



Consequences of phylogenetic conservativeness and functional trait similarity on aboveground biomass vary across subtropical forest strata

Arshad Ali^{a,b}, En-Rong Yan^{a,c,*}

^a Forest Ecosystem Research and Observation Station in Putuo Island, Tiantong National Forest Ecosystem Observation and Research Station, and Shanghai Key Lab for Urban Ecological Processes and Eco-Restoration; School of Ecological and Environmental Sciences, East China Normal University, Shanghai 200241, China

^b Spatial Ecology Lab, School of Life Sciences, South China Normal University, Guangzhou 510631, Guangdong, China

^c Institute of Eco-Chongming (IEC), 3663 N. Zhongshan Rd., Shanghai 200062, China



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ABSTRACT

Phylogenetically close and/or functionally similar species are generally assumed to compete more strongly than phylogenetically distant and functionally dissimilar species in a community. However, how coexisting species with different extents of variation in their phylogeny and functional traits determine community function such as aboveground biomass across forest strata remains an unresolved question. We hypothesize that phylogenetically close and functionally similar species of overstorey, but phylogenetically distant and functionally dissimilar species of understorey drive high aboveground biomass in structurally-complex subtropical forests. Multiple linear regression models were used to test the consequences of phylogenetic distances and functional traits of tree species, and environmental factors on aboveground biomass in a subtropical forest in Eastern China. Overstorey aboveground biomass was driven by functional evenness ($\beta = -0.21$), phylogenetic species evenness ($\beta = -0.27$) and phylogenetic diversity ($\beta = 0.31$). Understorey aboveground biomass was driven by functional richness ($\beta = 0.25$), functional dispersion ($\beta = -0.21$), soil nutrients ($\beta = -0.17$) and topography ($\beta = 0.36$). Whole-community aboveground biomass was best predicted by functional divergence ($\beta = 0.36$), functional dispersion ($\beta = -0.38$), phylogenetic diversity ($\beta = 0.24$) and soil nutrients ($\beta = -0.20$). Our results suggest that understorey aboveground biomass is great for groups of phylogenetically distant species having high functional richness due to specific functional strategy shared by all the species. By contrast, high overstorey aboveground biomass is related with groups of phylogenetically close species having low functional trait diversity (i.e. high functional trait similarity) due to the evolutionary relatedness. The mechanism at the whole-community level might result from the mixed effects of overstorey evolutionary relatedness and understorey functional trait diversity. This study highlights that disentangling the effects of evolutionary diversity and functional trait diversity across forest strata may be helpful for better understanding of ecological mechanisms for predicting aboveground biomass in a subtropical forest.

1. Introduction

Earlier ecologists, including Charles Darwin (1859), suggested that species belonging to the same genus would compete more intensely than species belonging to different genera (Simberloff, 1970; Valiente-Banuet and Verdú, 2007). The general notion is that phylogenetically close or functionally similar species would compete more strongly than phylogenetically distant or functionally dissimilar species, and may be less likely to coexist due to competitive exclusion (Cavender-Bares et al., 2009; Lyu et al., 2017). More recently, the same general notion has been revisited as the competition-relatedness hypothesis (Cahill et al., 2008) or the phylogenetic limiting similarity hypothesis (Violle

et al., 2011) for the understanding of biodiversity, community structure and functions (Cadotte et al., 2008; Cavender-Bares et al., 2009; Lyu et al., 2017). Therefore, phylogenetic diversity and/or functional trait dissimilarity are frequently considered as the main drivers of aboveground biomass or productivity across different ecosystems (Cadotte et al., 2009; Flynn et al., 2011; Paquette and Messier, 2011; Yuan et al., 2016). To date, direct tests for community assembly hypotheses on ecosystem function remain rare in (sub-) tropical forests, and not much is known about whether and how evolutionary diversity and functional trait dissimilarity drive aboveground biomass across each individual forest stratum (i.e. overstorey and understorey).

Functional trait dissimilarity and phylogenetic or evolutionary

* Corresponding author at: Forest Ecosystem Research and Observation Station in Putuo Island, Tiantong National Forest Ecosystem Observation and Research Station, and Shanghai Key Lab for Urban Ecological Processes and Eco-Restoration; School of Ecological and Environmental Sciences, East China Normal University, Shanghai 200241, China.

E-mail addresses: arshadforester@m.scnu.edu.cn (A. Ali), eryan@des.ecnu.edu.cn (E.-R. Yan).

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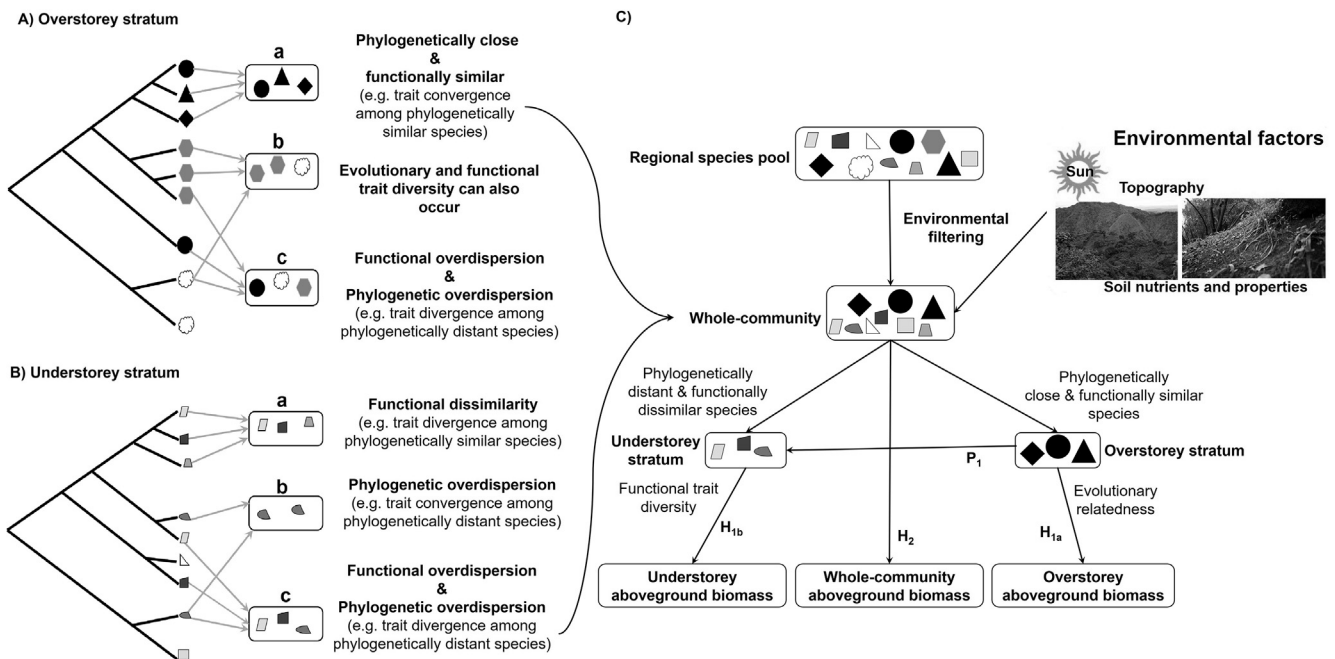


Fig. 1. An example patterns for functional trait diversity and evolutionary diversity when traits are conserved or labile on the phylogeny. (A) Individual species are represented by the shapes of symbols at the tips of the phylogenetic tree, the colors of the symbols indicate different traits, and rectangles represent species assemblage within a stratum. In this example (Fig. 1A), the similar trait is conserved on the phylogeny, such that phylogenetically close species tend to have the same traits (colors), i.e. phylogenetically close and functional similar species. Environmental filtering selects for species with similar traits (a in Fig. 1A) causing evolutionary relatedness and functional similarity. Functional trait diversity and evolutionary diversity that is no different from random expectation can also occur (b in Fig. 1A), such that less phylogenetically close and functionally similar species. Interspecific competition limits similarity between co-occurring species resulting in different traits (c in Fig. 1A) causing functional or phylogenetic overdispersion. (B) Functional dissimilarity in a stratum where a variety of traits are conserved on the phylogeny (a in Fig. 1B), such that phylogenetically close species tend to have the different traits (colors). Phylogenetic overdispersion (b in Fig. 1B) could be clustered in functional trait diversity, such that phylogenetically distant species tend to have the same traits. Both phylogenetic and functional overdispersion can also be expected (c in Fig. 1B), such that phylogenetically distant species tend to have the different traits. Note that these patterns (shown in Fig. 1A and B) can be interchangeably used for overstorey and understorey strata, but here we just present examples related to our expectations across forest strata. (C) Conceptual framework showing how changes in aboveground biomass are regulated by evolutionary diversity and functional trait diversity across forest strata and whole-community. Species pool having different symbols and colors represent different species and traits dissimilarity, respectively, while the size of the symbols represents the overstorey (big size) and understorey (small size) species. H_{1a} , H_{1b} , H_2 and P_1 indicate proposed hypotheses, prediction or questions (see introduction section).

diversity have often been treated as the two sides of the same coin, based on the assumption that functional traits are phylogenetically conserved (Cadotte et al., 2009; Paquette et al., 2015; Yuan et al., 2016). However, the relationships may be not that simple possibly due to the convergence in traits among phylogenetically distant species or divergent selection among phylogenetically close species (Fig. 1A and B), or vice versa (Wiens and Graham, 2005). In simple words, it is theoretically plausible that the decrease (i.e. the trait convergence) and increase (i.e. the trait divergence) of functional trait dissimilarity depend on the extent of habitat selection *versus* limiting similarity due to biotic interactions within communities (de Bello, 2012). On the one hand, phylogenetically close species are likely to assemble due to environmental filtering, and evolutionary relatedness and/or functional trait similarity are expected if traits are phylogenetically conserved (Fig. 1A) (Webb, 2000). On the other hand, it is possible that niche differentiation or ecological fitting mediates community assembly, and hence phylogenetic overdispersion and/or functional trait dissimilarity are expected (Fig. 1B) (Cavender-Bares et al., 2009).

Functional, evolutionary and ecological similarities of tree species might be fundamentally different across forest strata. Natural communities are assembled by niche-related, neutral and historical processes, where coexisting species are selected based on their functional traits, ecological similarity and evolutionary history (e.g. Cavender-Bares et al., 2009). More specifically, tree species with contrasting functional strategies are generally assembled in different vertical layers, probably due to the trait convergence and divergence across forest strata in complex natural forests (Rüger et al., 2012; Ali and Yan, 2017b; Ali

et al., 2018). Since whole-community species are selected from the regional species pool through natural assembly processes based on their functional traits and ecological similarity (Fig. 1C), how do evolutionary and functional trait dissimilarity measures explain variation in aboveground biomass at each individual forest strata in natural communities? It is expected that evolutionary relatedness would drive aboveground biomass at overstorey stratum, probably due to environmental filtering of phylogenetically close species with similar physiological or functional tolerances (Webb et al., 2002). By contrast, phylogenetic overdispersion can result from competition or other processes such as complementarity and facilitation among phylogenetically distant species in the resource-limited environment (Cavender-Bares et al., 2009), such as in the understorey stratum of the forest. At this juncture, it is expected that functional trait dissimilarity would drive aboveground biomass at understorey stratum, probably due to the niche complementarity (Ali and Yan, 2018).

We have previously reported that whole-community aboveground biomass is driven by the high functional trait diversity of understorey but low functional trait diversity of overstorey in a subtropical forest (Ali et al., 2018). This study aims to investigate whether the evolutionary and functional trait dissimilarity have differential consequences on aboveground biomass across forest strata along local environmental gradients in a natural subtropical forest. Specifically, we ask three major questions with the corresponding hypotheses and predictions. (1) How do evolutionary and functional trait dissimilarity indices affect aboveground biomass across each individual forest stratum? We hypothesize that phylogenetically close and functionally similar species

drive high aboveground biomass in overstorey stratum due to the evolutionary relatedness (H_{1a}), while phylogenetically distant and functionally dissimilar species drive high aboveground biomass in understorey stratum due to the functional dissimilarity (H_{1b}) (Fig. 1C). (2) Are evolutionary and functional trait dissimilarity predict aboveground biomass similarly across each individual forest stratum? Our proposed hypothesis (H_1) predicts: (i) based on the less stringent conditions for influencing species interactions at overstorey stratum, evolutionary relatedness would drive aboveground biomass better than functional similarity; and (ii) based on the dominant effect of overstorey stratum on understorey (P_1), functional dissimilarity would drive aboveground biomass better than phylogenetic overdispersion in understorey stratum. (3) What are the consequences of evolutionary and functional trait dissimilarity on whole-community aboveground biomass when the data is mixed across forest strata? If the above predictions are true, we, hypothesize (H_2) that the mixed effects of evolutionary relatedness of overstorey and functional dissimilarity of understorey would drive aboveground biomass at whole-community level (Fig. 1C).

2. Materials and methods

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

This study used the forest inventory, functional traits and environmental factors datasets from our previous studies, which was conducted in a 5-ha subtropical forest plot (i.e. 125 plots, 20 m × 20 m each) located in Tiantong National Forest Park, Zhejiang Province of Eastern China (Ali and Yan, 2017a, 2017b, 2018). All individual trees having a diameter at breast height (DBH) ≥ 1 cm were measured and identified to the species level. This forest inventory included 20,253 individuals belonging to 108 species across 125 plots. Measurement of plant functional traits consisted of three steps. First, for each of 20,253 individual trees, leaf samples were collected for the measurements of leaf physical functional traits: mean leaf area, specific leaf area and leaf dry matter content. Second, seven healthy mature trees 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). The data for leaf chemical traits and wood density were missing for 10 rare or less abundant species (Ali and Yan, 2017b), and hence 98 species were used in this study (Ali et al., 2018). Third, Chinese flora database was used for the extraction of the plant maximum height for each studied species. For further detailed information or description about study area, forest inventory and plant functional traits, see our previous study (Ali and Yan, 2017b), and supplementary text in Appendix A.

We considered the covariate effects of topographical and soil properties on the multivariate relationships between functional trait dissimilarity, evolutionary diversity, and aboveground biomass. The topographical properties were elevation, slope and convexity, whereas the soil properties were pH, volumetric soil water content, bulk density, humus depth, and soil carbon, phosphorus and nitrogen contents (see Appendix A for more details about the measurement of these soil properties). In all statistical analyses, we used the two multivariate axes of principal component analyses (PCA) for soil properties (soil PC1 and soil PC2) and for topographical variables (topography PC1 and topography PC2), separately, for the purpose to reduce the strong correlations among and within soil properties and topographical properties (see Tables A1 and A2). The soil PC1 was largely occupied (49%) by soil physicochemical properties whereas the soil PC2 was mostly characterized (27%) by soil phosphorus and nitrogen contents, i.e., the soil nutrients. With respect to the topography PCA, the PC1 was greatly defined (58%) by elevation, slope and convexity, whereas the PC2 was mostly characterized (25%) by slope and convexity.

2.2. Quantification of functional trait and evolutionary diversity across forest strata

Overstorey stratum included all individual trees having DBH ≥ 10 cm, and understorey stratum included woody vegetation (i.e. small trees and shrubs) having $1 \leq \text{DBH} < 10$ cm within each plot (Ali and Yan, 2017b). Two broad measures of biodiversity were used to test the strength and magnitude of the relationships between forest diversity and aboveground biomass at each of the overstorey and understorey stratum as well as at whole-community level in a subtropical forest. This conceptual framework (Fig. 1) separates two different broad characteristics of forest diversity in a community, such as functional trait diversity based on multivariate-trait space and evolutionary diversity based on plant species phylogeny or supertree (e.g., Cadotte et al., 2008; Conti and Díaz, 2013; Potter and Woodall, 2014; Finegan et al., 2015).

2.2.1. Quantification of functional trait diversity or dissimilarity

We used four multivariate-trait indices of functional trait diversity or dissimilarity: functional evenness, functional richness, functional divergence and functional dispersion. These four indices were quantified for each of overstorey, understorey and whole-community level. Functional richness is the amount of multivariate trait space filled by species at the level of the community or strata (in this study). Functional evenness indicates how species' basal area is disturbed over multivariate-trait space, being higher when species' basal area distribution is equal across this space. Functional divergence indicates how species' basal area is diverged from the center of the multivariate-trait space, being higher when extremes of the multivariate-trait space are occupied by most of the species' basal area. Functional dispersion is the average distance of the species to the basal-area weighted centroid of all species in community trait space (Mason et al., 2005; Villéger et al., 2008; Laliberté and Legendre, 2010). We used eight measured functional traits, including six leaf and two stem traits, for the quantification of multivariate-trait functional trait diversity, and the trait values were standardized before the quantification of four functional trait diversity indices (Ali et al., 2018). As suggested, the species' relative basal area was used to weight species' traits within each individual forest stratum and at whole-community (Prado-Junior et al., 2016; Ali et al., 2018). All diversity measures were calculated using the *vegan* (Oksanen et al., 2015), *FD* (Laliberté and Legendre, 2010).

2.2.2. Quantification of evolutionary diversity

For the quantifications of evolutionary diversity indices, we first constructed phylogenetic supertree of all species, for each of overstorey (Fig. A1), understorey (Fig. A2) and whole-community (Fig. A3), based on the 'R20120829 phylomatic tree for plants' in Phylomatic v3 (Webb and Donoghue, 2005). We then calculated five evolutionary diversity indices – phylogenetic diversity, phylogenetic species richness, phylogenetic species evenness, phylogenetic species variability, and phylogenetic species clustering. Phylogenetic diversity is conceptually simple and widely used phylogenetic index (Faith, 1992). The other four evolutionary diversity indices are the well-defined statistical properties of the phylogenetic measures (Helmus et al., 2007; Potter and Woodall, 2014). Phylogenetic species variability is a measure of the deviation from a star phylogeny, with its values ranging between 1 (low phylogenetically close species) to 0 (high phylogenetically close species). Phylogenetic species evenness incorporates relative species abundances into the phylogenetic species variability index, with its values ranging between 1 (equal abundances of the highly-unrelated species) to 0 (unequal abundances of the phylogenetically close species). Phylogenetic species richness is the number of species in a community multiplied by phylogenetic species variability, which can be considered as the species richness of a community after discounting by species relatedness, i.e., the value is maximum at the species richness, and decreases towards 0 as relatedness increases. Phylogenetic species

Table 1

The overstorey stratum, understorey stratum and whole-community level optimal models obtained from a series of multiple regression analyses for aboveground biomass and 12 predictors (4 functional trait diversity, 4 evolutionary diversity indices and 4 environmental factors axes within each model) using a linear model. Standardized regression coefficient (Beta), *t*-test and *P*-value are given. The coefficient of determination (R^2), *F*-test, *P*-value and Akaike Information Criterion (AICc) of the model are also given. Moran's *I* test was conducted on the residuals for the optimal linear model. *P* values < 0.05 are given in bold. The blank cells represent that predictor variables were not retained in the selected optimal model.

Predictors	Overstorey stratum model			Understorey stratum model			Whole-community model		
	Beta	<i>t</i>	<i>P</i>	Beta	<i>t</i>	<i>P</i>	Beta	<i>t</i>	<i>P</i>
Constant	0.00	0.00	0.997	0.00	−0.01	0.995	0.00	−0.01	0.996
<i>Niche complementarity hypothesis (multivariate functional trait diversity)</i>									
FRic				0.25	3.73	< 0.001			
FEve	−0.21	−2.60	0.010						
FDiv							0.36	3.48	< 0.001
FDis				−0.21	−3.23	0.002	−0.38	−3.66	< 0.001
<i>Niche complementarity hypothesis (Evolutionary diversity)</i>									
PD	0.31	3.85	< 0.001				0.24	2.81	0.006
PSE	−0.27	−3.37	< 0.001						
PSV									
PSC									
<i>Environmental factors effects (soil physicochemical properties and topography axes)</i>									
Soil PC1									
Soil PC2				−0.17	−2.66	0.009	−0.20	−3.14	0.002
Topography PC1				0.36	5.36	< 0.001			
Topography PC2									
<i>Model statistics</i>									
<i>F</i> -test (<i>P</i> -value)	14.28 (< 0.001)			36.05 (< 0.001)			8.88 (< 0.001)		
R^2	0.26			0.55			0.23		
AICc	326.2			268.0			334.0		
Moran's <i>I</i> -test (<i>P</i> -value)	0.00 (0.826)			0.08 (0.068)			0.07 (0.107)		

Abbreviations: FDiv, functional divergence; FRic, functional richness; FEve, functional evenness; FDis, functional dispersion; PD, phylogenetic diversity; PSV, phylogenetic species variability; PSE, phylogenetic species evenness; PSC, phylogenetic species clustering; PC1 and PC2, PCA axes.

clustering quantifies the branch-tip clustering of species across the phylogenetic tree, and its values range between 1 (less related species at the tips of the phylogenetic tree) to 0 (high related species). All evolutionary diversity indices were quantified using the *picante* package (Kembel et al., 2010).

Phylogenetic species richness was not included in our statistical analysis because of its similarity to and a high degree of correlation with phylogenetic diversity at overstorey ($r = 0.90$), understorey ($r = 0.94$) and whole-community ($r = 0.94$). Therefore, we used eight indices of forest diversity that were quantified for each of the overstorey and understorey stratum, and whole-community, separately: four complementary functional trait diversity and four evolutionary diversity indices.

2.3. Estimation of aboveground biomass

Aboveground biomass for each individual trees having DBH ≥ 5 cm was calculated using a general allometric equation for (sub-) tropical forests (Chave et al., 2014). For each individual of shrub and small trees having DBH < 5 cm, a locally developed multispecies generalized model was employed for the calculation of aboveground biomass (Ali et al., 2015). More detail about the estimation of aboveground biomass is provided in our previous studies (Ali and Yan, 2017a, 2017b). For more detailed information, see Appendix A.

2.4. Statistical analyses

Multiple linear regressions models were used to evaluate how aboveground biomass was driven by functional trait diversity (4 indices) and evolutionary diversity (4 indices) at each of overstorey and understorey stratum, as well as at whole-community level, across local environmental conditions. We evaluated all possible subsets of the multiple linear regression models and selected the most parsimonious optimal model that had the lowest AICc (i.e. AIC adjusted for small sample sizes) and lowest number of explanatory variables (Bartoń,

2016). Multiple linear regression models were conducted using the *stats* package and all subsets regression analyses were evaluated in *MuMIn* package (Bartoń, 2016). We also showed the bivariate model's response against each predictor's marginal effect from the optimal multiple linear models, by using the *plotmo* package (Milborrow, 2015).

To test the spatial autocorrelation in the studied variables, we used generalized least-squares models (GLS) (Pinheiro and Bates, 2016). We also used the Moran's *I* test for evaluating the spatial autocorrelation in the residuals of the selected optimal linear model, using the *spdep* package (Bivand, 2016). We did not find any clear indication of spatial autocorrelation (Fig. A4) because the non-spatial models had the lower AIC values (Table A3) as also shown by previous several studies in natural forests (Chiang et al., 2016; Ali and Yan, 2017b, 2017a; Ali et al., 2018). The corresponding correlations and relationships between variables used in the multiple linear models are shown in Tables A4–A6, and Figs. A5–A7 (also see Table A7), respectively.

A structural equation model (SEM) was used to assess whether functional trait diversity and evolutionary diversity of overstorey stratum affect understorey stratum and its relationship with aboveground biomass. Here, we designed an SEM using the best predictors from the optimal linear models for testing the following direct and indirect effects: (1) direct effects of overstorey functional trait diversity and/or evolutionary diversity on understorey functional trait diversity and/or evolutionary diversity; (2) indirect effects of overstorey functional trait diversity and/or evolutionary diversity via understorey functional trait diversity and/or evolutionary diversity on understorey aboveground biomass; and (3) direct effects of functional trait diversity and/or evolutionary diversity of understorey stratum on understorey aboveground biomass. The SEM was implemented using the *lavaan* package (Rosseel, 2012).

Functional trait diversity indices, evolutionary diversity indices and aboveground biomass were natural-logarithm transformed and standardized for the purpose to improve the normality and linearity of the studied variables (Zuur et al., 2009). See Appendix B for the summary of studied variables across 125 plots, used in this study. All ecological

Overstorey stratum

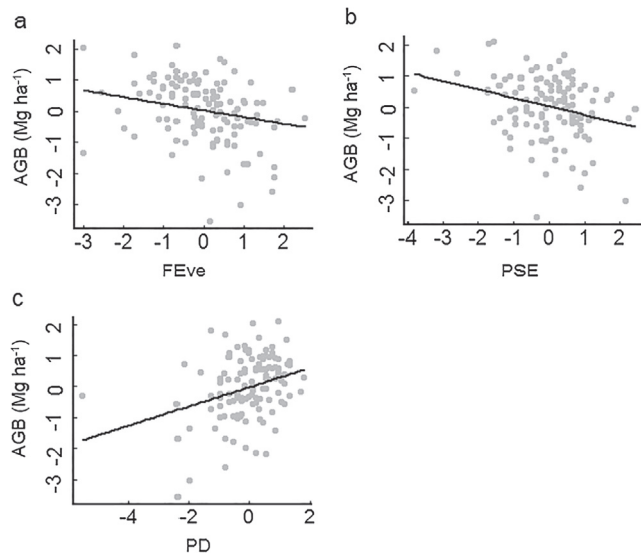


Fig. 2. The response of aboveground biomass to the retained predictors in the optimal model of overstorey stratum (see Table 1 for statistics). (a) Aboveground biomass (AGB; Mg ha^{-1}) as a function of functional evenness (FEve), (b) phylogenetic evenness (PSE) and (c) phylogenetic diversity (PD). The partial dependence plots represent an optimal linear model's response when varying predictor while holding the other predictors constant (i.e., marginal effect of a predictor). Solid lines represent significant ($P < 0.05$) relationships. See Fig. A5 for bivariate relationships.

and statistical analyses were conducted using R 3.4.2 (R Development Core Team, 2017).

3. Results

Overstorey aboveground biomass was best predicted ($R^2 = 0.26$) by functional evenness ($\beta = -0.21$, $P = 0.010$), phylogenetic species evenness ($\beta = -0.27$, $P < 0.001$) and phylogenetic diversity ($\beta = 0.31$, $P < 0.001$), with no spatial autocorrelation in the residuals (Table 1). This result indicates that overstorey stratum has high aboveground biomass when phylogeny is occupied by phylogenetically close species having highly different abundances, and low functional evenness (Fig. 2). Understorey aboveground biomass was best predicted ($R^2 = 0.55$) by functional richness ($\beta = 0.25$, $P < 0.001$), functional dispersion ($\beta = -0.21$, $P = 0.002$), soil nutrients ($\beta = -0.17$, $P = 0.009$) and topography ($\beta = 0.36$, $P < 0.001$), with no spatial autocorrelation in the residuals (Table 1). This finding indicates that understorey stratum has high aboveground biomass when they are occupied by the high functional richness and low functional dispersion, and located on nutrient-poor soils and high topography (Fig. 3).

In comparison, whole-community aboveground biomass was best predicted ($R^2 = 0.23$) by functional divergence ($\beta = 0.36$, $P < 0.001$), functional dispersion ($\beta = -0.38$, $P < 0.001$), phylogenetic diversity ($\beta = 0.24$, $P = 0.006$) and soil nutrients ($\beta = -0.20$, $P = 0.002$), with no spatial autocorrelation in the residuals (Table 1). This result indicates that whole-community has high aboveground biomass when minimum spanning distance of a phylogenetic tree in a given community is represented by all species having high functional divergence and low functional dispersion, and located on soils with low soil nutrients (Fig. 4).

The best-fit SEM showed that phylogenetic species evenness rather than functional evenness of overstorey species had a significant direct negative effect on understorey functional trait diversity ($\beta = -0.35$, $P = 0.002$), and as a consequence indirect negative effect on understorey aboveground biomass ($\beta = -0.23$, $P = 0.002$). Phylogenetic

Understorey stratum

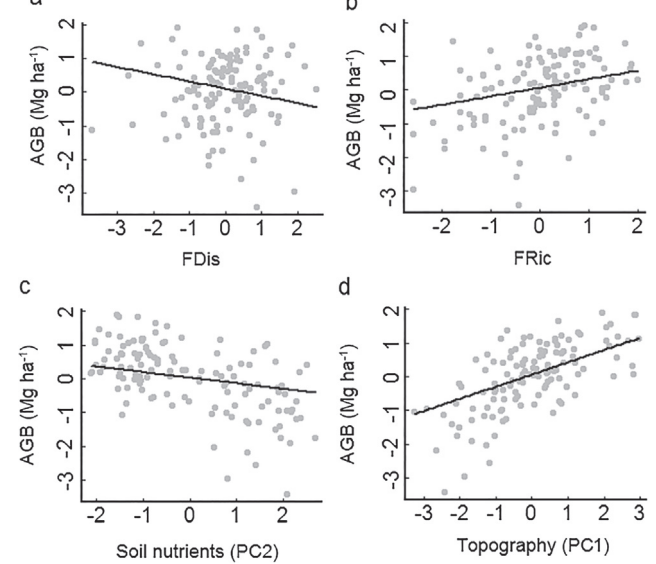


Fig. 3. The response of aboveground biomass to the retained predictors in the optimal model of understorey stratum (see Table 1 for statistics). (a) Aboveground biomass (AGB; Mg ha^{-1}) as a function of functional dispersion (FDis), (b) functional richness (FRic), (c) soil nutrients (PC2) and d) topography (PC1). See Fig. A6 for bivariate relationships.

Whole-community level

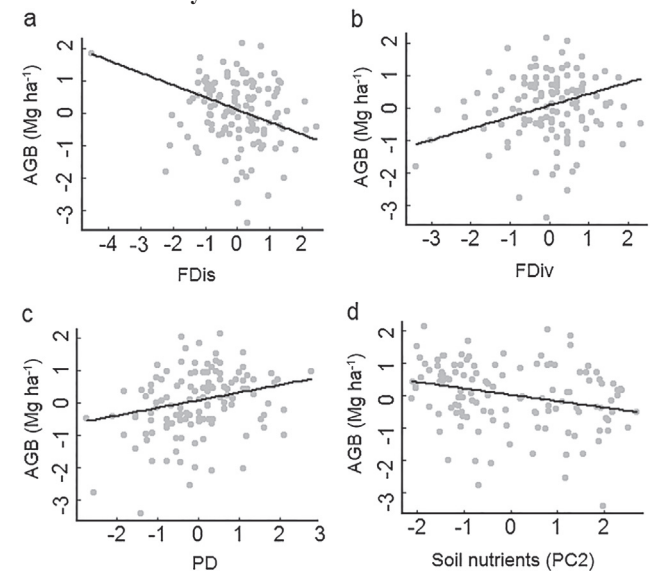


Fig. 4. The response of aboveground biomass to the retained predictors in the optimal model of whole-community (see Table 1 for statistics). (a) Aboveground biomass (AGB; Mg ha^{-1}) as a function of functional dispersion (FDis), (b) functional divergence (FDiv), (c) phylogenetic diversity (PD) and (d) soil nutrients. Solid lines represent significant ($P < 0.05$) relationships. See Fig. A7 for bivariate relationships.

diversity of overstorey species had a significant direct positive effect on understorey functional trait diversity ($\beta = 0.55$, $P < 0.001$), and as a result indirect positive effect on understorey aboveground biomass ($\beta = 0.36$, $P < 0.001$; Fig. A8). Understorey functional trait diversity (as a latent variable of functional richness and dispersion) had a significant positive direct effect on understorey aboveground biomass ($\beta = 0.66$, $P < 0.001$; Fig. A8). This result indicates that high evolutionary relatedness (high phylogenetic diversity and low phylogenetic species evenness) of overstorey stratum modulates the positive effect of

functional trait diversity on aboveground biomass at understory stratum.

4. Discussion

The main originality of this study is determining that high aboveground biomass in natural forests is greatly dependent on the species assembly based on their phylogenetic and functional similarity or the difference between forest strata. Our results suggest that functional trait similarity and phylogenetic conservatism at overstorey stratum whereas functional trait diversity at understory stratum are of great importance for driving high aboveground biomass in subtropical forest. We found that overstorey aboveground biomass is greater for the groups of phylogenetically close species with low functional trait variation (i.e. high functional trait similarity or convergence across phylogenetically close species). At understory stratum, high aboveground biomass is related to high functional trait diversity, after accounting for the effects of overstorey functional and evolutionary diversity, i.e., functional trait divergence across phylogenetically distant species. It is true that ecological differentiation among species relates to evolutionary diversity within a given habitat type (e.g. Cadotte et al., 2008). Greater ecological differentiation allows species to stably coexist together due to the efficient utilization of resources by co-occurring species (e.g., niche partitioning) (Ali et al., 2017). Greater niche and trait differences could, in turn, determine aboveground biomass in a community (Heemsbergen et al., 2004; Petchey et al., 2004; Hooper et al., 2005; Yuan et al., 2018).

Evolutionary and functional trait information may underpin similar ecological consequence for driving high aboveground biomass at each of the individual forest stratum and at a whole-community level. Our optimal models suggest that evolutionary diversity indices compared to functional trait diversity are better for predicting aboveground biomass at overstorey stratum, not at understory stratum, while a bit similarly important at a whole-community level. This is the case that evolutionary diversity can act as the proxy of functional trait diversity (Cadotte et al., 2008, 2009; Flynn et al., 2011; Paquette and Messier, 2011; Yuan et al., 2016). Additionally, we expected that functional trait diversity can better explain variation in aboveground biomass at understory stratum since trait differences should drive ecological differences – regardless of patterns of shared ancestry on the traits (e.g. Cadotte et al., 2009). We found that most of the effects of evolutionary diversity indices on understory aboveground biomass could be captured by functional trait diversity, whereas the opposite was not true or relatively unpredictable. As partially reported in our previous studies, functional traits of understory stratum contain some unique information and are most importantly relevant to functional conservative strategies, which are stronger predictors of aboveground biomass than phylogenetic information alone (Ali and Yan, 2017b; Ali et al., 2018).

The ecological mechanisms across forest strata and with the comparison at whole-community seem to be very different, which could be the results of biotic interactions and resource heterogeneity at each forest stratum (de Bello, 2012; Zhang et al., 2016; Ali and Yan, 2017a; Ali et al., 2017). We found that high aboveground biomass in overstorey stratum is dominantly contributed by phylogenetically close and functionally similar species. On the one hand, low phylogenetic species evenness and high phylogenetic diversity of overstorey stratum reflect the co-occurrence of phylogenetically close species, as an indication for environmental filtering on phylogenetically conserved traits (Webb, 2000; Kembel and Hubbell, 2006; Cavender-Bares et al., 2009). On the other hand, contrary to the niche complementarity hypothesis (Villéger et al., 2008; Ali et al., 2018), low functional evenness of overstorey species indicates that a restricted part of the multivariate-trait space is occupied by most of the species' basal area, and hence. In addition, the bivariate relationships suggest that overstorey stratum have high aboveground biomass when they are occupied by low functional trait diversity where branch-tip clustering of species across the phylogenetic

tree is occupied by highly different abundances of species with low phylogenetic variability (Helmus et al., 2007; Potter and Woodall, 2014). In combination, this study reveals that phylogenetically close overstorey species have high aboveground biomass due to ecological similarity, and the fact of the absence of strong biotic interactions among functionally similar species, which often share similar resources (e.g. Wiens and Graham, 2005; Cavender-Bares et al., 2009).

At understory stratum, high aboveground biomass is driven by species having a variety of functional traits with similar average functional distances (probably due to the dominance of conservative traits; Ali and Yan (2017b)) for efficient utilization of resources under resource-limited environments (Valiente-Banuet and Verdú, 2007). In agreement to the niche complementarity hypothesis (Heemsbergen et al., 2004; Hooper et al., 2005; Ali et al., 2018), high functional richness indicates that multivariate trait space is filled by most of the species' basal area (Villéger et al., 2008). Although aboveground biomass may increase with the sole effect of functional dispersion under the niche complementarity hypothesis, the lack of positive effect of functional dispersion on aboveground biomass might be attributable to the selection effect or resource complementarity among species (Loreau et al., 2001; Ali and Yan, 2017b). Consequently, the SEM result showed that functional richness and dispersion are positively correlated for driving high aboveground biomass under the niche complementarity mechanism, where functional dispersion has a negligible positive contribution. This result indicates that the selection effect was the strongest when functional richness is low, while complementarity effect is the greatest with high functional richness in the understory of the studied forest (Villéger et al., 2008; Ali et al., 2018). These opposing mechanism might be happening due to the effects of functional trait diversity of overstorey stratum on understory stratum (Ali et al., 2018). As such, high evolutionary relatedness (low phylogenetic species evenness and high phylogenetic diversity) of overstorey stratum might modulate the positive relationship between functional trait diversity (a latent variable of functional dispersion and richness) and aboveground biomass at understory stratum in our studied forest.

In addition to the functional richness and functional dispersion acting as the significant best predictors of aboveground biomass at understory stratum, we found that the bivariate relationships of aboveground biomass with phylogenetic diversity, phylogenetic species clustering and phylogenetic species variability were also significant. These bivariate relationships interpret the coexistence of phylogenetically distant species that share almost similar hypothetical traits (i.e. functional strategy) (Cavender-Bares et al., 2009). This can result either from the competition caused overdispersion of conserved traits or the environmental filtering mediated trait convergence (Webb, 2000; Kembel and Hubbell, 2006; Valiente-Banuet and Verdú, 2007). Our results are supporting the theories of earlier ecologists including Charles Darwin that similarity in resource use due to unshared ancestry would cause lower competition among phylogenetically distant species compared to phylogenetically close species, and hence higher phylogenetic diversity in natural communities (Simberloff, 1970; Webb, 2000; Valiente-Banuet and Verdú, 2007; Cadotte et al., 2008; Cavender-Bares et al., 2009). Taken together, our results suggest that high aboveground biomass in understory stratum is attributable to high clustering of phylogenetically distant species with high functional richness, similar average functional distances or a specific functional strategy (Ali and Yan, 2017b).

In comparison, high whole-community aboveground biomass was best predicted by high phylogenetic diversity, high functional divergence and low functional dispersion. However, the bivariate relationships suggest that overstorey stratum has high aboveground biomass as a result of high functional richness where branch-tip clustering of species across the phylogenetic tree is occupied by highly different abundances of species (Helmus et al., 2007; Potter and Woodall, 2014). As hypothesized, this mechanism at the whole-community level might be resulted from the mixed effects of overstorey evolutionary

relatedness and understorey functional trait diversity (Paquette et al., 2015; Yuan et al., 2016), which could be the cause of different functional strategies across forest strata in the studied forest (Ali and Yan, 2017b; Ali et al., 2018).

In conclusion, this study suggests that evolutionary diversity indices compared to functional trait diversity indices are important predictors for best-explaining variation in aboveground biomass at overstorey stratum, not at understorey stratum, while a bit similarly important at a whole-community level in a local forest. Our study suggests that disentangling the effects of evolutionary diversity and functional trait diversity across forest strata may be helpful for better understanding of ecological mechanisms for predicting aboveground biomass in a subtropical forest. From the practical point of view, this study suggests that high aboveground biomass and thus high carbon storage can be managed in naturally subtropical forests through the selective arranging of more phylogenetically close and functional similar species in overstorey stratum, and phylogenetically and functional distinct species in understorey stratum.

5. Data availability

The dataset used for analyses accompanies this paper as supplementary file (Appendix B). More information about dataset is available upon request to the authors.

6. Statement of authorship

AA and ERY conducted research; AA compiled and analyzed the data; AA and ERY designed the study and wrote the paper.

7. Conflict of interest

The authors declare no conflict of interest.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.foreco.2018.06.042>.

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