

# Multiple Drivers of Biomass Change in Subtropical Natural Forests

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## Research Article

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# Abstract

Forest ecosystems play an important role in regulating the global carbon, a substantial portion of terrestrial carbon pool which is stored in biomass stocks. However, how multiple biotic (i.e. topography) and abiotic (biodiversity, stand structure, and functional traits) influence forest biomass in natural forests, the relative important of these factors determine biomass is still controversial for subtropical natural forests. We used forest inventory data from nine 1-ha plots at different altitude gradients in China's subtropical forests. We used multiple analyse to quantify the relative importance of multiple facets of diversity, key functional traits, stand structural attributes, and topography variables in determining forest biomass. We found that multiple facets of diversity and stand structure variables enhances biomass. Specifically, large-diameter trees had a strong positive effect on biomass and were the most important factor in determining biomass. Plant functional traits were closely related to biomass. Community-weighted mean value (CWM) of maximum height positively correlated with biomass, but CWM of wood density negatively correlated biomass. Topographic factors including elevation and slope, had a positive effect on biomass. Moreover, among the aforementioned four types of variables, stand structure had the greatest impact on biomass and is linked to diversity-biomass relationship. Topography mainly indirectly affected biomass by altering multiple diversity and stand structure. Functional traits also directly and indirectly affected biomass. Overall, these results support niche complementarity effect and mass-ratio hypothesis. Our results indicate that biodiversity is essential for maintaining ecosystem functions of species-rich subtropical natural forests. Further, adjusting stand structure may be an effective forest management approach to increase forest carbon storage.

# Introduction

Forest ecosystems play an essential role in biodiversity conservation and carbon cycling (Pan et al. 2011; King et al. 2012). Species-rich subtropical forests cover an extensive area and are crucial in regulating global carbon cycling and maintaining high biodiversity (Li et al. 2019). Evidence is mounting that diverse forest communities generally accumulate biomass more rapidly than species-poor ones (Jucker et al. 2014; Liang et al. 2016). However, changing biotic and abiotic conditions are forcing ecosystems across thresholds into alternative stable, global environmental change and biodiversity loss strongly threaten the sustainability of ecosystem functions and services they underpin (Loreau et al. 2001; Worm et al. 2006; Ives and Carpenter, 2007; Cardinale et al. 2012). Our understanding of biodiversity and ecosystem functioning and their drivers in natural communities remains limited (Zhang and Chen 2015; Fotis et al. 2017). Therefore, more detailed studies are needed to better understand the mechanisms linking biodiversity to ecosystem functioning, especially for species-rich subtropical natural forests.

Recently, studies have revealed that species diversity may enhance productivity/biomass through a variety of mechanisms. For example, the niche complementarity hypothesis assumes that increasing diversity enhances forest productivity through niche differentiation and facilitation (Tilman et al. 1997). In contrast, the selection probability effect proposes that higher species richness increases community productivity through an increased chance of possessing highly productive species (Hooper et al. 2005).

An alternative but not mutually exclusive mechanism to the niche complementarity is the mass-ratio hypothesis (Grime 1998), which states that the most dominant species in the community drive the ecosystem processes by means of their traits. Moreover, species with acquisitive traits lead to faster carbon capture ability, while species with conservative traits possess a higher long-term carbon sequestration strategy (Díaz et al. 2009). Plant functional traits are the key aspects shaping forest biomass dynamics (Díaz et al. 2007; Lohbeck et al. 2015). Species-level differences are important in structuring highly diverse communities (Kraft et al. 2008). Functional trait trade-offs are useful metrics for understanding community response to global change (Kimball et al. 2016). In addition, previous studies reported that plant biomass accumulation predicted by phylogenetic diversity is stronger than by species richness and functional diversity (Cadotte et al. 2008; Liang et al. 2019).

In addition to species diversity, stand structural attributes in natural forests also have a strong influence on biomass and may interfere with the relationship between species diversity and biomass. Structural variability may influence ecosystem processes and functioning. Stand structural complexity increases light capture ability, light-use efficiency, plant water and nutrients use efficiency, promoting the accumulation of biomass in forest ecosystems (Hardiman et al. 2011). Forest biomass is intrinsically related to tree size. A study in natural boreal forests found that tree size inequality links to diversity and aboveground biomass and regulates above-ground biomass and species diversity by interactions among individuals (Zhang and Chen 2015). Studies at global and regional scales have shown that large-diameter trees comprise a large fraction of the stand basal area and biomass in many forests (Paoli et al. 2008; Lutz et al. 2012, 2018; Slik et al. 2013). Mensah et al. (2020) pointed out that structural complexity and large-sized trees explain shifting species richness and carbon relationship across vegetation. Stand density and age are more important modulators of forest productivity than diversity (Ouyang et al. 2018). Recent studies defined a stronger role of stand structure attributes over diversity in shaping forest biomass or productivity patterns (Fotis et al. 2008; Yuan et al. 2018).

It is noteworthy that environmental variation is also a key regulator of productivity/biomass in forests. Topography, for example, represents many aspects of microenvironmental changes. Topographic characteristics such as elevation, slope, and aspect influence microclimate, which are known to drive tree species distributions and abundances (McEwan and Muller 2006; Murphy et al. 2015), influence aboveground biomass (Valencia et al. 2009; McEwan et al. 2011), and forest dynamic (Bellingham and Tanner 2000; Robert 2003). For instance, topography plays a significant role in determining live tree biomass in tropical forests of Amazonia (de Castilho et al. 2006). Poor environmental conditions were found to have strongly limited forest biomass/productivity (van der Sande et al. 2017). In addition, soil type, soil water potential, and nutrient cycling are affected by topography, affecting tree biomass accumulation. Microclimate created by topography also changes stand attributes and leaf characteristics.

In this study, we set up plots at different elevation gradients in three subtropical forests. This ultimate goal is to determine how multiple diversity, plant functional traits, stand structure attributes, and topographic factors affect biomass in subtropical forests. Specifically, we address four questions. First,

we ask (i) is there a positive relationship between multiple diversity and biomass in a subtropical natural forest? Second, we incorporate data on key plant functional traits related to tree growth to ask (ii) is biomass influenced through the mass-ratio effects? Third, we ask (iii) how do stand structural attributes affect biomass of subtropical forests and maintain the diversity-biomass relationship? Finally, we ask (iv) how do topographic factors drive biomass other biotic factor? To answer these research questions, we used bivariate relationships, multiple linear regression, variation partitioning analysis and structural equation model based on existing research theories (Fig. 1a) to quantify the relative importance of multiple diversity, functional traits, stand structure, and topographic factors as the best predictors of variation in biomass.

## Materials And Methods

### Site description

We selected three Nature Reserves in Nanling National Forest Park to carry out this study, including Nanling (112°30'–113°04'E, 24°37'–24°57'N), Luoken (113°11'48"–113°25'55"E, 24°29'24"–24°3'40"N), and Shimentai (113°01'11"–113°46'22"E, 24°31'02"–24°17'49"N), respectively (Fig. 1b). The region experiences a monsoonal climate characteristic of subtropical regions. It is also a valuable natural heritage. Natural evergreen broad-leaved forests dominate the primary vegetation type. The annual precipitation ranges from 1615 to 1883 mm, with a yearly frost-free period lasting from 305 to 319 days, and the annual mean temperature and relative humidity level are 20.9°C and 78%, respectively, with a mean monthly maximum temperature of 9.5°C in January and 28.9°C in July, with distinct dry and wet seasons. The main soil types are red soil and yellow soils. The dominant trees in this region include *Schima superba*, *Castanopsis carlesii*, *Castanopsis eyrei*, *Pinus massoniana*, *Cunninghamia lanceolata*, *Diospyros morrisiana*, and *Machilus chinensis*.

### Plot settings and data collection

The forests in these three Nature Reserve have been well protected and with virtually no human disturbances or fire for a long time. The canopy is completely closed. From 2018 to 2020, we established three 1-ha study plots in different altitude gradients of the three Nature Reserves, a total of nine 1-ha forest plots were set up for vegetation census. Each forest plot consisted of twenty-five 20×20 m subplots. During the inventory, we recorded the geographic coordinates of each plot and the elevation of each subplot. Within each subplot, we followed the same procedures to map, tag, measure, and identify all woody-plant individuals with a DBH  $\geq$  1 cm. We also recorded the species names, DBH, height, crown width, health status, and spatial coordinates. The spatial coordinates of each individual had two-dimensional accuracy of  $\pm$  15 cm. A total of 33,172 individuals were recorded in the nine 1-ha plots, belonging to 343 species, 142 genera, and 61 families.

### Variables used in analyses

We estimated standing biomass for live trees each species (tons, t) in the 20×20m subplots using allometric equations based on DBH. The total biomass for each tree included leaves, branches, stems, and roots. We then calculated standing biomass, which represents the accumulated productivity since the stand establishment. Species richness or the number of species in a given area, a measure of changes in species dynamics, is the most common measure for characterizing community diversity. The often-recommended Simpson and Shannon-Wiener indices may still be highly correlated with species richness. Due to the strong correlation between log species richness and these indicators (Shannon:  $r = 0.83$ , Simpson:  $r = 0.55$ , with  $n = 225$  of subplot), species richness was selected as a key representative. We also calculated tree Faith's phylogenetic diversity based on species's evolutionary distances (Faith, 1992), which incorporates relative abundances and phylogenetic distances at set spatial scales. Further, trees with present branch lengths were generated according to Zanne et al. (2014), based on APG III. The generated phylogenetic tree is shown in Figure S1.

Functional diversity was quantified using the functional dispersion index (Laliberté and Legendre 2010). We calculated the functional diversity for each subplot using the wood density and maximum tree height for each species. Wood density data was extracted from the global wood density database (Zanne et al. 2009; <https://datadryad.org/handle/10255/dryad.235>). Tree maximum height for each species was obtained from the Flora of China (<http://iplant.cn>). Figure S1 shows wood density and maximum height for each species used in this study. We calculated the community-weighted means for wood density ( $CWM_{WD}$ ) and maximum height ( $CWM_{MH}$ ) of each trait weighted by the abundances of each species in each subplot. To ensure that our conclusions were not dependent on the functional indices used, we also calculated Rao's Quadratic entropy index (Rao's Q). The Rao's Q is a widely used multi-trait functional diversity metric that incorporates both the relative abundances of species and the pairwise functional distance between species (Laliberté and Legendre 2010; Cavanaugh et al. 2014). Functional indices were calculated using the R package 'FD' (Laliberté and Legendre 2010).

Stand structural variables in this study included DBH variation, stand density, and maximum DBH (Fotis et al. 2017; Ouyang et al. 2019). We calculated the coefficient of variation (CV) to represent tree size variation, which is the ratio of standard deviation of all DBH measurements to the mean DBH within each subplot. Stand density and maximum diameter were used to represent the number of individuals and dominant species in each subplot. Topographic variables included elevation, slope, and convexity. According to the elevation of each subplot, the slope and convexity within the subplot were calculated. Convexity was calculated as the elevation of the central subplot minus the average elevation of the eight adjacent subplots.

## Statistical analyses

With the ln-transformed biomass, we first tested correlations between individual continuous predictor variables and forest biomass using Pearson correlation coefficients. All indicators were standardized before the analysis. We used multiple linear regression to evaluate the effects of all predictors simultaneously. The full model included multiple diversity (species richness, phylogenetic diversity, and

functional diversity), functional traits ( $CWM_{WD}$ ,  $CWM_{MH}$ , and Rao's Q), structural variables (stand density, maximum DBH, and DBH variation), and topographic variables (elevation, slope, and convexity). The variance inflation factor (VIF) was used to diagnose the multicollinearity of the explanatory variables, with  $VIF > 10$  indicating excessive collinearity. The Akaike information criterion (AIC) was used to compare the model results. The VIF was calculated with the R package 'CAR' (Fox and Monette 1992). The comparison and averaging of models were conducted using the R package 'MuMIn' (Bartoń 2016).

We conducted a random forest classification analysis to identify the main predictors of forest biomass. The random forest analysis allowed us to identify the most important drivers of biomass among 12 variables. This analysis accounted for interactions and nonlinear relationships between predictors, and addressed the multicollinearity problem in multivariate regression. The fit for each tree was determined by randomly selecting cases. In addition, the importance of each predictor variable was estimated from the percentage increase in the mean square error between observation and prediction, and the decrease was averaged over all the trees to produce the final estimation of importance. This accurate measure was computed for each tree and averaged over the forest (i.e. 9999 trees) using the R package 'randomForest'.

Variation partitioning analysis was used to quantify the relative importance of multiple diversity diversity, functional traits, stand structure and topographic variables as predictors of biomass. In particular, the main goal of these analyses provides insights into whether these four types can explain a unique portion of the variance, which further explains the relative importance of the two underlying mechanisms. The variation partitioning analyses were conducted using the R package 'vegan' (Oksanen et al. 2017). All the above analyses were run in R version 3.3.3 (R Core Team 2017) (<http://www.R-project.org/>).

We first performed a principal component analysis was used to reduce the number of multiple diversity, functional traits, stand structure and topographic variables. Variables were standardized for the principal component analysis. We used the structural equation model (SEM) to investigate the impact of these four types of predictors on biomass directly and indirectly. We first designed a full conceptual model framework that included all possible pathways based on existing research theories. Path coefficients were obtained by using maximum likelihood estimation. We used  $\chi^2$  test, AIC, and the root mean square error (RMSE) of approximation to evaluate the model's fitness. All SEM analyses were performed using AMOS 21.0 (Amos Development Corporation, Chicago, IL, USA).

## Results

### Correlations between predictor variables and biomass

We found that all stand structural variables positively correlated with biomass. Specifically, both maximum DBH ( $R^2 = 0.43$ ,  $P < 0.001$ ) and DBH variation ( $R^2 = 0.13$ ,  $P < 0.001$ ) considerably explained the variation in biomass, followed by stand density ( $R^2 = 0.03$ ,  $P < 0.05$ ) (Figs. 2a-c). Similarly, species richness ( $R^2 = 0.28$ ,  $P < 0.001$ ), phylogenetic diversity ( $R^2 = 0.23$ ,  $P < 0.001$ ), and functional diversity ( $R^2 = 0.06$ ,  $P < 0.001$ ) positively correlated with biomass (Figs. 2d-f). Among the functional traits,  $CWM_{MH}$

positively correlated with biomass ( $R^2 = 0.08$ ,  $P < 0.001$ ),  $CWM_{WD}$  negatively correlated ( $R^2 = 0.08$ ,  $P < 0.001$ ) while Rao's Q had no significant correlation with biomass (Figs. 2g-i). Among topographic variables, elevation ( $R^2 = 0.08$ ,  $P < 0.001$ ) and slope ( $R^2 = 0.08$ ,  $P < 0.001$ ) showed positive correlations with biomass, while convexity had no correlation with biomass (Figs. 2j-l).

Among all individual predictor variables, species richness and phylogenetic diversity significantly and positively correlated with all stand structural variables ( $P < 0.05$ ). Rao's Q was negatively related to maximum DBH ( $R^2 = 0.03$ ,  $P < 0.01$ ) and DBH variation ( $R^2 = 0.05$ ,  $P < 0.001$ ), but positively correlated with stand density ( $R^2 = 0.04$ ,  $P < 0.01$ ).  $CWM_{MH}$  positively correlated with DBH variation ( $R^2 = 0.07$ ,  $P < 0.001$ ). Elevation ( $R^2 > 0.11$ ,  $P < 0.001$ ) and slope ( $R^2 > 0.02$ ,  $P < 0.05$ ) positively correlated with all diversity indices. Elevation negatively correlated with DBH variation ( $R^2 = 0.06$ ,  $P < 0.01$ ). Slope significantly positively correlated with all structural variables ( $R^2 > 0.02$ ,  $P < 0.05$ ). Elevation positively correlated with  $CWM_{MH}$  ( $R^2 = 0.03$ ,  $P < 0.01$ ) but negatively correlated with  $CWM_{WD}$  ( $R^2 = 0.07$ ,  $P < 0.001$ ). Slope positively correlated with  $CWM_{MH}$  ( $R^2 = 0.09$ ,  $P < 0.01$ ) and Rao's Q ( $R^2 = 0.10$ ,  $P < 0.01$ ) (Table S1).

## Relative importance of predictor variables on biomass

The final multiple regression model explained 67.35% of the variation in biomass (Fig. 3a). Among the all stand structural variables, the maximum DBH had the strongest effect on biomass, followed by stand density and DBH variation. Among the functional traits,  $CWM_{MH}$  had a positive effect on biomass, while  $CWM_{WD}$  and Rao's Q had a negative effect on biomass. Moreover, functional diversity and elevation had a positive effect on biomass. While species richness, phylogenetic diversity, and slope did not appear in the final model (Fig. 3a). Meanwhile, random forest model explained 62.79% of the variation in biomass. The most relative importance was the maximum DBH, followed by species richness, elevation, DBH variation and  $CWM_{MH}$ . The relative importance of the remaining indicators was relatively low (Fig. 3b).

## Direct and indirect effects of main drivers on biomass

Variation partitioning analysis revealed that the single effect of stand structure explained a much greater portion of variance in biomass (29%), followed by the combined effect of stand structure and multiple diversity explained 11%, respectively. Topography, multiple diversity and stand structure jointly explained 7% of biomass. The single effect of functional traits and the combined effect of stand structure and functional traits all explained 5% of biomass, respectively. The combined effect of topography and functional traits also explained 5% of biomass (Fig. 4a).

The SEM found that elevation directly and indirectly explained 59% of the variation in biomass via multiple diversity, stand structure, and functional traits (Fig. 4b). Stand structure ( $\beta = 0.54$ ) and multiple diversity ( $\beta = 0.45$ ) directly increased biomass, but functional traits directly decreased biomass ( $\beta = -0.32$ ). Importantly, multiple diversity indirectly increased biomass via increasing stand structure ( $\beta = 0.08$ ), but functional traits indirectly decreased biomass via reducing stand structure ( $\beta = -0.07$ ). Topography had a weak total direct ( $\beta = 0.03$ ) and indirect effect ( $\beta = -0.06$ ) on biomass. Notably,

topography indirectly increased biomass via increasing multiple diversity ( $\beta = -0.10$ ), but indirectly decreased biomass via stand structure ( $\beta = -0.16$ ) (Figs. 4b, c; Table S2).

## Discussion

### Multiple facets of diversity promotes forest biomass

A substantial body of evidence sustains that biodiversity enhances productivity or biomass in forest ecosystems (Tilman et al. 2014; Cavanaugh et al. 2014; Ruiz-Benito et al. 2014; Liang, et al. 2018, Huang et al. 2018). As expected, we found that species richness, phylogenetic diversity and functional diversity were positively related to biomass (Figs. 2d-f). The SEM showed that multiple diversity also increased biomass directly (Fig. 4b, c). Our results supports the idea that the niche complementarity is operating in species-rich subtropical natural forests. In addition, the relationship between species richness (or phylogenetic diversity) and biomass was not statistically significant when other factors were accounted for in the multiple regression model (Fig. 3a), indicating that species richness and phylogenetic diversity have independent effects on biomass, which is consistent with previous studies in temperate forests (Fotis et al. 2017; Yue et al. 2020). Linear regression analysis revealed that species richness and phylogenetic diversity are a better predictor of biomass than functional diversity. Our results indicate biodiversity promotes biomass in subtropical natural forests. Liang et al. (2019) have found that species richness and phylogenetic diversity in a subtropical forest are positively correlated with biomass for adult trees and seedlings across multiple spatial scales, while productivity is well predicted using phylogenetic diversity. Previous studies also indicate that significant effects of biodiversity on forest biomass during the succession of subtropical forest in south China (Ouyang et al. 2016).

### Effect of functional traits on forest biomass

Strategy differentiation among species contributes to the maintenance of diversity in tropical forests (Kraft et al. 2008). Plant functional traits have determined the trade-off between productivity and biomass in various forest ecosystems (Hao et al. 2018). Many studies generally find that the values of community-level traits respond to environmental gradients. We selected two key functional traits to reflect tree growth, species composition and response to environmental conditions. Wood density is a key trait driving the trade-off between growth and survival, as low wood density allows rapid growth of the canopy, higher diameter growth rate, and greater productivity, whereas high wood density results in a greater chance of survival (Chave et al. 2009). We found that the negative correlation between  $CWM_{WD}$  and biomass suggests that plots with lower  $CWM_{WD}$  have higher biomass accumulation rates (Fig. 2h).  $CWM_{WD}$  was negatively related to tree carbon storage in subtropical forests, emphasizing that the importance of the traits of dominant species in maintaining ecosystem function (Li et al. 2019). However, a study in neotropical forests showed that  $CWM_{WD}$  increased aboveground biomass, either directly because high wood density implies more stem biomass per wood volume or indirectly as wood density enhances stem longevity (Poorter et al. 2017). Furthermore, maximum tree height has universally been seen as ecologically important and included in ecological strategy schemes, which is an important

indicator of the strategy that a species uses for light-capture and competitive ability with neighbors (Westoby et al. 2012; Kraft et al. 2008). Our results found that  $CWM_{MH}$  positively correlated with biomass (Fig. 2g), indicating that more dominant trees are conducive to biomass accumulation. The effects of changes in  $CWM_{WD}$  and  $CWM_{MH}$  on biomass supports the mass-ratio hypothesis.

## **Stand structure as predictors of forest biomass**

Various studies have recently demonstrated that stand structural attributes strongly influenced on biomass compared with diversity (Fotis et al. 2017; Ouyang et al. 2019; Yue et al. 2020). For example, dominant species tend to determine community biomass (Slik et al. 2013; Zhou et al. 2013). Previous studies reported that large-diameter trees comprise a large fraction of the biomass of many forests and are predominant contributors of forest productivity (Lutz et al. 2018; Xu et al. 2019). Large-diameter trees play a key role in forest ecosystems and also store large quantities of carbon due to their high wood volumes (Lutz et al. 2012; Lindenmayer et al. 2012; Slik et al. 2013); however, they are more sensitive to drought than small trees, which can increase mortality disproportionately (Nepstad et al. 2007; Phillips et al. 2010; Bennett et al. 2015). Because tree biomass is dependent on tree size, our study indicated a significant positive relationship between maximum DBH and biomass (Fig. 2b). To be sure, our results suggest that maximum DBH had the greatest effect on biomass compared to other predictors.

Multiple analyses showed that the DBH variation was positively correlated with biomass (Figs. 2–3), suggesting that tree size inequality was the main regulation mechanism for biomass. Tree size inequality is caused by both differences with and among species and represents niche differentiation and facilitation (Coomes et al. 2009; Morin et al. 2011), a key process for maintaining species diversity and the positive diversity-productivity relationships. Together with previous studies, furthermore, we have demonstrated that the positive impact of stand density on forest biomass in natural forest ecosystems (van der Sande et al. 2017; Yuan et al. 2018; Yue et al. 2020). Stand density can reflect the available resources and space occupation of trees and may also, to some extent, reflect intraspecific interactions (Morin 2015; Fortunel et al. 2018). It has more potent effects on forest productivity than diversity based on large inventory datasets (Forrester and Bauhus 2016; Ouyang et al. 2019).

The SEM revealed that stand structure directly and strongly increased biomass and became the most important factor explaining variation in biomass. Notably, multiple diversity indirectly increased biomass via increasing stand structure (Fig. 4b,c). Collectively, this study suggests that a structurally complex forest stand increases biomass of subtropical natural forests and plays a major role in modulating diversity-biomass relationships. That is, these results demonstrate the complementarity effect in subtropical natural forests. Previous results have found that the positive diversity effects on forest biomass were mediated by promoting tree size inequality in boreal forests (Zhang and Chen 2015). Our finding is consistent with the reported variations among individuals in natural forests, critical to species coexistence (Clark 2010).

## **Effect of topographic factors on forest biomass**

Topography can influence multiple diversity, functional traits, stand structural attributes, and biomass in China's subtropical forests in multiple ways. Topography is strongly correlated with soil nutrient availability, temperature, hydrology, and light conditions (Mascaro et al. 2011; Tateno and Takeda, 2003), and thus is expected to play an important role in shaping the relationship between biodiversity and ecosystem functioning (Grossiord et al. 2014; Liu et al. 2014). Here, our results showed that diversity and biomass decreased with increasing elevation gradients. In contrast, our results found that species diversity and biomass increase with altitude gradient (Fig. 2j; Table S1), highlighting the role of habitat heterogeneity in regulating variation of diversity and biomass in subtropical natural forests. An increase in variation in aboveground live tree biomass with increasing elevation gradients has been observed in a central Amazonian (de Castilho et al. 2006).

Increasing temperatures are considered to be a key driver of upward migration of vascular plant species in mountains (Gottfried et al. 2012). A floristic composition study of alpine summit vegetation recorded that while plant species richness continued to increase, the trend in the upward shift of alpine plants accelerated (Walther et al. 2005). Furthermore, with the introduction of alien species, species richness of the region will usually increase (Sax and Gaines 2003), and due to the current warming of the cold and humid regions, the species richness is also expected to increase (Pauli et al. 2012). Moreover, due to climate change and global warming, some species may move to high altitude areas that were previously not suitable for plant growth, suggesting a widening of the adaptation range of such species. These reasons have also caused forest biomass of this area to increase with altitude.

Additionally, functional traits can be used to evaluate functional responses to restoration projects (Laughlin, 2014). First, we found that elevation (or slope) has a significant negative effect on  $CWM_{WD}$  (Table S1). We preliminarily predict that tree species with low wood density and higher diameter growth rate (e.g. large-diameter trees, fast-growing tree species) are increasing along elevation gradient, tree species with high wood density and lower growth rate (small tree, slow-growing tree species) are reducing change of survival. Second, our results also found that elevation has a significant positive effect on maximum DBH and  $CWM_{MH}$  (Table S1), suggesting that large diameter trees and higher trees are increasing along elevation gradient. Collectively, in response to global climate changes, these functional traits with altitude gradients will affect tree composition, life strategies and individual differences, emphasizing that functional traits respond to changes in elevation gradients that has important consequences for ecosystem functioning. Meanwhile, future studies should consider the impact of environmental changes caused by topography on ecological functions.

## Conclusions

This study shows the relative importance of multiple facets of diversity, key functional traits, stand structural attributes, and topographic variables on biomass variation in subtropical natural forests. We found that multiple facets of diversity were positively correlated with biomass. Plant functional traits also had a significant effect on biomass. More importantly, stand structure was a driver of biomass and regulated the diversity-biomass relationship. In addition, elevation and slope had a positive effect on

biomass. The SEM showed that topography mainly and indirectly affected biomass via altering multiple diversity and stand structure. In particular, the impact of elevation on biodiversity, functional traits and biomass was worthy of attention. Overall, this study advances our understanding of the mechanisms affecting biomass in complex subtropical natural forests. We also emphasize that many aspects of biodiversity are crucial for maintaining biomass of species-rich subtropical natural forests, supporting niche complementarity effect and mass-ratio hypothesis. Stand structure attributes should also be highly valued in the process of forest management, as well as the influence of environmental conditions on maintaining forest functioning.

## Declarations

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Declarations

**Conflict of interests** The authors declare that they have no conflict of interest.

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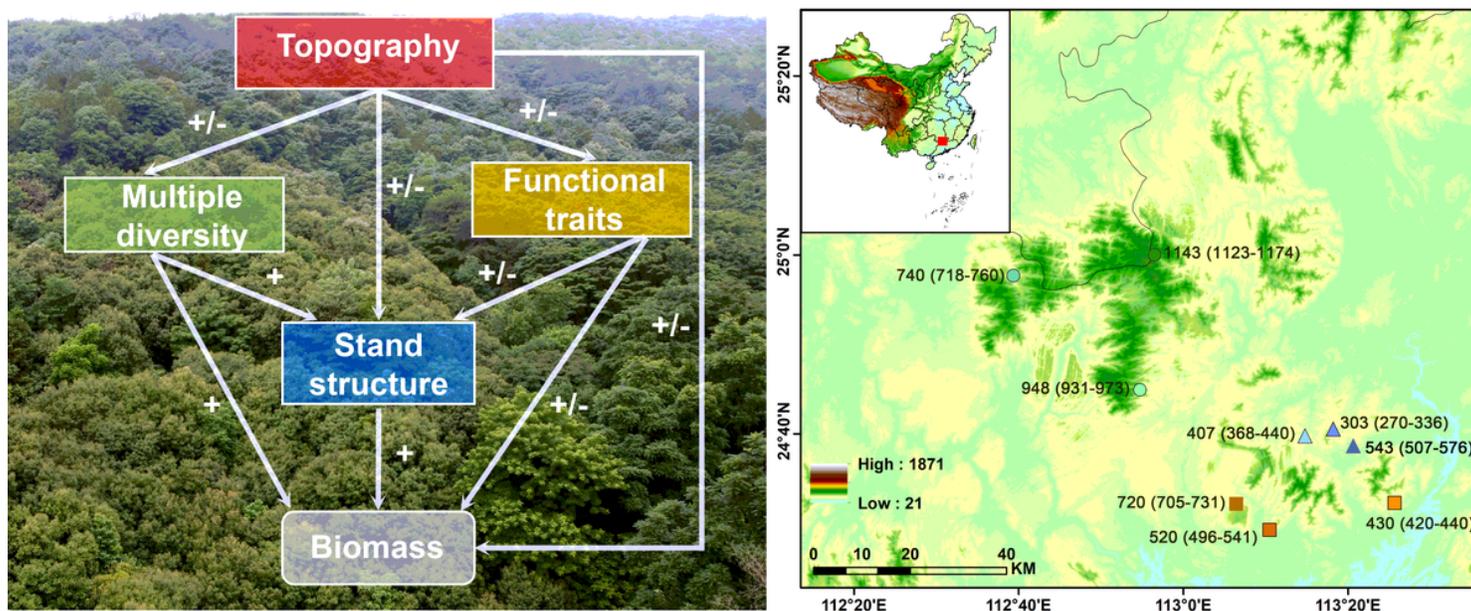
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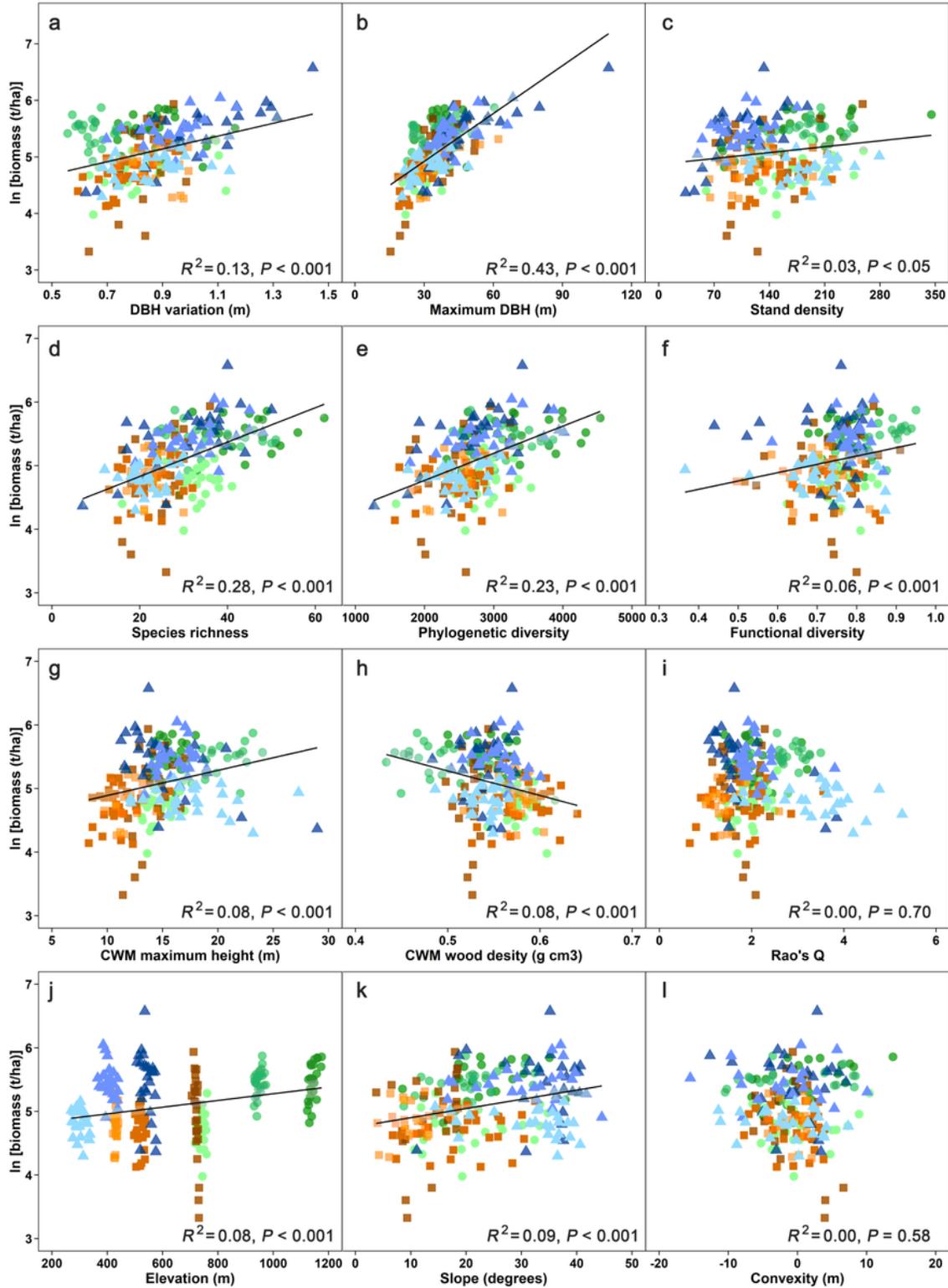
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## Figures



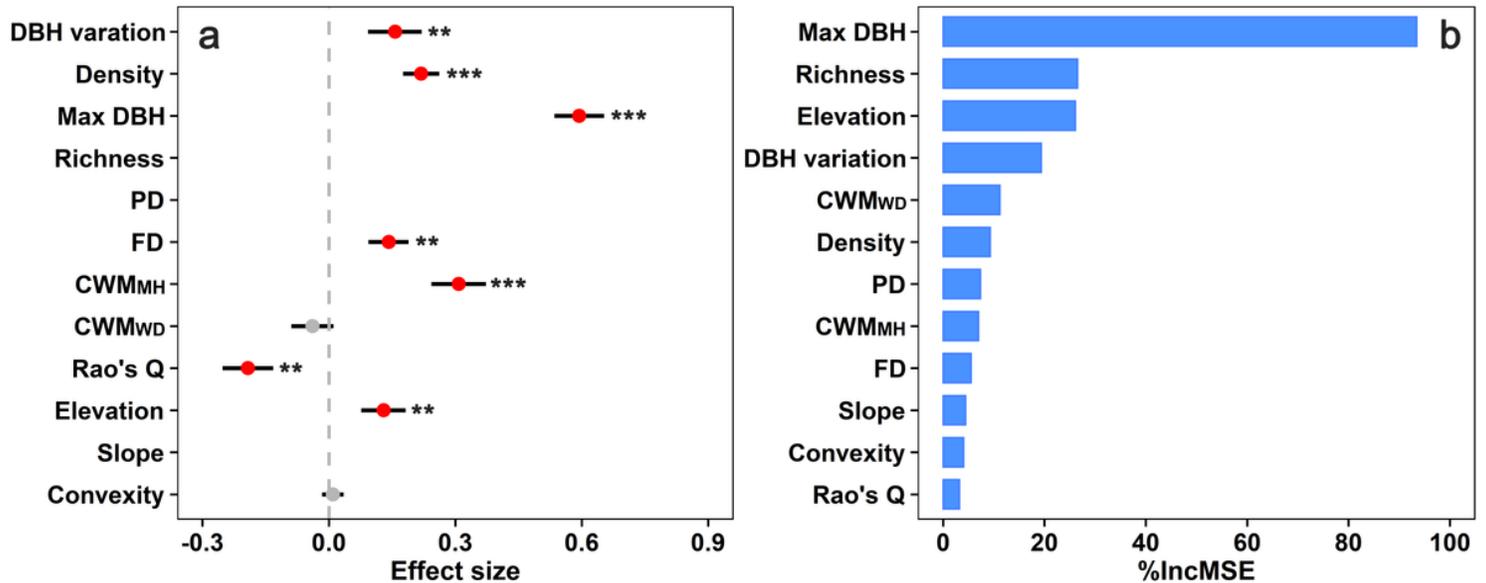
# Figure 1

Conceptual models for prediction of biomass and distribution of sample plots in a subtropical natural forest. (a) Hypothetical causal model for structural equation model exploring the effects of multiple diversity, functional traits, stand structure and topography on biomass. (b) Location of the nine 1-ha sample plots in subtropical forests in China (generated by ESRI ArcGIS 10.2). The text in the figure is the average altitude and range of the sample plot.



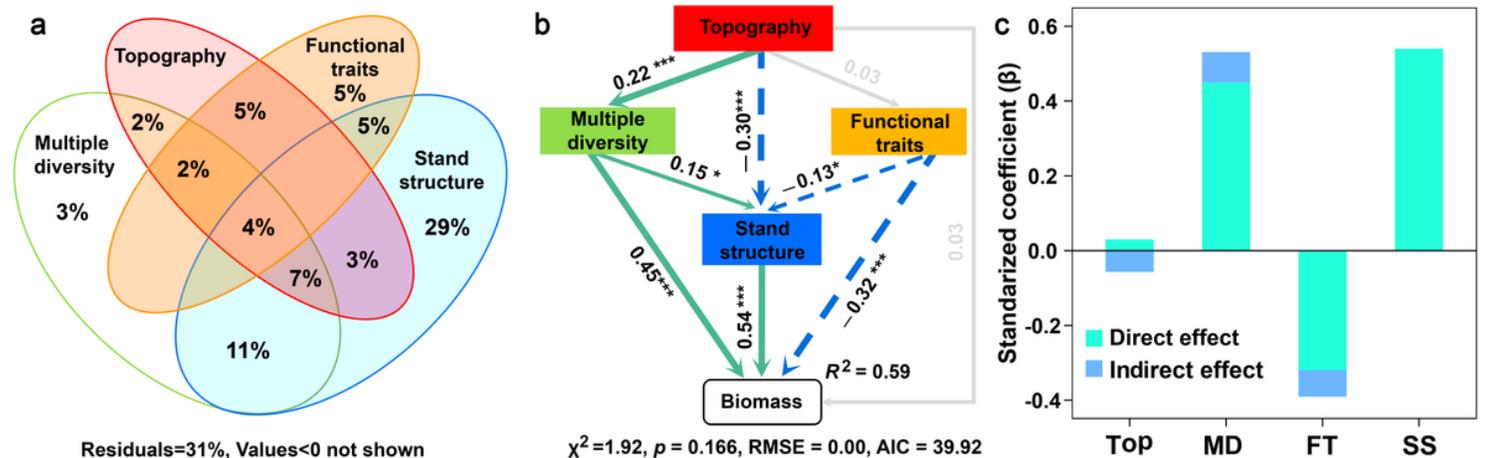
**Figure 2**

Relation between biomass and structural variables (stand density, maximum DBH and DBH variation), diversity indices (species richness, phylogenetic diversity and functional diversity), functional traits (Rao's Q and community-weighted mean (CWM) of maximum height and wood density) and topographic variables (elevation, slope and convexity). Light grey bands represent 95% confidence intervals, and the legend is shown in figure 1b.



**Figure 3**

Multiple regression and random forest model results of forest biomass using individual predictor variables. (a) Each variable was standardized and their effect sizes (circles) were compared to determine differences in the strength of predictor variables on biomass. Red circles indicate significant effects on biomass, and lines indicate standard errors. (b) Results from random forest analyses aiming to identify individual predictor variables of biomass. The increase in the mean square error (MSE, %) is displayed along the x-axes.



**Figure 4**

Effect of multiple factors on forest biomass. (a) Relative contributions of topography, multiple diversity, functional traits, and stand structure to biomass. (b) Direct and indirect effects of topography, multiple diversity, functional traits, and stand structure on biomass. Solid and dotted line indicate positive and negative effects, respectively. R<sup>2</sup> indicates the proportion of variance explained. The numbers on the arrows indicate standardized path coefficients (n=225). Significant effects are at P < 0.05(\*), P < 0.01(\*\*) and P < 0.001(\*\*\*). (c) Standardized coefficient of topography (Top), multiple diversity (MD), functional traits (FT), and stand structure (SS) on biomass.

## Supplementary Files

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