



Original Research Article

Environmental variation, functional diversity and identity predicting community biomass in an old-growth subtropical broad-leaved forest

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ABSTRACT

The relationship between biodiversity and ecosystem functioning (BEF) has emerged as a central issue in ecosystem ecology. Two broad classes of hypotheses, the mass ratio and niche complementarity effects, are proposed to explain the positive relation between biodiversity and ecosystem functioning in multiple experimental and natural systems. Environmental variation is noted as a key regulator of forest community biomass in natural systems and the under-story tree layer is often overlooked, as the canopy tree species are more likely to contribute to total community biomass. We determined community biomass of over-story, mid-story and under-story tree layers and employed environmental factors, functional diversity metrics of leaf traits to explain the variation in community biomass in an old-growth forest. We found that topographic and edaphic factors were of vital importance in regulating the standing biomass of each tree layer. Although functional diversity displayed positive effects on standing biomass across all tree strata, the standing biomass was more affected by functional identity than diversity in over-story and mid-story tree layers. Across all strata, the most significant correlation between functional diversity and standing biomass in under-story tree layer may suggest strengthened interspecific complementary interactions. Our study confirms that environmental variation is a strong driver of forest community biomass, and the relative importance of the mass ratio and the niche complementarity hypothesis vary across tree strata in explaining diversity effects on standing biomass.

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1. Introduction

Continuing species loss has the potential to impair ecosystem processes and the provision of ecosystem services to humanity (Balvanera et al., 2006; Cardinale et al., 2012). This recognition stimulated a rapid growth of research on

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relationships between biodiversity and ecosystem functioning (BEF for short) over the past two decades. The scientific community has reached a broad consensus that biodiversity and ecosystem functioning are intimately linked (Tilman and Downing, 1994; Hooper et al., 2005; Worm et al., 2006; Duffy, 2009). Numerous studies including both experimental and natural systems have shown a positive effect of biodiversity on ecosystem functioning (Worm et al., 2006; Duffy, 2009; Liang et al., 2016), with increasing diversity leading to enhanced productivity (Cardinale et al., 2006), stability (Gross et al., 2014), resistance to invisibility (Zavaleta and Hulvey, 2004), and nutrient cycling (Wall and Bardgett, 2013). As the most important terrestrial ecosystems harboring substantial biodiversity, forests gain more concerns on this issue in recent years (Ammer, 2019). Although species richness and functional diversity are inevitably correlated (Tobner et al., 2016), and both are widely used for measuring diversity in BEF studies, it has been reported that functional diversity is more closely linked to ecosystem process and dynamics (Díaz and Cabido, 2001; Cadotte et al., 2011), and shows a larger predictive power of community biomass than species diversity (Roscher et al., 2012; Ruiz-Benito et al., 2014; Tobner et al., 2016).

Niche complementarity hypothesis suggests that a higher level of functional diversity results in a greater ability to exploit resource pools, due to a greater variety of resource uptake strategies among species, thus the range or variety of species trait values is critical in determining ecosystem functioning (Conti and Díaz, 2013; Finegan et al., 2015). Four relatively independent components of functional diversity including functional richness (hereafter FRic), evenness (FEve), divergence (FDiv) and dispersion (FDis) can be applied to measure niche complementarity (Finegan et al., 2015). In contrast, the mass ratio hypothesis predicts that ecosystem functioning is mainly dependent on the functional identity and diversity of dominant species (Grime, 1998), which can be measured by community-weighted mean (hereafter CWM) trait values (Ruiz-Benito et al., 2014). While functional diversity metrics can be particularly useful for teasing apart the relative roles of niche complementarity and mass ratio effects, it is difficult to determine which traits should be included (Conti and Díaz, 2013). Hypothetically, traits associated with carbon and nutrient investment strategies (Poorter and Bongers, 2006) may be most important (Yuan et al., 2016), and thus should be considered in the studies of diversity effects on community biomass accumulation (Conti and Díaz, 2013; Finegan et al., 2015; Shen et al., 2016).

It has been suggested that the magnitude and direction of the relationship between diversity and community biomass is context specific and dependent on environmental conditions (Ratcliffe et al., 2017; Zhang et al., 2017). Specifically, diversity effects on community biomass may vary along environmental stress gradients and tend to peak at intermediate levels of environmental stress (Baert et al., 2018). In natural systems, abiotic environment exerts parallel influences on biodiversity and community biomass (Ma et al., 2010). The variations in resource availability along both horizontal (soil fertility and water supply) and vertical (forest strata and root systems) directions determine forest community structure and species composition (Oliveira-Filho et al., 2001; Russo et al., 2005), and also has important effects on forest community biomass accumulation by influencing the growth, mortality and regeneration of individual trees (Tateno and Takeda, 2003; Yasuhiro et al., 2004; de Toledo et al., 2011). Previous studies have supported that soil nutrients and topographic factors (e.g. convexity and slope) are important drivers of forest aboveground biomass (McEwan et al., 2011; Xu et al., 2015). Therefore, local environments should be considered in studying the relationship between diversity and biomass.

The DBH (diameter at breast height) class, stem density and neighbourhood species richness are also important factors in explaining the variation in community biomass (Fichtner et al., 2018; Fotis et al., 2017), especially in forest ecosystems as they are more complex-structured and harboring the mass of terrestrial species (Zhang et al., 2017). Although understories sustain considerable species and are crucial for some ecosystem process, e.g. nutrient dynamics and forest regeneration (Nilsson and Wardle, 2005), under-story tree layer is overlooked given that the canopy tree species are more likely to make a major contribution to community biomass. For instance, two studies examining functional diversity effects on above-ground biomass in tropical forests only included trees with DBH ≥ 10 cm (Cavanaugh et al., 2014; Finegan et al., 2015). Furthermore, empirical evidence of BEF relationships varying in different forest layers is still lacking, and there is less assessment of the relative importance of the niche complementarity and mass ratio hypotheses in driving biodiversity effects on standing biomass across forest layers (Mensah et al., 2018).

The present study aims to detect the influence of functional diversity, identity, and environments on community biomass in an old-growth subtropical broad-leaved forest, and to quantitatively evaluate their relative importance across tree strata. We hypothesized that abiotic environment (i.e. topographic and edaphic factors in this study) may explain more variation of community biomass than functional diversity or identity, as local environmental conditions can cause variation in resource availability and community dynamics, and the mechanisms driving BEF relationships may be dependent on environmental conditions (Ma et al., 2010; Ratcliffe et al., 2017; Zhang et al., 2017; Baert et al., 2018). Specifically, we hypothesized that BEF patterns may vary with the forest vertical structure, at least the magnitude of diversity effects in each layer may differ because 1) in natural forests, light resources vary for each tree layer, with canopy species exposed to more light and limited amount of light that reaches under-story layer (Mensah et al., 2018); 2) Species interaction and functional contribution change along environmental stress gradient (Baert et al., 2018); and 3) forest vertical stratification might also cause significant variation in important functional traits for both inter and intra-species within a forest community (Bassow and Bazzaz, 1997; Cavaleri et al., 2010; Jin et al., 2013).

2. Materials and methods

2.1. Study area

As the dominant vegetation type in subtropical area of Yunnan Province, evergreen broad-leaved forests are widely distributed with diverse species (Editorial Committee of the Vegetation of Yunnan, 1987). Data were collected from the Ailao Mountain National Nature Reserve, located in the southern branch of the Yunling Mountains (Jingdong County, Puer City; 24°32'N, 101°01'E; Fig. 1). The Ailao Mountain National Nature Reserve was established to conserve the unique mid-mountain moist evergreen forest ecosystems, and the rich diversity and abundance of wildlife found there. The annual average air temperature of the region is 11.3 °C, with a mean temperature in January of 5.4 °C and a mean temperature in July of 16.4 °C. The annual mean precipitation is approximately 1900 mm, about 85% of which occurs during the rainy season from May to October. The annual average evaporation and relative humidity is 1485 mm and 85%, respectively. The forest stands used for this study were over 300 years of age based on the study of the wood cores collected from most of the tree species (Tan et al., 2011), and the forests and their surrounding environments are well protected, as the human activities are strictly regulated there. The forest communities are dominated by *Lithocarpus xylocarpus*, *Castanopsis wattii* and *Schima noronhae* as canopy species, *Vaccinium duclouxii*, *Camellia forrestii* and *Symplocos ramosissima* as shrub species (Comprehensive Investigation Group of the Ailao Mountain National Nature Reserve, 1988).

2.2. Field survey

There is a large lake in the nature reserve, and thirty forest plots were randomly set around the lake and covering almost all the directions (Fig. 1). Each plot was set in the size of 20 m × 20 m by applying an electronic total station (NTS-310B/R). The total horizontal projection area of these plots added up to 1.2 ha and the average distance between each plot was over 200 m. All woody plants in plots were identified to species level. At beginning we set a criterion that only the trees and shrubs with DBH ≥ 1 cm could be measured in the plots, but we had to measure all of them, as they were all

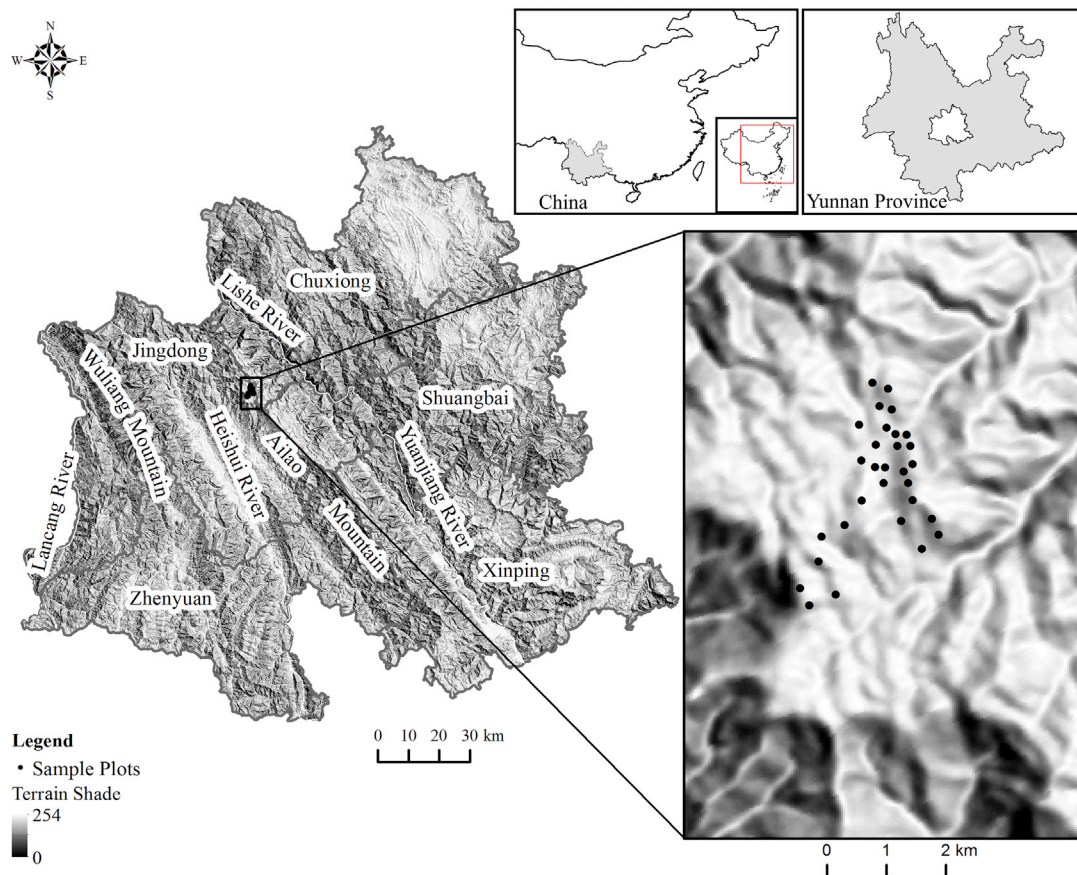


Fig. 1. Location of study area (generated by ESRI ArcGIS 10.2).

large enough. For instance, *Vaccinium duclouxii* and *Camellia forrestii* are the most dominant shrub species in the forest, and their mean DBH were 7.32 ± 4.08 cm and 3.67 ± 1.83 cm, ranging from 1.24 to 34.38 cm and 1.15–10.85 cm, respectively in our study. 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 most plots, probably due to regeneration difficulties imposed by a mature closed canopy, and they contributed little to the whole biomass in this old forest ecosystem, thus were not included in analyses. Out of these plots, more than 500 sample trees from 22 species (most of them are dominant tree and shrub species) were selected, with their DBHs and heights measured to establish allometric regression equations. The heights of these sample trees were determined either by a length rod (individual heights less than 10 m) or by a laser distance meter (Leica D810). Finally, each plot was divided into four equal quadrats, and soil samples were taken at depths of 0–20 cm from the centers of quadrats. Leaf samples were collected from sunlit tree crowns, with three to five adult individuals sampled for each species (Jin et al., 2013). All soil cores and leaf samples were stored in a cooler for the further determination in the laboratory.

2.3. Community biomass estimation

In total, 22 species-specific allometric equations between height and DBH were established based on the data from the field survey (all coefficients of determination (R^2) > 0.8). A general allometric equation was created for the rest of the species by using the inventory data of a 6 ha permanent forest dynamics plot that included more than 12,000 individuals (Yang et al., 2014). All these equations were in the form as following:

$$H = a + b \times D - c \times D^2 \quad (1)$$

where H and D represents tree height and DBH, respectively, and a – c are constants estimated via regression analysis (for details see Appendix1). The heights of trees in this study were estimated by using these equations.

Although biomass allometric equations for 5 canopy species were available (Qiu et al., 1984), we rebuilt them based on updated information from one of the original authors (personal communication, see these equations in Appendix2). Some of these trees were cut down during a road construction project in the nature reserve, which provided a chance to establish a general biomass equation by selecting 35 sample trees from more than 14 species with a DBH range from 5 to 100 cm. All sample trees were harvested and divided into trunks, branches, leaves, roots and flowers (only 10 individuals had flowers), and then dried to constant weights. The biomass allometric equations were constructed in the following form:

$$bio_i = d \times (D^2 \times H)^e \quad (2)$$

where bio , D , and H refers to biomass, DBH, tree height, respectively, i refers to the i th part of individual trees, e.g. leaves, d and e are constants are constants estimated via regression analysis (for more information see Appendix2). The biomass of each tree was calculated by adding the biomass values of all parts together, and the flower equation was used for a few individuals with flowers.

2.4. Predictive variables

Environmental predictor variables included topographic and edaphic factors. Elevation was determined by calculating the average value 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. Slope aspect was calculated as the angle between the projection of the slope normal line in the horizontal plane and due north (Lai et al., 2009). Edaphic factors were determined as following: oven-drying method for soil water content (SW), Walkley-Black analysis for 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 diversity metrics of leaf traits are widely used to predict forest standing biomass (Chiang et al., 2016; Finegan et al., 2015; Shen et al., 2016), as leaf traits influence the resource acquisition, growth and survival of species (Poorter and Bongers, 2006). Therefore, we selected leaf traits to construct functional diversity indices in this study. Specific leaf area (SLA) was determined as one-side area of a fresh leaf divided by its oven-dry mass. 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) (Cornelissen et al., 2003). In consideration of the higher correlations of multi-trait functional indices with niche differences than single-trait indices (Kraft et al., 2015), we used above five traits (weighted by basal area) to establish multi-trait functional indices including FRic, FEve, FDiv, FDis, RaoQ (Rao's quadratic entropy), and CWMs by applying R function “dbFD” of package “FD” (Laliberté and Legendre, 2010; Laliberté et al., 2014).

2.5. Data analysis

Individual trees within each plot were classified into under-story ($\text{DBH} \leq 5$ cm), mid-story ($5 \text{ cm} < \text{DBH} \leq 15$ cm) or over-story ($\text{DBH} > 15$ cm) tree layers (Yang et al., 2014). In order to determine the most important predictors and their relative contributions to the biomass variation in each tree layer, model selection and partial least squares regression were conducted in R package “plsVarSel” and “plsdepot”, respectively (Afara et al., 2017; Trogisch et al., 2016). Firstly, functional diversity indices and CWMs for each tree layer were combined with environmental factors to form an explanatory matrix. Secondly, a PLS model was fitted to the explanatory matrix of each tree layer, function “shaving” was employed to eliminate the least important predictors while keeping the most informative variables. Above procedure was repeated until an optimal model performance was achieved (Afara et al., 2017). Thirdly, variable importance for projection (VIP) was calculated for the remaining predictors by applying function “plsreg2” (Trogisch et al., 2016). VIP scores were then used to assess the explanatory power of each predictor. The predictors with a VIP score over 1 can be considered as major contributors to the model, which also means the predictors have a significant effect on the response variable. VIP scores between 1 and 0.8 represent a moderate contribution of predictors, while VIP scores lower than 0.8 indicate no contribution (Frameschi et al., 2013).

Based on the optimal PLS models and their included predictors, we performed the partial least squares path model (by using R package “plspm”) to explore the potential direct and indirect effects of environmental factors, and the relative importance of the mass ratio and the niche complementarity hypothesis (Li et al., 2019). We used latent variables by incorporating elevation, convexity and slope gradient to represent topography, soil chemicals to represent soil nutrient regime, functional diversity metrics to represent functional diversity (FD) and identity (CWM). Bootstrap validation (1000 resamples) was used to examine the significance of the estimated path coefficients (Li et al., 2019). Finally, the relationships between standing biomass of each tree layer and important predictors were displayed with linear regressions by using R package “ggplot2” (Mensah et al., 2018).

3. Results

Fifty-five woody species from 16 families were recorded in 30 forest plots. Species richness at the plot scale ranged from 4 to 26, with a mean value of 13. The mean standing biomass of under-story, mid-story and over-story tree layers were $3.40 \pm 2.89 \text{ Mg ha}^{-1}$, $59.42 \pm 32.56 \text{ Mg ha}^{-1}$ and $387.96 \pm 189.87 \text{ Mg ha}^{-1}$, respectively.

An optimal PLS model with six informative predictors for each tree layer was fitted. Functional richness, convexity, soil total phosphorus, functional divergence, community mean leaf potassium concentration and soil available boron were identified as informative predictors of the biomass of under-story tree layer, among which functional richness was of most importance, due to its VIP score over 1. Convexity and soil total phosphorus were less important ($0.8 < \text{VIP score} < 1$), and the other three predictors had low explanatory power ($\text{VIP score} < 0.8$) (Fig. 2). Elevation, community mean specific leaf area, soil total phosphorus and slope gradient were most relevant to the biomass of mid-story tree layer, and the other two predictors including soil available nitrogen and functional richness showed moderate correlations with it. Elevation and soil total phosphorus were the most important predictors for the biomass of over-story tree layer, with community mean leaf phosphorus concentration, functional dispersion, soil total potassium and soil available nitrogen as moderate predictors (Fig. 2).

The partial least squares path models explained 62.82%, 66.20% and 57.29% of the variation in the standing biomass of under-story, mid-story and over-story tree layer, respectively. The topographic factors and functional diversity showed significant positive direct effects on the standing biomass of under-story tree layer, whereas the edaphic factors showed significant negative effects on it. The topographic factors also showed significant positive indirect effects via functional diversity on it. The topographic factors showed positive indirect effects via functional diversity and functional diversity showed positive direct effects on the standing biomass of mid-story tree layer, whereas the soil factors and CWMs showed negative direct effects on it. The topographic factors displayed pronounced negative direct effects on the standing biomass of over-story tree layer, whereas the soil factors, functional diversity and CWMs showed positive direct effects on it. The other direct and indirect effects were insignificant thus neglected (Fig. 3 and Table 1).

The linear regression analysis displayed the relationships between the standing biomass of each tree layer and its informative predictors. Functional richness was positively correlated with the biomass of under-story tree layer at a highly significant level ($p < 0.01$). Convexity and functional divergence showed significantly and marginally positive associations with it while soil total phosphorus was negatively associated with it. Community mean leaf potassium concentration and soil available boron did not significantly correlate to it (Fig. 4). The biomass of mid-story tree layer showed highly positive trends with elevation, slope gradient and functional richness, and decreased with community mean specific leaf area, soil total phosphorus and soil available nitrogen at a highly significant level (Fig. 5). While the biomass of over-story tree layer decreased with elevation and soil total potassium significantly, it showed significantly positive associations with soil total phosphorus, community mean leaf phosphorus concentration, functional dispersion and soil available nitrogen (Fig. 6).

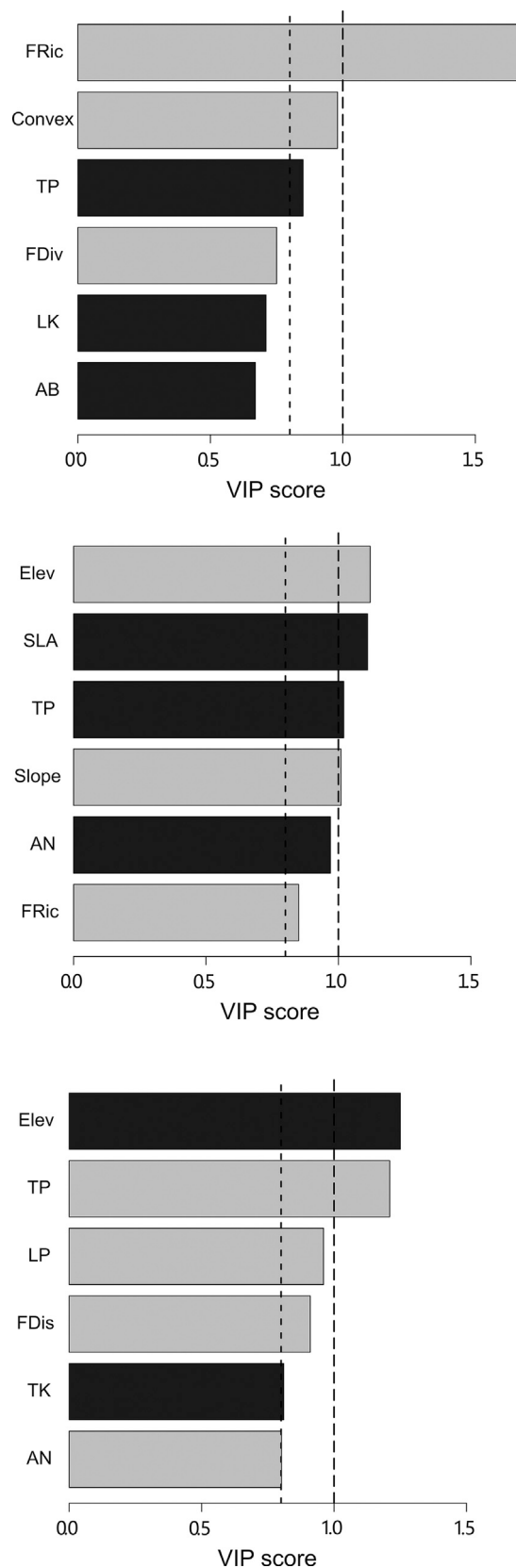


Fig. 2. Explanatory power of selected predictors expressed as variable importance for projection (VIP) for three tree layers (top, under-story tree layer; middle, mid-story tree layer; bottom, over-story tree layer). Grey bars indicate positive and black bars negative correlation with community biomass of each tree layer. The dash line left to line 1.0 indicates VIP score of 0.8. Elev: elevation, Slope: slope gradient, Convex: convexity, TP: soil total phosphorus, TK: soil total potassium, AN: soil available nitrogen, AB: soil available boron, FRic: functional richness, FDis: functional dispersion, FDiv: functional divergence, SLA: specific leaf area, LP: leaf phosphorus concentration, LK: leaf potassium concentration.

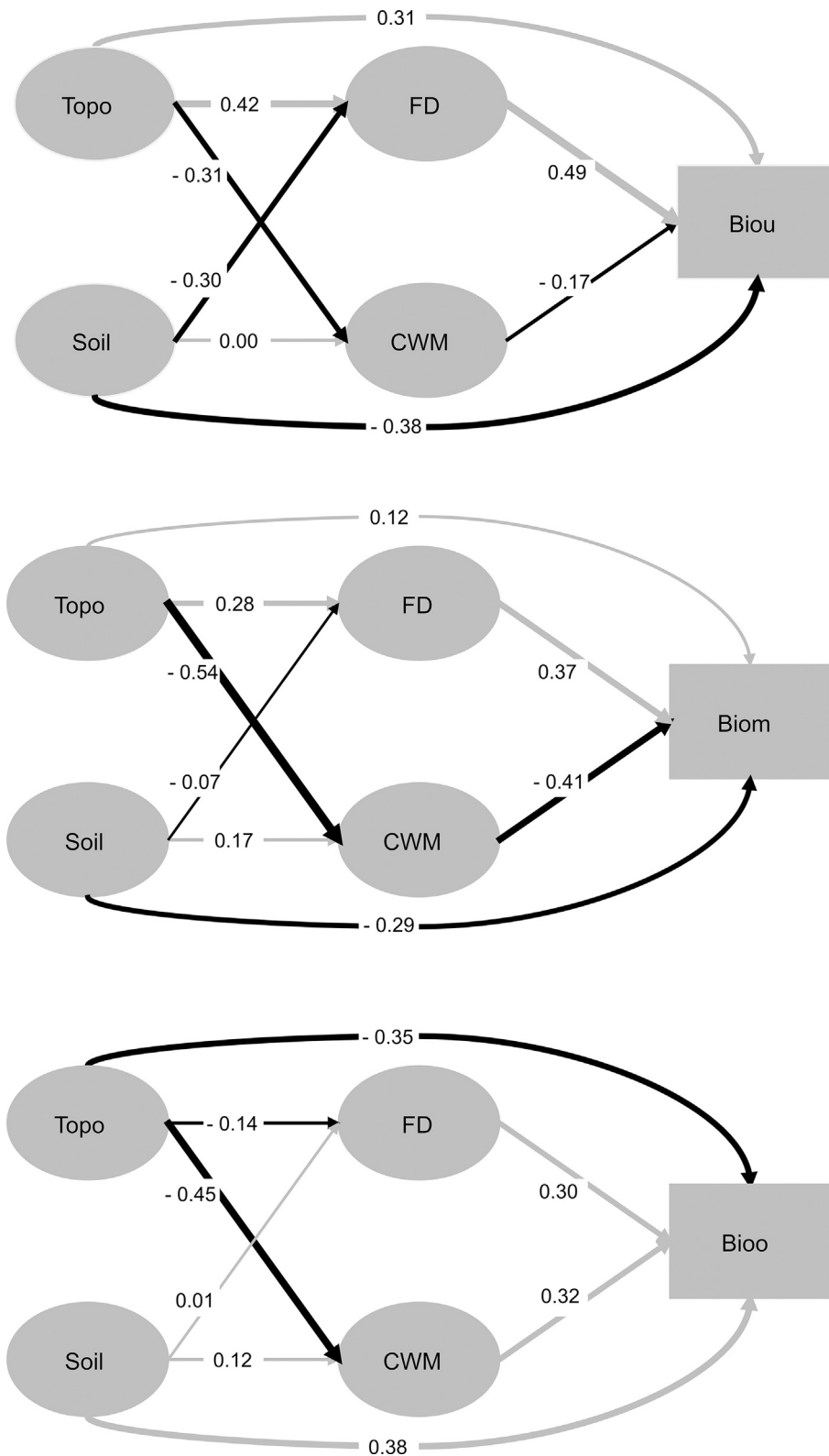


Fig. 3. Path models exploring the direct and indirect effects of topographic and edaphic factors, the mass ratio and niche complementarity hypothesis on standing biomass of three tree layers. Topo: topographic factors, Soil: soil factors, FD: functional diversity indices, CWM: community-weighted mean trait values. Biou, Biom and Bioo denote standing biomass of under-story, mid-story and over-story tree layer, respectively.

Table 1

Direct, indirect and total standardized effects of topographic and edaphic factors, the mass ratio and niche complementarity hypothesis on standing biomass of three tree layers. Notes see Fig. 1. Significant effects are at $P < 0.05$ (*), < 0.01 (**).

Predictor	Pathway to biomass	Biou	Biom	Bioo
Topo	Direct effect	0.31*	0.12	−0.35*
	Indirect effect via FD	0.21*	0.10	−0.05
	Indirect effect via CWM	0.05	0.22**	−0.14
	Total effect	0.52	0.22	−0.35
Soil	Direct effect	−0.38*	−0.29*	0.38**
	Indirect effect via FD	−0.15	−0.03	0.00
	Indirect effect via CWM	−0.00	−0.07	−0.04
	Total effect	−0.38	−0.29	0.38
FD	Direct effect	0.49**	0.37**	0.30*
CWM	Direct effect	−0.17	−0.41*	0.32*



4. Discussion

4.1. The importance of environmental variation in shaping forest standing biomass

Our results demonstrated that multiple covariates simultaneously drive community biomass in this old subtropical broad-leaved forest. **Environmental variation exerted remarkable influence on standing biomass across all tree strata, supporting our hypothesis that abiotic environment may explain more variation of community biomass than functional diversity or identity.** Standing biomass of the three tree layers differed markedly, and was largely influenced by environmental factors such as convexity, elevation, slope gradient, and soil nutrients. Abiotic environment led to high amounts of variation in forest community structure and composition, and habitat preferences of tree species might be a primary cause of differences in community biomass (Yasuhiro et al., 2004). Specifically, the variation in edaphic fertility and water availability caused by topographic heterogeneity showed a significant impact on the patterns of forest community biomass (Shen et al., 2016; Yuan et al., 2016), and significant direct and indirect effects (via functional diversity or CWMs) of topographic factors were also confirmed in this study. **Therefore, our results support previous findings that topographic factors including elevation, convexity and slope, and soil nutrients are effective predictors of community biomass** (Laurance et al., 1999; Slik et al., 2010; McEwan et al., 2011; Marshall et al., 2012).

Different tree layers achieved maximal biomass at opposite ends of some topographic and edaphic gradients, which may be partially due to the divergent soil preference of individual trees with different life-forms and life stages (Palow et al., 2012; Emilio et al., 2014), and the shifts of many species in habitat preference among growth stages (Comita et al., 2007; Lai et al., 2009). The topographic factors (mainly including elevation for the over-story tree layer) had strong negative direct effects on its standing biomass, indicating that large individual trees were filtered out of the higher altitudes. This is possibly caused by limited growth and wind disturbance (Hansen et al., 2000; Marshall et al., 2012), but the higher altitudes favored medium-sized individual trees. While the biomass in the over-story tree layer was concentrated primarily in flat areas, mid-story biomass was positively associated with slope steepness, as also reported by other studies (de Castilho et al., 2006; McEwan et al., 2011). This relationship is probably due to steep slopes led to mechanical instability of individual trees, and might even cause the collapse of large trees (Quesada et al., 2009). Moreover, high rates of soil erosion and leaching of nutrients caused by steep slopes might also reduce community biomass (Marshall et al., 2012). By comparison with the other layers, biomass accumulation in the under-story tree layer was promoted by increasing convexity, consistent with previous findings that concave areas often lead to poorly drained soils, which can be detrimental to young trees (Quesada et al., 2009). It was also reported that in an evergreen broad-leaved forest, under-story individual trees were restricted to convex sites with higher light availability (Enoki and Abe, 2004).

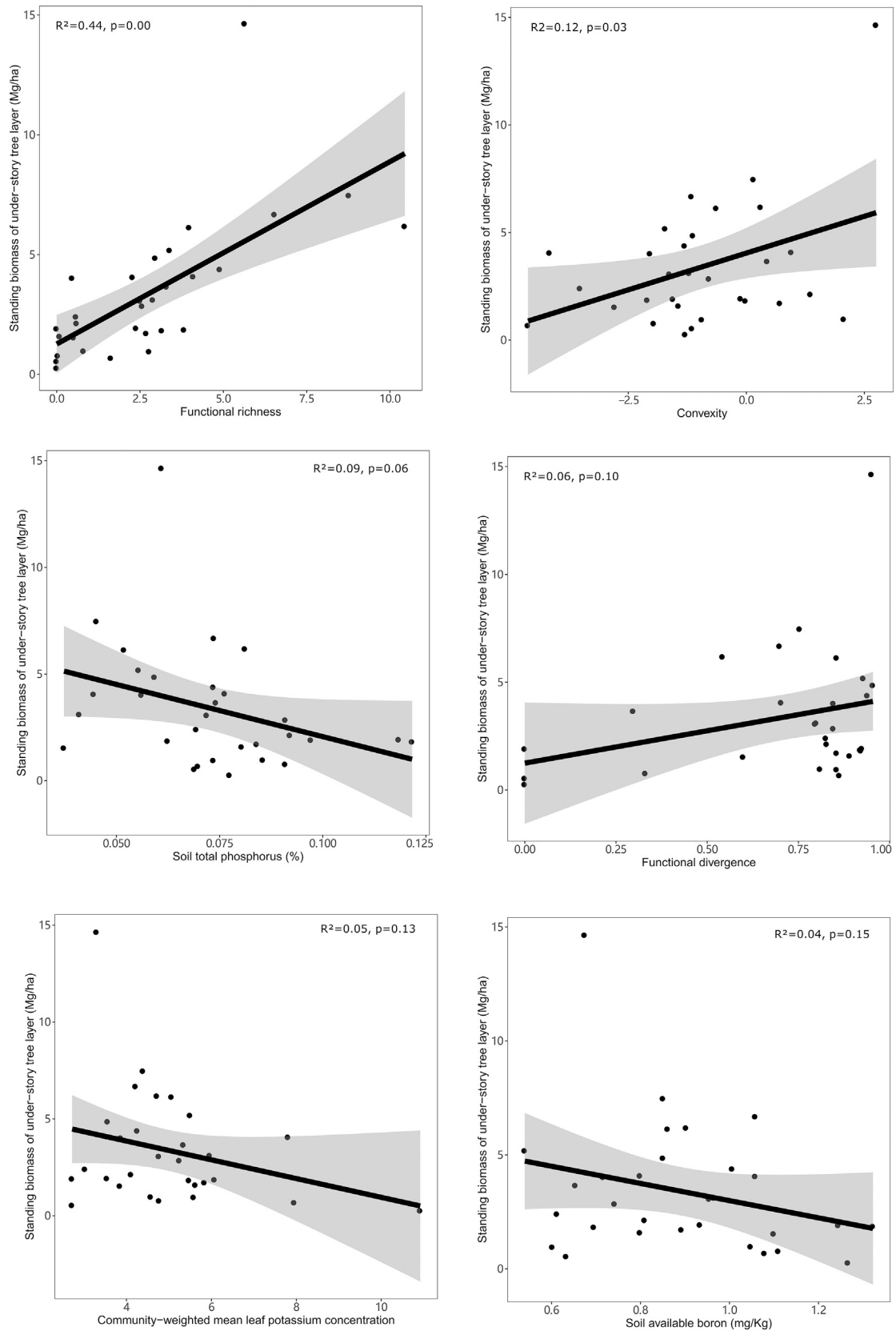


Fig. 4. Correlations between standing biomass of under-story tree layer and selected predictors.

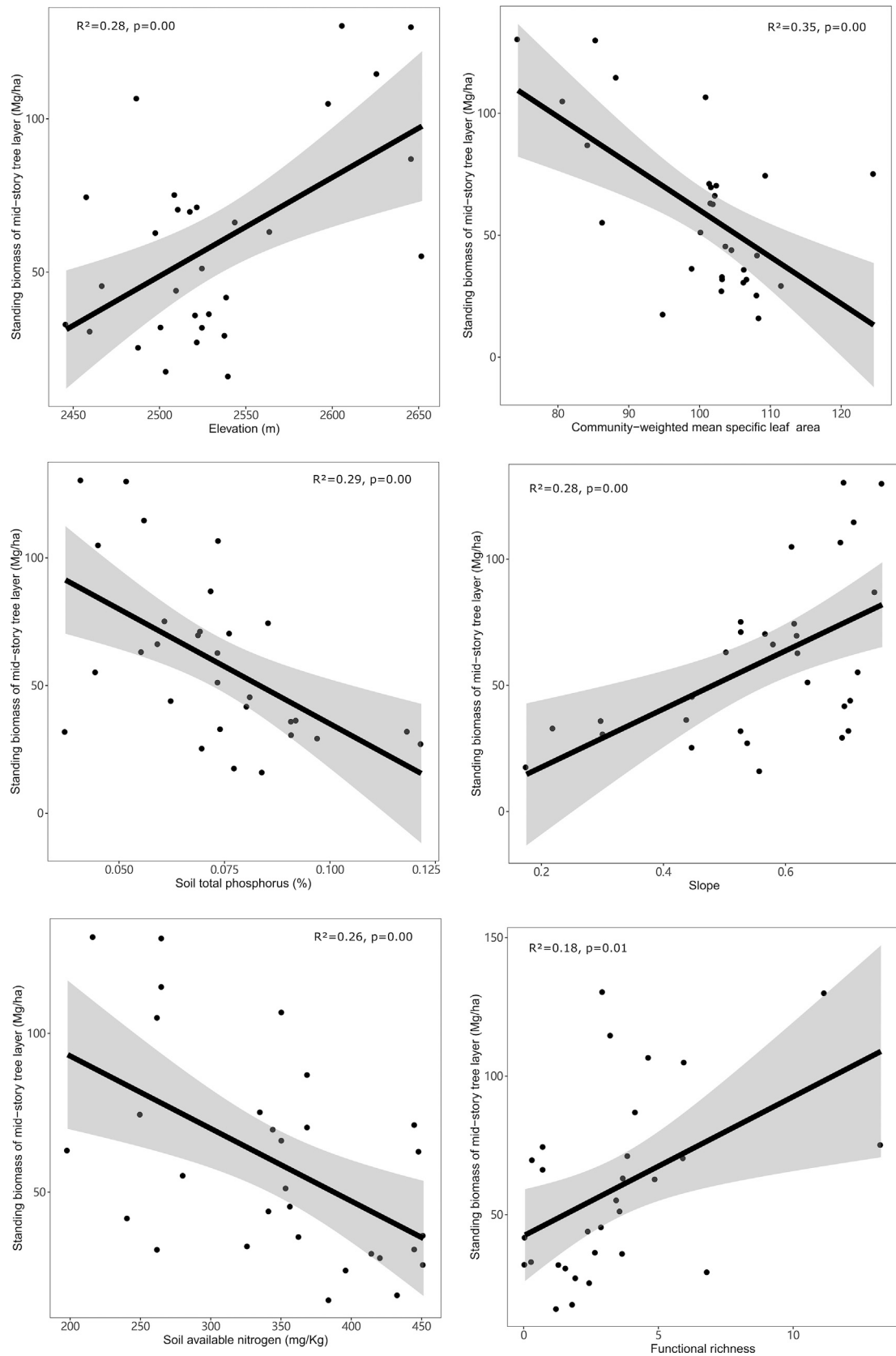


Fig. 5. Correlations between standing biomass of mid-story tree layer and selected predictors.

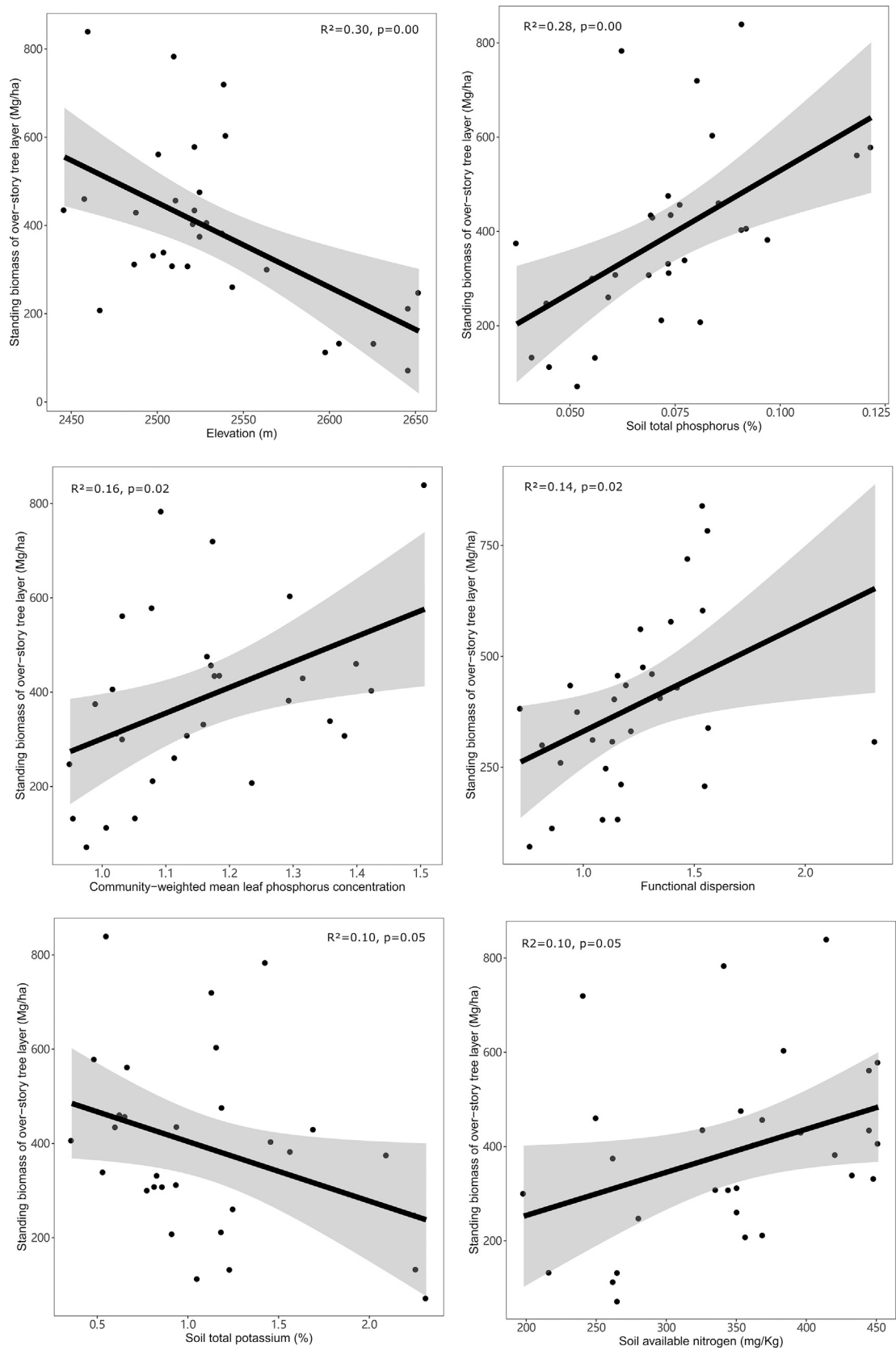


Fig. 6. Correlations between standing biomass of over-story tree layer and selected predictors.

We found significant direct effects of soil variables on standing biomass across all the tree strata. The biomass of over-story tree layer was positively correlated with almost all soil variables except for total potassium, whereas all soil nutrients showed negative effects on that of mid-story and under-story tree layers (Figs. 2–6). Several studies discovered positive links between soil fertility and large trees, which accounted for the large proportion of the standing biomass variation (Paoli et al., 2008; Slik et al., 2013; Xu et al., 2015; Yuan et al., 2016). One possible explanation is that edaphic resource acquisition of competing trees is size dependent. Specifically, competition for soil nutrients is often size symmetric (proportional to their sizes), and tends to be size asymmetry when soil nutrients are heterogeneously distributed (Rewald and Leuschner, 2009; Río et al., 2014; Schwinning and Weiner, 1998). Moreover, fertile soils could also lead to higher rates of forest turnover and mortality of young trees (Xu et al., 2015; Yuan et al., 2016). In addition, soil phosphorus concentration displayed more explanatory power than other soil nutrients, consistent with previous studies which considered soil phosphorus concentration as the most limiting nutrient for forest biomass (Quesada et al., 2012; Finegan et al., 2015).

4.2. The varying importance of functional diversity and identity in predicting forest standing biomass

Previous work on BEF suggested that niche complementarity is an effective mechanism applied to unstable and stressful environments, where beneficial interactions among species may be important. In contrast, the effects of niche complementarity may be weaker in stable and productive environments (Paquette and Messier, 2011; Cavanaugh et al., 2014). In addition, environmental filtering was found to be the main ecological process structuring tree species assemblages in the area we studied (Yang et al., 2014), and strong environmental filtering facilitated a small set of dominant species, whose traits might determine the stock of forest biomass (van der Sande et al., 2018). These findings might partly explain the greater influences of the mass ratio hypothesis in driving biomass of over-story and mid-story tree layers than that of under-story tree layer. Positive diversity-biomass relationship was also observed across three layers in a moist evergreen forest, with most evident complementarity effects in lower tree layer (Mensah et al., 2018). The weaker positive diversity effects in upper layers were ascribed to the fact that the increase of over-story biomass might be more related to the abundance of dominant and large trees (Mensah et al., 2018).

Multiple aspects of functional diversity, such as functional richness, functional divergence and functional dispersion, affected the standing biomass of the three tree layers. While high functional richness indicated well-occupied niches (Mason et al., 2005), high functional dispersion represented an even distribution of dissimilar traits (Frainer et al., 2014), and high functional divergence indicated a high degree of niche differentiation (Mason et al., 2005). Although our results confirmed the positive effects of functional diversity across all of the tree strata involving several components, some BEF studies found no relationships between functional diversity and community biomass (Finegan et al., 2015), or even a negative one (Conti and Díaz, 2013). The insignificant or negative effects of functional diversity might be ascribed to the fact that ecologically important traits are inherently correlated, and there can be positive, negative or no relationships between them (Wright et al., 2007). Diversity of some traits might promote community carbon sequestration, while other traits might not (Shen et al., 2016). While functional divergence of stem traits such as wood-specific gravity and height showed negative effects on above-ground biomass (Conti and Díaz, 2013), our study provides evidence for the positive relationship between the multiple functional indices of leaf traits and standing biomass across tree layers.

Although it has been reported that complementarity effects increased over time and were more apparent in old-growth forests (Cavanaugh et al., 2014; Tobner et al., 2016), in our study functional identity explained more variance than functional diversity in the biomass of mid-story and over-story tree strata. Actually, mass ratio and niche complementarity effects are not mutually exclusive and affect forest community biomass simultaneously (Conti and Díaz, 2013; Cavanaugh et al., 2014; Tobner et al., 2016). Other studies found old-growth forests were mostly dominated by conservative species with larger DBH, higher leaf mass per area (LMA) and lower SLA (Ruiz-Jaen and Potvin, 2011; Shen et al., 2016), supporting our results, for the biomass of mid-story tree layer was reduced with increasing SLA. The high resource use efficiency of dominant tree species resulted in high biomass production in forest communities (Lewandowska et al., 2016), which could be a possible explanation for the stronger effects of functional identity on community biomass, as well as for the absence of functional evenness as an important predictor of community biomass in our study.

5. Conclusions

Overall, our study suggests that topographic and edaphic factors together explain more variation in standing biomass across the tree strata than functional diversity and identity in this old moist evergreen forest, indicating that the diversity effect for biomass production is much weaker than the effect of resource availability. The functional diversity components, as well as magnitudes of the diversity-effect, vary with different tree strata in regulating community biomass, implying the significance of forest vertical stratification for functional diversity-community biomass relationships. The overlook of under-story tree layer or without separating it from over-story tree layer may underestimate the functional diversity roles in regulating community biomass. While other studies suggested that preservation of diverse forests and tree species with dominant functional traits is a key to maintaining ecosystem functioning, our findings support that protection of pristine environment benefitting tree species with suitable trait combinations is also of vital priority.

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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.gecco.2020.e01093>.
Photograph The unique mid-mountain moist evergreen forests in the study area.

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