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# Influence of tree functional diversity and stand environment on fine root biomass and necromass in four types of evergreen broad-leaved forests

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ABSTRACT

Positive effects of tree diversity on above-ground biomass have been well documented, whereas the relationships between tree functional diversity and fine root biomass and necromass remain unclear. This study explored the variation in fine root biomass and necromass among different evergreen broad-leaved forest types, the relative importance of the niche complementarity and the mass ratio hypotheses in driving biodiversity effects, as well as forest stand attributes and environmental factors causing variation in fine root biomass and necromass. We detected no significant differences between most forest types, and the prominently lower amount of fine root biomass and necromass in monsoon evergreen broad-leaved forests may be ascribed to the accelerated turnover rate caused by the elevated temperature. Conversely, the functional divergence showed marginally positive effects on fine root necromass, hence the effects of functional diversity may be negligible; however, community-weighted mean trait values, i.e. specific leaf area and leaf phosphorus concentration, demonstrated significantly negative effects on them. Basal area and stem density showed significant influence in regulating fine root biomass. The optimal GAM models explained 79.5% and 54.4% of the variation of fine root biomass and necromass, respectively. Our results suggest that fine root biomass and necromass may be determined by the functional characteristics of dominant tree species rather than collective functional diversity and closely linked to forest stand, topographic and edaphic factors.

## 1. Introduction

Current rates of species extinctions are 1000 times higher than that of natural background extinction (Pimm et al., 2014), which has aroused concerns about the potential consequences of species loss for ecosystem functioning and services (Balvanera et al., 2006). Therefore, studies of biodiversity and ecosystem functioning (BEF) relationships have been widely conducted in the past two decades, leading to an increasing consensus that biodiversity and ecosystem functioning are closely

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linked (Hooper et al., 2005; Duffy, 2009; Tilman et al., 2014). The positive effects of biodiversity on ecosystem functioning have been demonstrated in many ecosystems including grasslands (Tilman et al., 1996), wetlands (Engelhardt and Ritchie, 2001), oceans (Worm et al., 2006) and deserts (Bowker et al., 2010). Although recent studies also provide the evidence that species-diverse plots support more stand-level productivity than that of plots with low species richness in forest ecosystems (Liang et al., 2016; Liu et al., 2018; Huang et al., 2018), in most cases only the above-ground biomass is focused, and thus the current knowledge of biodiversity effects on forest fine root biomass and necromass is limited (Cardinale et al., 2011; Domisch et al., 2015), probably due to the methodological constrains (Brassard et al., 2013; Ma and Chen, 2016).

Most empirical studies of the biodiversity effects on fine root biomass and necromass are conducted by comparing the standing stocks of fine roots ($\leq$2 mm in diameter) in two or three species mixed forest plots with those of monospecific plots (Meinen et al., 2009; Jacob et al., 2013). While fine root necromass increases with tree species richness, which may lead to prompted interspecific competition thus high fine root mortality (Lei et al., 2012), present studies have shown discrepancies in the patterns between species richness and standing fine-root biomass. Some reported that species mixtures attained higher fine root biomass than monocultures (Brassard et al., 2013; Ma and Chen, 2016). This over-yielding can be ascribed to below-ground niche differentiation, giving rise to root spatial segregation, reduced root competition, fully occupied soil space and thus relative complete usage of soil resources (Brassard et al., 2011; Ma and Chen, 2017). Partial release from pathogens in species mixtures can also be responsible for below-ground over-yielding (de Kroon et al., 2012). Other studies found no evidence for below-ground over-yielding as well as vertical segregation of fine roots (Meinen et al., 2009; Jacob et al., 2013; Ravenek et al., 2014); however, species or functional group identity showed significant influences on root biomass (Gastine et al., 2003; Domisch et al., 2015). In addition, functional diversity can perform better in predicting above-ground biomass than species richness does (e.g., Roscher et al., 2012; Ruiz-Benito et al., 2014), thus the functional role of plant species is of vital importance in determining ecosystem functioning, specifically the overall above- or below-ground biomass.

To some extent the observed BEF relationships have been influenced by many co-varying environmental factors (Mokany et al., 2008; Ma et al., 2010; Ratcliffe et al., 2017). Moreover, roots are highly dynamic systems responsive to variations of soil environment (Brassard et al., 2009), hence the abiotic environment acts as a key regulator of fine root biomass allocation in forests. On a local scale, warmer soils lead to higher root production and mortality (Finér et al., 2011a); and fine root biomass is negatively correlated with soil nutrient availability (Espeleta and Clark, 2007; Yuan and Chen, 2010; van der Sande et al., 2018). A stressful environment, such as elevated concentrations of aluminium and highly acidic soils, stimulates a rapid death of fine roots (Leuschner and Hertel, 2003). Fine root biomass also responds across topographic gradients. There is a positive correlation between fine root biomass and elevation for both coniferous and broad-leaved forests (Leuschner and Hertel, 2003). Soil properties change markedly with slope position from ridge top to valley floor, giving rise to variations in soil-root interactions (Enoki et al., 1996). Besides, fine root biomass increases with stand basal area (Finér et al., 2011b). Both fine root biomass and necromass increase with stand age, but the former declines after 100-year old and the latter levels off at 200-year old (Yuan and Chen, 2012). Trees have deeper root systems in early-successional forest stands than in late-successional forest stands (Finér et al., 1997). These findings indicate stand factors as important determinants of fine root biomass and necromass in forests.

This study aims to detect the different standing stocks of fine roots in four types of evergreen broad-leaved forests (Mossy Dwarf Forests, MD; Mid-montane Moist Evergreen Broad-leaved Forests, MM; Monsoon Evergreen Broad-leaved Forests, MS; Semi-humid Evergreen Broad-leaved Forests, SH). Based on the functional trait approach (Ruiz-Benito et al., 2014), we investigated diversity effects on fine root biomass and necromass in these species-diverse forests, especially the relative explanatory strength of niche complementarity and mass ratio hypotheses, both of which prevail in addressing the mechanisms of positive BEF relationships. According to the niche complementarity hypothesis, high functional diversity indicates a greater variety of resource uptake strategies among species and thus enhances the collective ecosystem functioning (Finegan et al., 2015). The mass ratio hypothesis postulates that ecosystem functioning mainly depends on the functional traits and diversity of dominant species and is insensitive to species richness (Grime, 1998). This study also aims to explore the major stand attributes and environmental factors that affect fine root biomass and necromass accumulation. We specifically hypothesize that: 1) there may be a significant difference in fine root biomass and necromass among four types of forests, because of the pronounced differences of community structure and composition among them; 2) the mass ratio hypothesis may override the niche complementarity hypothesis in predicting fine root biomass and necromass, because some of the forest stands we studied are at late-successional stage, the fine roots of which may aggregate in the surface of soil profile without vertical segregation; 3) the most important stand and environmental factors influencing fine root biomass and necromass may differ, because of the different ecological processes for them, i.e. fine root biomass accumulation is determined by the net amount of fine root production minus fine root mortality, while the amount of fine root necromass depends on the trade-off between the mortality of fine roots and the decomposition of dead fine roots.

## 2. Materials and methods

### 2.1. Study site

As the dominant vegetation type in subtropical areas, evergreen broad-leaved forests support much more biodiversity than most other vegetation types in the Yunnan Province (Editorial Committee of Yunnan Vegetation, 1987). This study is conducted in the Ailao Mountains in the center of the Yunnan Province, and a national nature reserve has been established to conserve the largest mid-mountain moist evergreen forests in the world and its abundant wildlife. The evergreen broad-leaved forests in the Yunnan Province have been classified into five vegetation subtypes (Editorial Committee of Yunnan Vegetation, 1987), four of which are distributed in the Ailao Mountains (Comprehensive scientific survey group of the Ailao Mountain National Nature Reserve, 1988). Mossy Dwarf Forests (MD), Mid-montane Moist Evergreen Broad-leaved Forests (MM) and Monsoon Evergreen Broad-leaved Forests (MS) we studied are located on the western slopes of the Ailao Mountains along an altitudinal gradient from the top to the bottom, Semi-humid Evergreen Broad-leaved Forests (SH) are located on the eastern slopes with a lower altitude than MM forests. Among them only MS forests are distributed out of the nature reserve but are seldom disturbed by human activities for their remoteness. The annual average air temperature of this 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.

### *2.2. Field survey and sampling*

Due to the fact that MM forests represent the main type of regional ever-green broad-leaved forest and other forest types are distributed within relatively smaller areas, we randomly selected 24 plots for MM forests, and 6 plots for each other forest type (Fig. 1). All the plots were set in the size of 20 m × 20 m by applying an electronic total station (NTS-310B/R). A complete inventory of woody plants was conducted in plots, all individuals were identified to the species level, with diameters at breast height (DBH) measured. We also measured the relative altitude of the corners and centers of all plots in order to estimate topographic features such as elevation, convexity, aspect and slope. Herbs were rare in the plots, probably due to the handicap imposed by the mature closed canopies of the forest stands, and thus were not included in analyses. Each plot was divided into four equal quadrats, 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. The dynamics of fine root growth and death are highly synchronized with the seasonal patterns of foliage growth and senescence (Brassard et al., 2009), and fine roots affect photosynthesis rate by controlling the uptake efficiency of water and nutrients from the soil (Chen et al., 2004). Besides, several studies identified wood density associated with carbon sequestration in vegetation (Cavanaugh et al., 2014; Prado-Junior et al., 2016). In consideration of these findings, we used leaf traits and wood density to construct a series of functional diversity indices. Leaf samples were collected from sunlit tree crowns, with three to five adult individuals selected for each species (Jin et al., 2013), and wood cores were also collected from five individuals (Chiang et al., 2016). All soil cores, leaf samples and wood cores were stored in a cooler for further determination in laboratory. All the field work (including woody plant survey and sampling) was conducted from October 2014 to February 2015.

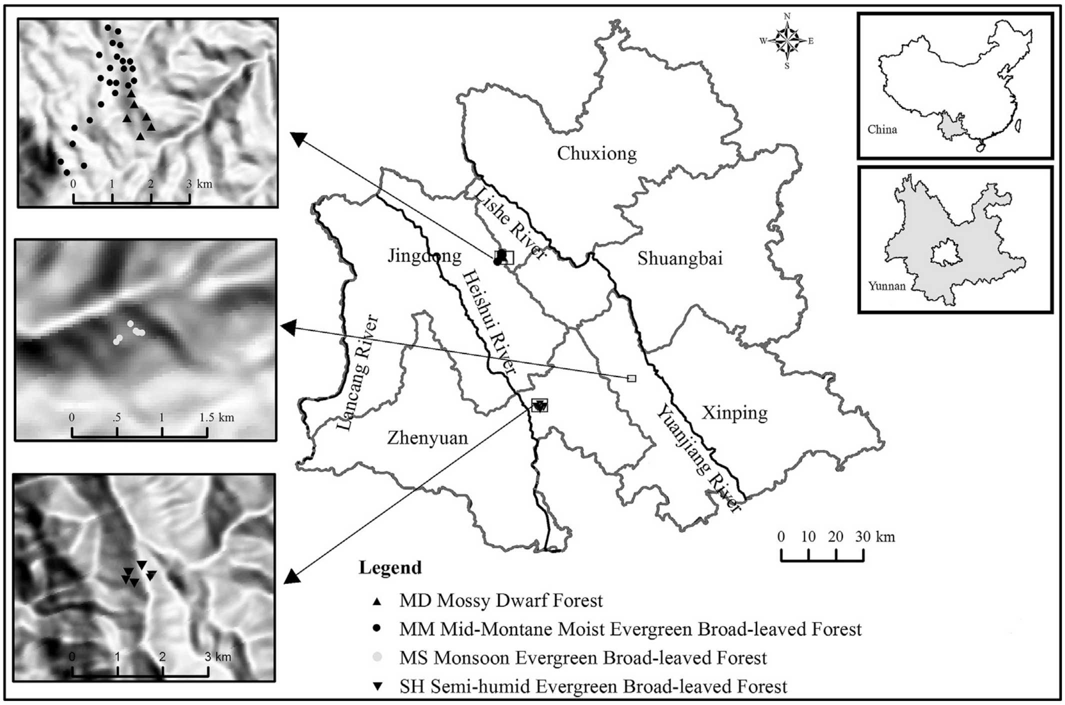

**Fig. 1.** Location of study area.

### 2.3. Determination of all variables

In the laboratory, fine roots were washed and picked out from soil cores and separated into living and dead roots based on their colors, textures, elasticity and whether floating or sinking in water. Then these fine root samples were dried to constant mass at 70 °C and weighed (Ostonen et al., 2005).

Leaf functional traits including specific leaf area (SLA), leaf nitrogen, phosphorus, potassium and carbon concentrations, and wood density (WD) were determined according to the methods suggested by Cornelissen et al. (2003), e.g., SLA was determined as one-side area of a fresh leaf divided by its oven-dry mass, and WD was measured as oven-dry mass of each wood core divided by its fresh volume. However, only SLA, leaf phosphorus (LP) and WD were included in measuring functional diversity indices because of the interspecific correlations among plant traits (Wright et al., 2007) and the relative independency of these three traits. Community functional diversity indices, including functional richness (FRic), evenness (FEve), divergence (FDiv), dispersion (FDis) and community-weighted mean trait values (CWMs) were calculated by applying R function “dbFD” of package “FD” (Laliberté and Legendre, 2010; Laliberté et al., 2014). Stand basal area (BA) was estimated by summing the stem area of each tree at breast height, and stem density (DEN) was determined by the counts of all individuals divided by the plot area.

Elevation was determined as the average values of the elevations at each four corners of the plot. Convexity was defined as the altitude of the plot center minus the average altitudes 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 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, including water content, organic matter, pH, total N, total P, total K, available N, available P, available K and B, were measured in laboratory for each plot following the methods mentioned by Bao (2005).

### 2.4. Data analysis

The fine root biomass and necormass for each plot was calculated by averaging the dry weight of live and dead fine roots from four quadrats, and then expanded into area of 1 $m^2$, respectively. Kruskal-Wallis tests and Dunn's tests were used to detect and examine the differences in fine root biomass and necormass of the four forest types. As a non-parametric multiple comparison method, Dunn's test can be used for pairwise comparisons between groups when the data do not meet the criterion of normal distribution or homogeneity of variance, and it often follows a Kruskal-Wallis test if the latter has detected significant differences among groups (Dinno, 2015).

Partial least squares (PLS) regression was applied to explore correlations between fine root biomass, necromass and functional diversity indices, stand basal area and stem density. We combined functional diversity indices, stand basal area (BA) and stem density (DEN) together as an explanatory matrix and then a PLS model with fine root biomass or necromass as response variables was fitted. The variable importance for projection (VIP) of the predictors was calculated to assess their performance in terms of their explanatory power to response variables. All these statistics were conducted in R package “plsdepot”. Only the predictors with VIP values higher than 1 were considered as major contributors to the model, VIP between 1 and 0.8 represented a moderate contribution of predictors, while VIP lower than 0.8 indicated no contribution (Frameschi et al., 2013). Relationships between response variables and important predictors were analyzed by using linear regressions.

Generalized additive models (GAM) were used to examine the complex relationships between fine root biomass, necromass and multiple environmental factors. Before analysis all the data were standardized (scaled values to zero mean then divided by standard deviations) with R function “decostand” in package “vegan”. To explore the most important predictors of fine root biomass and necromass, we applied function “dredge” to generate a set of models with all the combinations of predictors, then applied function “importance” to rank all the predictors in a descending order based on their importance values, and only the top four predictors were included in fitting optimal GAM models. Finally, the amount of variance explained by the models as well as the significance of included predictors was examined. Predictor selection and model fitting were conducted in R package “MuMIn” and “mgcv”, respectively.

## 3. Results

Overall, 105 tree and shrub species, belonging to 63 genera and 34 families, were recorded in these 42 forest plots. MD forests were dominated by *Lithocarpus crassifolius*, *Rhododendron irroratum*, *Clethra delavayi*, *Vaccinium duclouxii* and *Lyonia ovalifolia*; MM forests by *Lithocarpus xylocarpus*, *Castanopsis wattii*, *Stewartia pteropetiolata*, *Schima noronhae*, *Ilex coralline*, *Rhododendron leptothrium*; MS forests by *Castanopsis delavayi*, *Helicia nilagirica*, *Anneslea fragrans*, *Lithocarpus truncates*, *Castanopsis fleuryi*; and SH forests by *Alnus nepalensis*, *Cyclobalanopsis glaucoides*, *Lithocarpus craibianus*, *L. polystachyus*. The average fine root biomass and necromass of each forest type were $445.84 \pm 121.42$ g $m^{-2}$ and $59.09 \pm 25.68$ g $m^{-2}$, $399.24 \pm 73.88$ g $m^{-2}$ and $59.83 \pm 32.69$ g $m^{-2}$, $174.99 \pm 37.70$ g $m^{-2}$ and $29.82 \pm 9.75$ g $m^{-2}$, $420.88 \pm 92.29$ g $m^{-2}$ and $71.86 \pm 32.01$ g $m^{-2}$, respectively. The Kruskal-Wallis test indicated that at least one forest type's fine root biomass and necromass were significantly different from other forest types ($\chi^2 = 15.68$, $P = 0.00$; $\chi^2 = 8.06$, $P = 0.04$). Dunn's multiple comparison further demonstrated that fine root biomass of MS was significantly lower than that of MD ($z = -3.41$, $P = 0.00$), MM ($z = -3.56$, $P = 0.00$) and SH ($z = -3.10$, $P = 0.00$), and fine root necromass of MS was also significantly lower than that of

MD (z = −2.09, P = 0.02), MM (z = −2.24, P = 0.01) and SH (z = −2.68, P = 0.00). Additionally, there were no significant differences between other forest types of both fine root biomass and necromass (e.g. fine root necromass of MD vs. MM, z = 0.41, P = 0.34, etc.) (Fig. 2).

The variable importance for projection (VIP) value of each predictor is displayed in Fig. 3. SLA, LP and BA were identified as the most informative predictors of fine root biomass, SLA and FDiv were the most important predictors of fine root necromass, as their VIP values were over 1. We also included DEN as an informative predictor for fine root biomass, as its VIP value was over 0.9. According to the results of linear regression analysis, fine root biomass displayed significantly positive and marginally positive correlations with BA and DEN, respectively; and it significantly decreased with both SLA and LP (Fig. 4). While FDiv showed marginally positive effects on fine root necromass, SLA demonstrated significantly negative effects on it (Fig. 5).

Two optimal GAM models were fitted with four environmental factors of primary importance, which accumulatively explained 79.5% of the variance of fine root biomass and 54.4% of the variance of fine root necromass, respectively. Fine root biomass tended to descend along the AB gradient (F = 9.52, p = 0.00), raised with both slope (F = 10.46, p = 0.00) and soil water content (SW) linearly (F = 16.16, p = 0.00) and showed an unimodal pattern with soil organic matter (SOM) (F = 7.79, p = 0.00) (Fig. 6). Fine root necromass decreased with soil available boron concentration (AB) linearly (F = 29.07, p = 0.00), and showed a hump-shaped relationship with slope (F = 3.24, p = 0.06), increased with soil available P concentration (AP) linearly (F = 20.24, p = 0.00) and declined with soil available N concentration (AN) with a marginal significance (F = 2.34, p = 0.07) (Fig. 7).

## 4. Discussion

Our study revealed no significant differences between the three evergreen broad-leaved forest types for both fine root biomass and necromass, and only MS forests showed significantly lower fine root biomass and necromass than the other forest types, possibly due to the lower altitudes (1848 ± 25m) in comparison with other forest types (i.e., 2629 ± 23m for MD, 2509 ± 30m for MM, 2173 ± 37m for SH). Previous studies reported that broad-leaved forests increase in root biomass at higher elevation or lower temperature (Leuschner and Hertel, 2003). A decrease in temperature resulted in slower fine root turnover rates and increased root longevity (Finér et al., 2011a; Girardin et al., 2013), and increasing elevation slowed down root litter decomposition and enhanced fine root longevity (Leuschner et al., 2007; Graefe et al., 2008). In addition, species richness of MS forests ranged from 17 to 24 with a mean value of 20, higher than the other forest types (MD from 8 to 15 with a mean value of 12, MM from 4 to 26 with a mean value of 13, SH from 4 to 11 with a mean value of 8). This result is consistent with these studies that identified species diversity is not an important driver of fine root biomass, as species-rich forest stands had no more fine root biomass than the stands with lower species diversity (Meinen et al., 2009; Jacob et al., 2013; Ravenek et al., 2014).

We found significantly negative effects of SLA on both fine root biomass and necromass, as well as significantly negative effects of LP on fine root biomass. However, only FDiv showed marginally positive effects on fine root necromass, the other three functional diversity indices, i.e. FRic, FEve and FDis were insignificant to both fine root biomass and necromass. Hence fine root biomass and necromass were more closely linked to community-weighted mean trait values than to functional

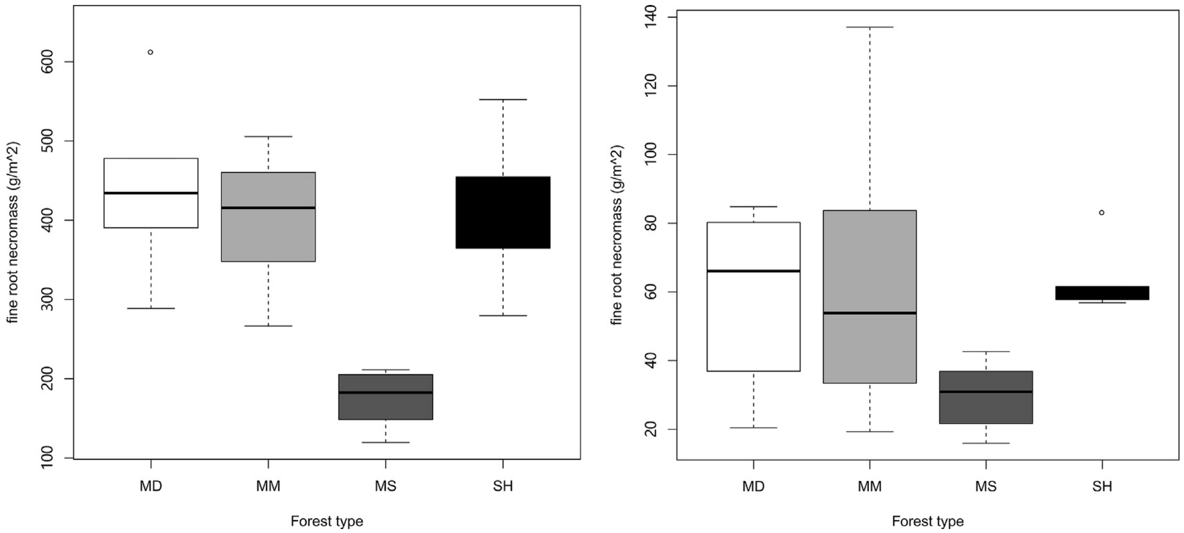

**Fig. 2.** Fine root biomass and necromass in four types of evergreen broad-leaved forests. MD: Mossy Dwarf Forests, MM: Mid-montane Moist Evergreen Broad-leaved Forests, MS: Monsoon Evergreen Broad-leaved Forests, SH: Semi-humid Evergreen Broad-leaved Forests.

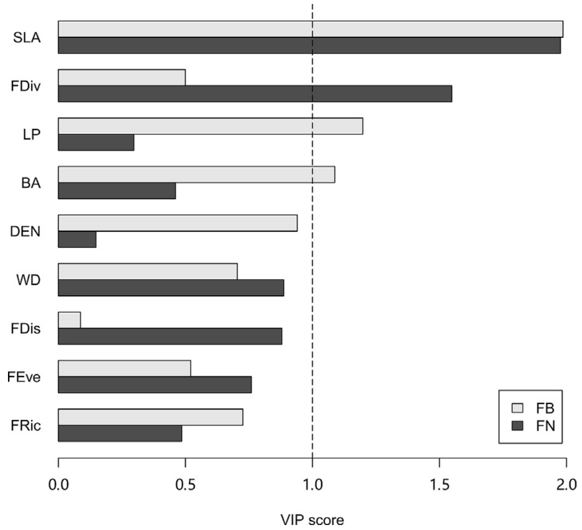

**Fig. 3.** Explanatory power of predictors expressed as variable importance for projection (VIP) for fine root biomass and necromass. FB: fine root biomass, FN: fine root necromass, SLA: specific leaf area, FDiv: functional divergence, LP: leaf phosphorus concentration, BA: stand basal area, DEN: stem density, WD: wood density, FDis: functional dispersion, FEve: functional evenness, FRic: functional richness.

diversity indices, indicating that the mass ratio hypothesis overrides the niche complementarity hypothesis in predicting fine root biomass and necromass. It's notable that the stand ages of MD and MM forests are over 300 years (Tan et al., 2011), and tree species with conservative traits (e.g. low SLA) can accumulate more biomass in old-growth forests (Shen et al., 2016). While SH forests are characterized by xerophytic species with small and thick leaves, tree species of MD and MM forests have adapted to the wet habitats (Editorial Committee of Yunnan Vegetation, 1987), and environmental filtering is the main ecological process structuring tree species assemblages in these MM forests (Yang et al., 2014). Strong environmental filtering facilitated a small set of dominant tree species, whose traits might determine the stock of fine root biomass. Moreover, positive biodiversity effects became weaker with increasing water availability (Guo et al., 2019), and decreased from boreal to subtropical forests (Wu et al., 2015), indicating diminished complementarity effects and increased interspecific competition in stable and productive environments (Paquette and Messier, 2011). The environmental dependence of complementarity effects could have also implications for fine root biomass. For the negative effects of LP on fine root biomass, we speculated that high leaf nutrient concentrations representing efficient resource-use, under which tree species enhanced biomass accumulation (van der Sande et al., 2018), while the species with low leaf nutrient concentrations relied on more fine roots to absorb soil nutrients. In addition, our results partly confirmed the findings that fine root biomass increased with stand basal area and had no relationships with stem density (Finér et al., 2011b).

Our results were partially consistent with a seven-year study showing the amount of fine root biomass and necromass declined along topographic gradient from slope crest to slope base (Espeleta and Clark, 2007), revealed the impact of topography especially slope gradient on fine root biomass and necromass. The topography shapes resource distribution patterns such as light availability and soil fertility, thus regulating forest structure, species distribution and plant growth (Tateno and Takeda, 2003). The negative effects of soil available boron concentration (AB) on fine root biomass and necromass might be attributable to the fact that the natural background value of soil boron in this area was reported as markedly higher than that of other forests (Wu et al., 1983). Soil available nitrogen showed a negative correlation with fine root necromass but it was insignificant for fine root biomass in our study. High soil nitrogen availability causes mortality of fine roots and decline of fine root biomass (Espeleta and Clark, 2007; van der Sande et al., 2018), however, high soil fertility also stimulates microbial activities and root-feeding herbivores, thus accelerating the decay rate of fine roots (Yuan and Chen, 2010). Above findings also partly explained the pattern between fine root biomass and SOM. Soil N availability is in excess of plant demand, whereas P limits primary production of fine roots (Wright et al., 2011), which explained the linear increase in fine root necromass with P availability we observed. Our results supported earlier studies that reported a significant increase of fine root biomass with rising soil moisture (Sundarapandian and Swamy, 1996), and found that water addition enhanced the proliferation of new roots and their longevity (Pregitzer et al., 1993). Additionally, trees are more susceptible to soil acidification under dry soil conditions, which could significantly reduce fine root growth and increase root mortality (Vanguelova et al., 2005). Therefore, our results highlighted the importance of soil water content to fine root biomass, especially in dry seasons.

In summary, this study indicates no significant differences between most forest types. The reduced fine root biomass and necromass of MS forest plots may be ascribed to the accelerated turnover rate caused by the elevated temperature. Forest types are associated with special habitats and dominated by certain tree species, which may perform better in taking up and utilizing resources at local scale, while other species perform less efficiently, thus not species richness or collective functional diversity but the functional characteristics of dominants determine biomass productivity. Our results also suggest that fine

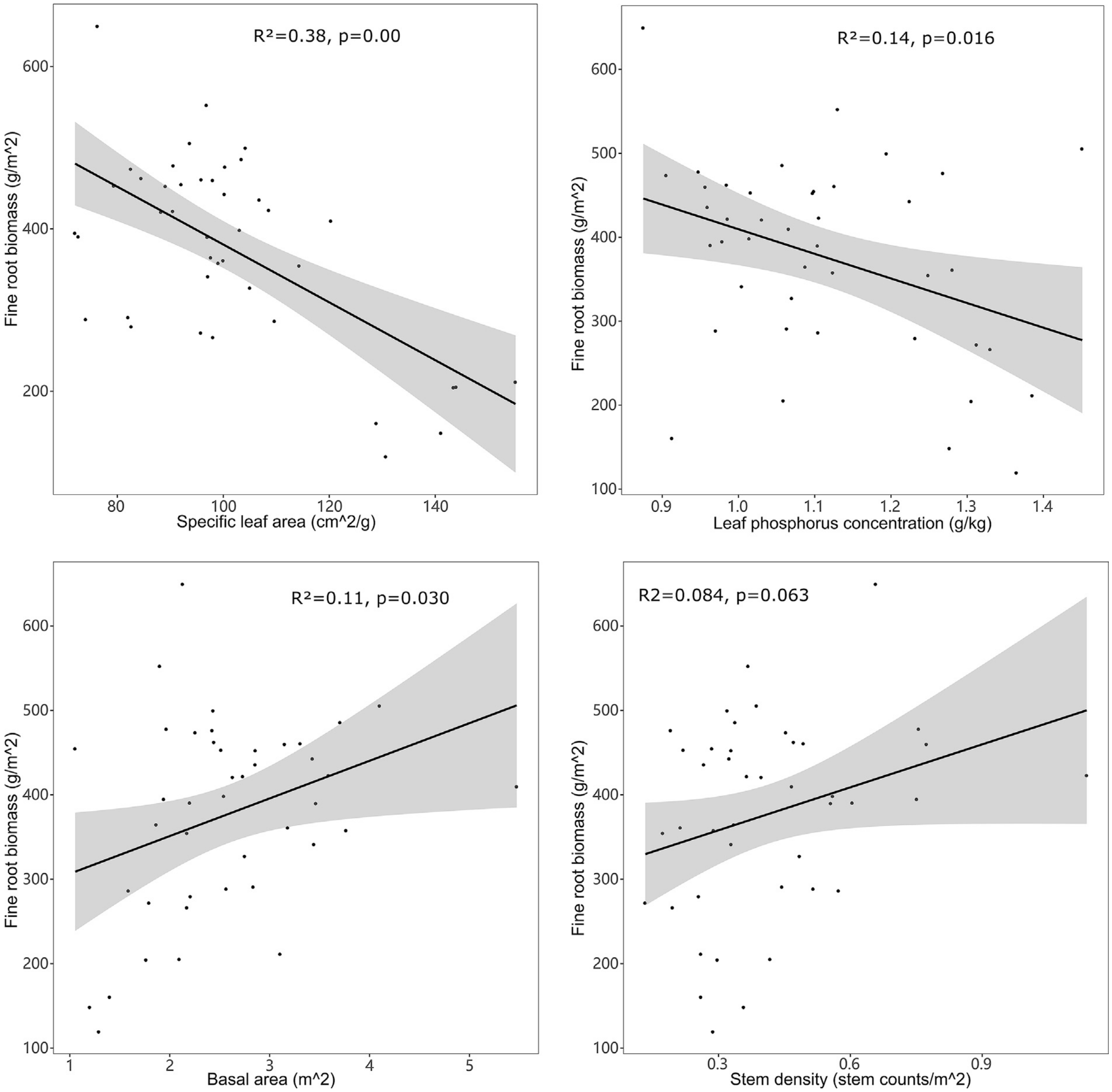

**Fig. 4.** Informative predictors for fine root biomass.

root biomass and necromass are closely linked to forest stand, topographic and edaphic factors. Based on the performance of their respective predictors and the variance explained by GAM models, we can conclude that the accumulation process of fine root necromass may be less clear than that of fine root biomass. In addition, although fine root production generally peaks in late spring to mid-summer (Brassard et al., 2009), this study was conducted out of that period, owing to the technical difficulties in rainy seasons. Future studies may take the whole phase of fine roots into consideration, and explore biodiversity effects on fine root biomass and necromass on a long-term scale.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

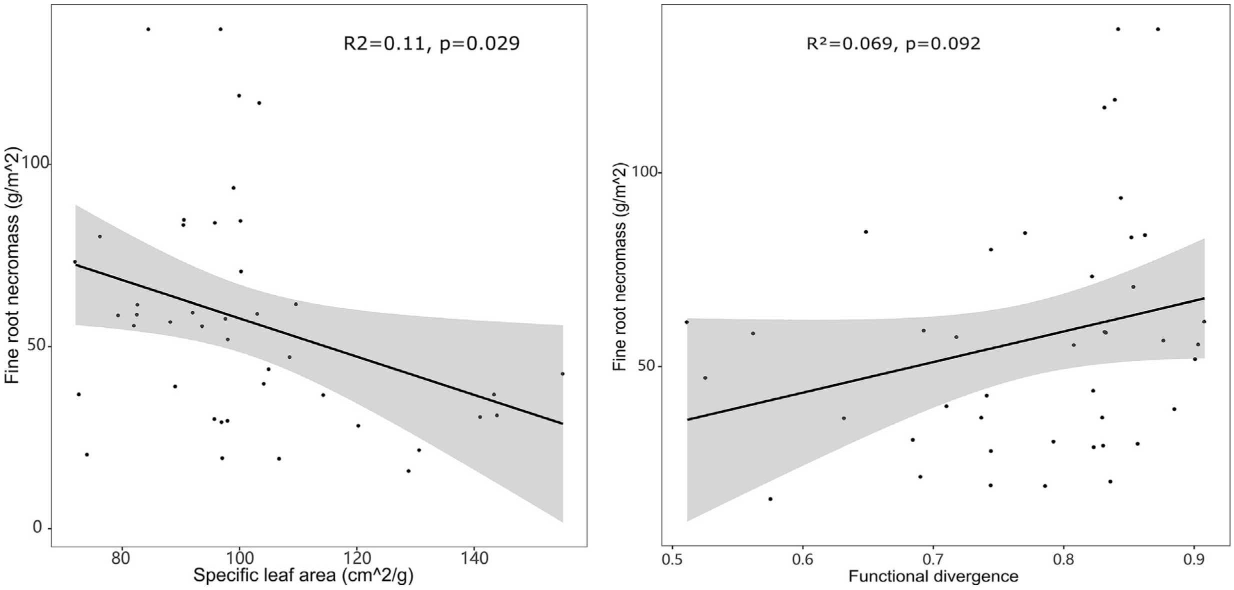

**Fig. 5.** Informative predictors for fine root necromass.

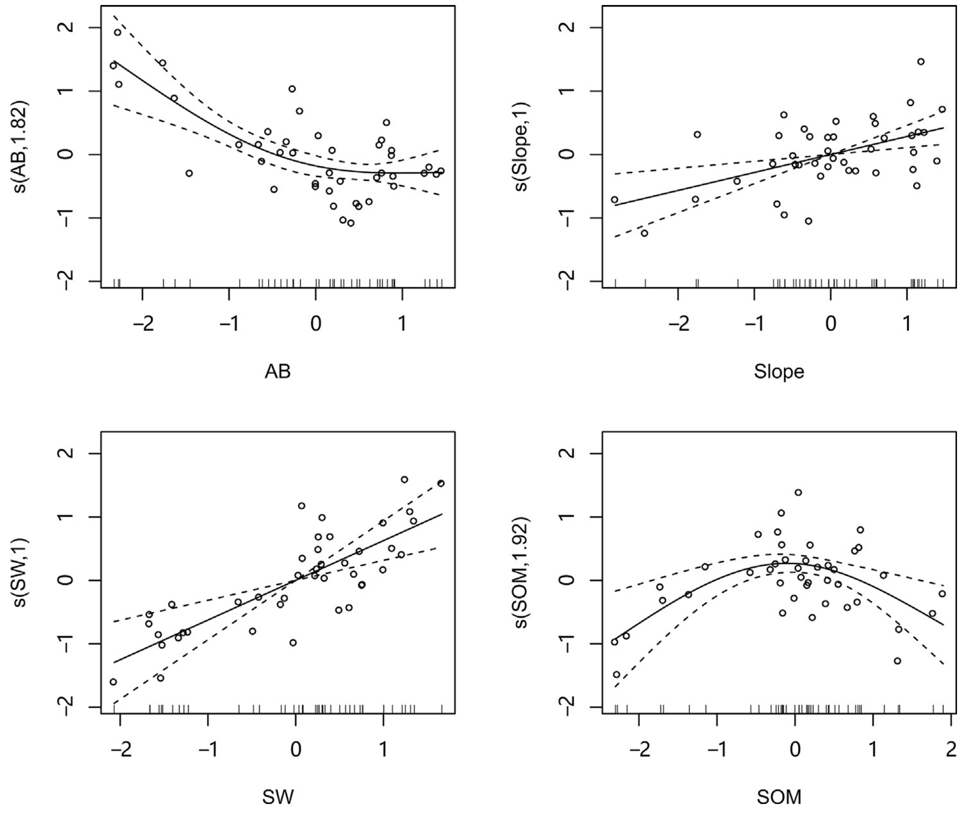

**Fig. 6.** Responses of fine root biomass to selected environmental factors. The solid line shows the estimations of fine root biomass, and the dashed lines indicate 95% confidence interval. s () is the fitted value of smoothing spline functions. AB: soil available boron, Slope: slope gradient, SW: soil water content, SOM: soil organic matter.

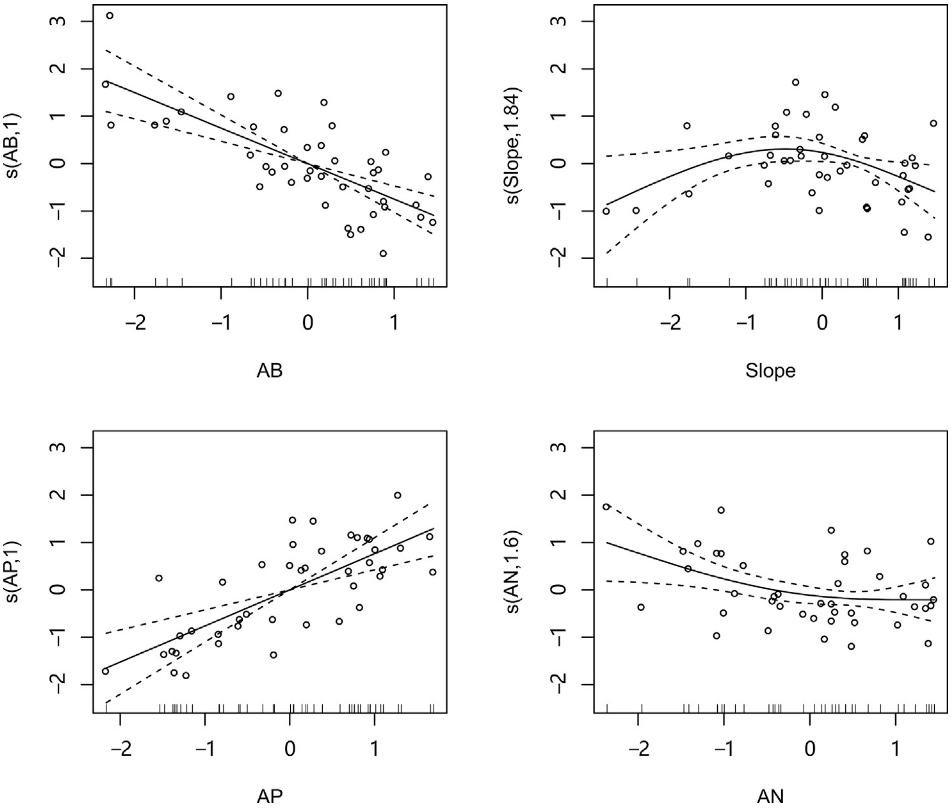

**Fig. 7.** Responses of fine root necromass to selected environmental factors. The solid line shows the estimations of fine root biomass, and the dashed lines indicate 95% confidence interval. s () is the fitted value of smoothing spline functions. AB: soil available boron, Slope: slope gradient, AP: soil available phosphorus, AN: soil available nitrogen.

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