphic variables, coarse-root biomass, fine-root biomass, and fine-root necromass in an old-growth broad-leaved evergreen forest, this study explores the relative predominance of the NC and MR hypotheses in regulating belowground biomass, as well as the predictive power of environmental variables. We specifically hypothesize that (*i*) MR may be more important in explaining the variation in belowground biomass, owing to the fact that this old-growth evergreen forest is probably dominated by late-successional species, the fine roots of which may be homogeneously distributed in the surface of the soil profile and (*ii*) the most informative predictive variables for coarse-root biomass and fine-root biomass may differ because coarse-root biomass increases with the forest stand development until maturity, whereas fine-root biomass largely depends on local environmental conditions.

Materials and methods

Study site

This study was conducted in the Ailao Mountains National Nature Reserve in Jingdong County, Pu'er City, Yunnan Province, P.R. China (24°32′N, 101°01′E; Fig. 1), which aims to conserve the largest midmountain moist evergreen forests in the world. The annual mean air temperature of the region is 11.3 °C, with a mean temperature of 5.4 °C in January and 16.4 °C in July. The annual mean precipitation is approximately 1900 mm, about 85% of which occurs during the rainy season from May to October. The annual mean evaporation and relative humidity are 1485 mm and 85%, respectively. The forest ecosystem is very unique and well protected, with a stand age over 300 years (Tan et al. 2011). The forest communities are dominated by *Lithocarpus xylocarpus* (Kurz) Markgr., *Castanopsis wattii* (King ex Hook.f.) A.Camus, *Schima noronhae* Reinw., *Stewartia pteropetiolata* W.C. Cheng, *Machilus bombycina* King ex Hook. f., and *Manglietia insignis* (Wall.) Blume as canopy species and *Vaccinium duclouxii* (H. Lév.) Hand.-Mazz., *Camellia forrestii* (Diels) Cohen-Stuart, and *Symplocos ramosissima* Wall. ex G. Don as shrub species (Comprehensive Investigation Group of the Ailao Mountain National Nature Reserve 1988).

Fig. 1. Location of the study area in the Ailao Mountains National Nature Reserve in P.R. China. Terrain shade (elevation) is measured in metres. [Color online.]



Field survey

Thirty 20 m × 20 m plots were randomly set with an electronic total station (NTS-310B/R; South Surveying & Mapping Technology Co., Ltd., Guangzhou, P.R. China), and the mean distance between each plot was >200 m. All woody plants with height > 1.3 m were identified to species level and had their diameter at breast height (DBH; breast height = 1.30 m) measured. In preparation for estimation of coarse-root biomass, we selected almost 500 sample trees from 22 species and measured their DBH and height to establish allometric regression equations. We also determined the relative elevation of the corners and centers of all plots to estimate topographic features such as elevation, convexity, aspect, and slope. Seedlings and herbs were rare in the plots because of regeneration difficulties imposed by a mature closed canopy and thus were not included in our analyses. Each plot was divided into four equal quadrats, and a soil core (10 cm in diameter and 20 cm in length) was taken from the center of each quadrat, where soil samples were also collected at depths of 0~20 cm. Leaf samples were collected from sunlit tree crowns, with three to five adult individuals sampled for each species, and then stored in a cooler for the determination of leaf functional traits in the laboratory (Jin et al. 2014). Wood cores were collected from five individuals for each species using an increment borer, with which the wood density for each species was measured in the laboratory (Wright et al. 2010).

Belowground biomass estimation

We used the conventional definitions of coarse roots as roots > 2 mm in diameter and fine roots as roots ≤ 2 mm in diameter (Leuschner and Hertel 2003). Coarse-root biomass of each plot was estimated using a series of allometric equations. Allometry, which relates easily measured variables (e.g., DBH and height) to other structural and functional characteristics, can be a reliable method for estimating biomass in forest ecosystems (Wang 2006). Although tree root systems are a major part of forest biomass, coarse-root equations are relatively rare, probably because the investigation of tree roots is laborious and time-consuming (Brassard et al. 2011*b*). Species-specific equations and DBH–height combined equations can enhance the accuracy of root-biomass estimation and are therefore useful for the calculation of global stand biomass (Wang 2006; Ouimet et al. 2008).

Twenty-two species-specific allometric equations relating height and DBH were established based on the data of sample trees (most coefficients of determination (R^2) > 0.8), most of which were for dominant species of both trees and shrubs. A general allometric equation was created for the remainder of the species based on an inventory data of a 6 ha permanent forest dynamics plot that included more than 12 000 individual trees. All equations were in the following form:

$$H = a + b \times D - c \times 2D^2$$

where H and D represent tree height and DBH, respectively; and a, b, and c are constants (see Supplementary file cjfr-2019-0254supplb[1]). All tree heights in this study were estimated by using these equations.

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[1] Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfr-2019-0254.

Table 1. Variable importance in projection (VIP) values of selected variables.

Type of biomass	FEve	FDis	FDiv	LN	LP	LK	LC	WD	BA	DEN
CR	—	0.87	0.93	—	1.02	—	—	1.14	1.45	0.73
FB	0.76	—	0.94	—	1.38	—	—	0.95	1.15	1.32
FN	—	—	0.75	0.72	0.75	1.65	1.35	0.82	—	—

Note: A missing value indicates that the variable was not included in the optimal model. Refer to Fig. 2 for partial least squares correlation circles of belowground biomass and selected predictors. CR, coarse-root biomass; FB, fine-root biomass; FN, fine-root necromass; FEve, functional evenness; FDis, functional dispersion; FDiv, functional divergence; LN, leaf nitrogen concentration; LP, leaf phosphorus concentration; LK, leaf potassium concentration; LC, leaf carbon concentration; WD, wood density; BA, stand basal area; DEN, stem density.

The allometric equations for biomass estimation of trunks, branches, leaves, and roots for five canopy species were constructed during the 1980s (when large field crews were available to excavate and measure tree roots) as follows: a series of sample trees with DBH ranging from 5 to 105 cm were selected for each species; for every DBH class (10 cm), one sample tree was cut at the soil surface; and the aboveground parts of sample trees were divided into trunks, branches, leaves, and flowers. For the whole root system, the taproots of sample trees were extracted by an excavator, and the lateral roots were harvested by manual digging. The ovendry mass of each part was measured and fitted to the DBHs and heights of the sample trees, and then the equations relating each part to the tree's DBH and height were generated (Qiu et al. 1984). Liu et al. (2002) used these equations to estimate aboveground and belowground biomass. We validated the equations by examining the original data and derivative procedures and then used them to calculate the coarse-root biomass of five canopy species. Some trees were cut down during a road construction project in this nature reserve, which provided a chance to establish general equations for biomass estimation of trunks, branches, leaves, roots, and flowers by selecting and measuring 35 sample trees from 14 species with a DBH range of 5–100 cm (see Supplementary file cjfr-2019-0254supplc[1]). The allometric equations we used to calculate coarse-root biomass in this study were as follows:

$$\mathrm{bio}(\mathit{Lithocarpus\ xylocarpus}) = 0.02431 \times (D^2 \times H)^{0.9512} \quad R^2 = 0.997$$

$$\mathrm{bio}(\mathit{Castanopsis\ wattii}) = 0.009105 \times (D^2 \times H)^{0.9339} \quad R^2 = 0.997$$

$$\mathrm{bio}(\mathit{Machilus\ bombycina}) = 0.04637 \times (D^2 \times H)^{0.9145} \quad R^2 = 0.992$$

$$\mathrm{bio}(\mathit{Schima\ noronhae}) = 0.5146 \times (D^2 \times H)^{0.3539} \quad R^2 = 0.944$$

$$\mathrm{bio}(\mathit{Manglietia\ insignis}) = 0.03460 \times (D^2 \times H)^{0.7911} \quad R^2 = 0.978$$

$$\mathrm{bio}(\text{other species}) = 0.02380 \times (D^2 \times H)^{0.8571} \quad R^2 = 0.950$$

where bio represents coarse-root biomass.

All soil cores were stored with ice packs in a cooler during transport and before processing. In the laboratory, fine roots were washed, picked out from soil cores, and separated into living and dead roots based on their colors, textures, and elasticity and whether they floated or sank in water. We found only a small fraction of herb roots (unlignified) in one or two soil cores, and they were thus excluded from woody roots. Then, the fine-root samples were dried to constant mass at 70 °C and weighed (Ostonen et al. 2005).

Explanatory variables

Elevation was determined as the mean value of the elevations at each of the four corners of the plot. Convexity was defined as the elevation of the plot center minus the mean elevations of the four corners. Slope was determined as the mean angle between the plane formed by any three corners and the horizontal plane, and slope aspect was determined as the angle between the projection of the slope normal line in the horizontal plane and due north (Lai et al. 2009). Ten soil variables were determined using the following methods: oven-drying method for soil water content (SW), Walkley–Black analysis for soil organic matter (SOM), potentiometry for pH, Kjeldahl method for total nitrogen concentration (TN), Mo-Sb colorimetry for total phosphorus concentration (TP), flame photometry for total potassium concentration (TK), diffusion method for available nitrogen concentration (AN), Bray I for available phosphorus concentration (AP), ammonium acetate method for available potassium concentration (AK), and azomethine-H method for available boron concentration (AB) (Bao 2005). Functional traits were determined as follows: wood density (WD) was measured as ovendry mass of each wood core divided by its fresh volume; specific leaf area (SLA) was determined as one-side area of a fresh leaf divided by its ovendry mass; and the Kjeldahl method, Mo-Sb colorimetry, flame photometry, and potassium dichromate method were applied to determine leaf nitrogen (LN), phosphorus (LP), potassium (LK) and carbon (LC) concentrations, respectively (Cornelissen et al. 2003). We used these six functional traits to establish multitrait functional indices, which showed higher correlations with niche differences than single-trait indices did (Kraft et al. 2015). We also calculated community-weighted means (CWMs) of these six traits by applying the R function "dbFD" of the FD package (R Core Team 2019). Specially, functional richness (FRic) represents the trait space filled by the community, functional evenness (FEve) measures the regularity of abundance distribution in filled niche space, functional divergence (FDiv) quantifies the distribution of abundances in trait space relative to an abundance-weighted centroid, and functional dispersion (FDis) simultaneously describes the volume of trait space occupied by a community and the spread of species within that space (Laliberté and Legendre 2010; Laliberté et al. 2014). CWMs were calculated as the mean trait value weighted by species-relative abundance in a given plot. Stand basal area (BA) was estimated by summing the stem area of each tree at breast height, and stand density (DEN) was determined by dividing the stem count by the plot area.

Data analysis

Coarse-root biomass for each plot was determined by summing the coarse-root biomass of all individual trees estimated by either a species-specific allometric equation or the general one. Fine-root biomass and necromass for each plot were calculated by averaging the dry mass of live and dead fine roots, respectively, from four quadrats and then each converted into an area of 1 ha. All data, including both response variables and predictive variables, were standardized (scaled values to mean of 0, then divided by standard deviations) in analysis using the R function "decostand" of the vegan package (R Core Team 2019). In addition, we calculated the variance inflation factor for each predictive variable by applying the R function "vif" of the car package (R Core Team 2019) and then excluded the candidate predictors that had a variance inflation factor > 2. Therefore, the collinearity among variables was largely reduced, given that this study included multiple predictive variables but limited samples.

We applied partial least squares (PLS) regression to explore correlations among functional diversity indices, other biological factors (i.e., BA and DEN), and belowground biomass. First, we combined all biological factors together as an explanatory matrix and then fitted them to coarse-root biomass, fine-root biomass, and fine-root necromass as response variables. Second, the R function "shaving" (R Core Team 2019) was performed to detect the most informative variables and improve prediction performance. Third, a parsimonious model was constructed based on the results of "shaving", and the variable importance in projection (VIP) for the remaining predictors was calculated to assess their performance in terms of their explanatory power to response variables.

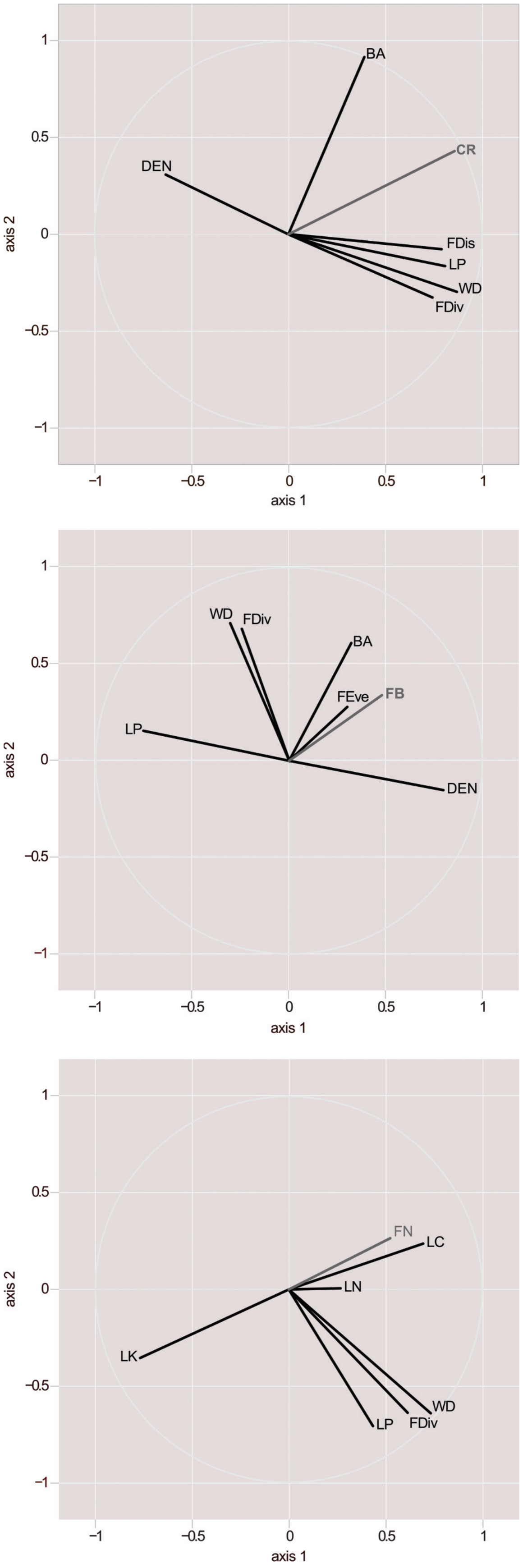


Fig. 2. Partial least squares (PLS) correlation circles of belowground biomass (top, coarse-root biomass (CR); middle, fine-root biomass (FB); bottom, fine-root necromass (FN)) and selected predictors. The length of a black line indicates the relative importance of the variable. A smaller angle between black lines indicates a higher degree of positive correlation between the variables. FDis, functional dispersion; FDiv, functional divergence; FEve, functional evenness; LC, leaf carbon concentration; LK, leaf potassium concentration; LN, leaf nitrogen concentration; LP, leaf phosphorus concentration; BA, stand basal area; DEN, stem density; WD, wood density. [Color online.]

Predictors with VIP > 1 were considered major contributors to the model, predictors with VIP between 1 and 0.8 were considered moderate contributors, and predictors with VIP < 0.8 were considered noncontributors (Frameschi et al. 2013). All of these statistics were conducted in R packages plsVarSel and plsdepot (R Core Team 2019).

Generalized additive models (GAMs) were used to examine the complex relationships among coarse-root biomass, fine-root biomass, fine-root necromass, and multiple environmental factors. To explore the most important predictors to each model, we applied the R function "dredge" to generate a set of models with combinations of different predictors, then applied the function "importance" to rank all the predictors in descending order based on their importance values (R Core Team 2019). Only the top three predictors were included in fitting new GAMs. Finally, the amount of variance explained by the models and the significance of included predictors were examined. Predictor selection and model fitting were conducted in R packages MuMIn and mgcv, respectively (R Core Team 2019).

Results

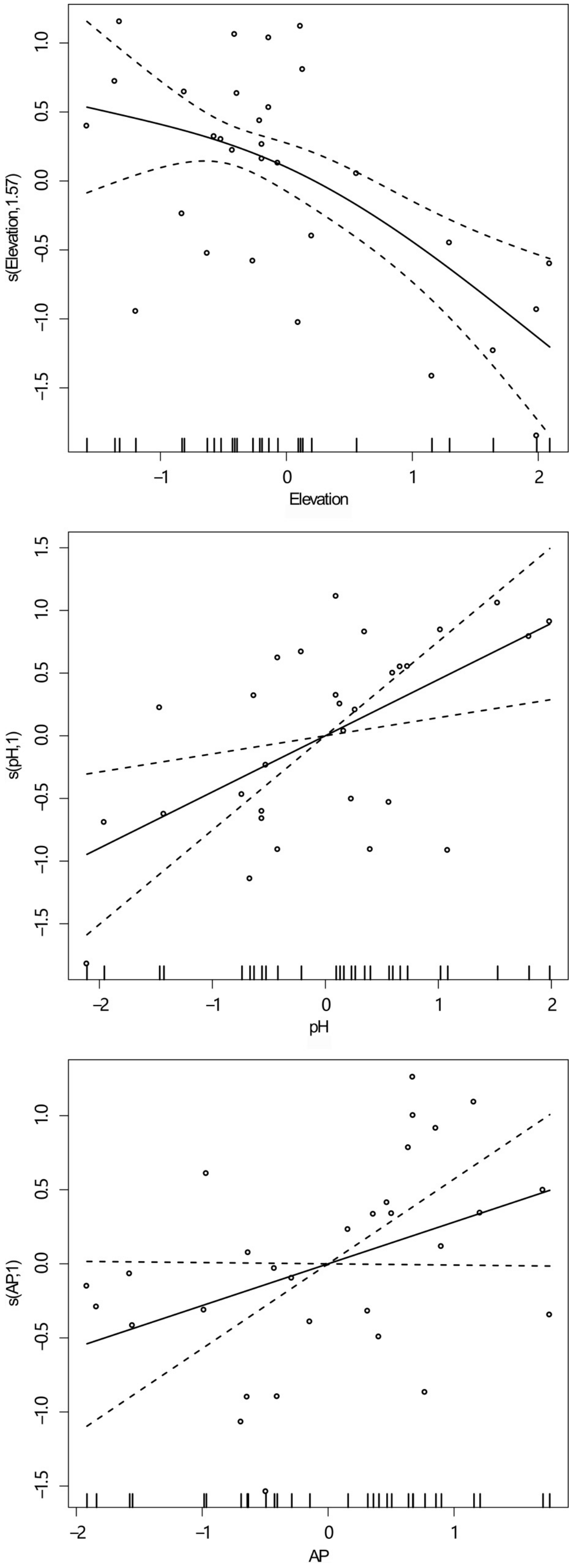
In total, 55 tree and shrub species from 16 families were recorded in 30 plots. Species richness of these plots ranged from 4 to 26 species, with a mean value of 13 species, which represented an ideal species-richness gradient. Stem count of these plots ranged from 30 to 256 stems, with a mean value of 102 stems. DBH ranged from 1 to 67 cm, with a mean of 11 cm. The mean values of coarse-root biomass, fine-root biomass, and fine-root necromass were 117.78 ± 54.00, 4.09 ± 0.85, and 0.60 ± 0.31 $\mathrm{Mg{\cdot}ha^{-1}}$, respectively.

Based on the results of variable selection, FEve, FDis, FDiv, and CWMs of LN, LP, LK, LC, WD, BA, and DEN were all identified as the most informative predictors of belowground biomass and were included to construct the optimal models. For coarse-root biomass, LP, WD, and BA were the most informative predictors; FDis and FDiv were moderate predictors; and DEN was a nonsignificant predictor. For fine-root biomass, LP, BA, and DEN were the most important predictors; FDiv and WD were moderate predictors; and FEve had little influence. For fine-root necromass, LK and LC were the most important predictors; WD was an inferior predictor; and the other variables, including FDiv, LN, and LP, were nonsignificant predictors (Table 1).

PLS correlation circles in Fig. 2 display correlations among belowground biomass and the previously mentioned predictors. FDis, FDiv, LP, WD, and BA were positively correlated with coarse-root biomass, whereas DEN was negatively correlated with it. FDiv, FEve, WD, BA, and DEN were positively correlated with fine-root biomass, whereas LP was negatively correlated with it. FDiv, LN, LC, and WD were positively correlated with fine-root necromass, whereas LP and LK were negatively correlated with it.

In terms of variable selection, elevation, pH, and AP were selected to generate a GAM, which explained 62.0% of the variation of coarse-root biomass. Coarse-root biomass declined nonlinearly with elevation ($F = 9.25$, $p = 0.004$) and increased monotonically with increasing pH ($F = 8.71$, $p = 0.007$). AP showed marginally significant positive effects on coarse-root biomass ($F = 3.77$, $p = 0.063$) (Fig. 3). The other two GAMs explained 53.2% and 37.8%

Fig. 3. Responses of coarse-root biomass to selected environmental factors (elevation, soil pH, and available phosphorus concentration (AP)). The solid line indicates the estimation of coarse-root biomass, and the dashed lines indicate the 95% confidence interval. s(·) is the fitted value of smoothing spline functions.



of the variation of fine-root biomass and fine-root necromass, respectively. Fine-root biomass tended to descend gradually along the AB gradient (F = 5.10, p = 0.038) and increased linearly with both slope (F = 16.40, p = 0.0002) and SW (F = 6.62, p = 0.016) (Fig. 4). Fine-root necromass decreased along the AB gradient (F = 12.84, p = 0.001) but increased linearly with AP (F = 7.10, p = 0.013). AN had no significant relation with fine-root necromass (F = 2.33, p = 0.138) (Fig. 5).

Discussion

According to the VIP values of selected variables (Table 1) and the correlation circles (Fig. 2), we can conclude that the CWMs (i.e., LP, LK, LC, and WD) performed better than the functional diversity indices (i.e., FDis and FDiv) in predicting all components of belowground biomass, which confirmed our hypothesis that MR explains more variation than NC in belowground biomass. Previous work suggested that the effects of NC were weaker in stable and productive environments because of the limited beneficial interactions among species (Paquette and Messier 2011); however, instead of mutually excluding each other, the NC and MR hypotheses both exert certain influence in ecosystems (Conti and Díaz 2013). Root biomass varies largely with tree species at the stand level (Wang et al. 2019), and tree species with conservative trait values (e.g., high WD and low SLA) can accumulate more biomass in old-growth forests (Shen et al. 2016). Additionally, functional traits of trees in this study were significantly clustered as a result of environmental filtering (Yang et al. 2014), so we can infer that those tree species with certain similar traits (i.e., larger DBH and WD) became dominant in the assembled forest communities and accumulated more biomass. Likewise, two previous studies also found that CWMs accounted for more variation of aboveground biomass accumulation than other functional diversity indices did in old-growth forests (Ruiz-Jaen and Potvin 2011; Cavanaugh et al. 2014).

Our results showed positive effects of functional diversity (specifically functional evenness, dispersion, and divergence) on belowground biomass. When functional dispersion is weighted by species abundance, it can be used as a surrogate measure of functional richness. It describes the distribution of multiple traits within the trait space and reflects the degree of niche complementarity within species assemblages (Laliberté and Legendre 2010). Previous studies also found that functional dispersion was a significant predictor of aboveground biomass (Chiang et al. 2016), and a positive correlation between functional dispersion and aboveground biomass existed in unmanaged forest stands (Ziter et al. 2013). Whereas functional divergence quantifies how species abundances diverge from the center of the functional space, functional evenness measures the regularity of the distribution of species functional traits (Mouchet et al. 2010). High functional divergence indicates a high degree of niche differentiation, and high functional evenness indicates effective resource utilization (Mason et al. 2005). Some studies reported no relationship between functional divergence and forest biomass accumulation (Finegan et al. 2015; Fotis et al. 2017), and some researchers have argued that high evenness in a forest community might not generate high biomass productivity because of the reduced dominant species, which perform better in uptake and utilization of resources (Lewandowska et al. 2016). The causes for such discrepancy may lie in the fact that different functional traits are associated with different niche axes and ecological processes and diversity of some traits might promote community carbon sequestration, whereas diversity of other traits might not (Shen et al. 2016).

Regarding the opposite effects of LP on coarse- and fine-root biomass, we speculated that the species with high concentrations of leaf nutrients used resources efficiently, which enhanced biomass accumulation (van der Sande et al. 2018), whereas the species

Fig. 4. Responses of fine-root biomass to selected environmental factors (slope, available boron concentration (AB), and soil water content (SW). The solid line indicates the estimation of fine-root biomass, and the dashed lines indicate the 95% confidence interval. s(·) is the fitted value of smoothing spline functions.

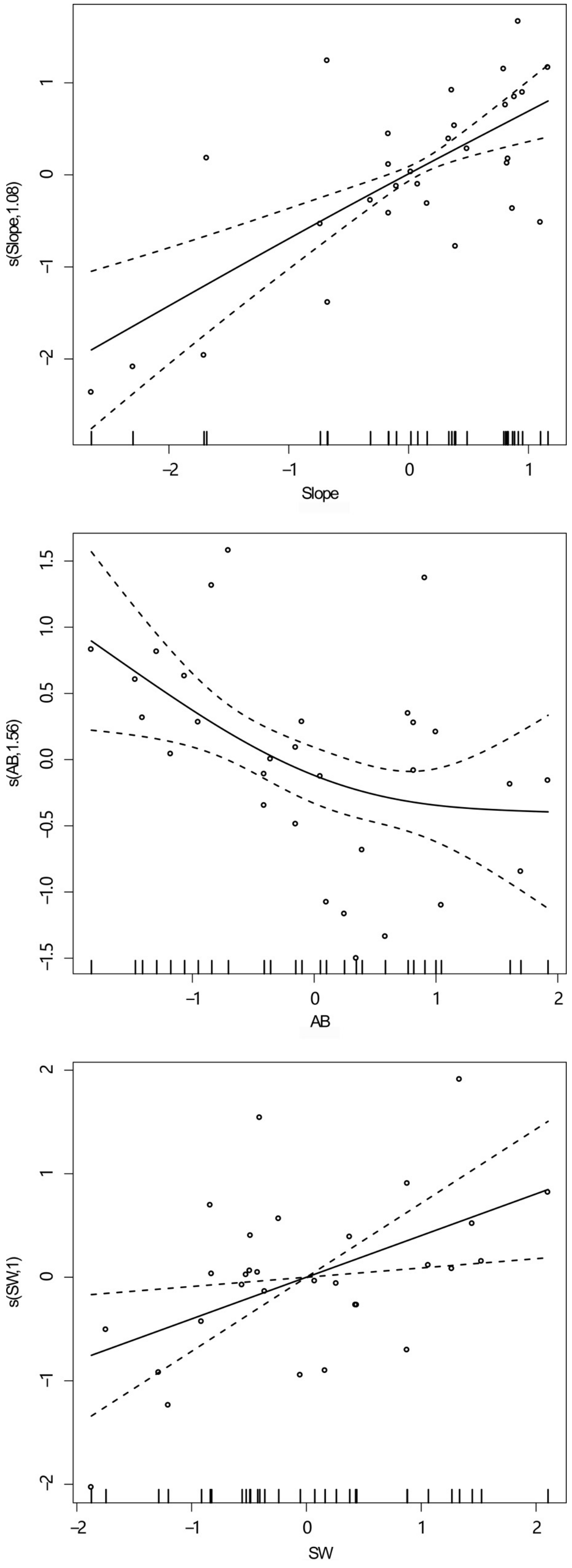
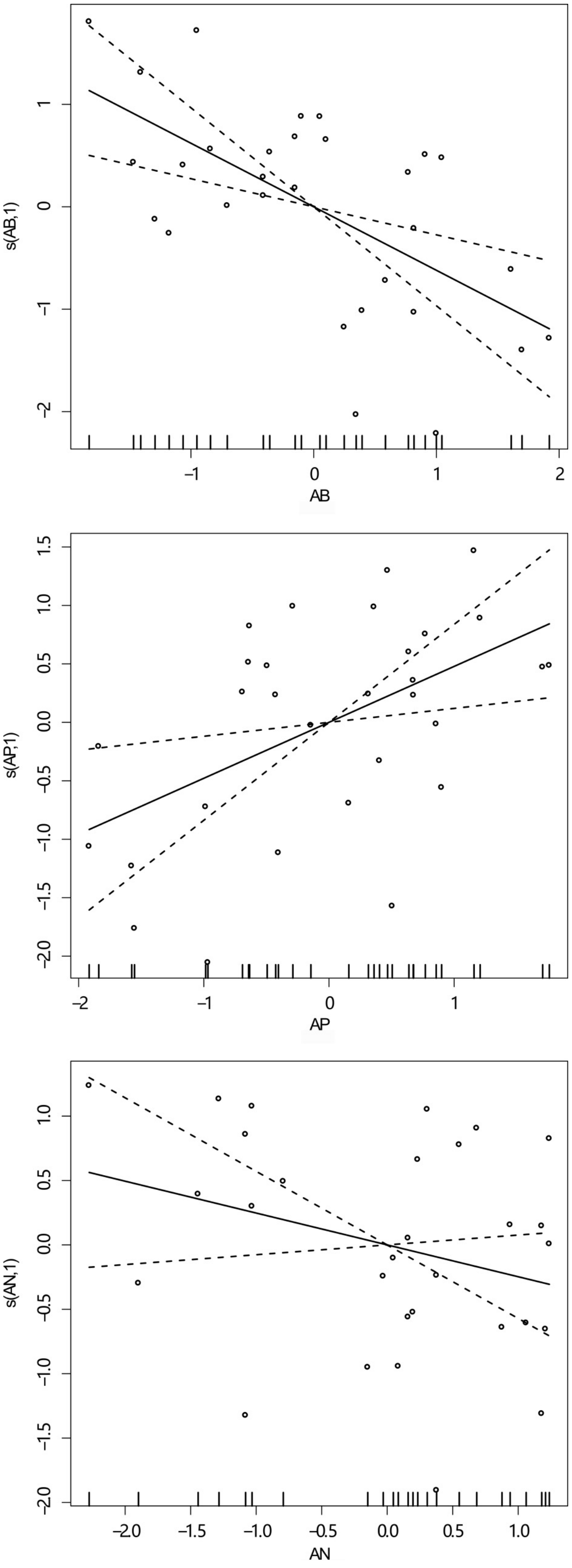


Fig. 5. Responses of fine-root necromass to selected environmental factors (available boron (AB), phosphorus (AP), and nitrogen (AN) concentrations). The solid line indicates the estimation of fine-root necromass, and the dashed lines indicate the 95% confidence interval. s(·) is the fitted value of smoothing spline functions.



with low concentrations of leaf nutrients relied on more fine roots to absorb soil nutrients. Our results identified the CWM of WD as an important factor for belowground biomass, which is consistent with previous studies that found WD of dominant trees influencing biomass storage in forest stands (Cavanaugh et al. 2014; Prado-Junior et al. 2016). Moreover, we found the positive effects of WD on all components of belowground biomass, which is consistent with the previous findings of high WD promoting biomass sequestration (Baker et al. 2004; Prado-Junior et al. 2016). This study also revealed the prominent effects of LK and LC on fine-root necromass, thus providing evidence for the CWMs of leaf traits and WD as important drivers of belowground biomass accumulation.

To provide adequate support for aboveground components, trees continuously allocate biomass production into coarse-root systems in proportion to their growing sizes, leading to an increment of coarse-root biomass until the forest stands are mature (Brassard et al. 2009). From this, we infer that high coarse-root biomass occurs in the forest plots with abundant larger trees; therefore, BA appeared to be a positive factor for coarse-root biomass, whereas DEN was a negative factor for coarse-root biomass, as thick stems might be associated with small trees in the forest stands. Elevation, one of the most important predictors, was negatively associated with coarse-root biomass, probably because of the limited growth and wind disturbance caused by high elevations (Marshall et al. 2012). The positive correlation between soil pH and coarse-root biomass indicated that acidic soils were not conducive to coarse-root biomass accumulation. As soil nutrient concentrations are intercorrelated, soil pH may be a key indicator of soil nutrient availability (Ledo et al. 2016). AP generally remained low, which widely limited aboveground biomass processes (Finegan et al. 2015; van der Sande et al. 2018), and our results also considered AP to be a notable determinant of coarse-root biomass.

We measured AB and treated it as a candidate predictor because of the notion of boron deficiencies in forest soils (Lehto et al. 2010). We included AB as a critical predictor for both fine-root biomass and necromass, but AB presented negative effects on both. The natural background value of soil boron in this area was reported as markedly higher than that of other forests (Wu et al. 1983), which might be relevant to the negative effects of AB on fine-root biomass and necromass. Our results suggested that AN had no relationship with fine-root biomass but showed an insignificantly negative correlation with fine-root necromass. Previous studies found that higher biomass was allocated to fine roots in stands with lower AN (Miyamoto et al. 2016) and high AN led to large fine-root necromass and reduced fine-root biomass (Espeleta and Clark 2007; van der Sande et al. 2018). The decline of root biomass along a natural gradient of increasing soil fertility indicates that trees reduce the partitioning of biomass to fine roots as nutrient limitation is alleviated (Wurzburger and Wright 2015). It is also important to note that ample soil nutrients stimulate microbial activities and root-feeding herbivores, thus enhancing the decay rate of fine roots (Yuan and Chen 2010). Whereas AN is in excess of plant demand, AP limits primary production of fine roots (Wright et al. 2011). AP had larger impacts on fine-root dynamics than AN (Ostertag 2001). These findings may partly explain the unimportant role of AN and the significantly positive effects of AP on fine-root necromass in this study. We found a positive correlation between fine-root biomass and SW, which supports the findings of previous studies that observed a significant increase of fine-root biomass with rising soil moisture (Sundarapandian and Swamy 1996) and the enhancement of the proliferation and longevity of new roots by adding water (Pregitzer et al. 1993). In addition, the soils in this forest area generally presented high acidity, with a mean pH of 3.95 (see Supplementary file cjfr-2019-0254suppla[1]). Trees are more susceptible to soil acidification under dry soil conditions (e.g., in dry seasons), which could significantly reduce fine-root growth and increase root mortality (Vanguelova et al. 2005). Topography intensely regulates species distribution and plant growth by mediating the resource gradient of light availability and soil fertility (Tateno and Takeda 2003). A long-term observation found a higher level of fine-root biomass on steep ridges than on flat bases of a slope (Espeleta and Clark 2007). Additionally, in most cases, slope gradient is positively correlated with elevation; therefore, we infer that stressful conditions on mountaintops may stimulate trees to generate more fine roots to capture limited resources and compensate for the short supply of soil nutrients.

In conclusion, this study detects moderately positive effects of functional diversity on belowground biomass and provides support for the NC hypothesis. However, the MR hypothesis exhibits more explanatory power than the NC hypothesis. Therefore, belowground biomass could be linked more to the functional identity of dominant tree species rather than functional diversity in such an old-growth evergreen forest. Multiple environmental variables, including topographic and edaphic factors, operate in combination to cause spatial heterogeneity in belowground biomass. Coarse-root biomass continuously increases with the development of forest stands from initiation to maturity, whereas fine roots show different biomass accumulation patterns, as they have shorter life-spans than coarse roots. In particular, fine-root accumulation is the outcome of the balance between fine-root production and mortality, and the amount of fine-root necromass mainly depends on the trade-off between the mortality of fine roots and the decomposition of dead fine roots (Jacob et al. 2013). Therefore, the relative importance of abiotic factors for coarse-root biomass, fine-root biomass, and fine-root necromass varies, which partly supports our second hypothesis. Our results suggest that environmental conditions, especially topographic and edaphic factors, should be considered when examining the relationships between biodiversity and ecosystem functioning. Other studies indicate that there are notable seasonal fluctuations of fine-root production and mortality (Brassard et al. 2009) and diversity effects may be more pronounced during the growing season when trees make demands for more soil nutrients and water (Brassard et al. 2013; Ma and Chen 2017). Because of technical difficulties and laborious fieldwork, our study was conducted at the end of the rainy season, not during the growing season. Future studies may take the growth phase of fine roots into consideration and explore the patterns of biodiversity and ecosystem functioning over a long period of time.

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