



Multiple abiotic and biotic drivers of aboveground biomass shift with forest stratum



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ABSTRACT

Insights into the underlying ecological mechanisms for diversity-biomass relationships across forest strata (i.e., overstorey and understorey) are crucial to understand the importance of vertical stratification on ecosystem function in natural forests. Yet, it remains unclear how multiple abiotic (i.e., soil nutrients) and biotic (i.e., biodiversity, functional identity and stand structural complexity) factors simultaneously determine aboveground biomass in each individual forest stratum and whole-community. To address this knowledge gap, we disentangled the relative effects of soil nutrients (soil fertility hypothesis), taxonomic, functional trait and evolutionary diversity (niche complementarity hypothesis), stand structural complexity (niche differentiation hypothesis based on tree sizes), and community-weighted mean trait values (mass ratio hypothesis) on aboveground biomass across forest strata and whole-community. We used forest inventory, functional traits and environmental factors datasets from 125 subtropical forest plots in Eastern China. Multiple linear regression models were performed for the selection of best predictors within each biotic group, and structural equation modelling was used to evaluating how multiple abiotic and biotic drivers determine aboveground biomass. In the overstorey, aboveground biomass was positively related to the community-weighted mean of tree height (i.e., functional dominance) and stand density but was negatively related to functional evenness on nutrient-rich soils. In the understorey, aboveground biomass was positively related to phylogenetic species richness and stand-level tree mean diameter (i.e., a proxy for forest growth) but was negatively related to Shannon's species diversity on nutrient-poor soils. Understorey aboveground biomass was also determined by overstorey stand structure and functional dominance through direct and indirect effects via understorey biotic drivers. These results suggest that functional dominance and stand structural complexity are the main biotic drivers of overstorey aboveground biomass. Whereas, functional dominance and stand structural complexity of overstorey, soil nutrients, and niche complementarity among understorey species with the conservative strategy determine understorey aboveground biomass. Whole-community aboveground biomass might be resulting from the superior role of overstorey functional dominance. This study highlights that the niche complementarity, mass ratio and soil nutrients effects are important for driving aboveground biomass, but in different ways across overstorey and understorey strata in natural subtropical forests. We argue that the relative effect of biodiversity loss on aboveground biomass depends critically on the functional and evolutionary identity of the lost species in the specific forest stratum. Better insights can be gained into forest management and biodiversity conservation by considering overstorey and understorey strata separately in complex natural forests.

1. Introduction

Plant diversity is a multifaceted concept and quantifies different aspects of biological variability, e.g., taxonomic diversity, functional

trait diversity and identity (or functional trait composition), and evolutionary diversity (Purvis and Hector, 2000; Díaz et al., 2007). In forest ecosystems, variations in the numbers of species, functional traits, and tree sizes along with abiotic factors (e.g., soils and topography)

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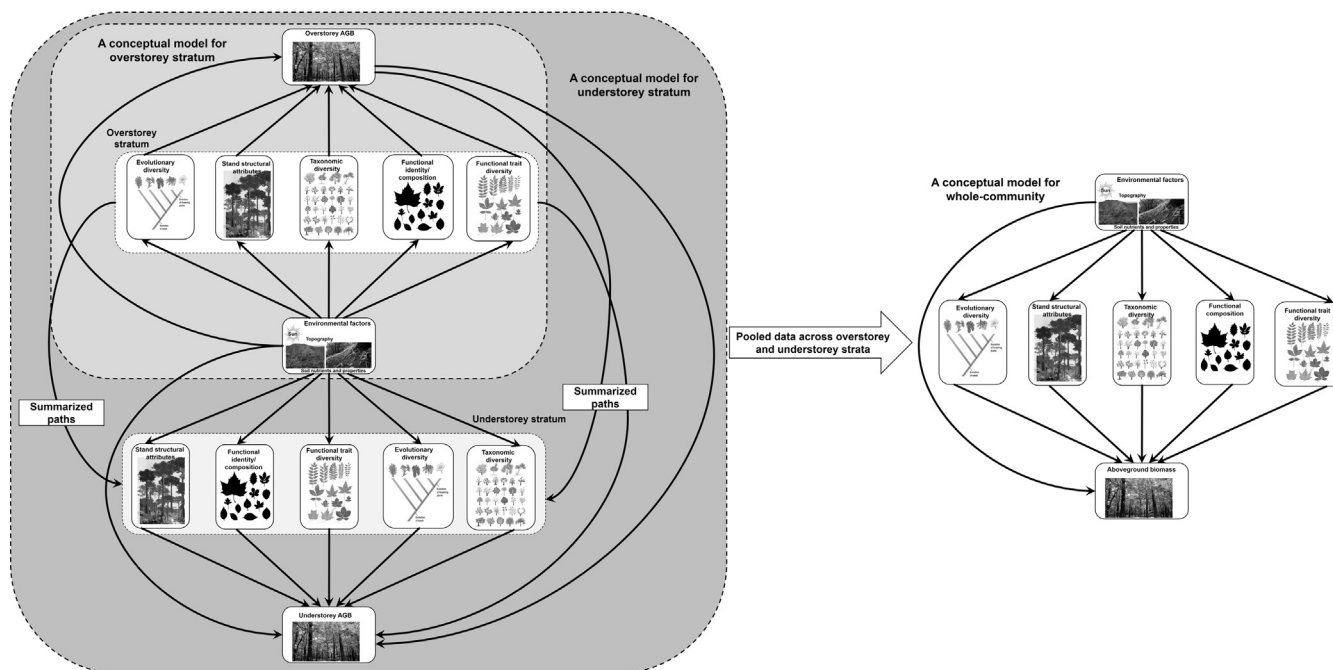


Fig. 1. Conceptual models showing the hypothesized relationships of how abiotic factors affect multiple biotic factors, and how abiotic and biotic factors concomitantly affect aboveground biomass at each individual forest stratum and whole-community level. Specifically, a conceptual model for understorey stratum also showing the hypothesized relationships of how abiotic and biotic factors of understorey (including overstorey biomass) affect biotic factors and aboveground biomass of understorey directly and indirectly via both overstorey and understorey biotic factors. The direct effects of overstorey biotic factors on understorey biotic factors and aboveground biomass are summarized in order to avoid complexity in the understorey conceptual model. Pictograms for abiotic and biotic factors are shown for visual interpretation only.

determine aboveground biomass or productivity (Paquette et al., 2015; Zhang and Chen, 2015; Prado-Junior et al., 2016; Yuan et al., 2016). Currently, the simultaneous effects of multiple abiotic (i.e., soil nutrients) and biotic (i.e., biodiversity and stand structure) factors on forest functioning at the whole-community level have been reported (Fotis et al., 2017; van der Sande et al., 2017; Yuan et al., 2018). However, the direct and indirect effects of multiple abiotic and biotic factors on aboveground biomass at each of individual forest stratum (i.e., overstorey and understorey) have rarely been examined, and the potential mechanisms associated with the effects of overstorey on understorey stratum remain unclear (Fig. 1).

The resource-use complementarity among co-occurring species is often considered as the mechanism underpinning the positive relationships of taxonomic, functional trait, and phylogenetic diversity with aboveground biomass or productivity in forests (Zhang et al., 2012; Poorter et al., 2015; Yuan et al., 2016; Ali and Yan, 2017a). Even though multivariate functional trait diversity has a negligible relationship with ecosystem function in several forests (Conti and Díaz, 2013; Finegan et al., 2015; Prado-Junior et al., 2016; Fotis et al., 2017), high functional trait variation due to the long evolutionary differentiation may lead to the niche complementarity effect (Cadotte et al., 2008; Flynn et al., 2011). Functional trait diversity is positively associated with phylogenetic and taxonomic diversity, due to the traits convergence among phylogenetically dissimilar species or traits divergence among phylogenetically similar species (Wiens and Graham, 2005; Flynn et al., 2011; de Bello, 2012; Ali and Yan, 2018). However, phylogenetic diversity, species richness, evenness, clustering and variability at the tips of phylogeny in a species-rich community might have different consequences on aboveground biomass (Ali and Yan, 2018).

Moreover, the mass ratio hypothesis (Grime, 1998) predicts that aboveground biomass should be strongly related (positive and/or negative) to the community-weighted mean (CWM) of a trait values (i.e., functional identity or trait composition), given that the dominant trait

value (not the variety of traits) drives aboveground biomass (Chiang et al., 2016; Prado-Junior et al., 2016; Ali and Yan, 2017b; Fotis et al., 2017). Traits that are associated with the plant growth rate and resource-acquisition are expected to be mechanistically relevant to high aboveground biomass or productivity (Garnier et al., 2004; Finegan et al., 2015). However, different patterns and magnitudes for the relationships between functional identity and aboveground biomass or productivity have been reported in different forest types. For instance, conservative traits that increase drought tolerance such as dense wood and lower specific leaf area, enhance aboveground biomass productivity in tropical dry forests (Prado-Junior et al., 2016); whereas these conservative traits constraint aboveground biomass or productivity in tropical wet and moist forests (Malhi et al., 2004; Finegan et al., 2015). In partial contrast to the tropical forests, both conservative and acquisitive traits promote aboveground biomass in subtropical forests (Chiang et al., 2016; Lin et al., 2016; Ali et al., 2017). As such, CWM of plant maximum height of overstorey and conservative traits (e.g., wood density) of understorey increase aboveground biomass in natural subtropical forests (Ali and Yan, 2017b). In addition, aboveground biomass or productivity is more strongly driven by functional dominance (i.e., the CWM of plant maximum height or diameter) than by CWM of leaf traits in natural (sub-) tropical forests (Cavanaugh et al., 2014; Prado-Junior et al., 2016; Ali and Yan, 2017b).

Aboveground biomass is not only determined by multiple aspects of biodiversity but also stand structural complexity such as individual tree size variation, tree diameter and height diversity, stand-level tree mean diameter, stand basal area, and stand diversity (Poorter et al., 2015; Zhang and Chen, 2015; Ali et al., 2016; Fotis et al., 2017). Individual tree size variation acts as a potential ecological mechanism for mediating a positive response of aboveground biomass to species diversity while simultaneously acts as a regulatory mechanism for species diversity via plant-plant interactions in natural forests (i.e., the niche differentiation based on tree sizes) (Yachi and Loreau, 2007; Zhang and Chen, 2015). As such, the effect of species diversity on productivity is

largely mediated by stand basal area in natural forests (Vilà et al., 2013). Therefore, both species diversity and stand structural complexity could influence aboveground biomass through their feedbacks or interactions, since high stand densities driven by biodiversity can lead to more light interception (Zhang and Chen, 2015; Ali et al., 2016; Dănescu et al., 2016). For instance, species diversity has indirect positive effects on aboveground biomass via tree diameter and height diversity or variation within forest stand (Zhang and Chen, 2015; Ali et al., 2016; Dănescu et al., 2016). The abundance of trees with large diameters and maximum tree height has a strong positive association with aboveground biomass (Chiang et al., 2016; Ali and Yan, 2017b, a).

Forest vertical stratification influences plant light capture and usage (Yachi and Loreau, 2007), thus shaping the patterns of species diversity, functional diversity, and aboveground biomass between overstorey and understorey strata. Light is more plentiful in the overstorey stratum relative to understorey, whereas the overstorey stratum imposes competitive constraints on the understorey light availability in natural forests (Bartels and Chen, 2010; Zhang et al., 2017). As such, understorey species may adopt a complementarity or conservative strategy, whereas functional dominance (adult stature) may be more apparent in the overstorey in structuring aboveground biomass (Bartels and Chen, 2010; Ali and Yan, 2017b). In addition, local abiotic factors (i.e., topography and soils) have both direct and indirect (via biotic factors) effects on aboveground biomass in natural forests (Yuan et al., 2012; Poorter et al., 2015; Zhang and Chen, 2015; Chiang et al., 2016; Jucker et al., 2016). For example, variation in light capture by component species can be influenced by topographic heterogeneity, and diversity, functional identity and/or stand structural complexity of overstorey trees (Yuan et al., 2012; Ali and Yan, 2017b). In the meantime, as soil fertility hypothesis suggested, soil physicochemical properties can strongly influence plant growth (Quesada et al., 2012), thereby species diversity, functional identity, stand structure and aboveground biomass across forest strata (Ali and Yan, 2017b, a). Therefore, the potential drivers of understorey biotic factors and aboveground biomass can be the result of direct and indirect effects of overstorey biotic factors and local soil nutrients (Fig. 1).

The objective of this study was to disentangle the relative effects of multiple abiotic and biotic drivers on aboveground biomass across overstorey and understorey, as well as at the whole-community level. Specifically, we addressed the following three questions. First, what are the relative effects of biotic drivers (i.e., taxonomic diversity, functional trait diversity, functional identity, evolutionary diversity and stand structural complexity) on aboveground biomass across each level of forest strata and at the whole-community? We hypothesized that taxonomic, functional trait, and evolutionary diversity have positive effects on aboveground biomass at the understorey stratum (through the niche complementarity effect), but have negative effects on that of the overstorey stratum (due to the niche overlap or functionally redundant species). Consistent with the mass ratio hypothesis, we expected that CWM of acquisitive traits and tree height would be positively associated with aboveground biomass while conservative traits constraint aboveground biomass in the overstorey stratum, whereas the opposite mechanisms are true for the understorey stratum. At the whole-community level, we expected almost the same relationships as hypothesized for the overstorey stratum due to the dominant contribution of the overstorey biomass to the whole community (Ali and Yan, 2017b). Because of the niche differentiation and facilitation associated with stand structural complexity (Yachi and Loreau, 2007; Zhang and Chen, 2015), we hypothesized that aboveground biomass increases with stand structural complexity at each individual forest stratum as well as at the whole-community level. Second, how do overstorey biotic factors (i.e., diversity, functional identity, stand structural complexity, and aboveground biomass) influence understorey biotic drivers and aboveground biomass? We hypothesized that: (1) overstorey functional identity and biomass exert negative effects on understorey biomass due to resource filtering; (2) overstorey diversity

and stand structural complexity enhance understorey due to their positive influences on understorey resource heterogeneity. Third, how do local abiotic factors affect biotic factors and aboveground biomass across forest strata and at whole-community? Following the soil fertility hypothesis (Quesada et al., 2012), we expected that multiple biotic factors and aboveground biomass would increase with increasing soil nutrient availability.

2. Materials and methods

2.1. Available datasets: Forest inventory, functional traits and abiotic factors

The forest inventory, functional traits and environmental factors datasets in this study were collected across contingent 125 (20 × 20 m) plots within a 5-ha subtropical evergreen broadleaf forest in the center of the Tiantong National forest park, Zhejiang province, in Eastern China. The elevation of the studied plot ranges from 320.4 to 489.4 m a.s.l., and slope ranges from 13.8 to 43.9°. The elevation is more pronounced in the northern section than in the southern edge of the plot, whereas the western and eastern edges of the plot extended through two north-south oriented valleys, with the interior of the plot spanning two small northwest-to-southeast oriented ridges, approximately 100 m apart (Ali and Yan, 2017a).

Measurement of plant traits consisted three steps (see Appendix A for details). First, mean leaf area, specific leaf area and leaf dry matter content were measured for 20,253 individual trees having the diameter at breast height (DBH) ≥ 1 cm and then averaged on species level (a total of 108 species) to capture both intraspecific and interspecific trait variations. Second, seven healthy individuals for each species were randomly selected for the measurements of leaf nitrogen concentration, leaf phosphorous concentration, leaf nitrogen to phosphorous concentrations ratio, and wood density (Cornelissen et al., 2003). Here, we selected healthy individual trees per species by following the standard protocols: (1) without leaf damage, (2) no oozing sap flow, and (3) no wilting or dieback. For leaf trait measurements, three branches were cut from three different positions (upper, mid, and lower) of the sunlit side of the tree crown, and then twenty to thirty mature leaves were harvested randomly from each branch. Finally, in this study, a total of 98 species were studied because leaf chemical traits and wood density values were unavailable for ten rare species (Ali et al., 2018). Third, the Chinese flora database was used for the extraction of the maximum plant height for each studied species.

To consider the effects of local abiotic factors, we included topographical and soil physicochemical properties as covariates. Topographical properties included elevation, slope and convexity, whereas soil properties were pH, volumetric soil water content, bulk density, humus depth, and soil carbon, phosphorus and nitrogen contents (see Appendix A for details). To minimize the correlations among soil and topographical variables (Tables S1 and S2 in Appendix B) and to prevent overfitting from a large number of abiotic predictors (Chiang et al., 2016), we used the two multivariate axes of principal component analyses (PCA) for soils and topographical variables, respectively. Soil PC1 accounted for 49% of the variation of soil physicochemical properties, while soil PC2 explained 27%, mostly soil phosphorus and nitrogen contents, i.e., the soil nutrients. The topography PC1 accounted for 58% of the variation of topography, mostly associated with elevation, slope and convexity, while the PC2 characterized 25%, associated with slope and convexity (Ali and Yan, 2018).

2.2. Quantification of multiple biotic factors

Overstorey stratum was defined as all individuals with DBH ≥ 10 cm in each forest plot, and understorey stratum included woody vegetation with 1 ≤ DBH < 10 cm (Ali and Yan, 2017b, a). At each forest stratum and whole-community, stand density (number of

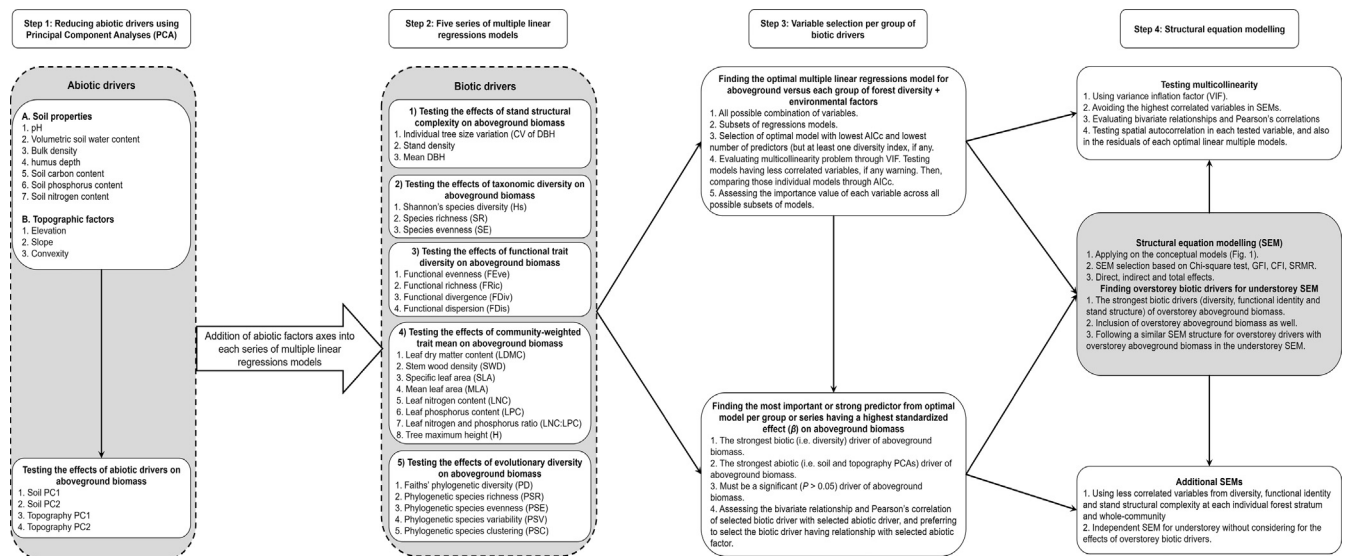


Fig. 2. Schematic representation of the steps proposed for statistical analyses. In step 1, abiotic drivers are reduced for the purpose to avoid complexity in multiple linear regressions models and structural equation models. In step 2, five series of multiple linear regressions models are tested for each group of biotic drivers in addition to abiotic drivers for predicting aboveground biomass at each of individual forest stratum and whole-community. In step 3, significant and strong drivers are selected in accordance to step 2. In step 4, structural equation models are applied to the conceptual models (Fig. 1), and additional statistical tests are performed for evaluating multicollinearity problems.

trees per hectare), stand-level mean DBH (in cm; i.e., an average value calculated from all individual trees DBHs within each stratum and/or plot), and coefficient of variation in individual tree DBHs (i.e., variations within and among species; expressed as a percentage) were calculated to represent stand structural complexity. Species richness, Pielou's species evenness and Shannon-Wiener species diversity indices were calculated to describe taxonomic diversity. The calculations of functional trait diversity and functional identity or composition (i.e., CWM) of trait values were based on eight traits, including mean leaf area, specific leaf area, leaf dry matter content, leaf phosphorous concentration, leaf nitrogen to phosphorous concentration ratio, plant maximum height, and wood density. Functional trait diversity was quantified based on the multivariate-trait space indices including functional evenness, functional richness, functional divergence and functional dispersion (Mason et al., 2005; Villéger et al., 2008; Laliberté and Legendre, 2010). The mean trait value weighted by the species' relative basal area was used to quantify the CWM of a trait value in a given stratum or at the whole-community level (Garnier et al., 2004). Five evolutionary diversity indices were calculated, including phylogenetic diversity, phylogenetic species richness, phylogenetic species evenness, phylogenetic species variability and phylogenetic species clustering (Faith, 1992; Helmus et al., 2007). The details for the quantification and summary of biotic factors are provided in Appendix A and Table S3, respectively (also see; Ali and Yan, 2017b; Ali and Yan, 2018).

2.3. Estimation of aboveground biomass

We calculated aboveground biomass for each tree with $DBH \geq 5$ cm (AGB_t) using a global allometric equation (Eq. (1)) (Chave et al., 2014), which is based on tree DBH, site-specific environment stress factor (E) and species' wood density (ρ).

$$AGB_t = \exp\{-1.803 - 0.976(E) + 0.976 \times \ln(\rho) + 2.673 \times \ln(DBH) - 0.0299 \times (\ln(DBH))^2\} \quad (1)$$

where the value of E for our study site was derived from Chave et al. (2014). The calculated E value for our study site was 1.11187 based on the geographic location of the 5-ha subtropical forest plot.

Extrapolating allometric equations beyond the size range used for

their development would lead to bias. To derive accurate estimates for the aboveground biomass of shrubs and small trees (AGBs) with $DBH < 5$ cm, we used the general multi-species allometric equation (Eq. (2)) developed locally for small trees and shrubs (Ali et al., 2015), which is also based on tree DBH and species' wood density (ρ).

$$AGBs = 1.450 \times \exp\{-4.97 + 2.20 \times \ln(DBH) + 3.06(\rho)\} \quad (2)$$

2.4. Statistical analyses

To account for the confounding effect of spatial autocorrelation in the variables of interest, we conducted generalized least-squares (GLS) models (Pinheiro and Bates, 2016). Here, we tested two types of GLS models, i.e., spatial (accounted for the effects of subplots X and Y coordinates) and non-spatial (i.e., no reference to subplots X and Y coordinates) GLS models. The forest strata effect was accounted as a grouping variable on the relationship between each predictor and aboveground biomass in both spatial and non-spatial GLS models, because overstorey and understorey strata had the same X and Y coordinates within each subplot. The influence of spatial autocorrelation was evaluated by comparing the AIC of spatial and non-spatial GLS models, and we found that non-spatial models had the lower AIC values (Table S4) which agrees with the previous suggestions in natural forests (Yuan et al., 2016; Ali and Yan, 2017a, b). Moreover, we also tested the Moran's I test on the residuals of each optimal multiple linear models, and did not find strong evidence for spatial autocorrelation, as also reported in our previous studies (Ali and Yan, 2017b; Ali et al., 2018; Ali and Yan, 2018). For a more explicit test, several other approaches were used, such as using the residuals of spatial GLS or autoregressive models as the proxy for original variables. We found almost the similar results as showed in the final selected models based on the original variables, indicating no strong effect of spatial autocorrelation. Therefore, we just showed the results based on the original variables.

We used structural equation models (SEMs) to examine the multivariate relationships of biotic factors and aboveground biomass, while considering for the direct and indirect effects of abiotic factors on aboveground biomass via each biotic factor at each stratum and the whole-community level (Fig. 1). For the understorey, we tested the effects of overstorey biotic factors (i.e., diversity, functional identity

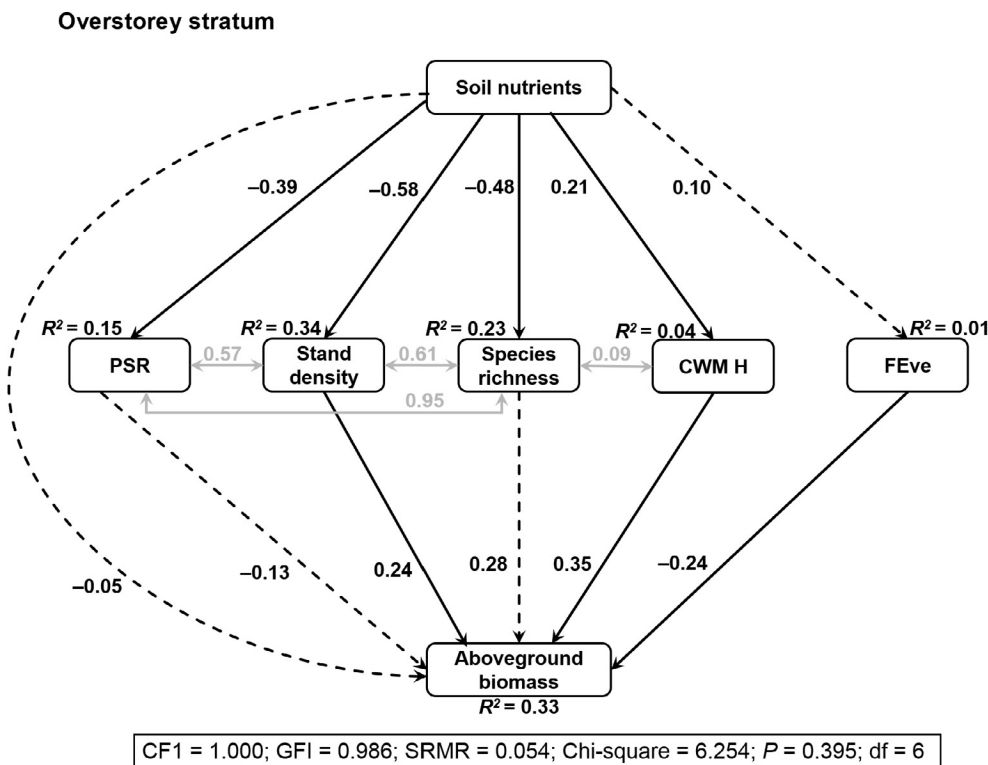


Fig. 3. Best-fit structural equation model for the effects of biotic factors on aboveground biomass at overstorey stratum in a subtropical forest, while accounting for the effects of soil nutrients. The one-sided black arrow represents regression path or direct effect, while double-sided gray arrow represents estimated covariance between two predictors. Solid arrows represent significant ($P < 0.05$) paths and dashed arrows represent non-significant paths ($P > 0.05$). For each path and covariance, the standardized coefficient is shown. R^2 indicates the total variation in a dependent variable that is explained by the combined independent variables. Model-fit statistics are provided. Abbreviations: CFI, comparative fit index; GFI, goodness of fit index; SRMR, standardized root mean square residual; df, degree of freedom.

and stand structure with the addition of aboveground biomass) on understorey biotic factors and aboveground biomass. Following previous studies (Conti and Díaz, 2013; Poorter et al., 2015; van der Sande et al., 2017), we selected only one important variable per biotic factors group because of strong multicollinearity among predictors within each group (see Fig. 2 for a schematic representation). For the selection of the strongest predictor variable for aboveground biomass within each biotic group, we performed five series of multiple linear regressions models for each of aboveground biomass in overstorey, understorey, and whole-community. We evaluated all possible subsets of the models and selected the optimal model that had the lowest AICc (i.e., adjusted AIC for small sample sizes) value within each series of models (Tables S5–S9). We critically selected the most parsimonious model by considering the lowest number of predictors and AICc (Ali et al., 2018). Also, the variance inflation factor was used to evaluate the multicollinearity issues in the multiple linear regressions models (Graham, 2003). If any warning reminds for the confounding effect of multicollinearity among predictor variables, we then separately tested the models by including one predictor variable per group in addition to abiotic factors as covariates and select the optimal model that had the lowest AICc across all individual models.

Finally, we selected the strongest predictor from optimal model per group or series having a highest standardized effect (β) on the variable of interest (i.e., aboveground biomass) (Tables S5–S9). In order to avoid complexity in SEM, we used soil PC2 as the main local abiotic factor because it basically represents the soil nutrient gradient (Table S2), and also retained in most of the optimal models across five series of multiple regressions models for explaining variation in aboveground biomass (Tables S5–S9), and also significantly correlated with topography PC1 and soil PC1 (Tables S10–S14). In addition, we evaluated which predictor variable within a given group of biotic factors contributed consistently across all possible subsets of models, for predicting aboveground biomass, by using an averaging approach in the synthetic model (e.g., Finegan et al., 2015). We found the same strong predictor for each group or series, as suggested by the optimal model for each group of biotic factors (Tables S5–S9). With respect to the understorey stratum, we selected the strong biotic factors of overstorey stratum (from the

final overstorey SEM) for testing the direct, indirect and total effects of overstorey on understorey stratum, as well as to keep consistency with the best-fit SEM of overstorey stratum. Moreover, in order to explicitly assess whether the multicollinearity among taxonomic, functional trait and phylogenetic diversity indices confound the main SEMs results, we further selected only one strong diversity index (i.e., a diversity index having a strong direct effect on aboveground biomass) among multiple metrics of biodiversity from each final selected SEMs, and then retested the SEMs by avoiding other high correlated biodiversity indices.

All recommended statistical tests were used to evaluate the goodness of fit for SEMs but Chi-square test was critically assessed for model-fit to the data, as suggested by previous studies (Jucker et al., 2016; Ali and Yan, 2017a; Poorter et al., 2017). We included all significant covariance between pairs of best predictors in order to test whether biotic factors provide any feedback to each other in the SEMs (Ali et al., 2016; Jucker et al., 2016). The SEMs were employed using the *lavaan* package (Rosseel, 2012). Prior to the statistical analyses, aboveground biomass, stand structural complexity and multiple metrics of biodiversity values were natural-logarithm transformed and standardized for the purpose to improve the normality and linearity. The Pearson's correlations matrices are shown in Tables S10–S14. The dataset used in the analyses is provided in Appendix C, and a summary of variables is provided in Table S3. For all statistical analyses, R 3.4.2 was used (R Development Core Team, 2017).

3. Results

The overstorey SEM revealed that aboveground biomass was influenced by the positive direct effects of CWM of tree height and stand density but the negative direct effect of functional evenness (Fig. 3). Soil nutrients had the significant negative direct effects on stand density, species richness and phylogenetic species richness, but a positive direct effect on CWM of plant height. As such, soil nutrients had a negative indirect effect via stand density while a positive indirect effect via CWM of tree height on aboveground biomass. Although the direct effect of soil nutrient on aboveground biomass was non-significant, there was a total negative effect of soil nutrients due to the strongest

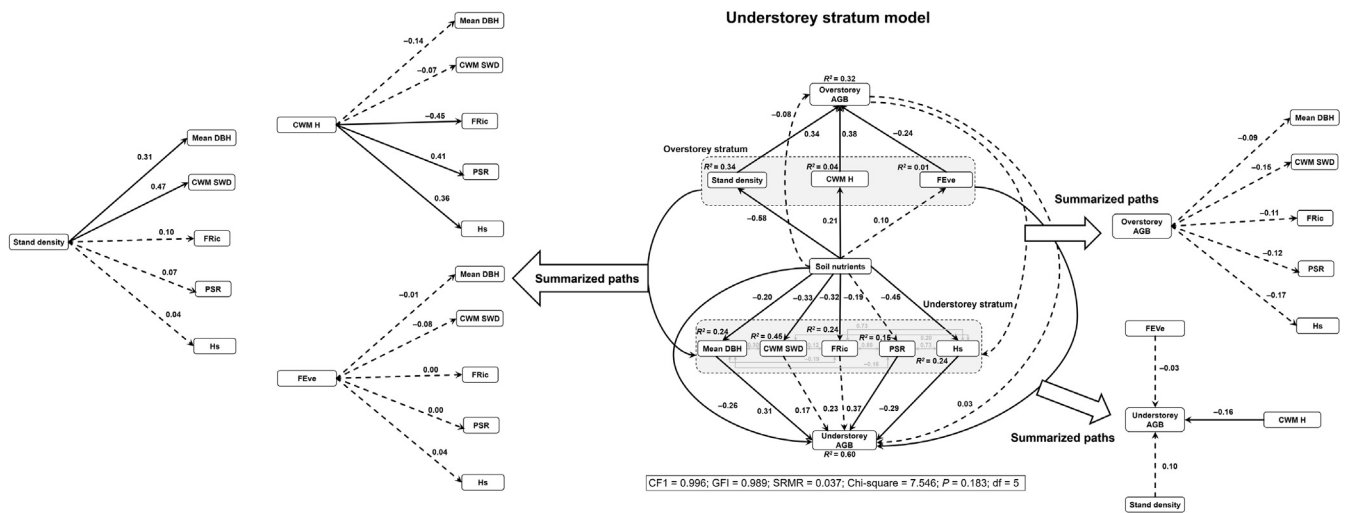


Fig. 4. Best-fit structural equation model for the effects of biotic factors on aboveground biomass at understorey stratum in a subtropical forest, while accounting for the direct and indirect effects of overstorey attributes and soil nutrients. The direct effects of overstorey biotic factors on understorey biotic factors and aboveground biomass are summarized in order to avoid complexity in the SEM (see the right and left hands paths for specific details).

indirect pathways via overstorey stand density and CWM of plant height (Table S15).

With respect to the understorey SEM, aboveground biomass was influenced by the positive direct effects of phylogenetic species richness and mean DBH but the negative direct effects of Shannon’s species diversity and soil nutrients (Fig. 4; Table S16). In addition, aboveground biomass of understorey was negatively and directly influenced by the CWM of overstorey tree height. The total effect of overstorey stand density on understorey aboveground biomass was significantly positive, whereas the total effects of CWM of tree height, functional evenness and aboveground biomass of overstorey on the understorey’s aboveground biomass were nonsignificant. More specifically, stand density of overstorey increased the aboveground biomass of understorey indirectly via increasing mean DBH of understorey. The CWM of overstorey tree height increased the aboveground biomass of understorey indirectly via increasing phylogenetic species richness but decreased indirectly via increasing Shannon’s species diversity (Table 1). Soil nutrients had a significant negative direct effect on overstorey stand density but a positive direct effect on CWM of overstorey tree height, and the negative direct effects on CWM of stem wood density, mean DBH, species diversity and functional richness of understorey. Soil nutrients had an indirect negative effect via Shannon’s species diversity of understorey on the aboveground biomass of understorey. The total effect of soil nutrients was significantly negative through the summation of variable direct and indirect effects mediated by both overstorey and understorey biotic factors (Table 1).

We also tested an additional SEM for understorey without considering the effects of overstorey, and the result showed almost similar direct effects of understorey biotic factors on the aboveground biomass of understorey (Fig. S1 and Table S17). Finally, our additional analyses showed that the strong multicollinearity among taxonomic, functional trait and phylogenetic diversity did not strongly change the above results (Figs. S2–S4). For example, the additional SEM for overstorey showed that functional evenness, the CWM of tree height, and stand density acted as direct, independent predictors of overstorey aboveground biomass (Fig. S2).

At the whole-community level, aboveground biomass was influenced by a negative direct effect of soil nutrients, but the positive direct effects of individual tree size variation (CV of DBH) and CWM of plant height (Fig. 5). Soil nutrients had the significant positive direct effects on the CV of DBH, phylogenetic species evenness and CWM of plant height, whereas a negative direct effect on species evenness (Fig. 5). Soil nutrients had the positive indirect effects via CV of DBH and CWM

of plant height on aboveground biomass. The total effect of soil nutrients on whole-community aboveground biomass was significantly negative (Table S18).

The significant bivariate relationships between aboveground biomass and predictors at overstorey, understorey, and whole-community are shown in Figs. S5, S6 and S8, respectively (also see Table S19). The significant bivariate relationships between understorey and overstorey strata are shown in Fig. S7 (also see Table S20).

4. Discussion

The main results of our study suggest that aboveground biomass in overstorey and understorey strata depends on different biotic factors and thus different ecological mechanisms along local soil nutrients gradients. Below we discuss these findings in the light of ecological mechanisms, in addition to the limitations and promises of the study.

4.1. Multiple biotic drivers of aboveground biomass in overstorey stratum

As hypothesized, we found that overstorey stratum dominated by tall trees (i.e., functional dominance) with low functional evenness and great stand density (canopy packing) had high aboveground biomass in the studied forest. However, evolutionary and taxonomic diversity appeared to be insignificant in affecting aboveground biomass, which may be attributable to the fact that functional trait, evolutionary and taxonomic diversity indices should outperform each other in predicting aboveground biomass (Yuan et al., 2016; Ali and Yan, 2018). In our analysis, we observed strong positive feedback between taxonomic and phylogenetic species richness but functional evenness was found to be independent, indicating that niche overlap determines aboveground biomass in overstorey stratum of the studied forest (Ali et al., 2018).

In addition, we observed strong positive feedback between stand density and species richness (taxonomic and phylogenetic), and hence strong direct effect of stand density on aboveground biomass but without significant effect of species richness. Species richness and functional dominance provided weak positive feedback to each other, whereas functional evenness was observed as an independent driver. It is well-understood that the niche complementarity and mass ratio effects on ecosystem function are maintained by the stand structural complexity because great stand density relates to both high biodiversity and aboveground biomass (Chiang et al., 2016; Jucker et al., 2016). This further suggests that high aboveground biomass in overstorey stratum is due to the high functional dominance of overstorey species

Table 1

The direct, indirect, subtotal indirect and total standardized effects of soil nutrients, and biotic factors of overstorey and understorey on aboveground biomass of understorey stratum, based on structural equation model (SEM; Fig. 4). Significant effects and covariance are indicated in bold ($P < 0.05$). The direct effects of biotic factors on aboveground biomass in understorey stratum are highlighted in gray shading color. All the abbreviations for variables are explained in Fig. 2. Full summary of the model is shown in Table S17.

Response variable	Mediator variable	Predictor variable	Effect	Beta	P-value
<i>Direct, indirect, subtotal indirect and total effects of soil nutrients on understorey aboveground biomass via understorey and overstorey drivers plus overstorey AGB</i>					
Understorey AGB	----	Soil nutrients (PC2)	Direct	-0.26	0.001
Understorey AGB	----	Understorey mean DBH	Direct	0.31	<0.001
Understorey AGB	Understorey mean DBH	Soil nutrients (PC2)	Indirect	-0.06	0.062
Understorey AGB	----	Understorey CWM SWD	Direct	0.17	0.051
Understorey AGB	Understorey CWM SWD	Soil nutrients (PC2)	Indirect	-0.06	0.080
Understorey AGB	----	Understorey FRic	Direct	0.23	0.120
Understorey AGB	Understorey FRic	Soil nutrients (PC2)	Indirect	-0.07	0.161
Understorey AGB	----	Understorey PSR	Direct	0.37	0.008
Understorey AGB	Understorey PSR	Soil nutrients (PC2)	Indirect	-0.07	0.131
Understorey AGB	----	Understorey species diversity	Direct	-0.29	0.005
Understorey AGB	Understorey species diversity	Soil nutrients (PC2)	Indirect	0.13	0.017
Understorey AGB	All indirect paths	Soil nutrients (PC2)	Subtotal indirect	0.05	0.033
Understorey AGB	Overstorey AGB	Soil nutrients (PC2)	Indirect	0.00	0.700
Understorey AGB	Overstorey stand density	Soil nutrients (PC2)	Indirect	-0.06	0.228
Understorey AGB	Overstorey CWM H	Soil nutrients (PC2)	Indirect	-0.03	0.098
Understorey AGB	Overstorey FEve	Soil nutrients (PC2)	Indirect	0.00	0.644
Understorey AGB	All indirect paths	Soil nutrients (PC2)	Subtotal indirect	0.04	0.055
Understorey AGB	Direct + Indirect paths	Soil nutrients (PC2)	Total	-0.50	<0.001
<i>Direct, indirect, subtotal indirect and total effects of overstorey stand density on understorey aboveground biomass via understorey drivers plus overstorey AGB</i>					
Understorey AGB	----	Overstorey stand density	Direct	0.10	0.223
Understorey AGB	Understorey mean DBH	Overstorey stand density	Indirect	0.10	0.012
Understorey AGB	Understorey CWM SWD	Overstorey stand density	Indirect	0.08	0.066
Understorey AGB	Understorey FRic		Indirect		
Understorey AGB	Understorey PSR	Overstorey stand density	Indirect	0.03	0.516
Understorey AGB	Understorey species diversity	Overstorey stand density	Indirect	-0.01	0.668
Understorey AGB	Overstorey AGB	Overstorey stand density	Indirect	0.01	0.664
Understorey AGB	All indirect paths	Overstorey stand density	Subtotal indirect	0.06	0.001
Understorey AGB	Direct + Indirect paths	Overstorey stand density	Total	0.32	<0.001
<i>Direct, indirect, subtotal indirect and total effects of overstorey CWM H on understorey aboveground biomass via understorey drivers plus overstorey AGB</i>					
Understorey AGB	----	Overstorey CWM H	Direct	-0.16	0.022
Understorey AGB	Understorey mean DBH	Overstorey CWM H	Indirect	-0.04	0.145
Understorey AGB	Understorey CWM SWD	Overstorey CWM H	Indirect	0.01	0.385
Understorey AGB	Understorey FRic	Overstorey CWM H	Indirect	0.11	0.137
Understorey AGB	Understorey PSR	Overstorey CWM H	Indirect	0.16	0.023
Understorey AGB	Understorey species diversity	Overstorey CWM H	Indirect	-0.10	0.020
Understorey AGB	Overstorey AGB	Overstorey CWM H	Indirect	0.01	0.663
Understorey AGB	All indirect paths	Overstorey CWM H	Subtotal indirect	0.05	0.018
Understorey AGB	Direct + Indirect paths	Overstorey CWM H	Total	-0.02	0.774
<i>Direct, indirect, subtotal indirect and total effects of overstorey FEve on understorey aboveground biomass via understorey drivers plus overstorey AGB</i>					
Understorey AGB	----	Overstorey FEve	Direct	-0.03	0.611
Understorey AGB	Understorey mean DBH	Overstorey FEve	Indirect	0.00	0.933
Understorey AGB	Understorey CWM SWD	Overstorey FEve	Indirect	-0.01	0.346
Understorey AGB	Understorey FRic	Overstorey FEve	Indirect	0.00	0.996
Understorey AGB	Understorey PSR	Overstorey FEve	Indirect	0.00	0.967
Understorey AGB	Understorey species diversity	Overstorey FEve	Indirect	-0.01	0.652
Understorey AGB	Overstorey AGB	Overstorey FEve	Indirect	-0.01	0.665
Understorey AGB	All indirect paths	Overstorey FEve	Subtotal indirect	0.04	0.574
Understorey AGB	Direct + Indirect paths	Overstorey FEve	Total	-0.06	0.383
<i>Direct, indirect, subtotal indirect and total effects of overstorey AGB on understorey aboveground biomass via understorey biotic drivers</i>					
Understorey AGB	----	Overstorey AGB	Direct	0.03	0.662
Understorey AGB	Understorey mean DBH	Overstorey AGB	Indirect	-0.03	0.349
Understorey AGB	Understorey CWM SWD	Overstorey AGB	Indirect	-0.02	0.183
Understorey AGB	Understorey FRic	Overstorey AGB	Indirect	-0.03	0.360
Understorey AGB	Understorey PSR	Overstorey AGB	Indirect	-0.05	0.263
Understorey AGB	Understorey species diversity	Overstorey AGB	Indirect	0.05	0.135
Understorey AGB	All indirect paths	Overstorey AGB	Subtotal indirect	0.05	0.135
Understorey AGB	Direct + Indirect paths	Overstorey AGB	Total	-0.05	0.592

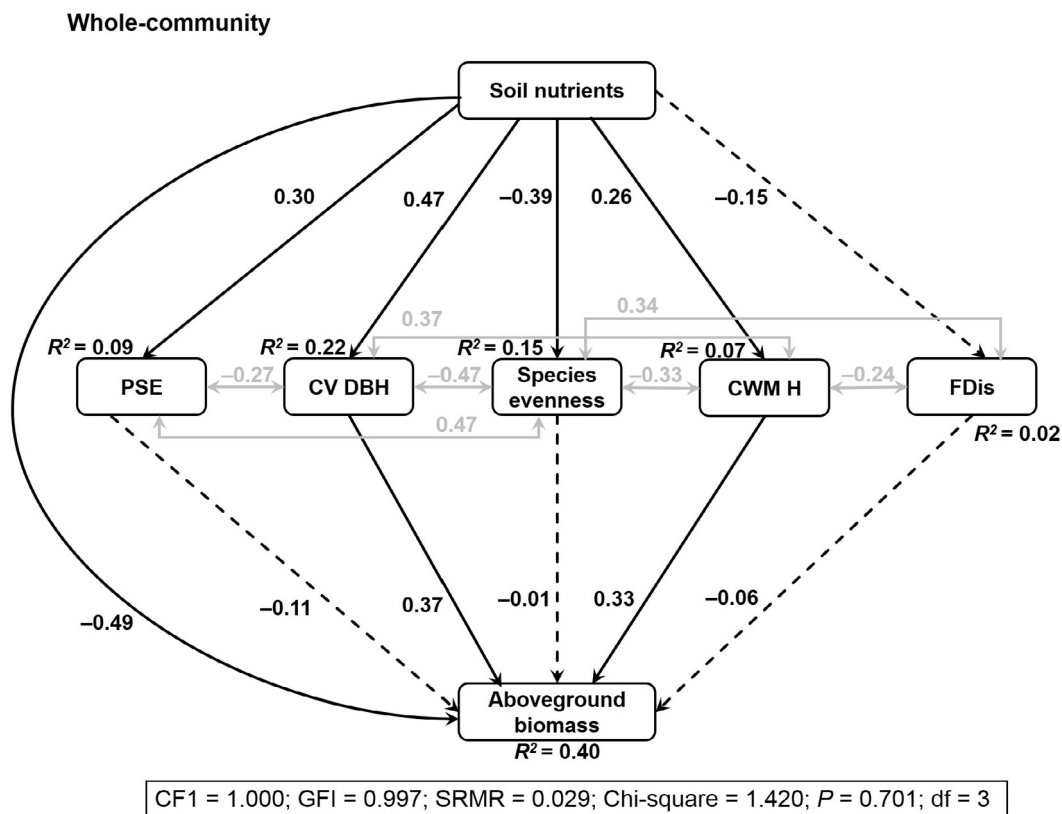


Fig. 5. Best-fit structural equation model for the effects of biotic factors on whole-community aboveground biomass in a subtropical forest, while accounting for the effects of soil nutrients.

with certain traits (e.g., the plant maximum height) and low functional evenness (i.e., niche overlap) in a complex stand structure (e.g., high stand density) (Villéger et al., 2008; Prado-Junior et al., 2016; Ali and Yan, 2017b; Fotis et al., 2017). These specific characteristics of the overstorey stratum, for driving high aboveground biomass, might be attributable to their strong capability to the environmental filtering (Lasky et al., 2014; Zhang et al., 2017; Ali et al., 2018). These findings strongly support the mass ratio hypothesis rather the niche complementarity hypothesis (Loreau and Hector, 2001; Fotis et al., 2017).

4.2. Multiple biotic drivers of aboveground biomass in understorey stratum

Most plants in the understorey stratum are slow-growing species as indicated by the positive feedback between CWM of wood density (an indicator for conservative strategy) and mean DBH (a proxy for plant growth), which result in high aboveground biomass (Ali and Yan, 2017b). Although aboveground biomass may increase with taxonomic diversity (Zhang et al., 2012), the negative direct effect of Shannon's species diversity on aboveground biomass indicates that high biomass in understorey may eliminate weak competitors under the assumption of competitive exclusion (Ali et al., 2016). Therefore, the dominance of certain productive species with a specific strategy (i.e., slow-growing conservative strategy) has a potent effect on aboveground biomass (Prado-Junior et al., 2016; Ali and Yan, 2017b).

This study also revealed that functional richness had a non-significant positive effect on aboveground biomass in understorey stratum. However, strong positive feedbacks among phylogenetic species richness, functional richness and species diversity were observed. In addition, we found that the main biotic drivers (i.e., mean DBH, phylogenetic species richness, species diversity and CWM of wood density) of aboveground biomass provided positive feedbacks to each other and to functional richness, but mean DBH had negative feedbacks with phylogenetic species richness and functional richness. These results

indicate that plant species in understorey stratum are phylogenetically, functionally and taxonomically rich, while keeping the conservative and slow-growing strategy for efficient utilization of limited resources to construct high aboveground biomass (Ali and Yan, 2017b, 2018).

The slow growth of understorey plants might be happened due to the strong light resource limitation, as a result of the high stand structural complexity, low functional evenness and high aboveground biomass of overstorey (Bartels and Chen, 2010; Ali and Yan, 2017a, b; Zhang et al., 2017). Also, this study showed that overstorey stand structure increased aboveground biomass indirectly via a slow-growing strategy of the understorey species. As such, overstorey functional dominance increased aboveground biomass indirectly via increasing phylogenetic species richness of understorey. These combined results suggest that biotic attributes of overstorey are the additional factors determining understorey aboveground biomass (Yuan et al., 2012; Ali and Yan, 2017a; Zhang et al., 2017).

4.3. Multiple biotic drivers of whole-community aboveground biomass

We found that communities with high aboveground biomass were characterized by species with high adult stature (or functional dominance), low functional dispersion and species evenness (taxonomic and phylogenetic), as well as great in tree size variation (complex stand structure) in the studied forests. The relationships observed at the whole-community level are almost similar to the observed relationships at overstorey stratum. The dominant effect of overstorey trees may weaken the effect of understorey trees on aboveground biomass (Zhang et al., 2017). Dominant species with the big size in overstorey stratum may effectively utilize light and water, thus resulting in the less availability of resources for understorey trees (Bartels and Chen, 2010). In this study, the significant positive effect of adult stature trees with low functional evenness on aboveground biomass at overstorey stratum suggests the functionally dominant effect of big trees on the slow-

growing understorey trees. In combination, the high functional dominance (probably more towards big-diameter trees and less towards small-diameter trees) strongly drives high aboveground biomass at the whole-community level (Ali and Yan, 2017a; Fotis et al., 2017).

In addition, we observed that functional dominance of adult stature trees and individual tree size variation provide positive feedback to each other, but both provide negative feedbacks to the taxonomic, functional trait and evolutionary diversity indices. These feedbacks indicate the complementarity strategy among adult stature tree species (i.e., the dominance of species with particular traits), which further impose negative influences on species with a variety of traits, phylogenetic distances and different taxonomies (Loreau et al., 2001; Ali and Yan, 2018). These results support the hypothesis of mass ratio or selection effect, i.e., dominant species or traits drive ecosystem functioning, and that the positive relationships between biodiversity and aboveground biomass arise simply because diverse communities are more likely to include few productive species and high-functioning traits (Loreau and Hector, 2001), thereby high aboveground biomass (Cavanaugh et al., 2014; Ali et al., 2018).

4.4. Soil nutrients modulate the effects of multiple biotic factors on aboveground biomass

In overstorey stratum, the species complementarity effect occurred at low-nutrients soils while functional dominance effect of big trees occurred at high-nutrient soils for driving high aboveground biomass. By contrary, in the understorey stratum, the species complementarity effect occurred at low-nutrients soils for driving high aboveground biomass, probably due to the competitive constraints caused by the overstorey trees (Bartels and Chen, 2010; Ali and Yan, 2017b; Zhang et al., 2017). At the whole-community level, these opposing mechanisms between overstorey and understorey strata are obscured. Therefore, species adaptations to the soil nutrients in overstorey and understorey strata may largely explain the observed negative direct and total effects of soil nutrients on aboveground biomass (Poorter et al., 2015; Jucker et al., 2016; Ali and Yan, 2017b).

Conservative strategy of plant species is expected to occur on nutrient-poor soils, whereas acquisitive strategy may be more closely related to nutrient-rich soils, because plant growth and survivor are positively related to soil nutrients (Poorter and Bongers, 2006; Coomes et al., 2009; Reich, 2014). In overstorey stratum, the observed positive indirect effect of soil nutrients on aboveground biomass via adult stature trees but a negative effect via stand density, could reflect the fact that fast-growing species are responsible for contributing high aboveground biomass on nutrient-rich soils. In understorey stratum, the strong negative indirect effects of soil nutrients on aboveground biomass via CWM of stem wood density and mean DBH but a positive indirect effect via species diversity, indicates that slow-growing species contribute high aboveground biomass on nutrient-poor soils (Ali and Yan, 2017b). At the whole-community level, soil nutrients had the positive indirect effects on aboveground biomass via functional dominance of adult stature tree species and individual tree size variation. This finding indicates the better capability of overstorey trees to uptake soil nutrients, and what is left available for understorey trees (Bartels and Chen, 2010; Ali and Yan, 2017b).

5. Concluding remarks

By specifically focusing on the overstorey and understorey strata, this study has tested the relative effects of biotic (functional identity, taxonomic, functional trait and evolutionary diversity, and stand structural complexity) and abiotic factors on aboveground biomass within a subtropical forest. The results showed that aboveground biomass in overstorey and understorey depends on different biotic factors and soil nutrients, and thus indicating different underlying ecological mechanisms. In general, the mass ratio and niche complementarity

effects are not necessarily mutually exclusive across forest strata. At the overstorey stratum, functional dominance effect (i.e., CWM of plant maximum height) occurs at high-nutrient soils while species complementarity effect occurs at low-nutrient soils for driving high aboveground biomass. Our results suggest that the mass ratio and stand structural complexity are the main mechanisms driving the aboveground biomass of overstorey on the nutrient-rich soils. By contrary, at the understorey stratum, the species complementarity effect with conservative plant strategy strongly occurs at low-nutrient soils for driving high aboveground biomass. Moreover, these potential mechanisms in understorey are simultaneously controlled by the diversity, stand structural complexity, functional dominance and aboveground biomass of overstorey trees. At the whole-community level, the functional dominance effect occurs on nutrient-rich soils for driving high aboveground biomass, suggesting that the mass ratio effect is more important at whole-community level. This study highlights that disentangling the relative effect of multiple metrics of biodiversity, stand structural complexity and environmental factors on aboveground biomass across forest strata will provide better understandings of observations into ecological mechanisms for carbon sequestration, forest management, biodiversity conservation and mitigation potential of natural forest ecosystems. We argue that the relative effect of biodiversity loss on aboveground biomass will depend critically on the functional and evolutionary identity of the lost species in the specific forest stratum in natural forests.

Data availability

Abiotic and biotic variables used in this study are included in Appendix C.

Statement of authorship

AA and ERY conducted research; AA compiled and analyzed the data; AA and ERY designed the study and wrote the paper through the support from HYHC and WHY.

Conflict of interests

The authors declare no conflict of interest.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2019.01.007>.

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