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華東師範大學

East China Normal University

博士学位论文

DOCTORAL DISSERTATION

论文题目：浙江天童森林生物多样性、地上生物量与环境关系的垂直层次依赖性

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Abstract

The relationships between biodiversity and aboveground biomass in forest ecosystems have been intensively studied in recent decades. However, natural forests are structurally complex and plant species with different functional strategies are generally assembled in different forest strata (i.e. overstorey and understorey). It is not very clear which ecological mechanism(s) underpin the relationships between biodiversity including stand structure and aboveground biomass across forest strata while accounting for the effects of environmental factors. This thesis focused on the linkage among environmental factors, biodiversity and stand structural attributes, and aboveground biomass across forest strata and at whole-community level (for comparison) of a subtropical evergreen broadleaved forest.

Aboveground biomass, multiple metrics of biodiversity (taxonomic, functional trait and phylogenetic diversity indices), stand structural attributes and environmental factors were quantified or measured for 125 plots in a 5-ha subtropical forest, located in Ningbo city, Zhejiang Province, in Eastern China. We[1] mainly used structural equation model and/ or multiple linear models for linking environment, biodiversity (including stand structure) and aboveground biomass across forest strata and at whole-community level. The complementary Pearson's correlations and bivariate relationships to the structural equation model and/ or multiple linear models were also evaluated. To account for spatial autocorrelation, we performed generalized least-squares models with (accounted for the spatial location of each plot) and without spatial autocorrelation among plots for each of the proposed relationships. In case of using multiple linear models, we also applied the Moran's I test for spatial autocorrelation in the selected optimal linear model residuals.

The main finding of this thesis is that no sole and ubiquitous relationship between biodiversity and aboveground biomass exists in a structurally complex forest, but rather that the magnitude and direction of this relationship is greatly dependent on the forest strata where available resources shift substantially. Specifically, we found that:

1) Aboveground biomass in overstorey strata was driven by high individual tree size variation and species diversity. In understorey strata, the mixture effects of tree development, high degree of biotic interaction, and increased resource heterogeneity complicated the relationship between biodiversity and aboveground biomass.

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[1] "we" is used when referring to research chapters in which co-author(s) are involved, and "I" for general thesis information in the general introduction and discussion (chapters 1 and 9).

2) High functional trait diversity of understorey enhanced aboveground biomass through the niche complementarity effect while low functional trait diversity of overstorey enhanced aboveground biomass through functionally-similar big trees effect.

3) Intraspecific and interspecific functional trait diversity positively mediated the response of aboveground biomass to species richness at understorey strata through niche differentiation, whereas negligible or negative roles at overstorey strata and whole-community indicated that only few large trees occupy larger niche space in a community.

4) Understorey aboveground biomass was 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 was related with groups of phylogenetically close species having low functional trait diversity due to the evolutionary relatedness. The mixed effects of overstorey evolutionary relatedness and understorey functional trait diversity on their corresponding aboveground biomass complicated these relationships at the whole-community level.

5) With respect to the species' functional strategies, high aboveground biomass was potentially driven by functional identity (community-weighted mean of a trait values) of tree height through making use of plentiful soil nutrients and light at overstorey strata, whereas by conservative strategy at understorey strata through enduring resource-poor conditions.

6) In combination, this study found that functional identity of tree height with low functional trait diversity at overstorey, whereas niche complementarity with conservative strategy on resource-poor soils were of great importance for driving aboveground biomass. At whole-community level, aboveground biomass was most strongly determined by soil nutrients, individual tree size variation and functional dominance of big trees.

The results in this thesis have highlighted the fundamental roles of forest strata where overstorey and understorey strata contribute to their corresponding aboveground biomass with contrasting functional strategies or ecological mechanisms across a range of soil nutrients. Hence, ecological models for predicting aboveground biomass would be improved by including separate effects of overstorey and understorey diversity. This study concluded that conserving biodiversity and maintaining stand structure at both overstorey and understorey strata in subtropical forests would be the beneficial and sustainable management strategies in the context of global change.

Key-words: biodiversity; ecosystem function; forest strata structure; functional traits; mass ratio hypothesis; niche complementarity hypothesis; soil nutrients

摘要 (Abstract in Chinese)

近年来，关于森林生物多样性和地上生物量关系的研究已经取得了深入进展。然而，在自然森林群落中，群落结构复杂，分布、配置于不同垂直层次（上木层和下木层）的物种功能策略差异显著。同时，当综合考虑环境因子的影响时，生物多样性、群落结构以及地上生物量在不同林层的潜在关系尚不清楚。本论文以亚热带常绿阔叶林为对象，主要聚焦研究上木层、下木层和群落整体层次上，环境因子、生物多样性、群落结构多样性和地上生物量的关系，及其潜在生态机制。

本研究主要基于浙江天童5公顷连续森林动态监测样地125个样方的地上生物量，不同维度生物多样性（包括物种多样性以及功能和系统发育多样性）指标，林分结构特征和环境因子数据集。我们主要采用结构方程模型和混合线性模型， 在不同林层及整个群落水平上分析环境、生物多样性与地上生物量之间的内在关系。其次，结合Pearson相关性分析和双变量对应关系对结构方程模型和混合线性模型进行了补充。考虑到空间自相关的问题，我们以广义最小二乘法进行模拟（考虑每个样地的空间位置），同时也对不考虑空间自相关的关系进行了分析比较。在使用混合线性模型的情况下，我们利用空间自相关Moran's I检验方法筛选最佳模型。

本研究的主要发现为：在结构复杂的亚热带森林群落内，生物多样性和地上生物量关系并非呈现单一的模式，其强度和方向完全取决于资源供给性变化剧烈的群落垂直层次。具体而言，本研究主要有如下发现：

1. 在乔木层，高的树木个体大小变异和物种多样性是决定地上生物量的主要驱动因素。在下木层，树木生长发育、高强度竞争以及环境异质性的混合效应导致了复杂的生物多样性和地上生物量关系。

2. 下木层高的功能多样性通过生态位互补效应对地上生物量有增强作用；在上木层，虽然物种功能多样性较低，但其通过具有相似功能的大树效应增强地上生物量。

3. 种内和种间功能多样性可以通过生态位分化正向调适下木层的地上生物量对于物种丰富度的响应。在上木层和群落整体，物种丰富度和地上生物量关系缺失，甚至为负向，间接表明了在上木层或整个群落水平，生态位空间可能主要由单优物种的大树占据。

4. 在下木层，物种的谱系距离越远，其功能多样性越高，越有利于增加地上生物量。与此相反， 在上木层，高的地上生物量主要归因于谱系距离较近、且功能多样性

较低的物种多样性组合。在群落水平，上木层的物种谱系相似性和下木层的功能多样性的混合效应使得物种多样性与地上生物量关系变得更加复杂。

5. 从物种功能策略角度而言，上木层较高的地上生物量主要归因于其具有较大的群落树高功能特性，功能特性是指某一功能特性的群落加权平均值，在这里是指其含有较大比例的高大个体物种，它们往往在竞争土壤养分和光线方面具有优势。相反，在下木层，物种更多的通过保守地耐受资源贫瘠策略而影响地上生物量。

6. 综合来看, 本研究发现：在森林上木层，物种的较高树高功能特性与较低的功能多样性有利于提高地上生物量；在下木层，具有耐瘠薄资源的保守策略的物种通过生态位互补效应提高其地上生物量。在群落整体尺度，地上生物量主要是由土壤养分、树木个体大小变异性以及大树的优势特征决定。

本研究结果强调了森林不同垂直层次在生物多样性与地上生物量关系中的重要性，在土壤养分梯度上，上木层和下木层物种功能策略差异显著，因而其影响生物多样性-地上生物量关系的机制也不同。因此， 在预测地上生物量的生态学模型中，如果能够区分上木层和下木层的多样性效应，将会提升预测性。总之，本论文研究结果表明，在全球变化背景下，同时保护亚热带森林上木层和下木层的生物多样性，且维持群落的结构多样性，将是非常有益且可持续的管理策略。

关键词：生物多样性；生态系统功能；功能性状；质量比率假说；生态位互补假说；土壤养分；林层结构

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Chapter 1. Introduction and background

1.1. Biodiversity and the functioning of forests in the changing world

Global biodiversity[1] is speedily decreasing due to anthropogenic disturbances such as deforestation and ecological habitat destruction, with potentially important concerns for the ecosystem functioning[2] (Bunker *et al.* 2005, Cardinale *et al.* 2012, Lohbeck *et al.* 2016). Ecosystem functions[3] can be defined as the stocks and fluxes of biological activity-driven substances and energy with time and space (Hooper *et al.* 2005) and biodiversity is considered as one of the main biotic drivers (Balvanera *et al.* 2006, Lohbeck *et al.* 2016, Midgley 2012). In forests, aboveground biomass productivity (a flux) and carbon storage in biomass or aboveground biomass (a stock) are two main ecosystem functions (Chisholm *et al.* 2013, Pacala & Kinzig 2002). Aboveground biomass (i.e. carbon storage) is of particular concern because globally forests hold more carbon than the atmosphere (Pan *et al.* 2011), and management of these carbon stores is an important tool for mitigating global climate change. Aboveground biomass stock is a state variable and a key ecosystem function that underlies many of the biogeochemical fluxes taking place in ecosystems (Poorter *et al.* 2015). Carbon is continuously removed from the atmosphere by forest ecosystem processes and stored both in vegetation and soils (McGuire *et al.* 2001). If carbon stocks of ecosystems increase, the carbon content of the atmosphere is reduced. On the other hand, if the carbon stocks in ecosystems were to reduce, the increase rate of carbon dioxide (CO_2) in the atmosphere would be much faster than currently observed (Reich 2011). Therefore, global forests are very diverse and provide a range of ecosystem services such as carbon sequestration, timber and non-timber products, flood and landslide protection, biodiversity preservations, aesthetic and health benefits (Pan *et al.* 2013).

Anthropogenic change threatens biodiversity worldwide, particularly (sub-) tropical forests, and increased the accelerating rate of species extinction up to one thousand times the background rate by modifying the environment (Andelman & Willig 2003, Millennium Ecosystem Assessment 2005, Sala *et al.* 2000). Subtropical forests in the East Asian monsoon region play a critical role in providing goods and services such as aboveground woody productivity and carbon cycling (Ali *et al.* 2016b, Niu *et al.* 2012, Wang *et al.* 2014), likely due to high nitrogen deposition, sufficient water, and heat availability (Yu *et al.* 2014). In total, forests account for approximately 75% of terrestrial productivity and 80% of biomass (Pan *et*

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[1] **Biodiversity:** the variety of life; synonym for ‘biotic conditions’ (e.g. individual tree size variation, species diversity, functional trait diversity and evolutionary diversity, in this thesis).

[2] **Ecosystem functioning:** the integrative effect of all ecosystem processes that are needed to sustain an ecosystem.

[3] **Ecosystem functions:** often used as a synonym for ‘ecosystem processes’. In this thesis ‘ecosystem functions’ mainly refer to aboveground biomass, carbon storage or productivity of forests. I use aboveground biomass in this research.

al. 2013). Tropical and subtropical forests are among the most productive ecosystems on Earth (Dixon *et al.* 1994, Melillo *et al.* 1993, Pan *et al.* 2013), interacting significantly with global biogeochemical cycles and regulating climate at regional and global scales (Bala *et al.* 2007, Yu *et al.* 2014). Although these ecosystems alone account for more than 50% of terrestrial species diversity (Wilson 1988), they are under increasing stress resulting from change and intensification of land-use, associated fragmentation, and climate change (Fan *et al.* 2016, Malhi *et al.* 2008, Yu *et al.* 2014, Zhao *et al.* 2013).

Besides the roles of (sub-) tropical forests in climate change mitigation capacity, these ecosystems are significantly important for various other functions that are relevant at local and global scales, such as timber and non-timber forest products and pollination (Malhi *et al.* 2008, Niu *et al.* 2012, Pan *et al.* 2013). Globally, the livelihood of more than a billion people depends directly on forests (e.g. Belcher 2005, and references therein), with most of them living in the (sub-) tropics. Humans are dependent on ecosystems for the services they offer; however, the capability for ecosystems to offer these services depends on how humans treat them (Millennium Ecosystem Assessment 2005). And, while it is plausible that ecosystem services are reliant on biota, there is incomplete knowledge in how exactly ecosystem services are reacting to the current trend of biodiversity loss. In an attempt to fill this gap in knowledge, ecologists have commenced a motivated research effort to quantify how biodiversity losses affect ecosystem functioning (Cardinale *et al.* 2012, Naeem 2002). Therefore, the study of the relationship between biodiversity and forest functioning is due to the understanding of the basic interests of forest communities and the practical need to protect and manage forest ecosystem services (Lohbeck *et al.* 2016, Poorter *et al.* 2015, Zhang *et al.* 2012b).

Subtropical evergreen broadleaved forest is ranged between 24 to 32° N latitude and 99 to 123° E longitude, accounting for about 25% of China, and becoming one of the most important vegetation types in China (Fan *et al.* 2016, Song 1988, Wang *et al.* 2007). This biome is seriously affected by the East Asian monsoon and human disturbance, and is expected to be affected by future climate change (Zhao *et al.* 2013). A recent study shows that the composition of subtropical evergreen broadleaved forest may has a special response to climate change in the late Quaternary, and the community assemblages of these forests may change over time (Fan *et al.* 2016). Despite the recognized importance of subtropical forests in climate change mitigation and even vulnerable to future climate change, uncertainties remain regarding the relationships between biodiversity and functioning of subtropical forests. Yet, few studies have tested these relationships within-site, and hence it is difficult to assess the role of these forests in global and regional carbon cycles. In this thesis I focused on the environmental factors[1] (abiotic conditions), biodiversity indices (biotic conditions), and aboveground biomass (a carbon stock) of the subtropical evergreen broadleaved forest in Ningbo region of Eastern China, given that the vegetation is most directly related to climate change mitigation and other globally important functions.

1.2. Current state of knowledge: Forest diversity and functioning

1.2.1. Taxonomic attributes and the functioning of forests

The relationships between biodiversity and ecosystem functions have been a subject of debate for more than four decades (Grime 1973). One of the most commonly studied relationships is that between species richness (i.e. taxonomic diversity) and aboveground biomass or productivity, or its surrogates (see Ali & Yan 2017a, and references therein). Most of the studies regarding species richness or diversity and aboveground biomass or productivity have been conducted in both experimental and natural environments including forests, and most of them have found positive or humpback relationships (Ali *et al.* 2016a, Balvanera *et al.* 2006, Hector *et al.* 1999, Isbell *et al.* 2011, Naeem *et al.* 1994, Tilman *et al.* 1996). These relationships between species richness or diversity and aboveground biomass or productivity are often attributed to the niche complementarity hypothesis, selection hypothesis and insurance hypothesis. The niche complementarity hypothesis postulates that species having different niches are able to utilize the available resources or facilitate each other, and hence increasing the productivity of a community (Tilman *et al.* 2001). The selection hypothesis states that increased productivity is due to the by chance occurrence of a very productive species in the community (Loreau & Hector 2001). The insurance hypothesis assumes that one species contributes more to the productivity in one year and another species are doing so in another year (Isbell *et al.* 2011, Yachi & Loreau 1999).

Species complementarity including niche differentiation and facilitation are often considered as the mechanisms for the positive relationships between species diversity or richness and aboveground biomass or productivity in natural forests (Poorter *et al.* 2015, Zhang & Chen 2015). It is, therefore, well known that species diversity or richness can be important for ecosystem functioning because it can influence the efficiency of resource acquisition and

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[1] **Environmental factors** (or conditions or drivers): In this thesis, environmental factors refer to local soil physicochemical properties (nutrients), and topographical factors (such as elevation, slope and convexity).

use of the plant community (Zhang *et al.* 2016a). Although the niche complementary hypothesis has received some empirical support (e.g. Cardinale *et al.* 2011), there are still differences in the contribution of species to ecosystem functions under the sampling effect prediction (Huston 1997). In natural forests, however, the relationships between species diversity or richness and aboveground biomass or carbon storage and productivity have been reported to either positive (Dayamba *et al.* 2016, Jucker *et al.* 2016, Wang *et al.* 2011, Zhang & Chen 2015), non-significant or even negative (Ali *et al.* 2016b, Edgar & Burk 2001, Vilà *et al.* 2003). In forest ecosystems, a recent meta-analysis has strongly supported the niche complementarity hypothesis in terms of both species richness and evenness (Zhang *et al.* 2012b). These results are important because it suggests that loss of biodiversity could have negative consequences for ecosystem functioning, and the ecosystem services that people depend on (Cardinale *et al.* 2011, Millennium Ecosystem Assessment 2005). However, increasing diversity may lead to niche overlap (functionally similar species that make use of the same resources) instead of niche complementarity (Walker 1992). This may explain why the relationship between species diversity and aboveground biomass sometimes does not supports the niche complementarity hypothesis in high-diverse natural forest ecosystems, where negative (Ali *et al.* 2016b, Szwagrzyk & Gazda 2007), or non-significant relationships are found (Vilà *et al.* 2003). The direction of this relationship depends on the resource-use complementarity of co-occurring species, and functional traits can be used as a proxy for this (e.g., Paquette & Messier 2011, Vilà *et al.* 2013, Vilà *et al.* 2007, Zhang *et al.* 2012b). Therefore, functional traits provide a more powerful link between species identity and ecosystem function, indicating that larger trait variation is associated with ecological niches and provide evidence for the niche complementarity hypothesis (Díaz *et al.* 2011a).

Alternately, relationships between species diversity and forest functioning may vary from linear, where all species contribute equally, to highly saturating, where few species contribute a lot and many species contribute little to the forest functioning (Balvanera *et al.* 2005, Lohbeck *et al.* 2016). Empirical evidence suggests that a small number of species contribute to most of the specific ecosystem function (Balvanera *et al.* 2005, Bunker *et al.* 2005, Lohbeck *et al.* 2016), due to the particular functional trait values (Mouillot *et al.* 2011). In natural ecosystems, this linkage is more complex because communities may also vary in species dominance and composition rather than species richness only (Maestre *et al.* 2012). In terms of size and/ or abundance, the contribution of dominant species to ecosystem functions is disproportionate (Creed *et al.* 2009, Slik *et al.* 2013, Winfree *et al.* 2015), and thus indirectly affecting the relationships between species richness and ecosystem function, from linear (low dominance) to asymptotic (high dominance) (Hillebrand *et al.* 2008, Lohbeck *et al.* 2016). Likewise, species dominance is expected to diminish the effect of biodiversity on ecosystem functioning, probably due to the outperforming effect of species dominance as compared to the effects of species functional traits on ecosystem function (see Lohbeck *et al.* 2016, and references therein). The asymptotic relationship between the cumulative number of species and the ecosystem function indicates that the functional identity of certain trait(s) is required, rather than the higher biodiversity, in order to optimize the ecosystem function (Lohbeck *et al.* 2016), as postulated by the mass ratio hypothesis (Grime 1998).

1.2.2. Functional traits and the functioning of forests

Compared to taxonomic attributes of biodiversity, functional traits of plant species in a given community provide a more mechanistic link between biodiversity and ecosystem functioning (Díaz *et al.* 2007, Díaz *et al.* 2011b, Petchey & Gaston 2006). According to Díaz *et al.* (2011b), plant functional trait diversity is the value, range, distribution, and relative abundance of the trait values of plant species that make up an ecosystem. Depending on the process and the associated service, the key components of functional trait diversity might be either the trait values of the most abundant species (i.e. functional composition), the variety of trait values found in the community (i.e. functional trait diversity) or the trait values of particular individual species, which may be rare (Díaz *et al.* 2011b). Functional trait diversity (referring to the niche complementarity) and community-weighted mean (CWM)[1] of trait values (the mass ratio, referring to the degree of a communities dominated by a single plant strategy) are two independent measures of biodiversity. These two measures determining the functional strategies for the quantification of functional attributes of biodiversity (Díaz *et al.* 2007), and have widely been used to elucidate the mechanisms behind the biodiversity and aboveground biomass relationships (e.g. Ali *et al.* 2017, Conti & Díaz 2013, Finegan *et al.* 2015).

The niche complementarity hypothesis predicting that communities with a higher diversity of species (Tilman 1999) or functional traits (Díaz *et al.* 2011b) use available resources more efficiently, thereby increasing the magnitude of ecosystem functions in natural forests (Zhang *et al.* 2012b). The mass ratio hypothesis predicting that ecosystem functions are driven by the (traits of the) most abundant species in plant communities (Grime 1998), and therefore communities dominated by plants with a single resource use strategy have higher

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[1] **CWM**: In this thesis, CWM of a trait values refer to functional identity or functional composition. CWM of tree height is also defined as functional dominance.

aboveground biomass (Conti & Díaz 2013, Díaz *et al.* 2007, Garnier *et al.* 2004). This mass ratio hypothesis (Grime 1998) is analogous to the hypothesis from biodiversity–ecosystem functioning experiments using plant monocultures and mixtures, which hypothesizes that variation in ecosystem productivity are determined by the presence or absence of highly productive species and not by the variety and complementarity of species (Cardinale *et al.* 2007). The mass ratio and niche complementarity effects are not necessarily mutually exclusive; both have been shown to operate in natural ecosystems and can have different relative importance in different situations (Ali *et al.* 2017, Conti & Díaz 2013, Finegan *et al.* 2015, Prado-Junior *et al.* 2016).

What mechanism (the mass ratio or the niche complementarity) would underlie the relationships between biodiversity (i.e. functional trait diversity and CWM of trait values) and aboveground biomass in natural forests? Traits that are associated with the growth rate of individual plants (Cornelissen *et al.* 2003) are also expected to be mechanistically associated to primary productivity of the vegetation (Finegan *et al.* 2015, Garnier *et al.* 2004). Plant trait values affect plant fitness and performance (Violle *et al.* 2007), trait-based approaches thus are rapidly emerging as a promising way to understand underlying ecological mechanisms that operate in plant communities. For instance, high CWM of specific leaf area and leaf chemical traits indicate a community dominated by fast-growing acquisitive species that are expected to be associated with high aboveground biomass productivity (Finegan *et al.* 2015). In contrast, high CWM of leaf dry matter content or wood density indicate a community dominated by conservative species and are expected to be associated with low productivity (Garnier *et al.* 2004, Wright *et al.* 2010). However, our understanding regarding the relationships between functional trait diversity and aboveground biomass or productivity remains patchy than that of CWM of trait values. For instance, four relatively independent components are put forward for the quantification of functional trait diversity based on multivariate-trait space, i.e. functional richness, evenness, divergence and dispersion (Laliberté & Legendre 2010, Villéger *et al.* 2008), and hence found to be not related with aboveground biomass or productivity in natural forests (Conti & Díaz 2013, Finegan *et al.* 2015, Lin *et al.* 2016, Prado-Junior *et al.* 2016). In addition, functional divergence of a single-trait strategy is an independent measure of functional trait diversity (Díaz *et al.* 2007), and hence found to be related with aboveground biomass in secondary subtropical forests (Ali *et al.* 2017). These functional properties are referring to the niche complementarity hypothesis (Petchey & Gaston 2006, Tilman 1999), and therefore high aboveground biomass or productivity is expected with high functional trait diversity in a community (Díaz *et al.* 2011a, Zhang *et al.* 2012b). The mass ratio and niche complementarity hypotheses can also be applied to aboveground biomass, since higher productivity may lead to faster accumulation of biomass (e.g. Poorter *et al.* 2015), and productivity and aboveground biomass are therefore positively related in natural tropical forests (Chisholm *et al.* 2013).

In addition, plant height is related with greater biomass and higher investment in structure of the plant per unit volume of the stem, and is expected to directly affect standing biomass and carbon storage (Conti & Díaz 2013, Moles *et al.* 2009). Tall and big plants are expected to emit more biomass in the form of leaf and woody litter per unit ground area (Garnier *et al.* 2004, Lavorel & Grigulis 2012). Generally, plant species having higher height and lower wood density are considered to be fast-growing acquisitive species because of cheap-production per cost, whereas opposite is true for slow-growing conservative species (e.g. Chave *et al.* 2009, Conti & Díaz 2013, Poorter *et al.* 2008, Prado-Junior *et al.* 2016). Tall and big trees with high biomass are also reasonable because the adult stature is potentially related to the growth and survival of trees in tall and closed-canopy forests (Poorter & Bongers 2006, Poorter *et al.* 2008) and hence may largely influence the ecosystem functioning (Finegan *et al.* 2015, Prado-Junior *et al.* 2016). Therefore, the strength and magnitude of the relationships of trait values with aboveground biomass in forest communities might be attributed primarily to trade-offs between 'grow fast and die young' *versus* 'grow slow and live long', as suggested by leaf (Wright *et al.* 2004), wood (Chave *et al.* 2009), and whole-plant (Reich 2014) economics spectra.

Although studies on the hypothetical relationships of aboveground biomass with functional trait diversity and composition are scarce, different hypotheses have been tested based on different multiple metrics of functional trait diversity in different forest ecosystems including (sub-) tropical, boreal and temperate forests. Here, I reported the following main findings from the reviewed papers. The non-significant relationships have been found for multivariate functional trait diversity indices with each of aboveground biomass, carbon storage and productivity in semi-arid subtropical forests, and tropical wet, moist and dry forests (Becknell & Powers 2014, Cavanaugh *et al.* 2014, Conti & Díaz 2013, Finegan *et al.* 2015, Prado-Junior *et al.* 2016). However, positive relationship of functional divergence while negative relationship of functional evenness with initial aboveground biomass have been reported in tropical forests in Southeastern Brazil (Prado-Junior *et al.* 2016). In addition, functional divergence of stem wood density has significant negative effect on aboveground carbon storage in semi-arid subtropical forests of Gran Chaco in central Argentina (Conti & Díaz 2013). Interestingly, functional dispersion (based on single functional trait) has significantly negative influence on aboveground biomass and productivity in subtropical broadleaved forests in northern Taiwan (Chiang *et al.* 2016), but negligible effect of functional dispersion (based on life history trait) on aboveground biomass has been found in Canadian temperate and boreal forests (Zhang *et al.* 2016b). Whereas negligible effects of multivariate functional trait diversity on aboveground biomass have been reported in subtropical evergreen broadleaved forests in southeast China (Lin *et al.* 2016). In contrast, the general positive effects of functional traits on terrestrial carbon storage and productivity have been reported in a wide variety of forests, ranging from the cold deciduous Atlantic to xeric Mediterranean evergreen forests in Continental Spain (Ruiz-Benito *et al.* 2014), and also in subtropical broadleaved forests in southeast China (Lin *et al.* 2016). More recently, it has been reported that functional divergence of wood traits (i.e. plant height and twig wood density) have significant positive relationships with aboveground biomass in secondary subtropical evergreen broadleaved forests in Eastern China (Ali *et al.* 2017). Moreover, it has also been recently reported that functional trait diversity based on a single trait consistently explains an additional variation in aboveground biomass or productivity than those with multivariate functional trait diversity in temperate forests in northeastern China (Yuan *et al.* 2016).

In most of the above reported studies, different observations are reported for the relationships between CWM of trait values with aboveground biomass or productivity in different forest types or ecosystems. For instance, conservative traits that increase drought tolerance, such as dense wood and lower specific leaf area, are found to enhance aboveground biomass productivity in tropical dry forests (Prado-Junior *et al.* 2016), whereas these conservative traits are found to diminish aboveground biomass productivity in tropical wet and moist forests (Finegan *et al.* 2015, Malhi *et al.* 2004). In partial contrast to the tropical forests, functional traits of (secondary) subtropical broadleaved forests have slightly different relationships with aboveground biomass. For instance, communities dominated by both conservative (i.e. lower leaf nitrogen concentration) and acquisitive strategies (higher leaf specific area), rather than only acquisitive or conservative strategy, have high aboveground biomass in secondary subtropical forests in Eastern China (Ali *et al.* 2017). In addition to higher wood density, higher specific leaf area has also been found to increase aboveground biomass in secondary dry tropical forests in Costa Rica, indicating both acquisitive and conservative strategies (Becknell & Powers 2014). Further, contrasting results have been reported for CWM of leaf and wood traits with aboveground biomass and productivity in evergreen broadleaved forests in southeast China (Lin *et al.* 2016) and northern Tiawan (Chiang *et al.* 2016), which also indicating both acquisitive and conservative strategies. More interestingly, it has previously been suggested that no consistent relationship exists between aboveground carbon storage and CWM of leaf traits (Conti & Díaz 2013), but it is strongly related to the relative abundance of plants with tall (CWM of plant height or diameter) and to a lesser extent dense-wooded in (sub-) tropical forests (Cavanaugh *et al.* 2014, Conti & Díaz 2013).

Based on systematic literature review, I found that most of the studies on the relationships between functional traits and aboveground biomass or carbon storage and productivity in the natural forests are recently conducted in (sub-) tropical forests compared to temperate and boreal forests. However, the relationships between functional traits and forest function are fundamentally different between wet or moist and dry (sub-) tropical (secondary) forests, due to the different limited resources of these forest types. For instance, the availability of water limits the growth of dry tropical forests, whereas the availability of light limits the growth wet and moist tropical forests (Lohbeck *et al.* 2013). The opposite relationships between functional trait values and aboveground biomass in forest communities might be attributed primarily to weak relationships between individual traits and broad functional strategies, particularly trade-offs between ‘grow fast and die young’ *versus* ‘grow slow and live long’, as suggested by leaf (Wright *et al.* 2004), wood (Chave *et al.* 2009), and whole-plant (Reich 2014) economics spectra. In addition, relationships between functional traits and aboveground biomass might be dependent on what functional traits are measured, because functional strategies of different organs are not necessarily coordinated, and leaf and stem economics spectra can be decoupled (Baraloto *et al.* 2010). Moreover, the shift in functional strategies of plants with forest succession (Yan *et al.* 2006) might also lead to uncertain relationships between growth/turnover rates and aboveground biomass in different aged forests. For instance, conservative traits that increase drought tolerance, such as dense wood indicating less hydraulic failure, and lower specific leaf area indicating less transpiration (Poorter & Bongers 2006), may improve species performance and hence, higher aboveground biomass and productivity in dry tropical forests (Prado-Junior *et al.* 2016). Alternately, these conservative traits are shown to diminish aboveground biomass productivity in wet and moist tropical forests, where acquisitive traits enhance aboveground biomass or productivity (Finegan *et al.* 2015, Malhi *et al.* 2004). For instance, high specific leaf area tends to have high aboveground biomass and that CWM of specific leaf area indeed indicates stand-level carbon gain (e.g., Ali *et al.* 2017, Finegan *et al.* 2015). However, another explanation for the positive association of CWM of specific leaf area with aboveground biomass or productivity would be that natural forests with complex vertical structures (i.e., high functional divergence of plant height) have a lot of unshaded leaves, which result mainly from the few dominant canopy species that are effective in light acquisition (Ali *et al.* 2017). Although forests with complex structure should have more shaded plants in the understorey, canopy tree species that effectively intercept light are larger than understorey species. Therefore, communities with a high proportion of unshaded leaves have high aboveground biomass. The strong support for the mass ratio hypothesis and no support for the niche complementarity hypothesis may be dependent on different attributes of functional trait diversity (Ali *et al.* 2017, Yuan *et al.* 2016). Lastly, I concluded that contrasting relationships between CWM of trait values and aboveground biomass or productivity in (sub-) tropical (secondary) forests may be dependent on what functional traits are measured, and weather the main effects of stand age or environment have been considered on the relationships between biodiversity and the functioning of forests.

1.2.3. Stand structural attributes and the functioning of forests

In forest ecology, much debate has been conducted on the influence of species diversity rather than stand structural diversity on ecosystem functions in general (Zhang *et al.* 2012b). However, it has long been recognized that complex and structurally diverse natural forests are critical for better providing ecosystem services than monoclonal and even-aged stands (Buongiorno *et al.* 1994). Moreover, the hypothetical relationships between stand structural diversity and ecosystem functions, such as aboveground biomass or carbon storage and stand productivity, have recently been recognized in forest ecosystems (Dănescu *et al.* 2016, Poorter *et al.* 2015, Zhang & Chen 2015). Stand structure attributes such as tree size (diameter and/or height) inequality or diversity among and within species are critical toward maintaining species diversity (Clark 2010), and in turn affect ecosystem functions in forest ecosystems (Zhang & Chen 2015). It has recently been recognized that stand structural diversity directly affect stand productivity or aboveground biomass, despite from the interference of species diversity in forest ecosystems (Dănescu *et al.* 2016).

Generally, species diversity is considered as a component of stand structure, but tree diameter diversity and height diversity alone or combined are typically defined as stand structural diversity (e.g., Dănescu *et al.* 2016, Staudhammer & LeMay 2001). However, in this section I aimed to evaluate the unique influences of the stand structural diversity on ecosystem functions, therefore, stand structural attributes such as average tree diameters or heights variations at the stand level, rather than species diversity attributes, were considered. Yet, two common methods for the calculations of stand structural diversity have frequently been reported in the ecological literatures for explaining ecosystem functions: Shannon's index and coefficient of variation. Initially, Shannon diversity is used for calculation of species diversity, but stand structural diversity can be calculated by replacing the species richness with the number of diameter or height classes of tree individuals within each stand (Buongiorno *et al.* 1994, Magurran 2004, Staudhammer & LeMay 2001). Stand structural diversity can also be computed as the coefficient of variations of tree diameter or height (Brassard *et al.* 2008), which is the ratio of the standard deviation of all diameter or height measurements to the mean diameter or height within each plot (Ali & Mattsson 2017, Zhang & Chen 2015). Shannon's index is using the relative abundance or relative basal area to weight the diameter or height classes within each plot, while coefficient of variance is not using any weighting variable.

Two fundamental mechanisms exist on the magnitude and patterns of biodiversity – ecosystem functioning relationships: (1) the niche complementarity effect and (2) the selection effect (e.g., Naeem 2002). These fundamental mechanisms have been explicitly tested in order to explain the relationships between species diversity and ecosystem functioning in in natural and controlled environments, including forests (Loreau *et al.* 2001, Tilman *et al.* 2001, Zhang *et al.* 2012b). However, stand structural diversity as a component of biodiversity has recently attained much importance in forest ecosystems (McElhinny *et al.* 2005, Staudhammer & LeMay 2001). Ecosystem functioning is influenced not only by species diversity but also by stand structural attributes in natural forests (Poorter *et al.* 2015). The niche complementarity hypothesis postulates that the magnitude of ecosystem functions increases with high species diversity through positive interactions such as niche differentiation or facilitation among species within a community (Loreau & Hector 2001).The selection effect hypothesis postulates that ecosystem function increases when the community contains a by chance a very productive species (Loreau & Hector 2001). These hypotheses about the relationship between species diversity or richness and productivity is also applicable for aboveground biomass or carbon storage, as higher stand productivity may lead to faster accumulation of aboveground biomass (e.g., Poorter *et al.* 2015).

It is rapidly increasing that aboveground biomass or carbon storage is significantly impacted by species diversity in forest ecosystems (Zhang *et al.* 2016a). It is theoretically plausible that the magnitude of a particular mechanism, e.g. the niche complementarity effect, increases asymptotically with the increase in number of species in an ecosystem, following the law of diminishing marginal benefit (Hooper *et al.* 2005). However, the question is whether different tree size (diameter or height) classes within and among component species, which represent diverse niches, may act similarly to different species in forest ecosystems (Clark 2010, Dănescu *et al.* 2016, Zhang & Chen 2015). It is also well known that different tree species have relatively different growth patterns and dimensions leading to different aboveground stratification and biomass productivity in complex forests (e.g., Lei *et al.* 2009, Liang *et al.*

2007, Poorter *et al.* 2016). Stand structural diversity contributes directly to ecosystem functions such as aboveground biomass and stand productivity, but multilayered forests may also enhance light capture and carbon gain and hence indirectly may influence ecosystem functions (Chu *et al.* 2009, Yachi & Loreau 2007, Zhang & Chen 2015). A supplementary question is whether species diversity may explain any extra variation in aboveground biomass or carbon storage and stand productivity once the role of stand structural diversity has explicitly been considered (Dănescu *et al.* 2016, Lei *et al.* 2009, Poorter *et al.* 2015, Van Con *et al.* 2013, Zhang & Chen 2015).

Although studies on the hypothetical relationships between stand structural diversity and ecosystem functions are scarce, different hypotheses have been tested based on different stand structure attributes in experimental and natural environments including boreal, temperate and tropical forests. Specifically, I reported the following main findings from the reviewed papers. A significant positive relationship has been found for stand structural diversity with each of aboveground carbon storage and stand productivity in the Canadian spruce-dominated forests (Lei *et al.* 2009, Wang *et al.* 2011). In contrast, stand composition and canopy vertical structure have been found to have negative influences on stand productivity in aspen forest stands (Edgar & Burk 2001). Moreover, negative and unimodal relationships have also been reported for stand productivity with tree size diversity in Douglas-fir – western hemlock and mixed coniferous stands in Canada, respectively (Liang *et al.* 2005, Liang *et al.* 2007). More recently, it has been reported that stand structural diversity has positive influence on the stand productivity, measured as stand basal area increment, in mixed and uneven aged forests in southwestern Germany (Dănescu *et al.* 2016). Similarly, stand structural attributes (i.e. tree density and tree average diameter) have strong positive relationships with aboveground biomass at all spatial scales (i.e., 0.1 and 1 ha) across 59 tropical forests, which covers nearly the full latitudinal range of Neotropical forests from Mexico to Bolivia (Poorter *et al.* 2015). Individual tree size inequality, measured as the coefficient of variance of diameter-at-breast-height, has positive influence on aboveground biomass relationships in the natural boreal forests of Canada (Zhang & Chen 2015), and also in agroforests (Ali & Mattsson 2017). In the tropical forests of Vietnam and Mexico, also strong positive relationships have been found for structure – species diversity with aboveground biomass, suggesting that uneven-aged and multistoried plantations should be encouraged for enhancing biomass or carbon storage (Martínez-Sánchez *et al.* 2016, Van Con *et al.* 2013). These findings are in contrast to the recent observations where lower tree size inequality are more productive than stands with higher tree size inequality in a temperate forest of France (Bourdier *et al.* 2016). In addition, it has also been found that stand structural heterogeneity have a strong negative influence on stand productivity in an experiment environment conducting on Eucalyptus clones in Brazil (Soares *et al.* 2016). Beside the positive and negative influences, stand structural diversity has insignificant relationship with stand productivity (i.e., stand growth) of ponderosa pine stands in the western region of the United States (Long & Shaw 2010). Similarly stand structural heterogeneity has only a marginal and inconsistent effect on stand productivity, measured as mean periodic annual increment, in Douglas-fir stands in Oregon (Kuehne *et al.* 2015). Heterogeneous stands have insignificantly lower light-use efficiency, gross primary productivity, and wood net primary productivity, compared to homogenous stands (Ryan *et al.* 2010).

In the natural forests, stand structure reflects autogenic development processes, such as regeneration, competition, and the consequent self-thinning effect, and disturbance history (Lei *et al.* 2009). Changes in stand structure resulting leaf layering and multilayered canopies, which in turn have an effect on ecosystem functions such as photosynthesis and respiration as well as stand productivity (Lei *et al.* 2009, Poorter *et al.* 2015). The reported positive effects of stand structural diversity on ecosystem functions are attributable to the enhancement of the resource use complementarity in forest ecosystems (Lei *et al.* 2009, Zhang *et al.* 2012b). Every species of a different size has its unique set of water and light requirements in a forest community. Therefore, high stand structural diversity will support their capacity to meet their specific requirements, whereas low stand structural diversity or homogenous structural arrangements may reduce complementarity effect (Lei *et al.* 2009, Wang *et al.* 2011). Positive stand structural diversity effects on ecosystem functions might result from greater packing densities due to the high vertical available space within a canopy, which in turn promote aboveground light capture, and hence greater light use efficiency within a stand (Chu *et al.* 2009, Yachi & Loreau 2007, Zhang & Chen 2015). Stand structural diversity appears to be the central regulating mechanism for the positive diversity effects on ecosystem functions, via increased resource acquisition and utilization as well as facilitation among tree individuals or species in natural boreal and temperate forest ecosystems (Dănescu *et al.* 2016, Zhang & Chen 2015). Similarly, structure – species diversity in natural tropical forests indicates that greater variation in tree size and species richness in each tree size class results in a multilayered forest canopy, which allows more efficiently light infiltration (Martínez-Sánchez *et al.* 2016, Poorter *et al.* 2015, Van Con *et al.* 2013). If this mechanism is also true for plantation forests, then mixed and uneven-aged plantations rather than mono-cultures and even-aged plantations should be encouraged, because they will be more efficient in promoting aboveground biomass, storing aboveground carbon and enhancing stand productivity (Zhang *et al.* 2012b).

The negative relationship between stand structural diversity and ecosystem functions might be attributable to the effect of overstorey or big sized trees on understorey or small sized trees in a forests (e.g., Zhang *et al.* 2016b). For instance, if the tree size diversity is positively related with canopy depth and leaf area index, this would suggest higher efficiency of light capture by structurally complex stands. However, this mechanism may necessarily be complemented by a loss of light transmittance of trees growing in the lower canopy strata (e.g., Zhang *et al.* 2016b), and hence low stand productivity in the forest ecosystem (Bourdier *et al.* 2016, Liang *et al.* 2005, Liang *et al.* 2007). A gain in light interception by bigger or overstorey trees is unlikely to compensate the loss of interception by smaller or understorey trees (Bourdier *et al.* 2016). It is also theoretically plausible that the total leaf area is allocated among trees within basically even-aged stands, e.g. many small trees versus fewer big trees, makes a difference in stand productivity of an ecosystem (Smith & Long 1989). In line with the ideas of competitive reduction, it can be hypothesized that understorey trees growing below the overstorey trees are likely to have a different influence on ecosystem functions than individuals growing in the overstorey strata (Kelty 1992, Zhang *et al.* 2016b). Further, it has recently been reported that aboveground biomass of understorey trees is negatively related with the diversity of the overstorey trees, possibly due to the greater resource filtration by overstorey trees in the forests (Zhang *et al.* 2016b). It has also been observed that a mixed overstorey strata, in contrast to a mono-cultures and even-aged overstorey strata, have negative influences on understorey production in boreal forests (Cavard *et al.* 2011). Lastly, I concluded that asymmetric competition for light therefore plays a central role for driving the negative influence of stand structural diversity or tree size inequality on ecosystem functions in forest ecosystems. These negative relationships between stand structural diversity and ecosystem functioning therefore challenge the universality of the broad positive effect of biodiversity on a range of ecosystem functions (Gamfeldt *et al.* 2013). However, our understanding regarding how overstorey and understorey stand structural diversity affect ecosystem functions, both in conjunction and individually, remains unclear in complex natural forests. For instance, light is limiting in understorey strata, and understory species co-occur by having complementary strategies to use the limited amount of light available. Instead, in the overstorey strata, the large trees have already escaped competition for light, and light-use complementarity becomes less important. Therefore, supplementary light has a strong influence on the productivity and growth of understorey trees in a stand (Messier *et al.* 1998, Onoda *et al.* 2014). An alternative explanation may also be that overstorey and big trees are often older and can suffer from physiological limitations of their light use efficiency due to aging, whereas small or understory trees are usually younger (e.g., Bourdier *et al.* 2016). The inconsistent or insignificant influence of stand structural diversity on ecosystem functions is generally plausible in the production aspect of forest ecology that stand composition and stand structural diversity have no influence on stand productivity (e.g., Long & Shaw 2010, Pretzsch 2005, Smith & Long 1992).

1.2.4. Evolutionary diversity and the functioning of forests

Biodiversity is a complex multifaceted concept (Purvis & Hector 2000), and therefore ecosystem functioning may be determined not only by taxonomic diversity and functional trait diversity but also by evolutionary diversity in a community (Cadotte *et al.* 2008, Flynn *et al.* 2011). Taxonomic diversity such as species richness is a simple measure that considers all species equally, and therefore may have more limitations as compared to the other measures of biodiversity such as evolutionary and functional trait diversity (Vane-Wright *et al.* 1991). However, taxonomically distinct species are expected to contribute more to the functional trait diversity and evolutionary diversity, present within a community (Faith 1992). So, measurements of evolutionary history within a set of co-occurring species are assumed to represent the functional trait diversity within a given community (Faith 2002). Thus, greater phylogenetic diversity in the community (a measure of evolutionary diversity) is associated with several ecosystem processes, goods and services such as nutrient cycling, resistance to invasion, and aboveground and soil carbon sequestration, and hence indicating that phylogenetic diversity is more powerful measure of biodiversity (Cavender-Bares *et al.* 2009).

Early ecologists, including Darwin, theorized that if closely-related species having common ancestry are ecologically similar, they should share similar environmental requirements and may therefore be likely to co-occur (Simberloff 1970, Valiente-Banuet & Verdú 2007). Alternately, it is also expected that closely-related species should experience strong competitive interactions due to their ecological similarity, thereby limiting coexistence (e.g. Cadotte *et al.* 2008, Cavender-Bares *et al.* 2009, Webb 2000). Functional trait diversity and phylogenetic or evolutionary 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 between distantly-related species or divergent selection between closely-related species (Wiens & Graham 2005). As such, there are two stringent basic assumptions under the competition-relatedness hypothesis. First, phylogenetically closely-related species are likely to be more ecologically similar than distantly-related species (e.g. Cadotte *et al.* 2008, Cavender-Bares *et al.* 2009, Webb 2000). Second, it is therefore expected that closely-related species should experience strong competitive interactions due to their ecological similarity, thereby limiting coexistence because they share similar niches, e.g., the limiting similarity hypothesis (MacArthur & Levins 1967). The rationale is that the phylogenetic distance between species can use as a proxy for the evolved ecological differences between them, assuming closely-related species are ecologically more similar to each other than more distantly-related species (Cavender-Bares *et al.* 2009). As such, functional trait diversification is due to the evolutionary diversification which sequentially may result in greater niche complementarity among and within species in a given community (e.g. Cadotte *et al.* 2008, Flynn *et al.* 2011, Paquette *et al.* 2015). Therefore, longer evolutionary differentiation has been theorized to generate greater functional trait variation related to ecological niches and provides evidence for the niche complementarity hypothesis (Cadotte *et al.* 2008, Flynn *et al.* 2011, Zuppinger-Dingley *et al.* 2014).

Evolutionary diversity can be quantified through 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, which is the minimum spanning distance (sum of all branch lengths) of a phylogenetic tree representing all the species from a given community, measured in millions of years of evolutionary time (Faith 1992). The other four evolutionary diversity indices are part of a series, synthesis and relatively easy to understand of phylogenetic measures of species richness, evenness, variability and clustering, with clear statistical properties (Helmus *et al.* 2007).

Most of the previous researches focusing on the relationships between phylogenetic diversity and aboveground biomass or productivity have been conducted in natural and experimental grasslands, while very few studies in natural forests and plantations. A meta-analysis of 29 biodiversity-ecosystem functioning experiments showed that phylogenetic diversity within the community explained more variations in aboveground biomas or carbon stocks than other measures of biodiversity in grasslands (Cadotte *et al.* 2008). This meta-analysis suggests that greater trait variation associated with ecological niche is due to the longer evolutionary differentiation under the niche complementary effect (Cadotte *et al.* 2008, Flynn *et al.* 2011, Zuppinger-Dingley *et al.* 2014). In contrast, the recent re-examination of 16 studies of grassland diversity has shown that phylogenetic diversity is a poor driver for aboveground biomass as compared to species richness (Cardinale *et al.* 2015, Venail *et al.* 2015). In natural forests, empirical evidence suggested that phylogenetic, functional trait and taxonomic diversity indices performed almost similarly well in explaining variation in aboveground biomass or productivity (Paquette & Messier 2011, Yuan *et al.* 2016). However, it has also been reported that evolutionary diversity indices may be more important for the better management of low quality forests, which is not previously considered for forest management activities (Potter & Woodall 2014). So, further experiments and analyses are required to clarify whether evolutionary diversity indices (not only phylogenetic diversity, but also phylogenetic species richness, evenness, clustering and variability) best predict forest functioning than other measures of biodiversity in natural forest ecosystems, and also in grasslands.

1.2.5. Effects of local environmental factors on biodiversity – ecosystem functioning relationships

Local soil physicochemical properties or site conditions that determine nutrient and water availabilities, may strongly influence ecosystem functions such as aboveground biomass or carbon storage and productivity (Chiang *et al.* 2016, Prado-Junior *et al.* 2016, Wang *et al.* 2003). Consequently, recent empirical evidences showed that local soil or site conditions strongly influence the relationships between biodiversity and ecosystem functioning through complex plant–soil feedback loops in forest ecosystems (Chiang *et al.* 2016, van der Putten *et al.* 2013, Zhang *et al.* 2016a). Soil fertility hypothesis predicts that aboveground biomass or productivity increases with increase in soil nutrients availability, and plants can grow faster when resource availability is high (Quesada *et al.* 2012, Wright *et al.* 2011). However, high nutrients availability may also lead to increased competition, and hence high mortality and biomass turnover rates of plant species (Prado-Junior *et al.* 2016). Consequently, high aboveground biomass or productivity in (sub-) tropical forests associates often with nutrient-poor soils (Chiang *et al.* 2016, Poorter *et al.* 2015, Prado-Junior *et al.* 2016).

Although soil fertility (i.e. cation exchange capacity) is thought to influence the relationship between species diversity and climate in forest ecosystems, it does not significantly (but negatively) influenced the relationships between biodiversity and aboveground biomass or carbon storage both in natural tropical forests (Poorter *et al.* 2015) and agroforests (Ali & Mattsson 2017). In temperate forests, aboveground biomass or productivity is often limited by nitrogen, whereas it is often limited by phosphorus in tropical forests because the soils are highly weathered due to a warm and wet climate (see Quesada *et al.* 2012, and references therein). However, a recent study has found that soil fertility (i.e. soil calcium) had a negative effect on the aboveground biomass of survivals in tropical dry forests (Prado-Junior *et al.* 2016).

It should be noted that aboveground biomass is a state variable, and hence indicating various underlying factors (Poorter *et al.* 2015). Biogeographical patterns in species traits determine aboveground biomass retention (Prado-Junior *et al.* 2016, Slik *et al.* 2013), whereas recent local disturbance history may determine aboveground biomass loss (see Poorter *et al.* 2015, and references therein). Therefore, soil nutrients can also indirectly affect aboveground biomass via edaphic filtering (Jucker *et al.* 2016, Reich 2014). For instance, nutrient-poor soils tend to be dominated by species with conservative strategy, whereas nutrient-rich soils tend to be dominated by species with acquisitive strategy (Fortunel *et al.* 2014, Poorter & Bongers 2006, Reich 2014).

Beside the influences of soil physiochemical properties or soil nutrients or fertility, the relationships between biodiversity and ecosystem functions are also greatly dependent on the topographical properties such as elevation, slope and convexity (Lin *et al.* 2016). The increase in aboveground biomass or carbon storage with increasing convexity is accompanied by a decrease in slope and elevation, and hence this pattern of topographic influence on ecosystem functions is widely observed on elevation transects in tropical forests (Galbraith *et al.* 2013, Girardin *et al.* 2014). The negative influences of elevation and slope on aboveground biomass or carbon storage are attributable to decline in net primary productivity, without increasing residence time (Galbraith *et al.* 2013). Alternately, a number of underlying factors have been shown to explain the declining pattern of aboveground biomass with elevation and slope, including temperature limitation of nutrient supply, limitation of nutrient uptake, high ultraviolet light exposure, low light levels and strong winds (see Girardin *et al.* 2014, and references therein). Further, steep slopes are associated with increased treefall rate and thus decline in aboveground biomass in tropical forests, while high aboveground biomass has also been found in topographically flat areas across subtropical evergreen broadleaf forests. Besides the direct effects, topographic factors greatly influence local site conditions, such as soil properties, soil nutrients, hydrology and light conditions, which may in turn influence growth, mortality and recruitment, and thereby higher contribution to variation in aboveground biomass (see Lin *et al.* 2012, and references therein).

1.3. Knowledge gap: Forest diversity and functioning across forest strata

In natural forests, positive biodiversity and aboveground biomass relationships have widely been observed (Zhang *et al.* 2016a), and the specific mechanism(s) of how higher biodiversity enhances aboveground biomass is highly debated (Finegan *et al.* 2015, Prado-Junior *et al.* 2016). Eminently, two non-mutually exclusive and alternative testable hypotheses, i.e., the mass ratio hypothesis and niche complementarity hypothesis, have been suggested to examine mechanisms underpinning positive biodiversity and aboveground biomass relationships in different forest types or ecosystems (Ali *et al.* 2017, Conti & Díaz 2013, Finegan *et al.* 2015, Lin *et al.* 2016, Prado-Junior *et al.* 2016). Among these empirical studies, the positive biodiversity and aboveground biomass relationships have been reported and explained at the level of either whole-community or overstorey strata only. Natural forests, however, are always structurally complex and plant species with different functional strategies are generally assembled in different vertical layers (Rüger *et al.* 2012, Wright 2002).

Understorey trees account for the majority of species richness, influence forest dynamics, and affect forest soil carbon and nutrient cycling (Gilliam 2007, Nilsson & Wardle 2005). Environmental conditions affecting plant performance can strongly differ between forest strata in natural forests (Zhang *et al.* 2014). Light, being one of the most important plant resources, is often limiting in the understorey of tropical forests, while in the overstorey light is abundant. As a consequence, understorey species co-occur by having complementary strategies to use the limited amount of light available (e.g., Brenes-Arguedas *et al.* 2011, Wright 2002) while in the canopy, complementarity in light-uptake strategies becomes unimportant (e.g., Cavanaugh *et al.* 2014). Indeed the niche complementarity effect has been found to be stronger under resource-limiting conditions (Paquette & Messier 2011). Understorey and overstorey trees may therefore contribute differently to the relationship between diversity and aboveground biomass. Therefore, to understand the mechanisms by which biodiversity affects aboveground biomass, it may be insightful to consider the different forest strata (understorey and overstorey) of the forest separately, as these represent different environments in which resources may or may not be limited.

Previous studies have suggested that the positive relationships between forest diversity (e.g., species diversity and individual tree size variation) and aboveground biomass are essential to the ability of forests to provide goods and services (Ali & Mattsson 2017, Poorter *et al.* 2015, Wang *et al.* 2014, Zhang & Chen 2015). Due to the dominant role of overstorey strata on the available resource and their influences on various ecological processes, the diversity and aboveground biomass of understorey strata are substantially influenced by overstorey trees in forests (Barbier *et al.* 2008). However, in most of the empirical studies, the effects of forest strata (e.g., overstorey and understorey) on the relationship between biodiversity and aboveground biomass are often ignored, making it impossible to assess the effects of overstorey trees on the patterns of biodiversity and aboveground biomass of understorey in forest ecosystems (Ali & Mattsson 2017, Cavanaugh *et al.* 2014, Poorter *et al.*

2015, Zhang & Chen 2015). Therefore, specific research is needed to improve our understanding about the patterns, magnitude and mechanisms of diversity – aboveground biomass relationships across forest strata in forests. Disentangling these ecological complexities requires integrative modelling considering how species diversity and tree size variation of overstorey and understorey strata affect their corresponding aboveground biomass, and at the same time how overstorey strata affect the diversity and aboveground biomass of understorey in species-rich forests.

One of the biggest challenges in functional ecology is to explain the underlying mechanisms for the relationships between functional attributes of biodiversity (i.e. functional trait diversity and identity) and ecosystem functions in forest ecosystems. Although the niche complementarity and mass ratio hypotheses have been put forward to explain the relationships between functional attributes of biodiversity and ecosystem functions (e.g. Ali *et al.* 2017, Conti & Díaz 2013, Finegan *et al.* 2015, Lin *et al.* 2016, Prado-Junior *et al.* 2016), few studies have tested these relationships across forest strata (i.e. overstorey and understorey). The niche complementarity hypothesis based on species richness has received some empirical support across forest strata (e.g. Zhang *et al.* 2016a), but species differ in functional strategies for their contribution to ecosystem functions (Rüger *et al.* 2012) as predicted by the mass ratio hypothesis (Grime 1998). As such, the relationships between functional attributes of biodiversity and aboveground biomass, especially the associated mechanisms might be fundamentally different across forest strata. To date, few studies have teased apart the contributions of functional attributes of trees with either conservative or acquisitive strategies at overstorey and understorey strata to aboveground biomass in forests.

Previous studies have described species by mean functional trait values for relating functional trait diversity and ecosystem functioning (e.g. aboveground biomass), i.e. to have intraspecific functional trait diversity negligible compared with interspecific functional trait diversity (Ali *et al.* 2017, Conti & Díaz 2013, Finegan *et al.* 2015, Lin *et al.* 2016). Intraspecific functional trait diversity has been recognized as a critical driver for maintaining individuals within species, co-occurring species dynamics, total functional trait diversity and functioning of communities (e.g. Chesson 2000, Chu *et al.* 2009, Clark 2010, Kichenin *et al.* 2013, Siefert *et al.* 2015). Therefore, it is insufficient to use only interspecific functional trait diversity to represent total functional trait diversity of a community because of the multifaceted nature of biodiversity (de Bello *et al.* 2011, Purvis & Hector 2000). To date, intraspecific functional trait diversity are not usually assessed explicitly, making it impossible to assess its effect on aboveground biomass in natural forests (e.g. Ali *et al.* 2017, Conti & Díaz 2013, Finegan *et al.*

2015). In addition, using mean trait values per species can lead to critical misinterpretations of the conclusions regarding functioning of an ecosystem (Siefert *et al.* 2015). For instance, considering mean trait values per species can underestimates the ability of a species to endure the presence of others in a community, and ultimately underestimates the degree of niche differentiation and facilitation between species (e.g. Violle *et al.* 2012). In this thesis I investigate whether the interspecific and intraspecific functional trait diversity have differential effects on aboveground biomass at each of individual strata and whole-community level, using specific leaf area and leaf dry matter content of 20,253 individuals from 125 plots inside 5-ha natural subtropical forest in Eastern China.

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 & 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. More recently, this 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 diversity are frequently considered as the main drivers of aboveground biomass or productivity in both experimental and natural environments, including forests (Cadotte *et al.* 2009, Flynn *et al.* 2011, Paquette & 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 diversity drive aboveground biomass across forest strata (i.e. overstorey and understorey).

Biodiversity is a multifaceted concept that includes the diversity of life on different levels of organization from genes, to species, to entire ecosystems (Purvis & Hector 2000). Therefore, biodiversity itself can be quantified in many different ways, e.g., taxonomic diversity, functional trait diversity and composition, and evolutionary diversity. Biodiversity as such is not an ecosystem function but is important to many ecosystem functions such as aboveground biomass and productivity (Cadotte *et al.* 2008, Finegan *et al.* 2015, Prado-Junior *et al.* 2016, Yuan *et al.* 2016). In addition, stand structural diversity or attributes have been recognized as the coupling factors with some of the above metrics of biodiversity for explaining variation in ecosystem functions (Ali *et al.* 2016b, Chiang *et al.* 2016, Poorter *et al.* 2015, Zhang & Chen 2015). Most of previous studies on the relationships between these multiple drivers and aboveground biomass or productivity in the natural forests have been focused on the ecological hypotheses (i.e. the mass ratio and niche complementarity). However, our understandings regarding the effects of these multiple drivers on aboveground biomass across forest strata (overstorey and understorey) and at whole-community level in natural forests remain unclear, since light limits plant performance in different vertical layers (e.g., Brenes-Arguedas *et al.* 2011, Wright 2002).

To date, forest strata are not usually assessed explicitly, but rather as part of the whole-community, making it impossible to assess their effect on aboveground biomass or carbon storage in natural (sub-) tropical forests (e.g. Ali *et al.* 2017, Conti & Díaz 2013, Finegan *et al.* 2015, Lin *et al.* 2016, Poorter *et al.* 2015). Recent empirical study in Canadian temperate and boreal forests reported that positive relationships between species richness and aboveground biomass are ubiquitous across all forest strata, but the relationship was strongest for the overstorey strata (Zhang *et al.* 2016a). It is possible that relationship between biodiversity and aboveground biomass is obscured when mixing understorey and overstorey species, as these may be subjected to different assembly mechanisms due to differences in resource limitation (Balvanera *et al.* 2014, Bartels & Chen 2013). In this thesis I investigated whether the stand structural attributes and multiple metrics of biodiversity of overstorey and understorey strata have differential effects on aboveground biomass of each individual strata and whole-community level after accounting for the effects of environmental factors, using biophysical, functional traits and environmental factors data from 125 plots inside 5-ha natural subtropical forest in Eastern China.

1.4. Thesis synopsis

1.4.1. Thesis structure or frame work

This thesis is focusing on the hypothetical relationships of environmental factors, stand structural attributes, multiple metrics of biodiversity and aboveground biomass across forest strata (overstorey and understorey), as well as at whole-community level (for comparison), across 125 plots inside 5-ha natural subtropical forest in Tiantong, Zhejiang Province, Eastern China. Specifically, I focused on four parts or six research chapters (Fig. 1.1). In the part 1 (chapters 3-5), I focused on the relationships among species diversity, stand structure, functional trait diversity, environmental factors and aboveground biomass across forest strata and at whole-community as: 1) the relationships of individual tree size inequality and species diversity with aboveground biomass; 2) functional trait diversity of overstorey and understorey strata with whole-community aboveground biomass; and 3) species richness, intraspecific and interspecific functional trait diversity with aboveground biomass, for testing the niche complementarity, big trees and soil nutrients hypotheses. In part 2 (chapter 6), I focused on the effects of the evolutionary diversity and functional trait diversity on aboveground biomass in addition to environmental factors, in order to test the effects of phylogenetically close and distant, as well as functionally similar and dissimilar species on aboveground biomass across forest strata and at whole-community level. In part 3 (chapter 7), I focused on the functional strategy of species across forest strata and at whole community in order to assess the effect of functional identity (CWM of a trait values) on aboveground biomass, and to test the mass ratio hypothesis based on conservative and acquisitive strategies. In part 4 (chapter 8), I disentangled the effects of stand structural attributes, multiple metrics of biodiversity and environmental factors on aboveground biomass across forest strata and at whole community, in order to test the niche complementarity, mass ratio, big trees and soil nutrient hypotheses.

This thesis consists of nine chapters: the introduction and background (this chapter), general methodology (chapter 2), six research chapters (chapters 3-8) ordered from individual to phylogeny level data (but scaled up to forest strata or community level) for testing the niche complementarity, mass ratio and big trees hypotheses in addition to soil nutrient hypothesis (Fig. 1.2): individual tree size variation (chapters 3 and 8), species diversity or richness (chapters 3, 5 and 8), functional trait diversity (chapters 4, 6 and 8), functional identity (chapters 7 and 8), and evolutionary or phylogenetic diversity (chapters 6 and 8), and the general discussion and concluding remarks (chapter 9). I conduct a systematic literature review on the hypothetical relationships between multiple measures of biodiversity and the functioning of forests, in order to collect the current state of knowledge in the existing literature (chapter 1). In research chapters (3-8), I first focus on stand structural attributes and taxonomic diversity indices i.e. the using of data at individual tree-scale and species-identity (chapter 3), then I focus on the main components of functional trait diversity (chapters 4 and 6), functional trait variation within and between species (chapter 5), phylogenetic differences among species (chapter 6), and functional identity based on functional traits (chapter 8) at each of overstorey and understorey strata, and whole-community level. In chapter 4, I investigated the relationships of functional trait diversity of overstorey and understorey strata with whole-community aboveground biomass, whereas all other research chapters dealing relationships at each of overstorey and understorey strata, as well as at whole-community level, in addition to the effects of overstorey on understorey strata in chapters 3, 5, 6 and 7. Lastly in chapter 8, I disentangled the effects of stand structural attributes, multiple metrics of biodiversity and environmental factors on aboveground biomass at each of the overstorey and understorey strata, and whole-community level.

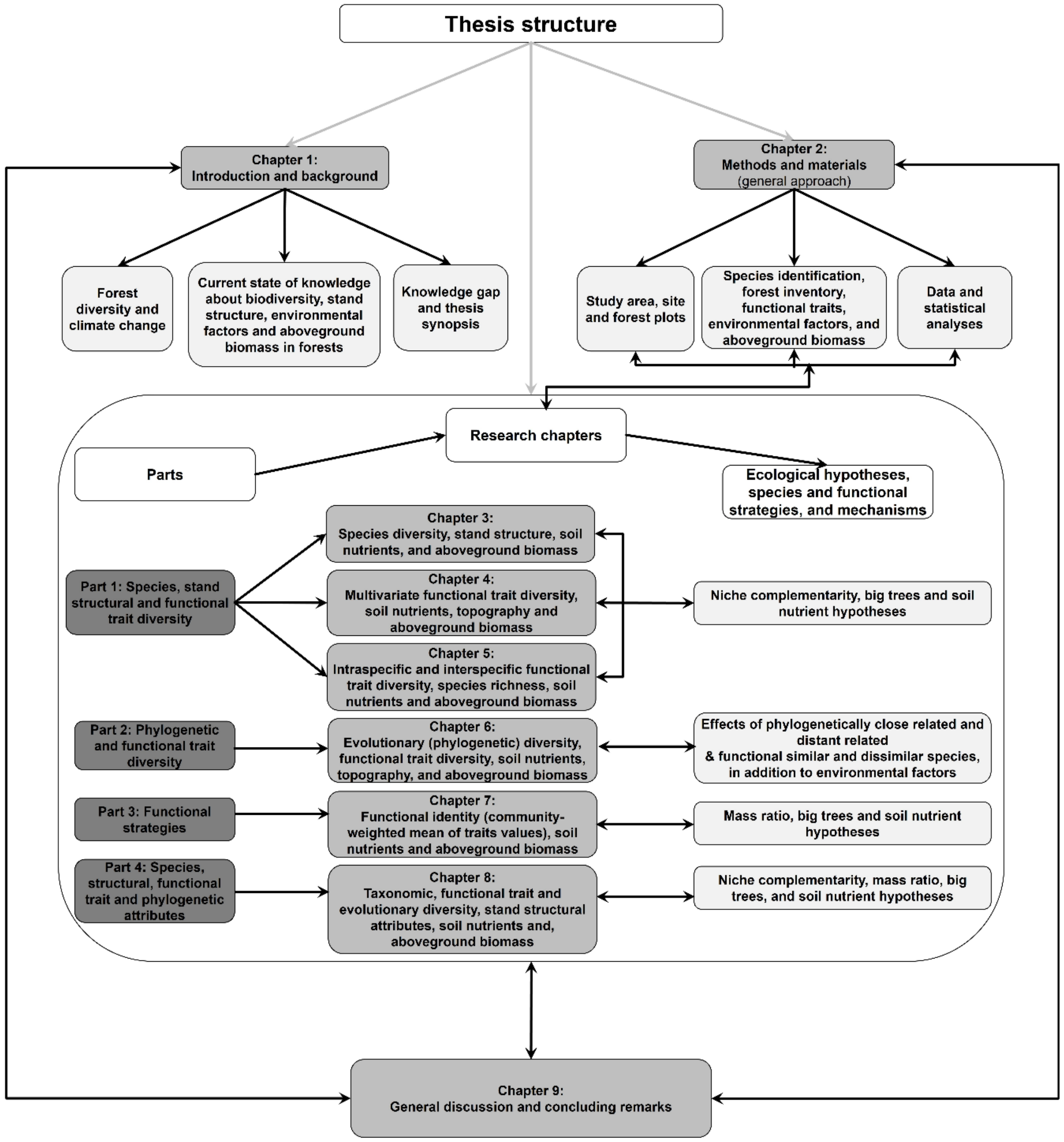

Fig. 1.1. Thesis structure and framework of the chapters. Research chapters are arranged from species, structural and functional trait diversity (chapters 3-5) to phylogenetic diversity (chapter 6), and then to functional strategies (chapter 7) and combination of all these aspects (chapter 8).

1.4.2. Thesis focus, major questions, hypotheses and predictions

This thesis mainly focuses on ecological aspects or mechanisms, and aims to understand how stand structural attributes, multiple metrics of biodiversity and environmental factors determine aboveground biomass across forest strata (overstorey and understorey) and at whole-community level in a subtropical forest (Fig. 1.2). To understand the multivariate relationships of aboveground biomass with multiple metrics of biodiversity, stand structural attributes and environmental factors, I performed a systematic literature review in this chapter. To do so, I tried to explore the current state of knowledge regarding the influences of biodiversity and stand structural attributes on ecosystem functions such as aboveground biomass or carbon storage and productivity in forest ecosystems. Based on the knowledge gap in the current state of knowledge, the main objectives of this thesis are:

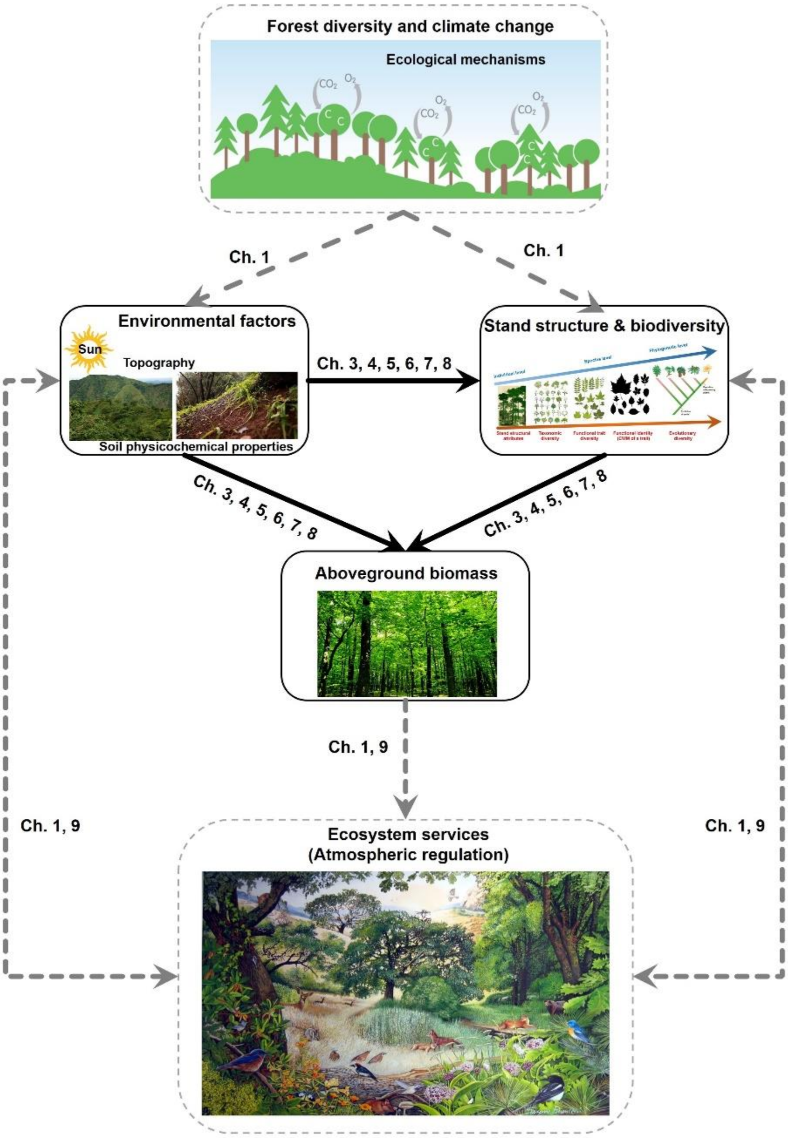

Fig. 1.2. General conceptual framework linking environmental factors (e.g. soil nutrients and properties and/ or topography), stand structure and biodiversity (e.g. tree size inequality, taxonomic diversity, functional trait diversity, CWM and evolutionary diversity indices) with aboveground biomass across forest strata (overstorey and understorey) and whole-community level. The chapters in which these relationships are addressed are provided. The black arrows represent directly analysed relationships, whereas the grey dashed arrows represent relationships that are discussed or hypothesized but not measured in this thesis. The boxes with a black, solid border represent measured variables, whereas the box with a grey, dashed border represents non-measured variables. For more detailed description, see Fig. 1.1.

1) To understand the effects of multiple metrics of biodiversity, stand structural attributes, and environmental factors on aboveground biomass across forest strata and at whole-community level in a subtropical forest.
2) To evaluate how these relationships depend on the individuals (i.e. individual tree size inequality, and intraspecific functional trait diversity), species (taxonomic and functional trait diversity and identity) and phylogenetic (evolutionary diversity indices based on phylogenetic distances) scales (data was used across different scales, but scaled up to strata or community level) across forest strata and at whole-community level.
3) To assess how overstorey strata affect understorey strata while considering environmental factors.
4) Finally, to assess what determines aboveground biomass across forest strata and at whole-community level in a subtropical forest.

The specific research questions, hypotheses and predictions are:

1. How do species diversity and individual tree size variation of overstorey and understorey strata affect their corresponding aboveground biomass, and at the same time how overstorey strata affect the diversity and aboveground biomass of understorey strata in a subtropical forest, after accounting for the effects of soil nutrients (chapter 3)?

   a) We hypothesize that overstorey species diversity and individual tree size variation contribute to aboveground biomass and understorey species diversity through the niche complementarity effect, while weaken the relationship between understorey aboveground biomass and individual tree size variation due to the mixed effects of tree development, biotic interaction and reduced available resources by overstorey strata. This hypothesis leads to four main predictions:
   i) With respect to the niche complementarity hypothesis, we predict that species diversity and individual tree size variation have positive effects on aboveground biomass across forest strata alone and combined.
   ii) Considering the soil fertility hypothesis, we predict that aboveground biomass, species diversity and individual tree size variation increase with an improvement of soil nutrients in both overstorey and understorey strata, and in whole-community.

iii) We predict that overstorey strata would decrease aboveground biomass and individual tree size variation in understorey strata, due to the dominant role of overstorey strata in competing and/or consuming available light and soil nutrients.

iv) We predict that species diversity of overstorey strata may promote species diversity of understorey, due to increased resource heterogeneity and reduced interspecific competition in understorey.

2. How do functional trait diversity of overstorey and understorey strata affect whole-community aboveground biomass, after accounting for the effects of environmental factors (chapter 4)?

a) We hypothesize the high functional trait diversity of understorey strata due to the niche complementarity, while low functional trait diversity of overstorey strata due to the presence of a few large trees would drive high aboveground biomass in a community. In addition, we predict that functionally-similar big trees (i.e., overstorey trees) will have a larger effect than functionally-dissimilar small trees (i.e. understorey trees) on the aboveground biomass due to the large stem volumes present in the overstorey, and dominant role over the understorey strata in the forests, which we call the big trees effect.

b) If the above prediction is true, as a consequence, we further hypothesize low functional trait diversity of whole-community would drive high aboveground biomass in a community due to the dominant role of functionally-similar large trees (i.e. overstorey) on understorey strata and available resources.

3. How do intraspecific and interspecific functional trait diversity mediate the response of species richness to aboveground biomass at each of forest strata and whole community level, after accounting for the effects of soil nutrients (chapter 5)?

a) We hypothesize that intraspecific and interspecific functional trait diversity mediate the response of aboveground biomass to species richness in understorey strata through niche complementarity, whereas only intraspecific functional trait diversity would mediate this response in overstorey strata or whole-community due to the presence of a few large trees occupying larger niche space in a community. This hypothesis leads to the following three key predictions:

i) Positive direct relationship between species richness and aboveground biomass at each of forest strata and whole-community level.
ii) Intraspecific and interspecific functional trait diversity will strongly affect aboveground biomass in understorey strata.
iii) Intraspecific rather than interspecific functional trait diversity will strongly affect aboveground biomass in overstorey strata or whole-community.

4. Whether evolutionary diversity and functional trait diversity would explain variation in aboveground biomass at each of forest strata and whole-community, after accounting for the effects of soil nutrients and properties (chapter 6)?

a) We hypothesize that phylogenetically close and functionally similar species drive high aboveground biomass in overstorey strata due to the evolutionary relatedness, while phylogenetically distant and functionally dissimilar species drive high aboveground biomass in understorey strata due to the functional dissimilarity. This hypothesis leads to the following two key predictions:
i) Based on the less stringent conditions for influencing species interactions at overstorey strata, we predict that evolutionary relatedness would drive aboveground biomass better than functional similarity.
ii) Based on the dominant effect of overstorey strata on understorey, we predict that functional dissimilarity would drive aboveground biomass better than phylogenetic overdispersion.
b) If the above predictions are true, we therefore hypothesize that the mixed effects of evolutionary relatedness of overstorey and functional dissimilarity of understorey would drive aboveground biomass at whole-community level.

5. Whether high aboveground biomass was driven by the functional identity of tree height, conservative and/ or acquisitive strategies of plant species across forest strata and whole-community level in a subtropical forest (chapter 7)?

a) Considering the mass ratio effect in overstorey strata where light condition is favorable, we hypothesize the positive relationships of aboveground biomass with CWM of acquisitive traits, especially with functional identity of potential maximum tree height, while the negative relationships of aboveground biomass with CWM of conservative traits.

b) With regard to the mass ratio effect in light-stressful understorey, we hypothesize the positive relationships of aboveground biomass with CWM of conservative traits, while negative relationships of aboveground biomass with CWM of acquisitive traits.

c) Due to the dominant role of big trees on available resources, we hypothesize that functional identity of overstorey strata negatively relates with functional identity and aboveground biomass of understorey strata.

d) For the comparison to whole-community level, we hypothesize that high aboveground biomass is potentially driven by high CWM of acquisitive traits due to the dominant role of big trees on the available resources.

e) We hypothesize that high CWM of acquisitive trait values relates to nutrient-rich soils while high CWM of conservative trait values of understorey associates with nutrient-poor soils in driving high aboveground biomass across forest strata.

6. Whether aboveground biomass was strongly driven by taxonomic diversity, functional trait diversity, functional trait composition, evolutionary diversity and stand structural attributes, after accounting for the effects of local environmental factors across overstorey and understorey strata and whole-community level in a subtropical forest (chapter 8)?

a) We hypothesize that taxonomic diversity, functional trait diversity and evolutionary diversity have positive effects on aboveground biomass at understorey strata (through the niche complementarity effect) whereas the negative effect at overstorey strata (due to the presence of few dominant and functionally-similar big trees).

b) Under the mass ratio hypothesis, we hypothesize: i) the positive relationships of aboveground biomass with CWM of acquisitive traits and tree height while negative relationships with conservative traits at overstorey strata; and ii) the positive relationships of aboveground biomass with conservative traits while negative relationships with CWM of acquisitive traits at understorey strata.

c) At whole-community level, we expect almost the same relationships as hypothesized for the overstorey strata due to the dominant role of overstorey strata on understorey, and hence may be obscured the role of understorey when mixed data across forest strata.

d) Under the niche complementarity hypothesis based on the stand structural attributes, we hypothesize that as stand structural attributes increase there will be greater aboveground biomass across forest strata and at whole-community level, and that they have stronger effects on aboveground biomass than individual effect of each biodiversity attributes.

e) Under the soil fertility hypothesis, we hypothesize that with an increase in soil nutrients there will be an increase in aboveground biomass, biodiversity and stand structure at each of the overstorey and understorey strata, and whole-community level.

Chapter 2. Materials and methods

Research in this thesis includes four broad steps[1] (see framework in Fig. 2.1): 1) selection of study site and forest plots; 2) field sampling and measurements; 3) data analyses; and 4) statistical analyses.

2.1. Study site and forest plots

Research in this thesis was conducted in a 5-ha subtropical forest plot in Tiantong National forest park (29°48´N, 121°47´E, 200 m a.s.l), located in Ningbo city, Zhejiang province, in Eastern China. The area is characterized by a warm and humid subtropical monsoon climate, and has an average temperature of 28 °C and 4.2 °C in the warmest and coldest months, respectively. The average annual precipitation is 1375 mm, most of which falls between May and August; annual evaporation is 1320 mm and annual relative humidity is 82% (Yan *et al.* 2013). The vegetation is characterized as a subtropical evergreen broadleaf forest, and the soils are classified as Ferralsols in the FAO soil classification system (World Reference Base for Soil Resources 2006), with pH values that range from 4.4 to 5.1. The parental material is mostly composed of Mesozoic sediments and intrusive acidic rocks, including quartzite and granite (Yan *et al.* 2013).

The studied 5-ha forest plot is located in the center of the Park, and is divided into 125 20 × 20 m subplots. The topography of the plot is very heterogeneous and rugged (Fig. 2.2), with elevation varying from 320.4 to 489.4 m a.s.l. The slopes of the subplots within the plot ranges from 13.8 to 43.9°. The elevation is more pronounced in the northern section than in the southern section of the plot. 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 (Fig. 2.3).

The vertical structure of community and species composition varied with changes in topography. In the ravine area, the canopy tree layer (~15-20 m in height) was dominated by *Choerospondias axiliaris*, which is a deciduous species, whereas the sub-canopy tree layer (4 < height < 15 m) was dominated by evergreen species such as *Machilus leptophylla*. The dominant species in the shrub layer (< 4 m in height) was composed of evergreen species such as *Litsea elongate* and *Eurya loquaiana*. On slopes and ridge areas, the dominant species in the shrub layer was similar to the ravine area. In contrast, the canopy tree layer was occupied by evergreen species including *Lithocarpus harlandii* and *Cyclobalanopsis nubium*, and the sub-canopy tree layer was also dominated by evergreen species, such as *Lithocarpus harlandii*.

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[1] Description about materials and methods provided here are generally broad or frequently used in the research chapers. Therefore, specific data and statistical analyses are provided in each research chapter.

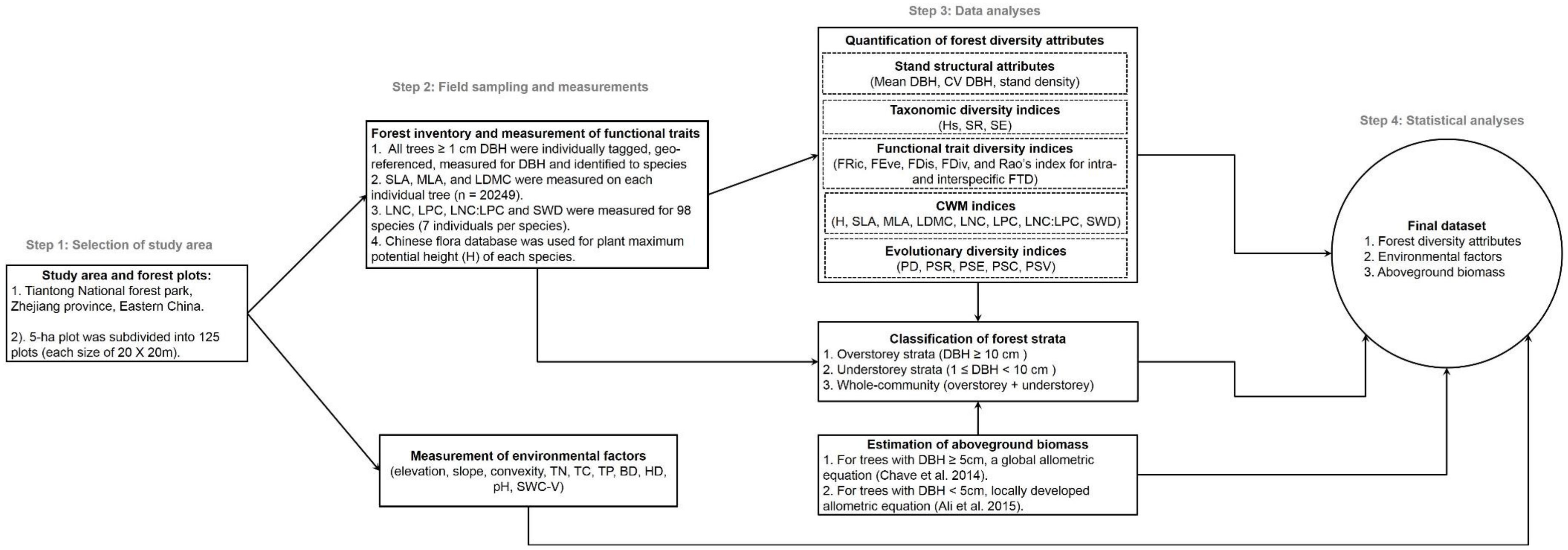


Fig. 2.1. Framework for research conducted in this thesis.
Abbreviations: DBH, diameter at breast height; CV DBH, individual tree size inequality (coefficient of variance); SR, species richness; SE, species evenness; Hs, species diversity; FRic, functional richness; FEve, functional evenness; FDiv, functional divergence; FDis, functional dispersion; FDiv, functional divergence; FTD, functional trait diversity; CWM, community-weighted mean; H, plant maximum potential height; SLA, specific leaf area; LDMC, leaf dry matter content; MLA, mean leaf area; LNC, leaf nitrogen concentration; LPC, leaf phosphorus concentration; LNC:LPC leaf nitrogen to phosphorus ratio; SWD, stem wood density; PSC, phylogenetic species clustering; PSE, phylogenetic species evenness; PSV, phylogenetic species variability; PD, phylogenetic diversity; PSR, phylogenetic species richness; TN, soil total nitrogen; TC, soil total carbon; TP, soil total phosphorus; BD, soil bulk density; HD, humus depth; pH, soil pH; SWC-V, soil volumetric water content.

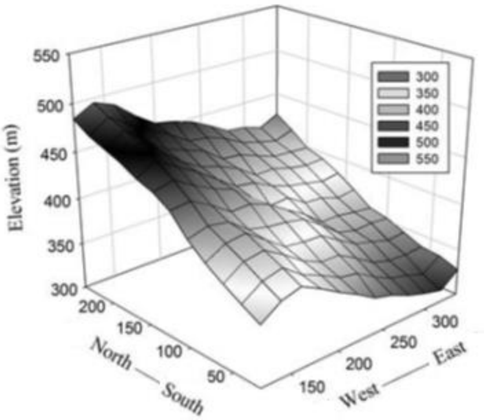


Fig. 2.2. Topographic heterogeneity of the study area, covering a 5-ha subtropical evergreen broadleaf forest located in Tiantong National Forest Park, Zhejiang Province, in Eastern China.

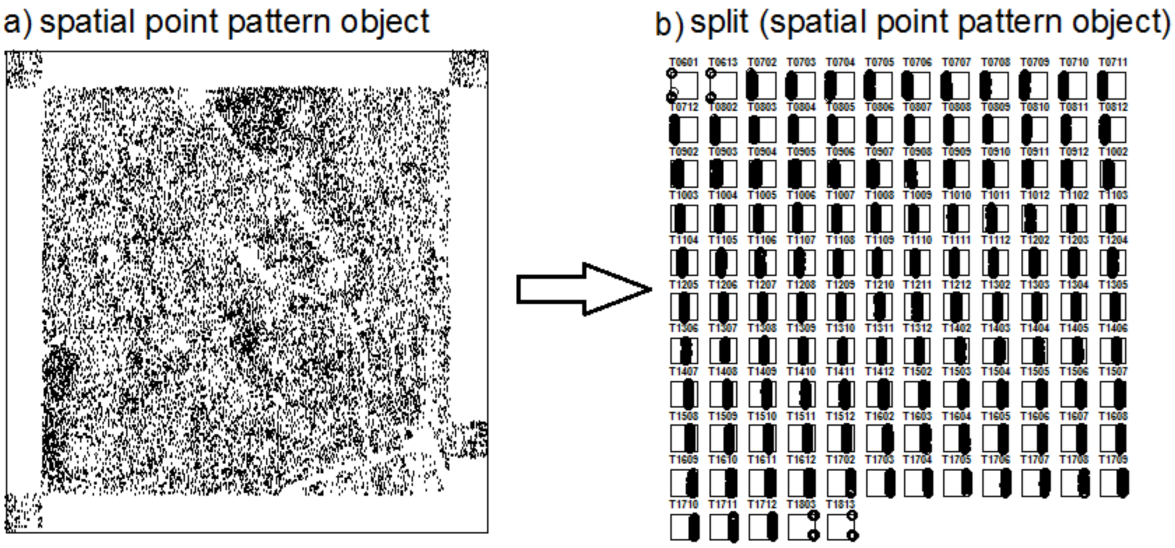


Fig. 2.3. Spatial point pattern object gives the locations of trees occurring in a 5 ha subtropical forest plot (125 subplots with each size of 20 × 20 m) of a study area. a) Showing the spatial point pattern object with mark of DBH for 5-ha plot. b) Showing the split of 5-ha plot into 125 subplots with each size of 20 × 20 m.

2.2. Forest inventory and measurement of plant functional traits

All stems ≥ 1 cm diameter at breast height (DBH) were individually tagged, geo-referenced, measured for DBH using a diameter tape and identified to species-level in June to August 2009 (Fig. 2.3). A total of 20,253 stems were recorded belonging to 108 species, 76 genera and 43 families. The relationships between functional traits and aboveground biomass might be dependent on what functional traits are measured (Ali *et al.* 2017), because functional strategies of different organs are not necessarily coordinated, and leaf and stem economics spectra can be decoupled (Baraloto *et al.* 2010). Mean leaf area, specific leaf area and leaf dry matter content are the key traits in the leaf economic spectrum, and wood density as an important trait in wood economic spectrum while plant maximum height as a key whole-plant trait, and thus robust indicators for plant ecological strategy and biodiversity indices. Leaf chemical traits, mean leaf area and specific leaf area are closely related to photosynthetic capacity, nitrogen content per mass and leaf life span while leaf dry matter content reflects the fundamental tradeoff in investing resources in structural tissues *versus* hydraulic processes (Cornelissen *et al.* 2003, Reich 2014). We therefore measured eight key functional traits, including two stem traits and six leaf traits, across 98 species in a 5-ha subtropical forest: stem wood density, plant maximum height, specific leaf area, mean leaf area, leaf dry matter content, leaf nitrogen content, leaf phosphorous content, and leaf nitrogen to phosphorous ratio (LNC:LPC). Leaf trait measurements were obtained in the summer (i.e., June to August) of 2010-2013, when trees had fully developed leaves. We measured mean leaf area, specific leaf area and leaf dry matter content for each of the 20,253 individuals in the plots following (Cornelissen *et al.* (2003). For leaf chemical traits (leaf nitrogen and phosphorous contents) and wood density trait measurements were taken for seven randomly-selected healthy mature trees for each species (Cornelissen *et al.* 2003, Pakeman & Quested 2007). The trait plant maximum height was collected from the Chinese flora database.

For leaf trait measurements, three branches were cut from three positions (upper, mid, and lower position) in the sunlit side of the tree crown. Twenty to thirty mature leaves (without apparent physical damage) were collected from each branch. The leaves were transported to the laboratory wrapped in a moist paper towel placed in a sealed plastic bag inside a cooler. Functional traits were measured within 12 hours after arriving in the laboratory. Twenty leaves were randomly selected from the leaves from each tree, leaf area was determined (using LI-3100C, Li-Cor, USA) and weighted. After that, the leaves were dried at 75 °C for 48 hours to determine leaf dry mass. Specific leaf area was calculated as the one-sided area of a leaf divided by its oven-dried mass, mean leaf area as the average leaf area of 20-30 leaves, and leaf dry matter content as the oven-dried mass of a leaf divided by its water-saturated fresh mass (Cornelissen *et al.* 2003). Finally, the leaf samples collected from an average of seven randomly-selected healthy mature trees were ground to determine leaf nitrogen and phosphorous contents using a flow-injection auto analyser (Skalar-1000, Netherland), and then the ratio of leaf nitrogen content and phosphorous content was calculated.

For wood density, wood cores were taken on seven individuals for each species with a 5-mm increment corer. In the laboratory, the volume of the tree core was estimated using the length of the tree core, measured using an electronic vernier caliper, and the known diameter. Wood cores were dried at 75 °C in an oven for 72 hrs to determine dry mass. Wood density was calculated by dividing the dry mass over the volume of the wood sample (Cornelissen *et al.* 2003).

2.3. Classification of forest strata and quantification of forest diversity attributes

Overstorey strata were defined as all individuals with DBH ≥ 10 cm in each forest plot, and understorey strata included trees with 1 ≤ DBH < 10 cm (Barrufol *et al.* 2013, Zhang *et al.* 2016a). This resulted in a total of 3,224 stems belonging to 75 species, 51 genera and 29 families in the overstorey strata, and a total of 17,025 stems belonging to 103 species, 65 genera and 37 families in the understorey strata across 125 plots in a 5-ha subtropical forest (chapters 3 and 5). However, leaf chemical traits and wood density were missing for ten rare species, and hence a total of 3,213 stems belonging to 71 species, 47 genera and 27 families were used in the overstorey, and a total of 17,004 stems belonging to 94 species, 57 genera and 33 families were used in the understorey across 125 plots in a 5-ha subtropical forest (chapters 4, 6, 7 and 8).

In this thesis, stand structural attributes and four metrics of biodiversity (collectively called as ‘forest diversity attributes’) in addition to inter- and intraspecific functional trait diversity (Rao’s index) were used to test the multivariate relationships between forest diversity and aboveground biomass at each of the overstorey and understorey strata, and whole-community level in a subtropical forest. This framework distinguishes five different generic attributes of forest diversity in a community, i.e. the structural variation, the variation in component species based on taxonomic features, the dominant (most abundant) trait values, functional trait diversity based on multivariate-trait space, functional trait variation within species, evolutionary diversity based on plant species phylogeny or supertree (e.g., Ali *et al.* 2017, Conti & Díaz 2013, de Bello *et al.* 2011, Finegan *et al.* 2015, Poorter *et al.* 2015, Zhang & Chen 2015). More details about the quantification of each group of forest diversity attributes are provided in the method section of each chapter.

2.4. Environmental factors dataset

To take into account any effects of environment conditions on the relationships of stand structural attributes and biodiversity with aboveground biomass, we included as covariates the soil physicochemical properties: soil carbon content, phosphorus content, nitrogen content, pH, volumetric soil water content, bulk density and humus depth and the topographical properties: elevation, slope and convexity. The original dataset of soil physicochemical and topographical properties for each sampling plot within a 5-ha forest plot were used from the study of Zhang *et al.* (2012a). Summary of the environmental factors used in this thesis is provided in Table 2.1.

In March 2011 soil samples were collected by following the standard method of Center for Tropical Forest Science (CTFS; John *et al.* 2007). To this end, the 5-ha plot was divided into 125 subplots. Starting from the South-West corner of each subplot, samples were taken at 2, 5 and 8 m in a randomly chosen compass directions (East, West, North, South, South-East, South-West, North-West, and North-East). At of these sample points, we collected two topsoil samples (0-10 cm depth) that were mixed together to make a composite soil sample for measurement of soil physiochemical properties. Soil samples were collected using a bulk density corer with a known volume. Thus, soil samples were collected from a total of 375 points to capture fine scale variation in soil properties. The soil samples were immediately transported to the laboratory in sealed plastic bags, where they were sieved (< 2 mm) to homogenize the soil samples and to remove visible roots and small stones. In the laboratory, soil physical properties were measured by following (Lu 2000). The soil total carbon and total nitrogen contents were determined using the “Elemental analyzer” (vario MICRO cube, Elementar, Germany), while total phosphorous content was determined using flow-injection autoanalyser (Skalar, Netherlands).

Table 2.1. Summary for environmental factors, from 125 subtropical forest plots used for analysis of biodiversity – aboveground biomass in this thesis.

Variables	Unit	Mean	S.E.	Minimum	Maximum
*Topography**					
Elevation	m	399.70	3.55	320.44	489.37
Slope	degree	33.66	0.54	13.81	43.92
Convexity	m	0.04	0.24	-5.16	6.90
*Soil properties**					
Soil total phosphorous (TP)	g kg^{-1}	0.26	0.01	0.09	0.58
Soil total nitrogen (TN)	g kg^{-1}	3.12	0.05	1.85	4.49
Soil total carbon (TC)	g kg^{-1}	43.45	0.82	26.30	73.06
pH	unitless	4.14	0.01	3.76	4.55
Volumetric soil water content (SWCV)	unitless	0.29	0.00	0.24	0.38
Soil bulk density (BD)	g cm^{-3}	0.86	0.01	0.64	1.04
Humus depth (HD)	cm	7.49	0.15	5.25	13.42

*Principle Component Analysis was used for the purpose to reduce variables and avoid multicollinearity among the variables. PCA axes were used in the statistical analyses of this thesis, instead of original variables. See Table 2.3 for PCA results.

_ENREF_59In order to reduce the number of local environmental conditions and to avoid the strong correlations among them (see Table 2.2 for correlations), we ran principal component analyses (PCA) based on the soil physicochemical and topographical properties separately. In statistical analyses, we used two PCA axes for soil properties and for topographical variables (soil PC1, soil PC2, topography PC1 and topography PC2), to represent environmental conditions (see Table 2.3).

Table 2.2. Pearson's correlation coefficient between environmental factors among 125 sub-plots in a subtropical evergreen broadleaf forest in Eastern China. Bold numbers indicate significant correlations ($P < 0.05$). All the abbreviations for variables are explained in Table 2.1.

	Soil properties							*Topography*		
	TP	TN	TC	pH	SWCV	BD	HD	Elevation	Slope	Convexity
Soil properties										
TP	---									
TN	**0.67**	---								
TC	**0.33**	**0.81**	---							
pH	0.01	-0.16	**-0.45**	---						
SWCV	-0.13	0.14	**0.57**	**-0.61**	---					
BD	0.00	**-0.24**	**-0.60**	**0.57**	**-0.89**	---				
HD	**-0.18**	0.06	**0.44**	**-0.33**	**0.59**	**-0.48**	---			
Topography										
Elevation	**-0.32**	**-0.31**	0.02	**-0.64**	**0.48**	**-0.39**	**0.34**	---		
Slope	**-0.36**	**-0.28**	0.04	**-0.25**	**0.41**	**-0.37**	**0.22**	**0.37**	---	
Convexity	**-0.37**	**-0.22**	**0.18**	**-0.52**	**0.61**	**-0.51**	**0.56**	**0.47**	**0.27**	---

Table 1.3. Principal Component Analysis (PCA) of 125 forest plots for soil properties and topography. Values in parentheses indicate the variance (%) accounted for by each axis. Values in the table indicate the eigenvector scores of each of the variables on the two PCA axes. All the abbreviations for variables are explained in Table 2.1.

Variables	Soil properties		Variables	Topography	
	PC1 (49%)	PC2 (27%)		PC1 (58%)	PC2 (25%)
TP	-0.09	0.63	Elevation	0.62	-0.17
TN	-0.29	0.58	Slope	0.52	0.82
TC	-0.46	0.27	Convexity	0.58	-0.55
pH	0.38	0.15			
SWCV	-0.47	-0.27			
BD	0.47	0.16			
HD	-0.34	-0.27			

2.5. Estimation of aboveground biomass

We calculated aboveground biomass for each tree with DBH ≥ 5cm (AGB*t*) using a global allometric equation (Eq. 2.1) (Chave *et al.* 2014), which is based on tree DBH, site-specific environment stress factor (E) and species' wood density (ρ).

$$\mathrm{AGB}t = \exp\{-1.803 - 0.976(\mathrm{E}) + 0.976 \times \ln(\rho) + 2.673 \times \ln(\mathrm{DBH}) - 0.0299 \times (\ln(\mathrm{DBH}))^2 \quad (2.1)$$

Where E for our study site was derived from Chave *et al.* (2014).

Applying generalized allometric equations developed for large trees (DBH ≥ 5cm) (Chave *et al.* 2014) to shrubs and small trees may overestimate or underestimate the actual biomass, because of their restriction in the DBH range, and different growth forms and physiognomies, as compared to large trees (Litton & Kauffman 2008). Global allometric equation for trees with DBH ≥ 5cm (Chave *et al.* 2014) tended to overestimate, but to a very lesser extent, biomass of individual small trees and shrubs (DBH < 5 cm) as compared to the estimations obtained using Ali *et al.* (2015) site-specific equation for small trees and shrubs, but the results of the two equations were highly consistent ($R^2 = 0.96$, $P < 0.001$, PMSE = 0.01, $n = 13799$; Fig. 2.4).

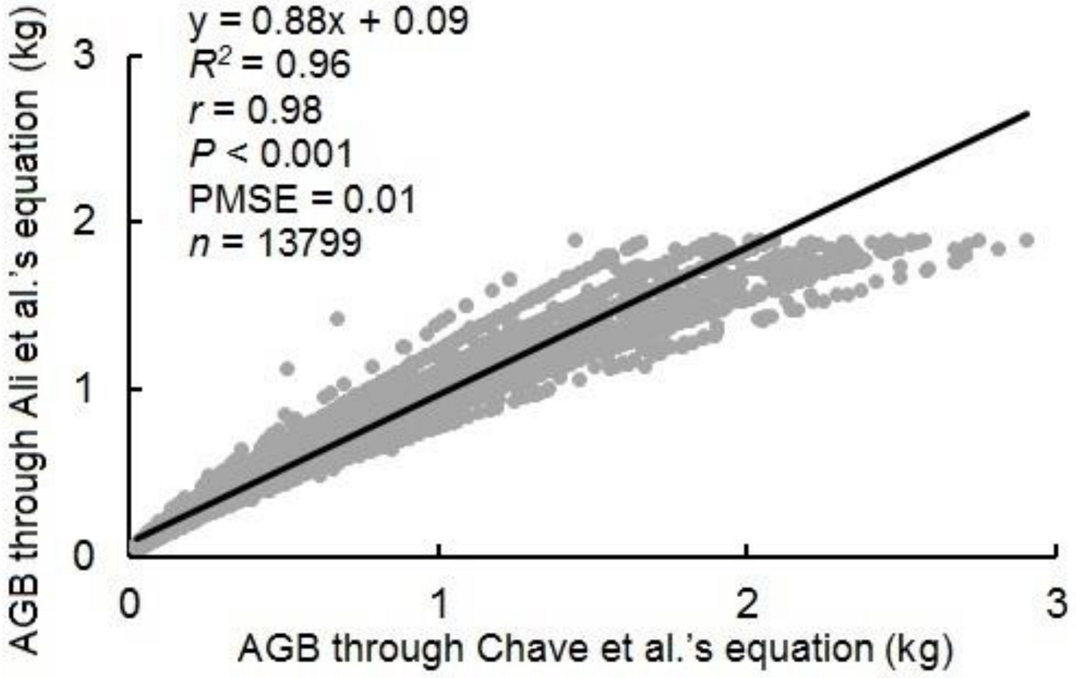


Fig. 2.4. Comparison of the individual tree aboveground biomass (DBH < 5 cm) estimated with Chave et al.'s equation for big trees (DBH ≥ 5 cm) and Ali et al.'s equation for small trees and shrubs (DBH < 5 cm). Abbreviations: R^2 = coefficient of determination; *r* = Pearson's correlation; PMSE, predictive mean square error; *n* = number of small trees and shrubs.

Therefore, we tried to accurately estimate the aboveground biomass of shrubs and small trees (AGB*s*) with DBH < 5 cm by using a general multi-species allometric equation (Eq. 2.2) developed locally for small trees and shrubs (Ali *et al.* 2015), which is similarly based on tree DBH and species' wood density (ρ).

$$\mathrm{AGBs} = 1.460 \times \exp\{\text{-}3.23 + 2.17 \times \mathrm{Ln}(\mathrm{D})\} \qquad (2.2)$$

2.6. Statistical analyses

In this thesis, I used the following four main steps for statistical analyses: 1) data transformation; 2) spatial autocorrelations, bivariate relationships and correlations; 3) multiple linear regressions models, and/ or structural equation modelling; and 4) Moran's I test for spatial autocorrelation in the final selected model (Fig. 2.5). Note that the third step varies according to the specific conceptual model or framework within each specific research chapter.

Prior to the statistical analyses, Shapiro-Wilk goodness-of-fit test was used to assess the normality for all variables. All numerical variables were natural-logarithm transformed and standardized, as suggested by previous studies (Hoyle 2012, Zhang *et al.* 2016a). Transformations of the variables were conducted for the following purposes: 1) to meet the assumptions of normality and linearity; 2) to reduce the effect of outliers; 3) to account for possible nonlinear relationships between variables; and 4) to allow comparisons among multiple predictors and models (Zuur *et al.* 2009).

Study design may confound statistical results when there is spatial autocorrelation in the variables of interest. To account for this, we performed generalized least-squares (GLS) models (Pinheiro & Bates 2016) by accounting for subplots with spatial autocorrelation (including subplots X and Y coordinates as a spatial effect) and without spatial autocorrelation (no reference to subplots X and Y coordinates) among subplots for all relationships between predictors and aboveground biomass (Chisholm *et al.* 2013, Yuan *et al.* 2016). GLS model is a reliable method for testing whether subplots sharing similar abiotic conditions are independent from each other within a forest (Zuur *et al.* 2009). The goodness of fit of spatial and non-spatial GLS models was evaluated by Akaike information criterion (AIC).

For the interpretation of results in multiple linear regressions model and/or structural equation model (Grace *et al.* 2016, Prado-Junior *et al.* 2016), I identified bivariate relationships between each of the hypothesized causal paths or effects according to the hypothesis in the conceptual model or framework, using simple regression analysis and Pearson's correlation. Multiple linear regressions models (i.e., general linear models) were used to evaluate how aboveground biomass related to multiple predictors, as hypothesized in conceptual model or framework. I used all subsets regression analysis and selected the optimal model that had lowest AICc (i.e. AIC adjusted for small sample sizes). Models were considered to be equally supported if the difference in AICc was less than two units (Bartoń 2016). When models were equally supported, I selected the most parsimonious model by considering the lowest number of predictors. General linear models were performed using the *stats* package and all subsets regression analyses using the *MuMIn* package (Bartoń 2016). I plotted a bivariate model's response (optimal linear model) against each predictor's marginal effect (i.e. holding all other predictors in constant), by using the *plotmo* package (Milborrow 2015). After that, I applied the Moran's I test for spatial autocorrelation in the selected optimal linear model residuals, while assessing the range and type of spatial autocorrelation in lag classes by plotting the correlograms, by using the *spdep* package (Bivand 2016).

Finally, I employed structural equation modelling in order to evaluate the direct, indirect and total effects, based on proposed conceptual model(s). Here, I used two steps: 1) direct use of structural equation modelling to test the proposed specific conceptual model (chapters 3 and 5); and applied on the final optimal multiple linear model. In the latter case, I selected the best predictors for the response variable which were retained in the selected optimal model(s). Several tests were used to assess the goodness of fit for structural equation model (Malaeb *et al.* 2000), i.e., the Chi-square (χ^2) test, goodness-of-fit index (GFI), comparative fit index (CFI), standardized root mean square residual (SRMR) and AIC. Indicators for a best model fit to the data critically included an insignificant χ^2 test statistic ($P >$ 0.05; indicates that sample and observed covariance matrices are statistically indistinguishable), SRMR < 0.08, and both GFI and CFI > 0.95 (Grace *et al.* 2016, Hoyle 2012). I critically used χ^2 test, representing the maximum likelihood estimation, to assess how well the hypothesized structural equation model fits the data (Ali *et al.* 2016b, Grace *et al.* 2016). The indirect effect of a predictor was calculated by multiplying the standardized effects of all paths on one route from one predictor to mediator and then to aboveground biomass, while total effect was calculated by adding standardized direct and indirect effects (Ali *et al.* 2016b, Grace *et al.* 2016). The structural equation model were employed using the *lavaan* package (Rosseel 2012). For all statistical analyses R 3.2.2 was used (R Development Core Team 2015).

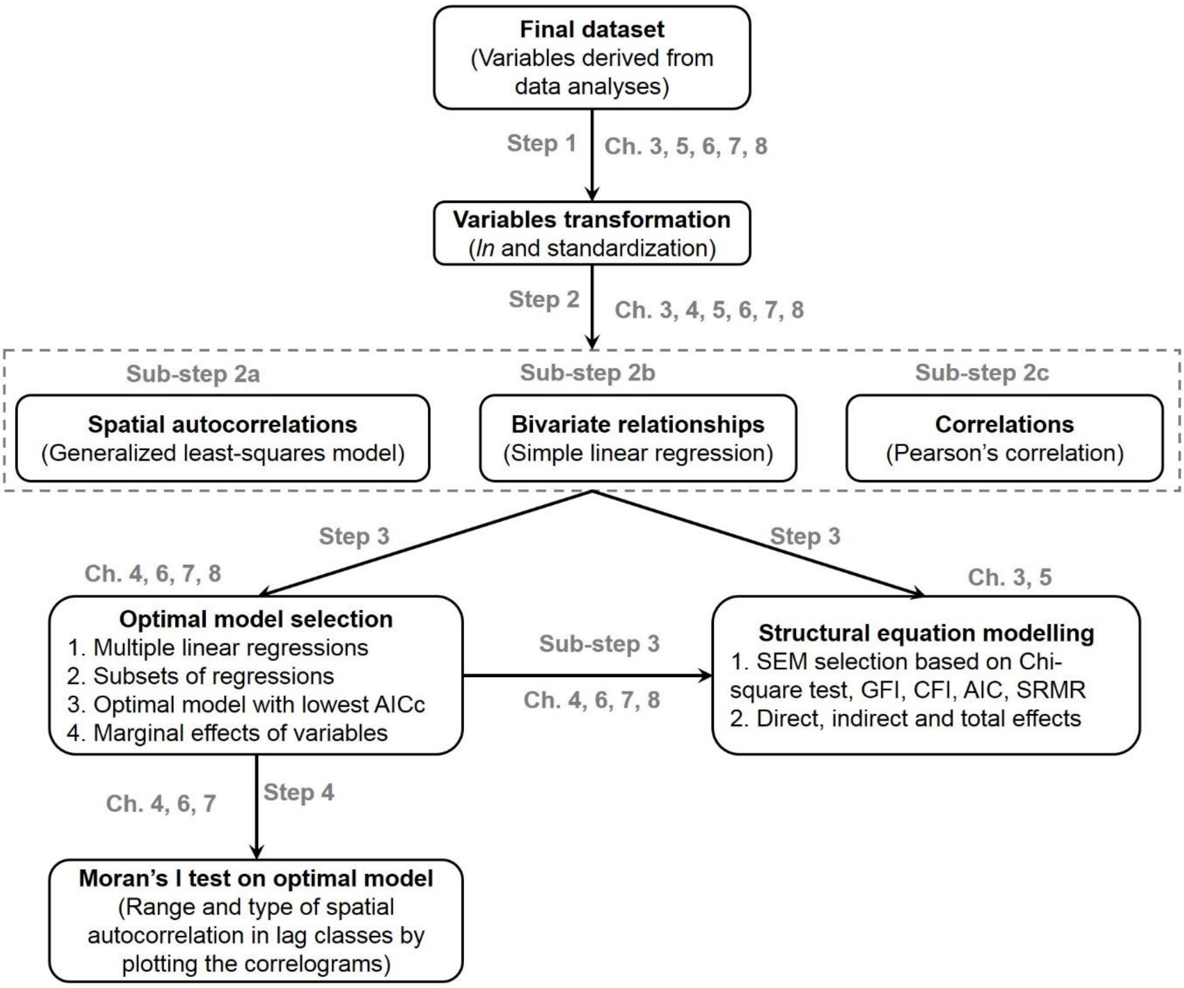
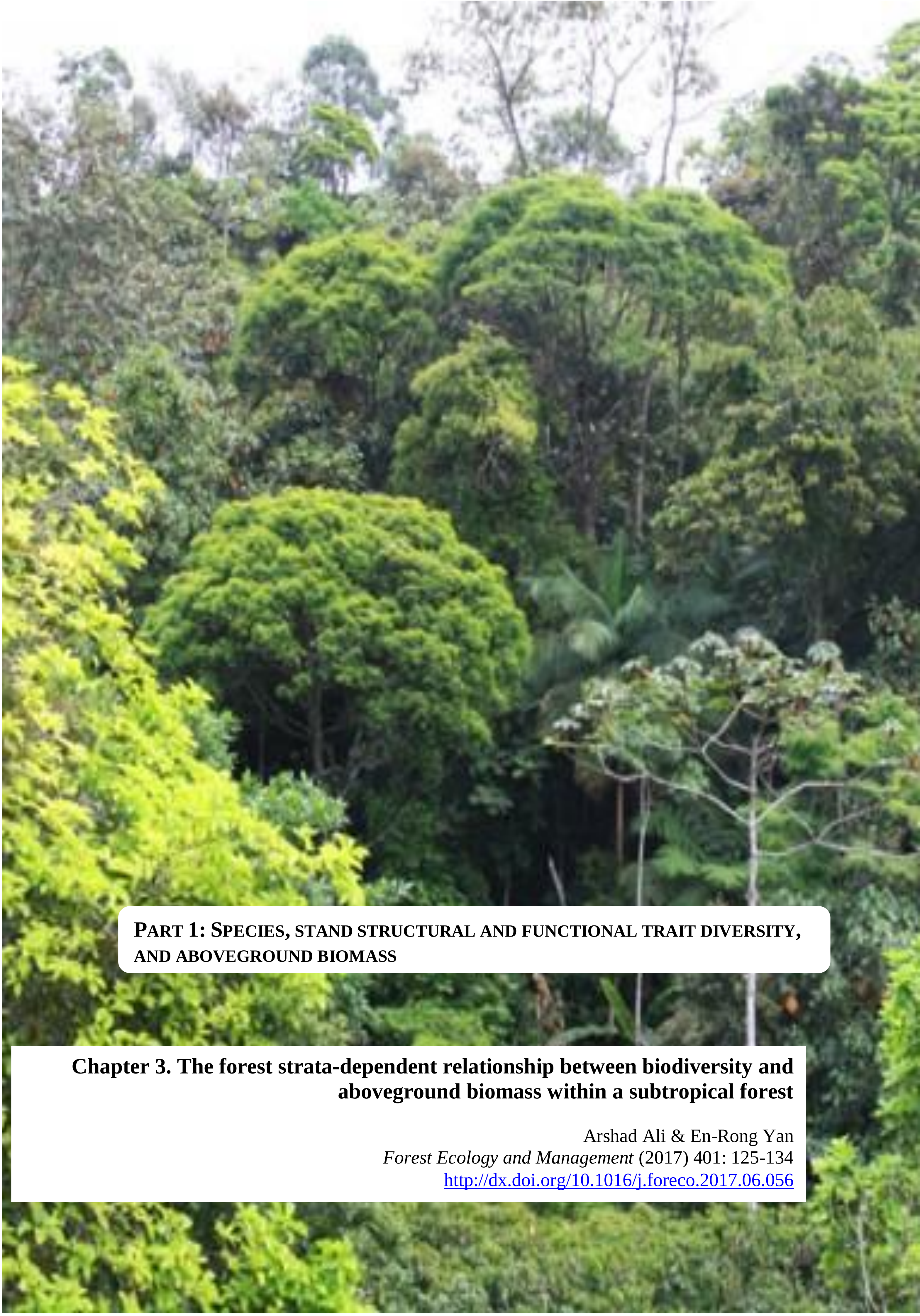


Fig. 2.5. Statistical steps used in this thesis. Chapters are indicated.



PART 1: SPECIES, STAND STRUCTURAL AND FUNCTIONAL TRAIT DIVERSITY, AND ABOVEGROUND BIOMASS

Chapter 3. The forest strata-dependent relationship between biodiversity and aboveground biomass within a subtropical forest

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3.1. Introduction

Previous studies have suggested that the positive relationships between forest diversity (e.g., species diversity and individual tree size variation) and aboveground biomass are essential to the ability of forests to provide goods and services (Ali & Mattsson 2017, Poorter *et al.* 2015, Wang *et al.* 2014, Zhang & Chen 2015). Due to the dominant role of overstorey strata on the available resource and their influences on various ecological processes, the diversity and aboveground biomass of understorey strata are substantially influenced by overstorey trees in forests (Barbier *et al.* 2008). However, in most of the empirical studies, the effects of forest strata (e.g., overstorey and understorey) on the relationship between biodiversity and aboveground biomass are often ignored, making it impossible to assess the effects of overstorey trees on the patterns of biodiversity and aboveground biomass of understorey in forest ecosystems (Ali & Mattsson 2017, Cavanaugh *et al.* 2014, Poorter *et al.* 2015, Zhang & Chen 2015). Therefore, specific research is needed to improve our understanding about the patterns, magnitude and mechanisms of diversity – aboveground biomass relationships across forest strata in forests. Disentangling these ecological complexities requires integrative modelling considering how species diversity and tree size variation of overstorey and understorey strata affect their corresponding aboveground biomass, and at the same time how overstorey strata affect the diversity and aboveground biomass of understorey in species-rich forests (Fig. 3.1).

The positive relationships between biodiversity and ecosystem functions are often attributed to the niche complementarity hypothesis (Tilman *et al.* 2001), which postulates that species with different niches are able to use available resources more efficiently, and thus enhancing aboveground biomass or productivity (Zhang *et al.* 2012b). Species diversity and individual tree size variation are important for ecosystem functions because they can influence the efficiency of resource acquisition and utilization among and within component species in forests (Chu *et al.* 2009, Zhang & Chen 2015). Species diversity generally interpreted as a result of niche differentiation and facilitation (i.e., species complementarity), is recognized to be responsible for the positive relationships between biodiversity and aboveground biomass in both experimental and natural environments, including forests (Loreau *et al.* 2001, Poorter *et al.* 2015, Zhang & Chen 2015). Recent studies have suggested that multilayered stand structure also promotes aboveground biomass due to the niche complementarity effect in both natural forests and agroforests (Ali & Mattsson 2017, Ali *et al.* 2016b, Poorter *et al.* 2015, Zhang & Chen 2015). Individual tree size variation is a key stand structural attribute being generally quantified by variances among all individual tree sizes across component species in a community (Clark 2010, Zhang & Chen 2015). Theoretically, individual tree size variation enhance aboveground biomass through complementary light-use (Ali & Mattsson 2017, Yachi & Loreau 2007, Zhang & Chen 2015).

In forest ecosystems, overstorey strata store large quantities of aboveground biomass due to their high wood volumes and disproportionate contribution of large trees to the aboveground biomass at whole-community level (Slik *et al.* 2013). In contrast, understorey strata contribute much to the majority of biodiversity (Barbier *et al.* 2008, Gilliam 2007, Nilsson & Wardle 2005). Moreover, local environmental conditions strongly affecting plant performance (Barbier *et al.* 2008, Bartels & Chen 2010, 2013), thus the ensuing patterns of species diversity and tree size variation across forest strata. Light, being one of the most important plant resources, is often limiting for understorey trees, while it is abundant for overstorey trees (Brenes-Arguedas *et al.* 2011, Wright 2002). A dense forest with great aboveground biomass can positively contribute to ecosystem functions through large stem volumes of overstorey trees, but slows down ecosystem functioning rates in understorey due to low light availabilities (Poorter *et al.* 2015, Slik *et al.* 2013, Zhang *et al.* 2016a). Additionally, species diversity of overstorey strata may promote species diversity in understorey strata as a result of reduced interspecific competition (Bartels & Chen 2013, Zhang *et al.* 2016a). Therefore, to understand the mechanism(s) by which aboveground biomass is interactively affected by biodiversity in both overstorey and understorey strata within forests, it may be insightful to consider understorey and overstorey strata separately.

In this study, we tested hypothesis of the niche complementarity in terms of species diversity and individual tree size variation by using linear structural equation model (SEM) through analyzing biophysical data from 125 plots inside a 5-ha subtropical forest in Eastern China. Studies in tropical forests reveal that soil nutrients or physicochemical variables should be included when testing multivariate relationships between diversity and aboveground biomass because it determines nutrients availability which strongly influences the relationships between biodiversity and aboveground biomass (Poorter *et al.* 2015, Prado-Junior *et al.* 2016). Considering this, we constructed four conceptual frameworks for overstorey and understorey strata both in integration (Fig. 3.1a) and in isolation (Fig. 3.1b and 3.1c), as well as in whole-community (Fig. 3.1d). Specifically, we asked the following two questions. First, how do species diversity, individual tree size variation and soil nutrients relate with aboveground biomass across forest strata and whole-community level? With respect to the niche complementarity hypothesis, we predicted that species diversity and individual tree size variation have positive effects on aboveground biomass across forest strata alone and combined (Prediction 1). Considering the soil fertility hypothesis (Quesada *et al.* 2012, Wright *et al.*

2011), we predicted that aboveground biomass, species diversity and individual tree size variation increase with an improvement of soil nutrients in both overstorey and understorey strata, and in whole-community (Prediction 2).

The second question is whether species diversity, individual tree size variation and aboveground biomass of overstorey strata affect biodiversity and aboveground biomass of understorey strata, when soil nutrients are considered simultaneously? We predicted that overstorey strata would decrease aboveground biomass and individual tree size variation in understorey strata (Prediction 3), due to the dominant role of overstorey strata in competing and/or consuming available light and soil nutrients (Anderson *et al.* 1969, Bartels & Chen 2010, Zhang *et al.* 2016a). In addition, we predicted that species diversity of overstorey strata may promote species diversity of understorey (Prediction 4), due to increased resource heterogeneity and reduced interspecific competition in understorey (e.g., Gamfeldt *et al.* 2013, Zhang *et al.* 2016a).

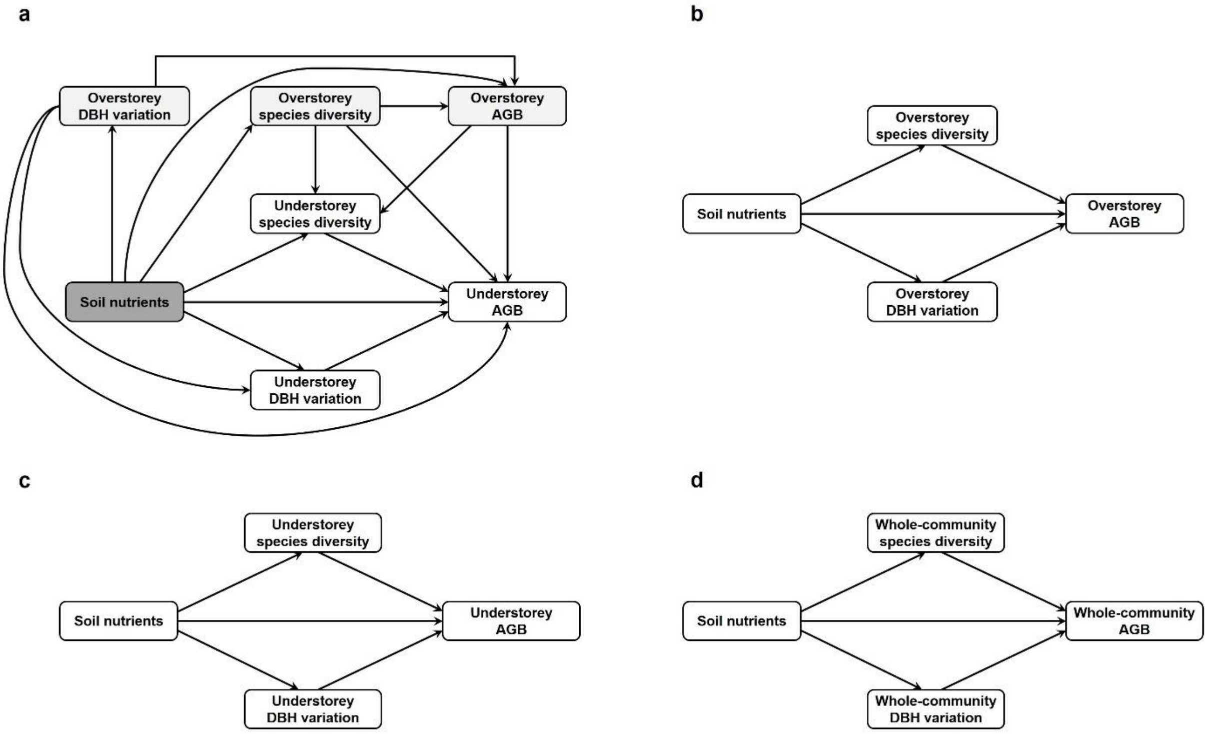


Fig. 3.1. Conceptual models for the relationships of aboveground biomass with species diversity and individual tree size variation (DBH variation) across forest strata in a subtropical evergreen broadleaf forest. a) integrative modelling showing hypothesized relationships of how species diversity and individual tree size variation in overstorey and understorey strata affect their corresponding aboveground biomass, and at the same time how overstorey strata affects the diversity and aboveground biomass of understorey strata, in addition to the effects of soil nutrients. b) and c) isolation modelling showing hypothesized relationships of how species diversity and individual tree size variation of overstorey and understorey strata affect their corresponding aboveground biomass; and d) whole-community modelling showing hypothesized relationships of how species diversity and individual tree size variation of whole-community affect whole-community aboveground biomass.

3.2. Materials and methods

3.2.1. Quantification of forest diversity

Overstorey strata were defined as all individuals with DBH ≥ 10 cm in each forest plot, and understorey strata included trees with 1 ≤ DBH < 10 cm (Barrufol *et al.* 2013, Zhang *et al.* 2016a). This resulted in a total of 3,224 stems belonging to 75 species, 51 genera and 29 families in the overstorey strata, and a total of 17,025 stems belonging to 103 species, 65 genera and 37 families in the understorey strata across 125 plots in a 5-ha subtropical forest.

We used two measures of forest diversity that were quantified for overstorey and understorey strata separately: Shannon's species diversity and DBH variation. This resulted in four diversity measures per plot for integrative modelling analyses, while two measures per plot for whole-community level and forest strata level analyses. We used the Shannon-Wiener biodiversity index (Eq. 3.1) to quantify tree species diversity at each plot (Magurran 2004). The species' relative basal area (relative to the total understorey/ overstorey basal area) was used to weight the number of tree species at overstorey and understorey strata at each plot, because basal area is a better indicator of plant performance than abundance (Ali *et al.* 2016b, Zhang & Chen 2015). Similarly, the species' relative basal area (relative to the whole-community basal area) was used to weight number of tree species at whole-community level at each plot. We chose Shannon's species diversity index to account for species richness and evenness, two of the important aspects of species diversity in biodiversity – productivity studies (Zhang *et al.* 2012b).

$$\mathrm{H_s} = -\sum_{i=1}^{s} \mathrm{p}_i \times \ln(\mathrm{p}_i) \qquad (3.1)$$

where p_i is the proportion of basal areas of *i*th species, while *s* is the number of tree species. The calculations on the Shannon-Weiner diversity index was performed using the *vegan* package (Oksanen *et al.* 2015).

We used DBH variation among individual trees within each plot as proxy of individual tree size variation (Ali & Mattsson 2017, Zhang & Chen 2015), because the overall DBH variation represents the degree of the realized niche differentiation via positive plant-plant interactions (Clark 2010, Yachi & Loreau 2007). Coefficient of variation of DBH (Eq. 3.2), the ratio of the standard deviation of all DBH measurements to the mean DBH, was used to calculate DBH variation within each plot, expressed as percentage.

$$\mathrm{CV_j} = \frac{\mathrm{s_j}}{\mathrm{\bar{x}_j}} \times 100 \qquad (3.2)$$

where CV_j is the individual tree size (DBH) variation of all species within *j*th plot, s_j is the standard deviation of all DBH measurements within *j*th plot, i.e. $s_j = \sqrt{\frac{\sum(x_j - \bar{x}_j)^2}{n_i - 1}}$, $\bar{x}_j$ is the mean DBH of the *j*th plot, i.e. $\bar{x}_j = \frac{\sum_{i=1}^{n} x_i}{n_i}$, and x_j is the value of each individual tree DBH in the *j*th plot being averaged.

The calculations on the coefficient of variation was performed using *cv* function of *raster* package. The descriptions about the estimation of aboveground biomass and measurement of soil nutrients are provided in Chapter 2. Summary of DBH variation, species diversity and aboveground biomass across forest strata and whole-community, and soil nutrients (soil PC2) is provided in Table 3.1.

Table 3.1. Summary of variable used in analyses, from 125 subtropical forest plots. Abbreviations: UAGB, understorey aboveground biomass; OAGB, overstorey aboveground biomass; WAGB, whole-community aboveground biomass; UDV, understorey DBH variation; ODV, overstorey DBH variation; WDV, whole-community DBH variation; USD, understorey species diversity; OSD, overstorey species diversity; WSD, whole-community species diversity; SN, soil nutrients (soil PC2).

Variable	Unit	Mean	S.E.	Minimum	Maximum
Overstorey strata					
ODV	%	49.56	1.11	24.19	89.41
OSD	unitless	2.15	0.03	1.17	2.80
OAGB	Mg ha^{-1}	69.53	2.26	17.59	149.56
Understorey strata					
UDV	%	63.56	0.52	49.26	84.34
USD	unitless	2.08	0.04	1.13	3.12
UAGB	Mg ha^{-1}	5.01	0.15	1.25	9.34
Whole-community level					
WDV	%	126.87	2.03	82.84	183.74
WSD	unitless	2.35	0.03	1.54	3.27
WAGB	Mg ha^{-1}	74.54	2.29	21.93	154.79
Soil nutrients					
SN	unitless	0.00	0.12	-2.11	2.69

Note: logarithm-transformed and standardized data were used in statistical analyses.

3.2.2. Statistical analyses

Our study design may confound statistical results when there is spatial autocorrelation in the variables of interest. To account for this, we performed generalized least-squares (GLS) models (Pinheiro & Bates 2016) by accounting for subplots with spatial autocorrelation (including subplots X and Y coordinates as a spatial effect) and without spatial autocorrelation (no reference to subplots X and Y coordinates) among subplots for all relationships between predictors and aboveground biomass (Chisholm *et al.* 2013, Yuan *et al.* 2016). In addition, forest strata may also confound the spatial autocorrelation in the variables of interest, as overstorey and understorey strata within a plot have similar spatial location (X and Y coordinates). We therefore explicitly accounted for the effect of vertical strata (overstorey and understorey) by using grouping variable on the relationship between predictor and aboveground biomass in both spatial (i.e., subplots X and Y coordinates are grouped within strata) and non-spatial (no reference to subplots X and Y coordinates within strata) GLS models. GLS model is a reliable method for testing whether subplots sharing similar abiotic conditions are independent from each other within a forest (Zuur *et al.* 2009). The goodness of fit of spatial and non-spatial GLS models was evaluated by AIC, and we found that models without spatial autocorrelation always had the lower AIC values (Table 3.2), which is similar to the recent observations in 25-ha broad-leaved Korean pine mixed forest and 5-ha secondary poplar-birch forest in northeastern China (Yuan *et al.* 2016).

Table 3.2. Summary of the generalized least-squares (GLS) models of aboveground biomass on predictors at forest strata and whole-community level. To account for the confounding effect of forest strata, the grouping effect of forest strata, i.e. the grouping variable of overstorey and understorey, was included in both spatial and non-spatial GLS models. Abbreviations: AGB, aboveground biomass; DV, DBH variation; SD, species diversity; SN, soil nutrients.

GLS model	Hypothesized model	Coefficient	*t*-value	*P*-value	AIC	R^2_{pseudo}
Forest strata						
AGB ~ SD	Non-spatial	0.19	3.13	0.002	693.91	0.036
	Spatial	0.19	2.92	0.004	704.13	0.036
AGB ~ DV	Non-spatial	0.27	4.46	<0.001	686.10	0.032
	Spatial	0.27	4.36	<0.001	695.69	0.032
AGB ~ SN	Non-spatial	-0.28	-5.69	<0.001	675.07	0.148
	Spatial	-0.28	-5.90	<0.001	682.49	0.148
Whole-community level						
AGB ~ SD	Non-spatial	0.14	1.61	0.110	363.14	0.021
	Spatial	0.15	1.62	0.109	367.04	0.021
AGB ~ DV	Non-spatial	0.32	3.72	<0.001	352.56	0.101
	Spatial	0.42	4.71	<0.001	352.35	0.101
AGB ~ SN	Non-spatial	-0.17	-2.68	0.008	359.35	0.055
	Spatial	-0.17	-2.68	0.008	363.35	0.055

Having confirmed that spatial autocorrelation is not likely to strongly confound our results, we employed linear SEM to examine the relationships of species diversity and DBH variation with aboveground biomass, in addition to the effects of soil nutrients. We constructed SEM based on known hypothetical multivariate causes of forest diversity and aboveground biomass within each vertical strata for integrative and isolation modelling, and also for whole-community level analyses (Fig. 3.1).

Several tests were used to assess the goodness of fit for SEMs (Malaeb *et al.* 2000), i.e., the Chi-square (χ^2) test, goodness-of-fit index (GFI), comparative fit index (CFI), standardized root mean square residual (SRMR) and Akaike information criterion (AIC). Indicators for a best model fit to the data critically included an insignificant χ^2 test statistic ($P > 0.05$; indicates that sample and observed covariance matrices are statistically indistinguishable), SRMR < 0.08, and both GFI and CFI > 0.95 (Grace *et al.* 2016, Hoyle 2012). We critically used χ^2 test, representing the maximum likelihood estimation, to assess how well the hypothesized SEM fits the data (Ali *et al.* 2016b, Grace *et al.* 2016). The indirect effect of a predictor was calculated by multiplying the standardized effects of all paths on one route from one predictor to mediator and then to aboveground biomass, while total effect was calculated by adding standardized direct and indirect effects (Ali *et al.* 2016b, Grace *et al.* 2016). The SEMs were employed using the *lavaan* package (Rosseel 2012).

Table 3.3. Pearson's correlation coefficient between variables used in the structural equation models (Figs. 3.5, 3.6 and 3.7). Bold numbers indicate significant correlations ($P < 0.05$). All the abbreviations for variables are explained in Table 3.1.

	Overstorey			*Understorey*			*Soil PC2*
	ODV	OSD	OAGB	USD	UDV	UAGB	SN
Overstorey							
ODV	---						
OSD	-0.10	---					
OAGB	**0.38**	**0.26**	---				
Understorey							
USD	-0.05	**0.19**	0.06	---			
UDV	0.05	-0.08	0.04	-0.13	---		
UAGB	**-0.30**	**0.28**	0.17	0.12	-0.02	---	
Soil PC2							
SN	**0.39**	**-0.35**	**-0.20**	-0.05	0.02	**-0.57**	---
Whole-community							
	WDV	WSD	WAGB				
WDV	---						
WSD	**-0.25**	---					
WAGB	**0.32**	0.14	---				

Soil PC2							
SN	**0.47**	**-0.18**	**-0.23**				---

Shapiro-Wilk goodness-of-fit test was used to assess the normality for all variables. As recommended (Grace *et al.* 2016), all numerical variables including aboveground biomass, species diversity and DBH variation were natural-logarithm transformed and standardized in order to meet the assumptions of normality and linearity, and to allow comparisons among multiple predictors and models (Zuur *et al.* 2009). For the interpretation of results (Grace *et al.* 2016), we conducted the bivariate relationships indicating each hypothesized path according to the conceptual model in Fig. 3.1, using Pearson's correlation and regression analyses. The complementary Pearson's correlations and bivariate relationships to the SEMs are provided in Table 3.3 and Figs 3.2-3.4, respectively. For all statistical analyses R 3.2.2 was used (R Development Core Team 2015). Dataset used in the analyses can be found at http://dx.doi.org/10.1016/j.foreco.2017.06.056.

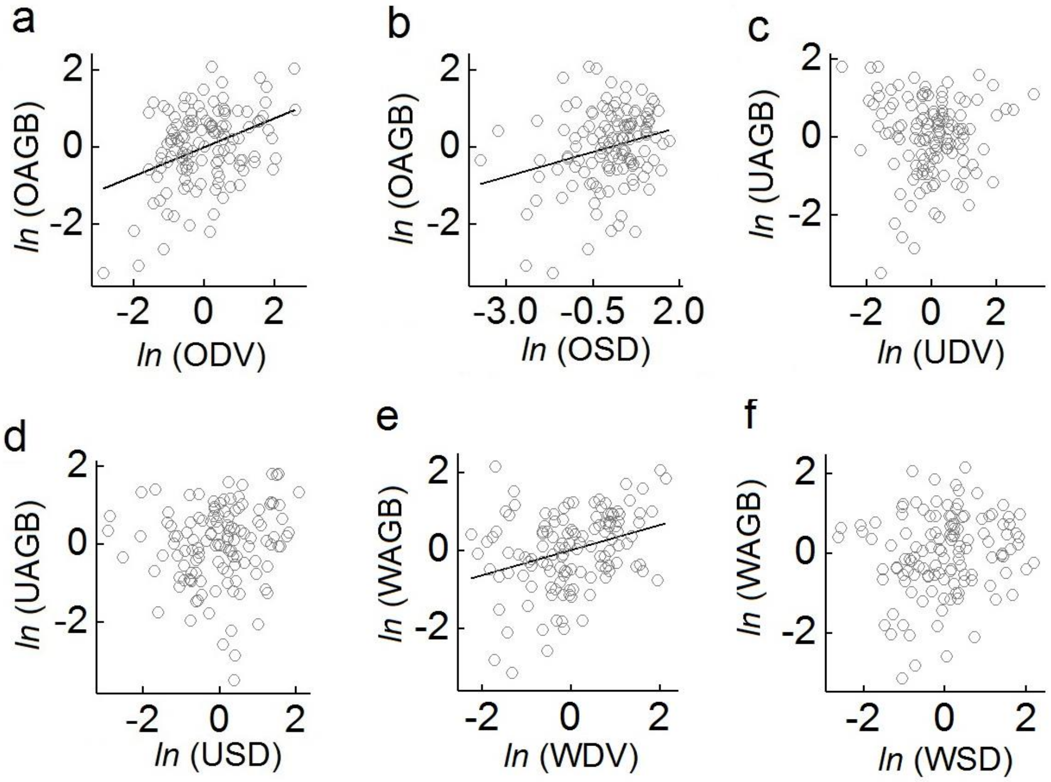


Fig. 3.2. The bivariate relationships between endogenous and exogenous variables (n = 125) for hypothesized causal paths in the structural equation models (Figs 3.5, 3.6 and 3.7) in a subtropical evergreen broadleaf forest in Eastern China. Fitted regressions are significant at $P < 0.05$. All the abbreviations for variables are explained in Table 3.1.

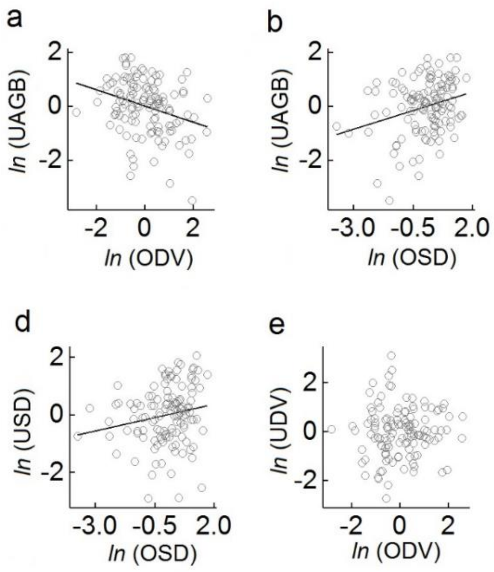


Fig. 3.3. The bivariate relationships between endogenous and exogenous variables (n = 125) for hypothesized causal paths in the structural equation models (Figs. 3.5) in a subtropical evergreen broadleaf forest in Eastern China. Fitted regressions are significant at $P < 0.05$. All the abbreviations for variables are explained in Table 3.1.

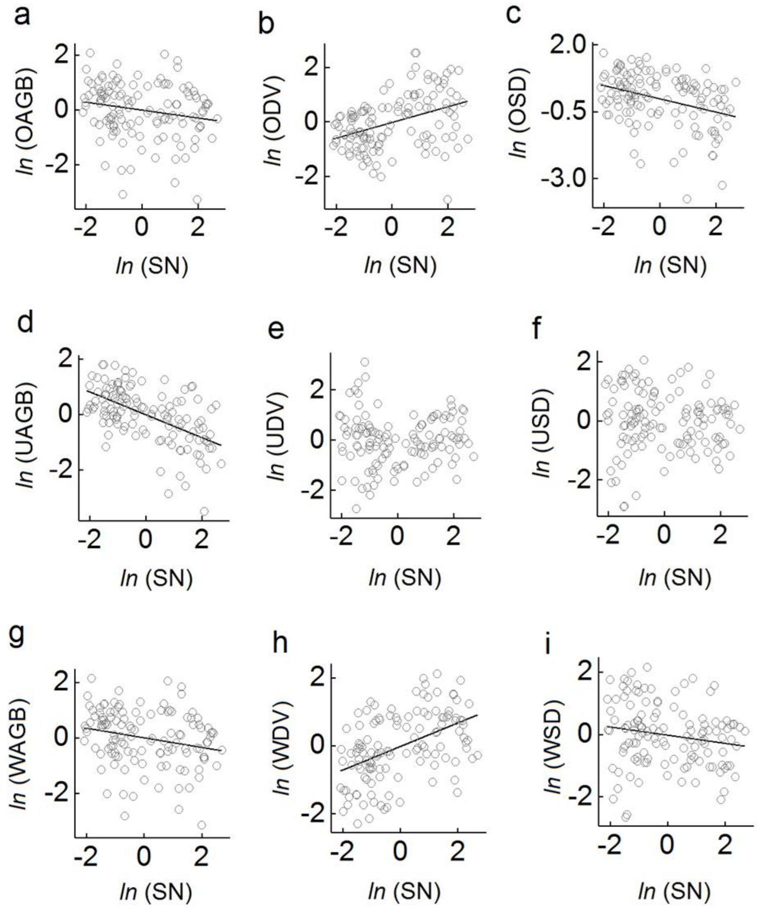


Fig. 3.4. The bivariate relationships between endogenous and exogenous variable (soil nutrients) (*n* = 125) for hypothesized causal paths in the structural equation models (Figs. 3.5, 3.6 and 3.7) in a subtropical evergreen broadleaf forest in Eastern China. Fitted regressions are significant at $P < 0.05$. All the abbreviations for variables are explained in Table 3.1.

3.3. Results

According to the χ^2 test, the integrative SEM which included the overstorey and understorey strata in conjunction was accepted ($\chi^2 = 5.98$, $P = 0.425$). In comparison, the isolation SEMs for overstorey ($\chi^2 = 0.27$, $P = 0.605$) and understorey ($\chi^2 = 2.03$, $P = 0.155$) strata were also accepted, whereas the whole-community SEM was rejected ($\chi^2 = 4.72$, $P = 0.030$; Table 3.4). The goodness of fit for the integrative and forest strata SEMs showed that including overstorey and understorey trees in an integration (Fig. 3.5) or in isolation (Fig. 3.6) performed equally well for predicting aboveground biomass (Tables 3.4 and 3.5).

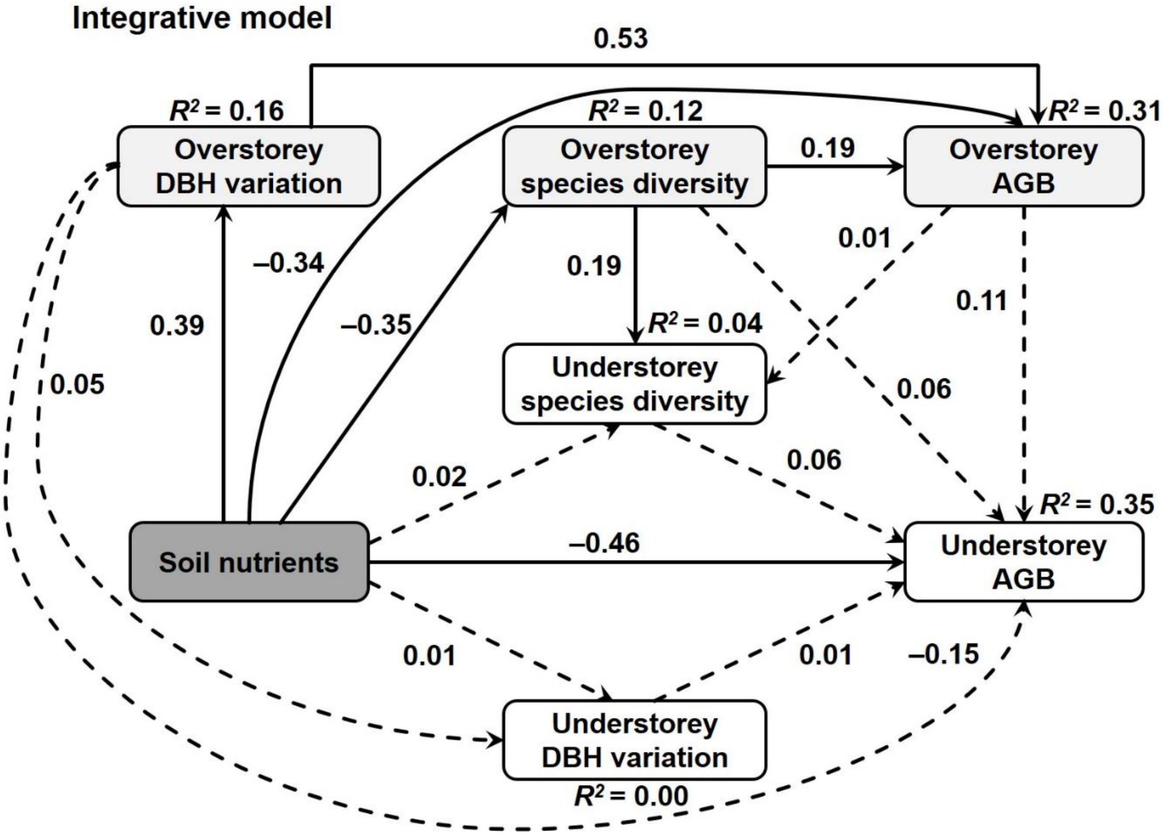


Fig. 3.5. The best-fit structural equation model for the integrative modelling of the relationships of species diversity and individual tree size variation in overstorey and understorey strata with their corresponding aboveground biomass, and the relationships of overstorey strata with understorey strata, in addition to the effects of soil nutrients. Solid arrows represent significant ($P < 0.05$) paths and dashed arrows represent non-significant paths ($P > 0.05$). For each path the standardized regression 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 shown in Table 3.4. For abbreviations, see Table 3.5.

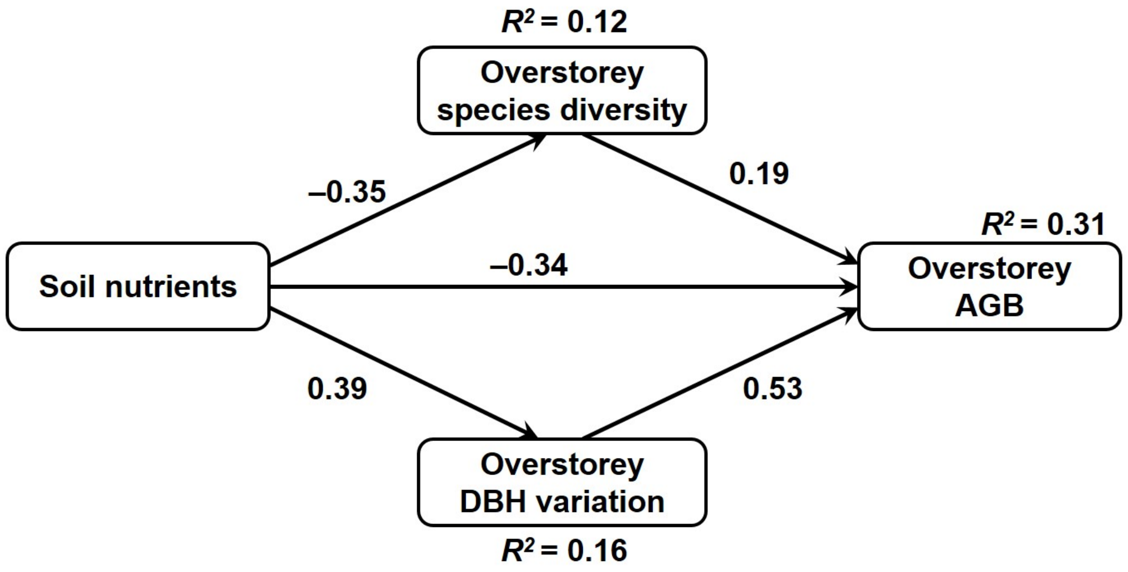
The integrative SEM accounted for 35, 31, 16, 12, 4, and 0 % of the variation in understorey aboveground biomass, overstorey aboveground biomass, overstorey DBH variation, overstorey species diversity, understorey species diversity, and understorey DBH variation, respectively (Fig. 3.5). Overstorey DBH variation ($\beta = 0.53$, $P < 0.001$) and species diversity ($\beta = 0.19$, $P = 0.016$) had positive direct effects on overstorey aboveground biomass. Overstorey species diversity had positive direct effect on species diversity ($\beta = 0.19$, $P = 0.046$), but not on aboveground biomass of understorey strata. Understorey species diversity and DBH variation did not significant affect understorey aboveground biomass. Soil nutrients had positive direct effect on overstorey DBH variation ($\beta = 0.39$, $P < 0.001$), but negative direct effects on aboveground biomass in both overstorey ($\beta = –0.34$, $P < 0.001$) and understorey ($\beta = –0.46$, $P < 0.001$), and on species diversity in overstorey ($\beta = –0.35$, $P < 0.001$). In contrast, soil nutrients did not directly affect understorey species diversity and DBH variation (Table 3.5; Fig. 3.5).

Overstorey species diversity, DBH variation and aboveground biomass did not indirectly affect understorey aboveground biomass via understorey species diversity and DBH variation (Table 3.5). Soil nutrients had indirect positive effect on overstorey aboveground biomass via overstorey DBH variation ($\beta = 0.21$, $P < 0.001$), while negative indirect effect on overstorey aboveground biomass via overstorey species diversity ($\beta = –0.07$, $P = 0.037$). The indirect effect of soil nutrients on understorey aboveground biomass was not found. There were significant total negative effects of soil nutrients on understorey and overstorey aboveground biomass, but the strength of the effect varied at understorey ($\beta = –0.58$, $P < 0.001$) and overstorey ($\beta = –0.20$, $P = 0.023$) strata (Table 3.5).

The overstorey SEM (Fig. 3.6a) showed that overstorey DBH variation ($\beta = 0.53$, $P < 0.001$) and species diversity ($\beta = 0.19$, $P = 0.016$) had positive direct effects on overstorey aboveground biomass (Fig. 3.6a). Soil nutrients had negative direct effects on overstorey aboveground biomass ($\beta = –0.34$, $P < 0.001$) and species diversity ($\beta = –0.35$, $P < 0.001$), but positive direct effect on overstorey DBH variation ($\beta = 0.39$, $P < 0.001$). Soil nutrients also had indirect positive effect via overstorey DBH variation ($\beta = 0.21$, $P < 0.001$) while negative indirect effect via overstorey species diversity ($\beta = –0.07$, $P = 0.037$) on overstorey aboveground biomass. The total effect of soil nutrients on overstorey aboveground biomass was significantly negative ($\beta = –0.20$, $P = 0.023$; Table 3.5).

The SEM for understorey strata (Fig. 3.6b) showed that species diversity and DBH variation did not directly affect aboveground biomass in understorey. Aboveground biomass significantly decreased with soil nutrients ($\beta = –0.57$, $P < 0.001$). Soil nutrients did not directly affect understorey species diversity and DBH variation. There were not significant indirect effects of soil nutrients via understorey species diversity and DBH variation on understorey aboveground biomass. The total effect of soil nutrients on aboveground biomass was relatively similar to the direct effect ($\beta = -0.57$, $P < 0.001$; Table 3.5). In comparison, the whole-community SEM (Fig. 3.7) showed almost similar results to the overstorey SEM (Fig. 3.6a), but the SEM was rejected based on χ^2 test ($P < 0.05$).

a) Overstorey strata model



b) Understorey strata model

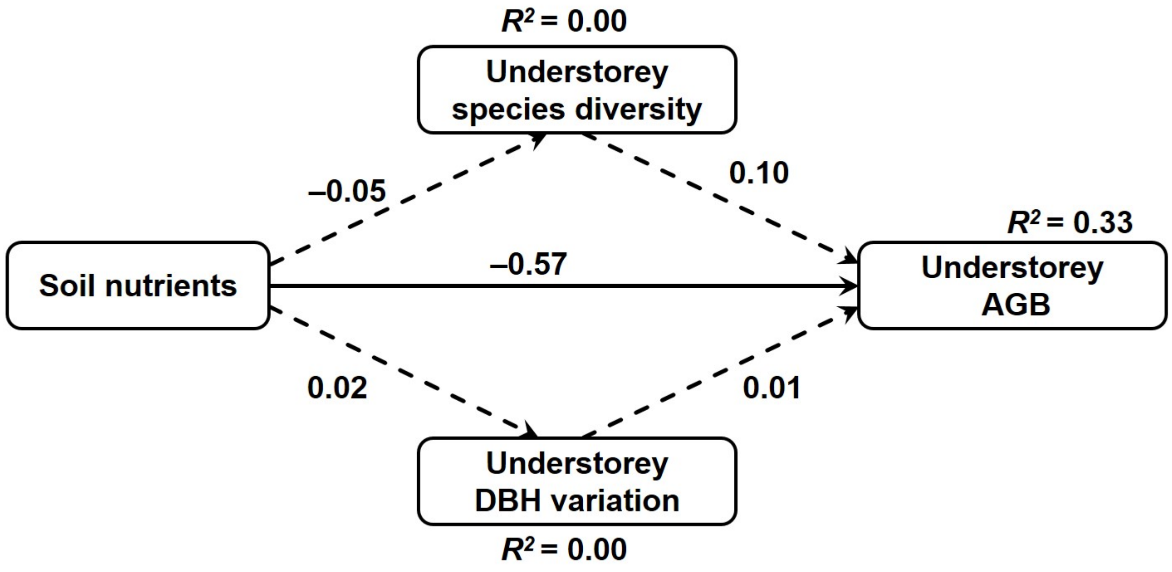


Fig. 3.6. The best-fit structural equation models for the isolation modelling of forests strata. a) the relationships of species diversity and individual tree size variation with aboveground biomass at overstorey strata, and (b) understorey strata, in addition to the effects of soil nutrients. Solid arrows represent significant ($P < 0.05$) paths and dashed arrows represent non-significant paths ($P > 0.05$). For each path the standardized regression 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 shown in Table 3.4. For abbreviations, see Table 3.1.

Table 3.4. Model fit statistic summary of the structural equation models (SEMs) for the relationships of species diversity and individual tree size variation with aboveground biomass, in addition to the effects of soil nutrients, in a subtropical forest. SEMs were accepted or rejected based on χ^2 test. Abbreviations: AGB, aboveground biomass; df, degrees of freedom; CFI, comparative fit index; GFI, goodness of fit index; SRMR, standardized root mean square residual; AIC, Akaike information criterion; χ^2, Chi-square test; R^2 indicates the total variation in aboveground biomass that is explained by the combined independent variables.

Hypothesized model	df	Model fit statistics summary						Model remarks	SEM
		CFI	GFI	SRMR	AIC	R^2	χ^2 (*P*-value)		
Integrative model (Fig. 3.1a)	5	1.00	0.99	0.030	2456.07	0.31 (overstorey AGB) 0.35 (understorey AGB)	3.24 (0.664)	Accepted	Fig. 3.5
Overstorey strata model (Fig. 3.1b)	1	1.00	0.99	0.015	1426.38	0.31	0.27 (0.605)	Accepted	Fig. 3.6a
Understorey strata model (Fig. 3.1c)	1	0.98	0.99	0.040	1459.81	0.33	2.03 (0.155)	Accepted	Fig. 3.6b
Whole-community model (Fig. 3.1d)	1	0.96	0.98	0.064	1424.33	0.36	4.72 (0.030)	Rejected	Fig. 3.7

Note: *df* is based on the number of ‘knowns’ minus the number of free parameters in the model, not on the sample size.

Table 3.5. The direct, indirect, and total standardized effects on aboveground biomass based on structural equation models (SEMs). Effects values of accepted SEMs are shown here (see Table 3.4 for model fit statistics, and Figs 3.5 and 3.6 for accepted SEMs). Significant effects are indicated in bold ($P < 0.05$). Abbreviations: DBH, diameter at breast height; AGB, aboveground biomass; S.E., standard error.

Predictor	Pathway to response variable	Response variable	Integrative model in Fig. 3.5			Overstorey strata model in Fig. 3.6a			Understorey strata model in Fig. 3.6b		
			Effect	S.E.	*P*-value	Effect	S.E.	*P*-value	Effect	S.E.	*P*-value
Soil nutrients	Direct effect	Overstorey AGB	−0.34	0.06	**<0.001**	−0.34	0.06	**<0.001**	---	---	---
	Direct effect	Understorey AGB	−0.46	0.06	**<0.001**	---	---	---	−0.57	0.05	**<0.001**
	Indirect effect via overstorey species diversity	Overstorey AGB	−0.07	0.02	**0.037**	−0.07	0.02	**0.037**	---	---	---
	Indirect effect via overstorey DBH variation	Overstorey AGB	0.21	0.04	**<0.001**	0.21	0.04	**<0.001**	---	---	---
	Indirect effect via overstorey species diversity	Understorey AGB	−0.02	0.02	0.460	---	---	---	---	---	---

	Indirect effect via overstorey DBH variation	Understorey AGB	−0.06	0.03	0.115	---	---	---	---	---	---
	Indirect effect via overstorey AGB	Understorey AGB	−0.04	0.02	0.222	---	---	---	---	---	---
	Indirect effect via understorey species diversity	Understorey AGB	0.00	0.00	0.853	---	---	---	−0.01	0.01	0.604
	Indirect effect via understorey DBH variation	Understorey AGB	0.00	0.00	0.964	---	---	---	0.00	0.00	0.925
	Total effect	Overstorey AGB	−0.20	0.06	**0.023**	−0.20	0.06	**0.023**	---	---	---
	Total effect	Understorey AGB	−0.58	0.06	**<0.001**	---	---	---	−0.57	0.05	**<0.001**
Overstorey species diversity	Direct effect	Overstorey AGB	0.19	0.08	**0.016**	0.19	0.08	**0.016**	---	---	---
	Direct effect	Understorey AGB	0.06	0.08	0.453	---	---	---	---	---	---
	Indirect effect via understorey species diversity	Understorey AGB	0.02	0.02	0.350	---	---	---	---	---	---
	Indirect effect via overstorey AGB	Understorey AGB	0.02	0.02	0.258	---	---	---	---	---	---
	Total effect	Overstorey AGB	0.19	0.08	**0.016**	0.19	0.08	**0.016**	---	---	---
	Total effect	Understorey AGB	0.10	0.08	0.217	---	---	---	---	---	---
Overstorey DBH variation	Direct effect	Overstorey AGB	0.53	0.08	**<0.001**	0.53	0.08	**<0.001**	---	---	---
	Direct effect	Understorey AGB	−0.15	0.09	0.095	---	---	---	---	---	---
	Indirect effect via understorey DBH variation	Understorey AGB	0.00	0.00	0.893	---	---	---	---	---	---
	Indirect effect via overstorey AGB	Understorey AGB	0.06	0.05	0.209	---	---	---	---	---	---
	Total effect	Overstorey AGB	0.53	0.08	**<0.001**	0.53	0.08	**<0.001**	---	---	---
	Total effect	Understorey AGB	−0.09	0.08	0.242	---	---	---	---	---	---
Understorey species diversity	Direct effect	Understorey AGB	0.08	0.07	0.291	---	---	---	0.10	0.07	0.188
Understorey DBH variation	Direct effect	Understorey AGB	0.01	0.07	0.888	---	---	---	0.01	0.07	0.920

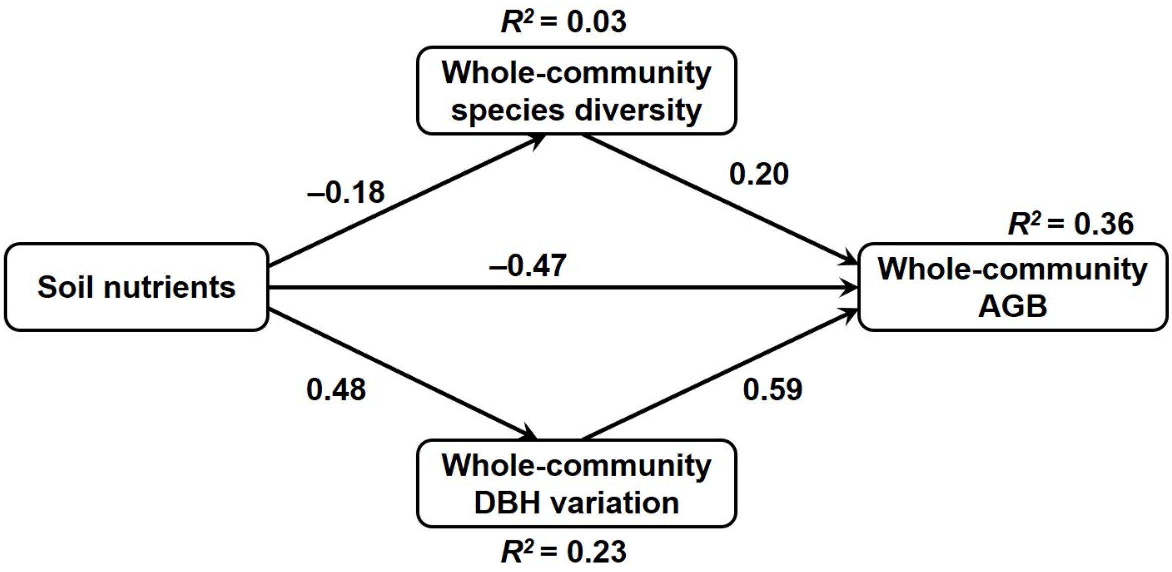


Fig. 3.7. The structural equation model for the relationships of species diversity and individual tree size variation with aboveground biomass (AGB) at whole-community level, in addition to the effects of soil nutrients. Solid arrows represent significant ($P < 0.05$) paths and dashed arrows represent non-significant paths ($P > 0.05$). For each path the standardized regression 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 shown in Table 3.4.

3.4. Discussion

Using both integration and isolation modelling, we assessed how species diversity and individual tree size variation drive aboveground biomass in overstorey and understorey strata, and whether overstorey species diversity and individual tree size variation affect understorey species diversity, tree size variation and aboveground biomass in a subtropical forest, when soil nutrients were considered simultaneously. In partial agreement with our Prediction 1 and Prediction 2, we found that aboveground biomass significantly increases with species diversity and individual tree size variation in overstorey strata, whereas the positive relationships are not statistically significant in understorey strata. With increase of soil nutrients, there is an increase of individual tree size variation in overstorey strata, but the decrease of overstorey species diversity and aboveground biomass in both forest strata. Our Prediction 3 was rejected, as we found that overstorey strata did not affect aboveground biomass and individual tree size variation in understorey strata. Markedly, species diversity of overstorey strata promotes species diversity of understorey, which is in full agreement with our Prediction 4.

3.4.1. The relationship between biodiversity and aboveground biomass depends on forest strata

The observed positive relationships of aboveground biomass with species diversity and individual tree size variation in overstorey strata might be attributable to the niche complementarity effect, which progressively leads to great site resource utilization (Díaz *et al.* 2011a, Poorter *et al.* 2015, Slik *et al.* 2013, Zhang *et al.* 2016a). Within forests, complex tree sized structures associate with increased light capture and light use efficiencies (Ali & Mattsson 2017, Dănescu *et al.* 2016, Yachi & Loreau 2007, Zhang & Chen 2015). Tree species with high size variation or variable tree sizes in forest communities are likely to have their own set of habitat requirements for water and soil nutrients (Ali *et al.* 2016b, Lei *et al.* 2009). Therefore, a multilayered forest structure allows for more efficient utilization of resources in species diverse forests, leading to enhance of aboveground biomass due to niche differentiation (Ali *et al.* 2016b, Dănescu *et al.* 2016, Poorter *et al.* 2015, Zhang & Chen 2015). Generally, aboveground biomass increases exponentially or power-functionally with tree diameter at tree scale (Ali *et al.* 2015, Chave *et al.* 2014), and large trees in overstorey strata thus contribute disproportionally to stand biomass compared with small trees in natural forests (Poorter *et al.* 2015) and agroforests (Ali & Mattsson 2017).

We found that the magnitude of the effects of species diversity and individual tree size variation on aboveground biomass in understorey strata is relatively weaker compared to the observations at overstorey strata. The non-significant relationships between biodiversity and aboveground biomass in understorey strata might be attributable to developmental effect of tree species. Understorey strata include both shrub species and regeneration of canopy tree species, which are functionally different in coping with biotic interaction and resource competition. Regeneration of trees could have a different ecology than developed trees, as trees grow they may experience varying biomechanical burdens and environmental conditions, or pre-programmed ontogenetic switch, which can induce concomitant changes in tree structure and function (Meinzer *et al.* 2011). Therefore, the relationship between biodiversity and aboveground biomass might be weakened in understorey strata by the mixture effects of development or life stage and high degree of biotic interaction and resource heterogeneity. In addition, tree species in overstorey strata with high aboveground biomass and great tree size may consume a large part of resource, thus probably reducing resources availability to understorey species (Gilliam 2007, Mason *et al.* 2011). As such, the dominant role of overstorey strata on the available resources likely weakens the biodiversity – aboveground biomass relationships in understorey strata (Hooper *et al.* 2005, Zhang *et al.* 2016a). The strong response of overstorey species diversity and weak response of understorey species diversity to soil nutrients collectively suggest a dominant filtering role of the overstorey trees in shaping understorey structure and function (Zhang *et al.* 2016a). Moreover, the absence of evidence for the effects of species diversity and individual tree size variation on aboveground biomass in understorey strata might be also attributable to the inability of diversity indices to gauge the actual range of positive interactions in the analyzed understorey strata, rather than an intrinsic ecological mechanism (Dănescu *et al.* 2016).

In this study, we found that species diversity are positively related between overstorey and understorey strata. Understandably, if there are more seed trees of different species in overstorey strata, high species diversity in understorey strata is nursed and promoted due to abundant seed availability from different species. Moreover, overstorey or large tree species may adjust the habitat to sustain the suitability of understorey or small tree species (e.g., Gamfeldt *et al.* 2013, Lefcheck *et al.* 2015). For instance, high species diversity of overstorey strata may increase resource heterogeneity in the understorey strata or facilitate understorey trees, which in turn promotes understorey species diversity (Bartels & Chen 2010, 2013, Zhang *et al.* 2016a).

3.4.2. High species diversity and aboveground biomass on nutrient-poor soils

We found a clear trend toward high aboveground biomass across forest strata on nutrient-poor soils in the studied forest, with a high species diversity and low individual tree size variation in overstorey strata, and without any biodiversity mediation in understorey strata. This might be attributable to the specific adaptations of conservative species to the nutrient-poor soils that increase species longevity and biomass retention, thus enhancing the storage of aboveground biomass at the stand level (Ali & Mattsson 2017, Poorter *et al.* 2015, Prado-Junior *et al.* 2016). Nutrient-poor soils are widely thought to be advantageous to species with conservative strategy, whereas nutrient-rich soils support species in favor of acquisitive strategy (Coomes *et al.* 2009, Fortunel *et al.* 2014, Poorter & Bongers 2006, Reich 2014). In the studied forest, the canopy trees or large trees and understorey trees are generally conservative evergreen species, which tend to dominate to infertile soils (Yan *et al.* 2009, Yan *et al.* 2006). Therefore, with slow growth and high longevity, they may accumulate and contribute to large part of aboveground biomass at the stand level (Prado-Junior *et al.* 2016).

Soil fertility hypothesis predicts that aboveground biomass or productivity increases with increasing soil nutrients availability, and plants grow fast when resource availability is high (Quesada *et al.* 2012, Wright *et al.* 2011). However, high nutrients availability may also lead to increased competition, and hence high mortality and biomass turnover rates of plants (Prado-Junior *et al.* 2016). Consequently, high aboveground biomass or productivity in (sub-) tropical forests associates often with nutrient-poor soils (Chiang *et al.* 2016, Poorter *et al.* 2015, Prado-Junior *et al.* 2016). In this study, we also found that nutrient enhancements depress species diversity in overstorey strata of the studied forest. This mismatch between conventional theory and empirical pattern is potentially due to an interaction between tree size and niche overlap among canopy tree species (Prado-Junior *et al.* 2016). Emergent tree species with large maximum size in overstorey strata can grow large and may integrate resource patches both above- and belowground by reducing the niche complementarity with functionally dissimilar species and by increasing niche overlap with functionally similar species (Prado-Junior *et al.* 2016, Walker 1992). As such, species diversity in overstorey strata is depressed (e.g. Jucker *et al.* 2016).

3.5. Concluding remarks

Our results provide strong evidence for the forest strata-dependent relationship between biodiversity and aboveground biomass in a subtropical forest. Particularly, the integrative model of this study suggests the general notion that no sole and ubiquitous relationship between biodiversity and aboveground biomass exists, but rather that the magnitude and direction and the underlying mechanisms of this relationship is forest strata-specific where available resources shift greatly. In overstorey strata, the positive relationship of aboveground biomass with species diversity and individual tree size variation might be attributed to the niche complementarity effect. In understorey strata, the mixture effects of tree development, high degree of biotic interaction, and increased resource heterogeneity might complicate the relationship between biodiversity and aboveground biomass. Importantly, the positive association of species diversity between overstorey and understorey strata indicates a crucial role of taxonomic diversity in overstorey trees for fostering species diversity of understorey strata in a subtropical forest. The strong and consistent negative effects of soil nutrients on aboveground biomass and overstorey species diversity suggest an important mechanism that high species diversity of overstorey strata with great tree size variation on nutrient-poor soils is crucial for driving high aboveground biomass in subtropical forest ecosystems. Insightfully, ecological models for predicting aboveground biomass would be improved by including separate effects of overstorey and understorey diversity.

Chapter 4. Forest strata-dependent effects of functional trait diversity on aboveground biomass in a subtropical forest

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For submission to Journal

4.1. Introduction

Understanding the relationship between biodiversity and ecosystem function has been a central pursuit in ecology for more than four decades (Chisholm *et al.* 2013, Grime 1973). A number of ecological hypotheses exist on how the magnitude of ecosystem function would respond to variation in species and/or functional trait diversity (e.g., Naeem 2002). A prominent hypothesis is the niche complementarity hypothesis predicting that communities with a higher diversity of species (Tilman 1999) or functional traits (Díaz *et al.* 2011a) use available resources more efficiently, thereby increasing the magnitude of ecosystem functions in natural forests (Chisholm *et al.* 2013, Zhang *et al.* 2012b). Most of the recent studies found no or a little support for the niche complementarity hypothesis, based on functional trait diversity, driving aboveground biomass in forest ecosystems (Chiang *et al.* 2016, Conti & Díaz 2013, Finegan *et al.* 2015, Fotis *et al.* 2017). Among these empirical studies, the relationships between functional trait diversity and aboveground biomass have been assessed at the level of either whole-community or overstorey strata only. Natural forests, however, are always structurally complex and plant species with different functional strategies are generally assembled in different vertical layers or forest strata (i.e. overstorey and understorey) (Rüger *et al.* 2012, Wright 2002).

Understorey strata contribute much to the majority of biodiversity, and have higher turnover rate in comparison with overstorey strata (Barbier *et al.* 2008, Gilliam 2007, Nilsson & Wardle 2005). Overstorey strata store large quantities of biomass due to their large wood volumes and disproportionate contribution of large trees to the whole-community level aboveground biomass (Slik *et al.* 2013). Environmental conditions affecting plant performance can strongly differ between forest strata in natural forests (Zhang *et al.* 2014), and therefore important resources like light is often limiting in the understorey while abundant in overstorey strata of forests (e.g., Brenes-Arguedas *et al.* 2011, Wright 2002). Indeed the niche complementarity effect may be less important in stable and productive environments of the overstorey, while competition may be driving species interactions in a more stressful understorey environment (Paquette & Messier 2011). Therefore, it is expected that high functional trait diversity of understorey would drive high aboveground biomass probably due to the niche complementarity in the resource-limited environment, whereas low functional trait diversity of overstorey would drive aboveground biomass probably due to the presence of few large trees. By evaluating the mass ratio hypothesis, we have previously reported that high aboveground biomass was potentially driven by functional identity of overstorey tree height on nutrient-rich soils, whereas by understorey conservative traits on nutrient-poor soils (Ali & Yan 2017b).

In this study, we tested whether the functional trait diversity of overstorey and understorey strata have differential effects on whole-community aboveground biomass using biophysical data from 125 plots inside a 5-ha natural subtropical forest in Eastern China. Studies in natural (sub-) tropical forests also reveal that environmental factors such as topography and soil nutrients or physicochemical properties may modulate the multivariate relationships between functional trait diversity and ecosystem functions because of nutrients availability (Ali & Yan 2017b, Chiang *et al.* 2016, Prado-Junior *et al.* 2016). Specifically, we addressed the following questions: 1) what is the contribution of functional trait diversity of overstorey and understorey strata to whole-community (overstorey plus understorey strata) aboveground biomass (hereafter simply referred to 'aboveground biomass')? 2) how do functional trait diversity of overstorey and understorey strata, alone or jointly, affect aboveground biomass? and 3) whether functional trait diversity of overstorey strata affects functional trait diversity of understorey strata and its relationship with aboveground biomass, after accounting for the effects of environmental factors in a subtropical forest?

Specifically, we first hypothesize (H_1) the high functional trait diversity of understorey strata due to the niche complementarity, while low functional trait diversity of overstorey strata due to the presence of a few large trees would drive high aboveground biomass in a community (Fig. 4.1). In addition, we predict that functionally-similar big trees (i.e., overstorey trees) will have a larger effect than functionally-dissimilar small trees (i.e. understorey trees) on the aboveground biomass due to the large stem volumes present in the overstorey (Ali & Yan 2017c, Slik *et al.* 2013) and dominant role over the understorey strata in the forests (Ali & Yan 2017b, Zhang *et al.* 2016a), which we call the big trees effect (H_{1b}, P_1). As a consequence, we further hypothesize (H_{1c}) low functional trait diversity of whole-community would drive high aboveground biomass in a community due to the dominant role of functionally-similar large trees (i.e. overstorey) on understorey strata and available resources (Fig. 4.1) (Ali & Yan 2017b, Bartels & Chen 2010, Zhang *et al.* 2016a).

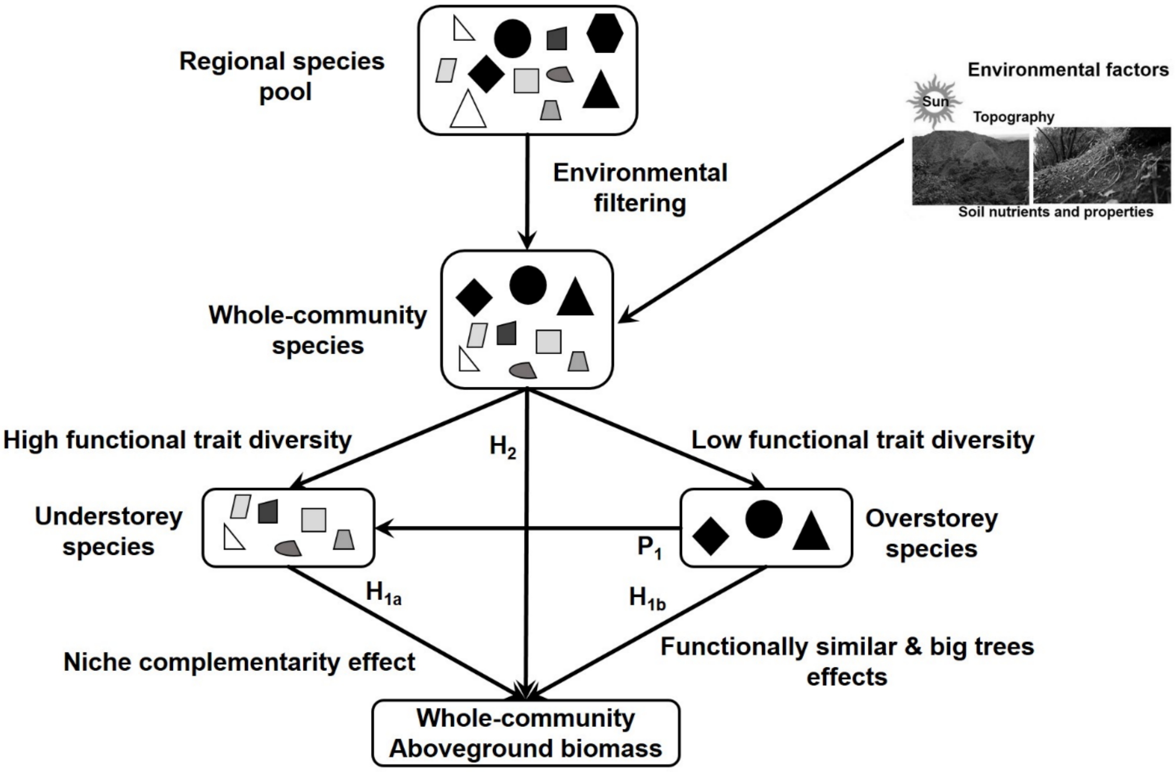


Fig. 4.1. Conceptual framework showing how changes in aboveground biomass are determined by underlying mechanisms (niche complementarity and/ or niche overlap and big trees effects). Species pool having different symbols and colors represent different species and traits dissimilarity, respectively, while size of the symbols represent 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).

4.3. Materials and methods

4.2.1. Quantification of functional trait diversity

Overstorey trees were defined as all individuals with DBH ≥ 10 cm in each forest plot, and understorey plants included woody vegetation with 1 ≤ DBH < 10 cm (Barrufol *et al.* 2013). This resulted in a total of 3,213 stems belonging to 71 species, 47 genera and 27 families in the overstorey, and a total of 17,004 stems belonging to 94 species, 57 genera and 33 families in the understorey across 125 plots in a 5-ha subtropical forest.

For calculation of functional trait diversity of the overstorey, understorey, and the whole-community within each plot, we used eight functional traits that are important for plant growth and survival (Poorter & Markesteijn 2008, Wright *et al.* 2010), and hence for standing aboveground biomass, biomass productivity and carbon storage (Finegan *et al.* 2015, Prado-Junior *et al.* 2016). We used four measures of functional trait diversity that were quantified for the overstorey and understorey separately: functional evenness, functional richness, functional divergence and functional dispersion. This resulted in 8 diversity measures per plot for forest strata level analyses, while four measures per plot for whole-community level analyses. Functional richness is the amount of multivariate trait space filled by the community. Functional evenness indicates how species' basal area is spread over multivariate-trait space, being higher when basal area distribution is homogeneous across this space. Functional divergence is the degree of divergence from the center that most dominant species occupy in multivariate-trait space and it is higher when most of basal area is concentrated in the extremes of the multivariate-trait space. Functional dispersion is the average distance of the species to the basal-area weighted centroid of all species in community trait space (Laliberté & Legendre 2010, Mason *et al.* 2005, Villéger *et al.* 2008). These functional trait diversity indices were shown to be orthogonal (Mason *et al.* 2005). The species' relative basal area (relative to the total understory/ overstorey basal area) was used to weight species' traits in each plot, because basal area is a better indicator of plant performance than abundance (Prado-Junior *et al.* 2016). Trait values were standardized before the calculation of four functional trait diversity indices. All diversity measures were calculated using the *vegan* (Oksanen *et al.* 2015), *FD* (Laliberté & Legendre 2010).

The descriptions about the measurement of functional traits, estimation of aboveground biomass and measurement of environmental factors are provided in Chapter 2. Summary of functional trait diversity across forest strata and whole-community, and environmental factors axes and whole-community aboveground biomass is provided in Table 4.1.

Table 4.1. Descriptive statistics for explanatory variables, from 125 subtropical forest plots used for analysis of biodiversity –aboveground biomass.

Variables	Unit	Mean	Standard error	Minimum	Maximum
a) Overstorey strata					
Functional dispersion (FDis)	unitless	2.28	0.03	0.83	3.46
Functional divergence (FDiv)	unitless	0.77	0.01	0.45	0.97
Functional evenness (FEve)	unitless	0.63	0.01	0.38	0.95
Functional richness (FRic)	unitless	0.22	0.06	0.00	5.03
b) Understorey strata					
Functional dispersion (FDis)	unitless	1.92	0.03	1.07	2.80
Functional divergence (FDiv)	unitless	0.64	0.01	0.42	0.86
Functional evenness (FEve)	unitless	0.50	0.01	0.11	0.75
Functional richness (FRic)	unitless	2.23	0.32	0.01	21.94
c) Whole-community level					
Functional dispersion (FDis)	unitless	2.31	0.03	1.04	3.48
Functional divergence (FDiv)	unitless	0.77	0.01	0.55	0.96

Functional evenness (FEve)	unitless	0.42	0.01	0.20	0.69
Functional richness (FRic)	unitless	4.94	0.50	0.12	27.83
d) Environmental factors axes					
Soil PC1	unitless	0.00	0.17	-6.25	2.87
Soil PC2	unitless	0.00	0.12	-2.11	2.69
Topography PC1	unitless	0.00	0.12	-3.25	2.97
Topography PC2	unitless	0.00	0.08	-2.75	2.06
e) Response variable					
Whole-community aboveground biomass	Mg ha^{-1}	74.32	2.31	19.64	154.84

4.2.2. Statistical analyses

Our study design may confound statistical results when there is spatial autocorrelation in the variables of interest. To account for this we performed generalized least-squares models, (Pinheiro & Bates 2016), with (accounted for the spatial location of each subplot, i.e. local X and Y coordinates within a 5-ha plot) and without spatial autocorrelation among subplots for each of the relationships between predictors and aboveground biomass, as recommended by previous studies (Chisholm *et al.* 2013, Yuan *et al.* 2016). Generalized least-squares model is a reliable method for testing whether subplots sharing same abiotic conditions are independent from each other within a forest (Zuur *et al.* 2009). By plotting semivariogram of the spatial GLS models with accounted for the nugget effect (intercept), we found no clear indication of spatial autocorrelation (Fig. 4.2). In addition, the goodness-of-fit of spatial and non-spatial models was evaluated by the Akaike Information Criterion (AIC), and we found that models without spatial autocorrelation always had the lower AIC values (Table 4.2), which is similar to the recent observations in 25-ha broad-leaved Korean pine mixed forest and 5-ha secondary poplar-birch forest in northeastern China (Yuan *et al.* 2016).

Having confirmed that spatial autocorrelation is not likely to confound our results, we then performed multiple linear regressions models (i.e. general linear models) to evaluate how aboveground biomass (overstorey plus understorey) was driven by functional trait diversity (functional dispersion, functional divergence, functional richness and functional evenness) of overstorey and understorey species across local environmental conditions (hereafter referred as ‘forest strata model’). More specifically, we conducted three series of forest strata model in order to find the best subset of predictor(s) (i.e. optimal model) for each of the overstorey strata effect (the first series; overstorey model), the understorey strata effect (the second series; understorey model), and the joint effect of overstorey and understorey strata (the third series; joint model for forest strata), in addition to the local environmental factors, on aboveground biomass. For the first and second series of the forest strata model, we included functional trait diversity indices (4 multivariate-trait indices) of overstorey and understorey species, respectively. With respect to the third series, we jointly included all indices of functional trait diversity (8 indices) in order to test the joint effects of overstorey and understorey species on aboveground biomass._ENREF_3 For comparison, we also evaluated how aboveground biomass was driven by whole-community functional trait diversity across local environmental conditions (hereafter referred as ‘whole-community model’). In all models, we included local environmental factors, i.e. soil PC1, soil PC2, topography PC1 and PC2, as covariates. We used all subsets regression analysis and selected the optimal model that had lowest AICc (i.e. AIC adjusted for small sample sizes). Models were considered to be equally supported if the difference in AICc was less than two units (Bartoń 2016). When models were equally supported, we selected the most parsimonious model by considering the lowest number of predictors. General linear models were performed using the *stats* package and all subsets regression analyses using the *MuMIn* package (Bartoń 2016). In addition, we applied the Moran's I test for spatial autocorrelation in the selected optimal linear model residuals, while assessing the range and type of spatial autocorrelation in lag classes by plotting the correlograms (Fig. 4.3), using the *spdep* package (Bivand 2016).

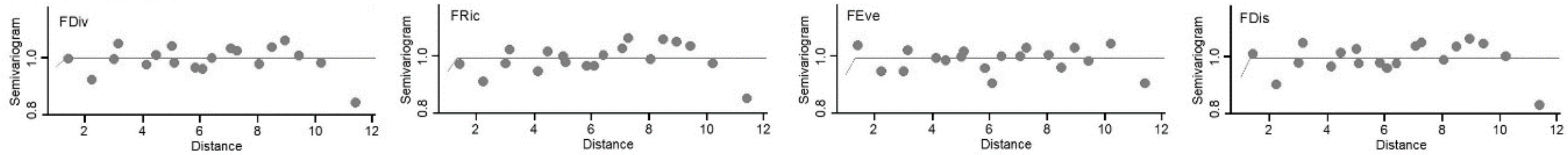
Table 4.2. Summary of the generalized least-squares (GLS) models of whole-community aboveground biomass (AGB) on functional trait diversity of overstorey, understorey and whole-community species, in addition to environmental factors, in subtropical forests. All the abbreviations for variables are explained in Table 4.1.

GLS model	Model	Coefficient	*t*-value	*P*-value	AIC	R^2_{pseudo}
AGB ~ Understorey FDiv	Non-spatial	29.09	1.13	0.262	1159.09	0.010
	Spatial	26.30	1.02	0.309	1162.27	0.010
AGB ~ Understorey FRic	Non-spatial	0.09	0.14	0.888	1167.74	0.000
	Spatial	0.11	0.16	0.873	1170.58	0.000
AGB ~ Understorey FEve	Non-spatial	52.33	2.45	0.007	1153.56	0.058
	Spatial	51.07	2.70	0.008	1156.82	0.058
AGB ~ Understorey FDis	Non-spatial	-13.43	-2.18	0.032	1158.55	0.037
	Spatial	0.42	0.05	0.959	1165.61	0.000
AGB ~ Overstorey FDiv	Non-spatial	-56.93	-2.34	0.021	1155.08	0.043
	Spatial	-53.78	-2.22	0.029	1158.80	0.043
AGB ~ Overstorey FRic	Non-spatial	-5.76	-1.64	0.104	1161.68	0.021
	Spatial	-5.53	-1.58	0.117	1164.82	0.021
AGB ~ Overstorey FEve	Non-spatial	-93.13	-4.47	<0.001	1142.13	0.140
	Spatial	-92.82	-4.46	<0.001	1145.15	0.140
AGB ~ Overstorey FDis	Non-spatial	0.29	0.04	0.972	1162.69	0.000

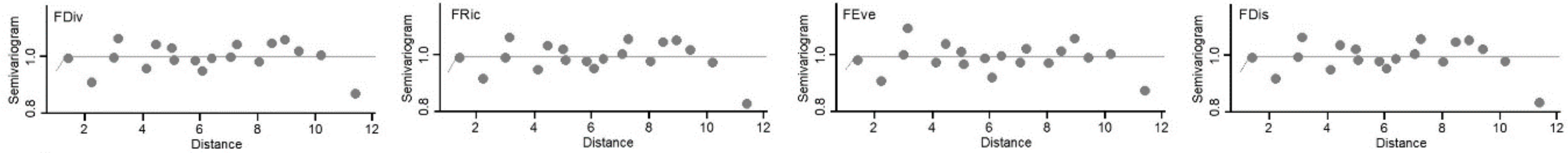
	Spatial	-14.30	-2.33	0.022	1160.91	0.037
AGB ~ Whole-community FDiv	Non-spatial	21.71	0.68	0.497	1159.48	0.004
	Spatial	30.44	0.96	0.338	1162.00	0.004
AGB ~ Whole-community FRic	Non-spatial	0.31	0.75	0.457	1168.08	0.005
	Spatial	0.33	0.76	0.449	1170.90	0.005
AGB ~ Whole-community FEve	Non-spatial	-26.66	-1.12	0.264	1159.27	0.010
	Spatial	-26.35	-1.12	0.266	1162.23	0.010
AGB ~ Whole-community FDis	Non-spatial	-10.63	-1.78	0.077	1160.14	0.025
	Spatial	-10.63	-1.77	0.079	1163.09	0.025
AGB ~ Topo PC1	Non-spatial	4.25	2.48	0.015	1159.76	0.047
	Spatial	4.34	2.38	0.019	1163.04	0.047
AGB ~ Topo PC2	Non-spatial	-4.20	-1.57	0.119	1162.44	0.020
	Spatial	-4.10	-1.49	0.138	1165.57	0.020
AGB ~ Soil PC1	Non-spatial	-0.80	-0.64	0.524	1166.01	0.003
	Spatial	-0.74	-0.55	0.583	1168.91	0.003
AGB ~ Soil PC2	Non-spatial	-4.62	-2.82	0.006	1158.11	0.061
	Spatial	-4.68	-2.70	0.008	1161.67	0.061

The percent variation explained by each predictor was represented by the relative contribution of that predictor to the total variation explained (i.e., R^2), determined using the *relaimpo* package (Groemping 2013). The importance of each predictor to the explained variance was assessed based on both relative contribution and the marginal effect of each predictor within the optimal model. We plotted a bivariate model's response (optimal linear model) against each predictor's marginal effect (i.e. while holding all other predictors constant), by using the *plotmo* package (Milborrow 2015). The complementary Pearson's correlations and bivariate relationships to the general linear models are shown in Tables 4.3 and 4.4, and Figs 4.4-4.7, respectively.

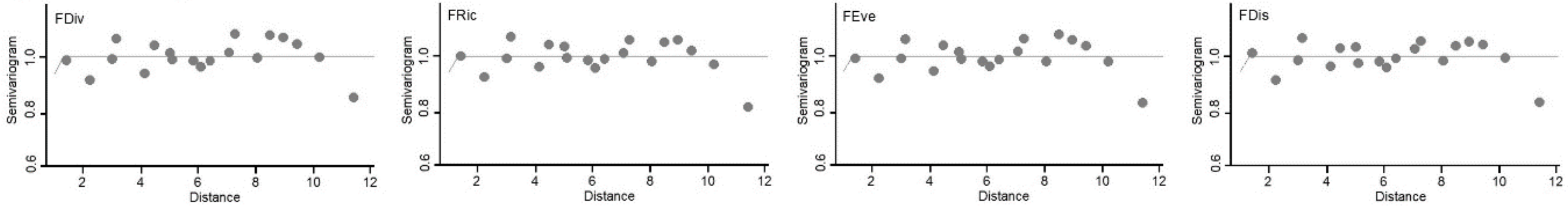
A) AGB ~ Overstorey FTD



B) AGB ~ Understorey FTD



C) AGB ~ Whole-community FTD



D) AGB ~ Environmnetal factors axes

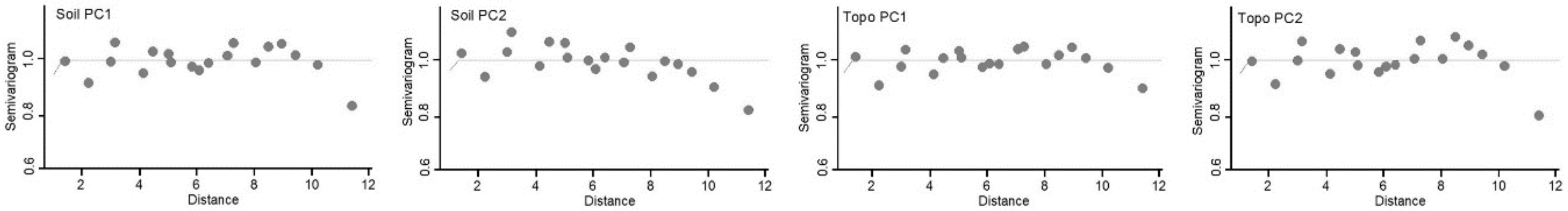


Fig. 4.2. Semivariogram plots of the Generalized least squares (GLS) models in order to check the range and type of spatial autocorrelation in distance classes. A) whole-community aboveground biomass (AGB) as a function of overstorey functional trait diversity (FTD); B) AGB as a function of understorey FTD; C) AGB as a function of whole-community FTD; and D) AGB as a function of environmental factors axes. All the abbreviations for variables are explained in Table 4.1.

Table 4.3. Pearson's correlation coefficient between predictors of aboveground biomass, used in forest strata models, among 125 sample plots in subtropical evergreen broadleaf forests in eastern China. Bold numbers indicate significant correlations ($P < 0.05$). All the abbreviations for variables are explained in Table 4.1.

	Understorey species				*Overstorey species*				*Environmental factors*			
	FDis	FDiv	FRic	FEve	FDis	FDiv	FRic	FEve	Topo PC1	Topo PC2	Soil PC1	soilPC2
Understorey species												
FDis	---											
FDiv	-0.10	---										
FRic	-0.04	0.06	---									
FEve	-0.03	**0.25**	0.10	---								
Overstorey species												
FDis	-0.07	**0.73**	0.33	0.30	---							
FDiv	**0.67**	-0.15	-0.07	**-0.11**	-0.04	---						
FRic	0.06	-0.04	-0.08	-0.02	-0.05	**0.18**	---					
FEve	**0.25**	-0.17	-0.13	-0.23	-0.03	**0.23**	**0.19**	---				
Environmental factors												
Topo PC1	0.04	**0.23**	0.10	0.00	**0.28**	**-0.18**	-0.13	-0.14	---			
Topo PC2	0.07	-0.08	0.03	-0.09	0.03	**0.19**	0.03	0.04	0.00	---		
Soil PC1	0.18	**-0.23**	**-0.24**	-0.06	-0.11	**0.25**	0.12	0.10	**-0.47**	0.16	---	
Soil PC2	-0.14	-0.16	-0.09	-0.12	**-0.22**	0.12	-0.02	0.13	**-0.69**	0.03	0.00	---

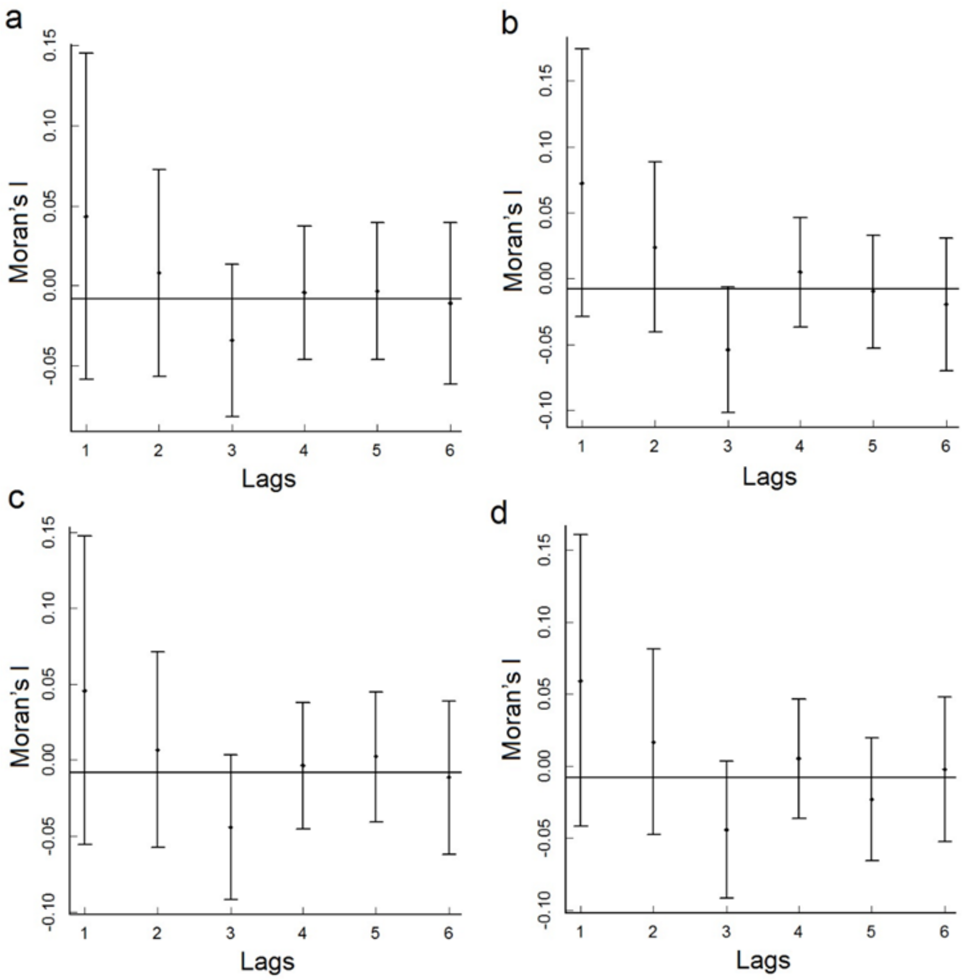


Fig. 4.3. Correlograms plots of the Moran's I test on the residuals of linear multiple models in order to check the range and type of autocorrelation in lag classes. a) Overstorey optimal model, b) understorey optimal model, c) joint optimal model for forest strata (Table 4.5), and d) whole-community optimal model (Table 4.6).

Table 4.4. Pearson's correlation coefficient between predictors of aboveground biomass, used in whole-community model, among 125 sample plots in subtropical evergreen broadleaf forests in eastern China. Bold numbers indicate significant correlations ($P < 0.05$). All the abbreviations for variables are explained in Table 4.1.

	Whole-community diversity				*Environmental factors*			
	FRic	FEve	FDiv	FDis	Topo PC1	Topo PC2	Soil PC1	Soil PC2
Whole-community diversity								
FRic	---							
FEve	0.00	---						
FDiv	-0.02	0.04	---					
FDis	0.00	0.14	**0.59**	---				
Environmental factors								
Topo PC1	**0.19**	0.11	0.02	0.11	---			
Topo PC2	-0.03	0.01	0.11	0.10	0.00	---		
Soil PC1	**-0.31**	-0.01	0.07	0.12	**-0.47**	0.16	---	
Soil PC2	-0.15	-0.08	0.09	-0.14	**-0.69**	0.03	0.00	---

Finally, we employed structural equation model (SEM) in order to evaluate whether functional trait diversity of overstorey species affects understorey species and its relationship with aboveground biomass, after accounting for the effects of environmental factors. Here, we selected best predictors for aboveground biomass which were retained in the joint optimal model for forest strata (i.e. the third series of linear models). In order to keep possible consistency with the optimal linear model and to answer our question, we constructed SEM based on the following three hypothesized paths: 1) direct effect of overstorey functional trait diversity on understorey functional trait diversity; 2) indirect effects of overstorey functional trait diversity via understorey functional trait diversity on aboveground biomass; and 3) direct effects of overstorey functional trait diversity, understorey functional trait diversity and environmental factors on aboveground biomass. Best-fit SEM was assessed through several tests (Malaeb *et al.* 2000); the Chi-square (χ^2) test, goodness-of-fit index (GFI), comparative fit index (CFI) and standardized root mean square residual (SRMR). The SEM was implemented using the *lavaan* package (Rosseel 2012). The summary of predictors and aboveground biomass, used in the analyses is listed in Table 4.1. For all statistical analyses R 3.2.2 was used (R Development Core Team 2015).

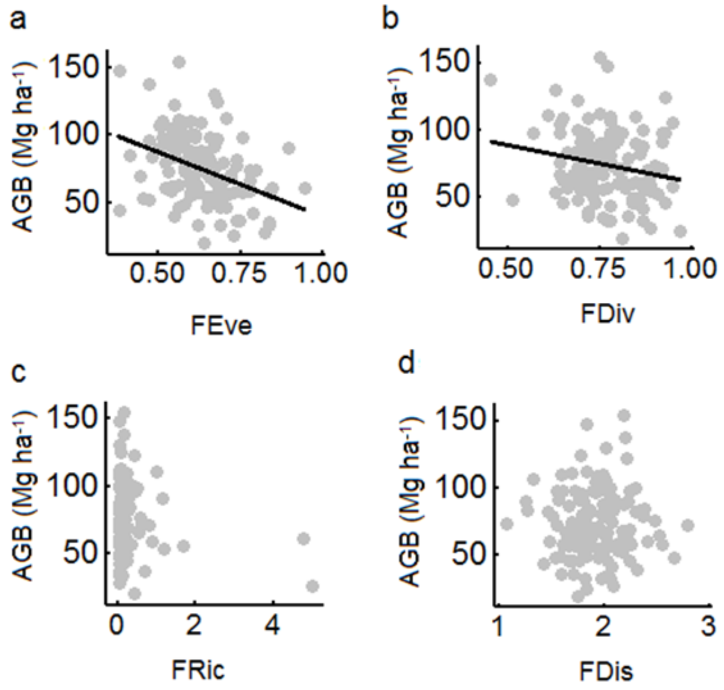


Fig. 4.4. The bivariate relationships between aboveground biomass (AGB) and overstorey species diversity (n = 125) in subtropical evergreen broadleaf forests in Eastern China. Fitted regressions are significant at $P < 0.05$. All the abbreviations for variables are explained in Table 4.1.

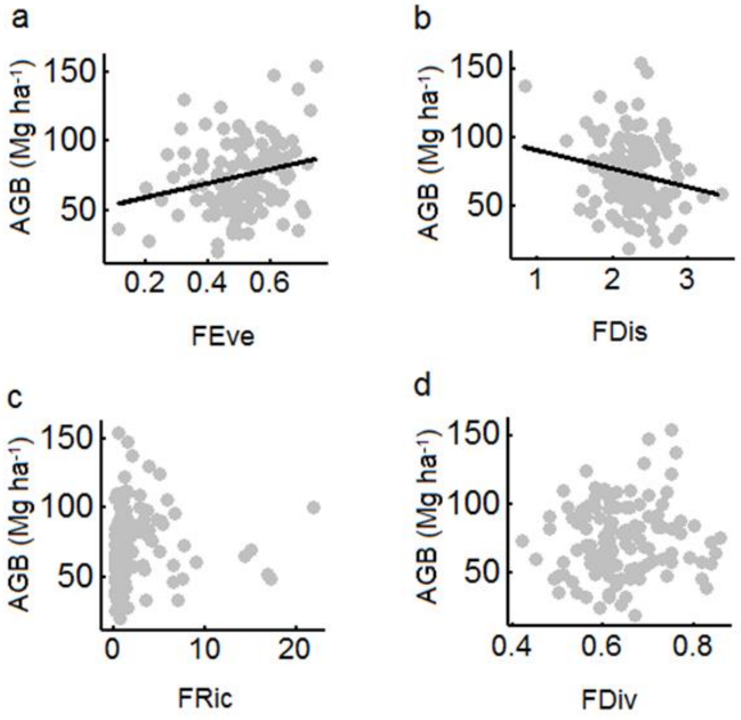


Fig. 4.5. The bivariate relationships between aboveground biomass (AGB) and understorey species diversity (n = 125) in subtropical evergreen broadleaf forests in Eastern China. Fitted regressions are significant at $P < 0.05$. All the abbreviations for variables are explained in Table 4.1.

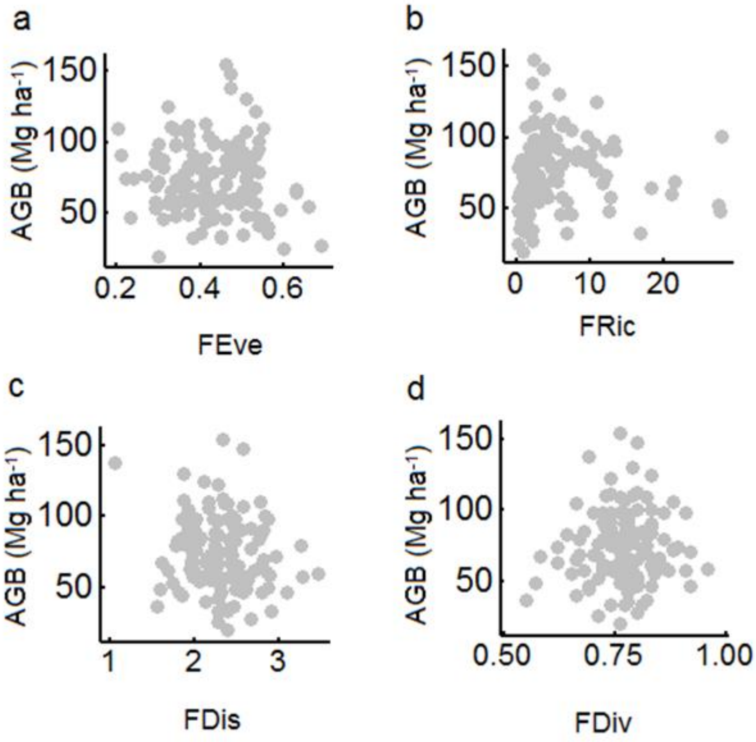


Fig. 4.6. The bivariate relationships between aboveground biomass (AGB) and whole-community diversity (n = 125) in subtropical evergreen broadleaf forests in Eastern China. Fitted regressions are significant at $P < 0.05$. All the abbreviations for variables are explained in Table 4.1.

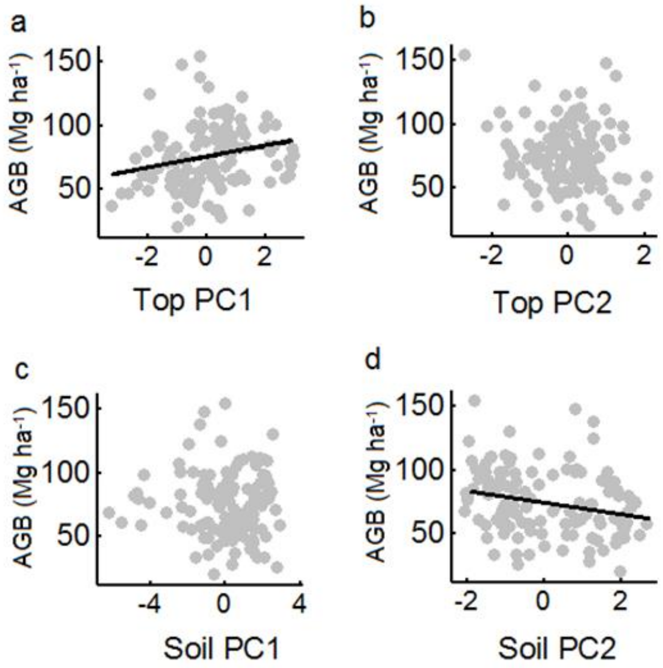
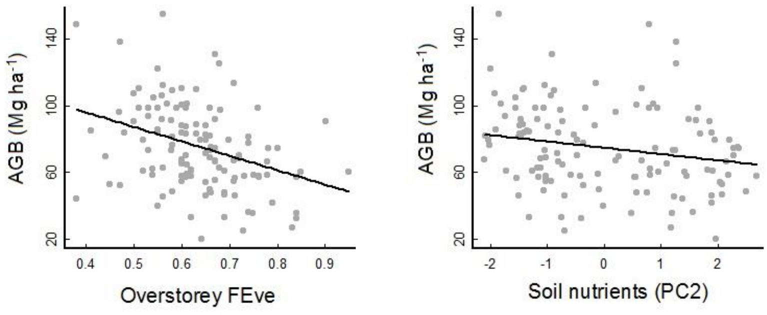


Fig. 4.7. The bivariate relationships between aboveground biomass (AGB) and environmental factors (n = 125) in subtropical evergreen broadleaf forests in Eastern China. Fitted regressions are significant at $P < 0.05$. All the abbreviations for variables are explained in Table 4.1.

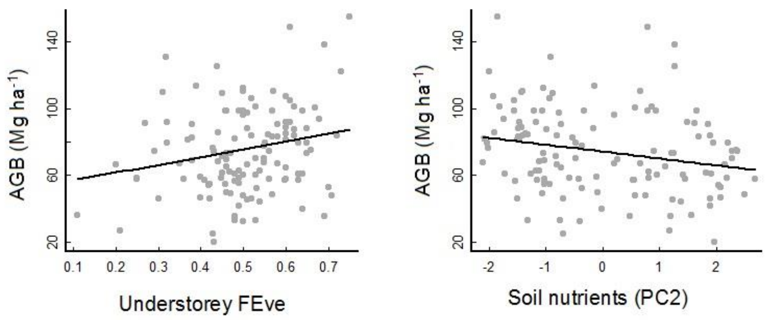
4.3. Results

The overstorey optimal model showed that aboveground biomass was best predicted ($R^2 = 0.18$) by functional evenness ($\beta = -0.35$, $P < 0.001$; contributed 71.99%) and soil nutrients ($\beta = -0.20$, $P = 0.016$; contributed 28.01%), with no spatial autocorrelation in the residuals (Table 4.5). This result indicates that aboveground biomass is high in plots with low functional evenness where most of overstorey tree species' basal area is concentrated in a constrained area of the multivariate-trait space, and located on soils with low soil nutrients (Fig. 4.8A). The understorey optimal model showed that aboveground biomass was best predicted ($R^2 = 0.11$) by functional evenness ($\beta = 0.21$, $P = 0.014$; contributed 48.74%) and soil nutrients ($\beta = -0.22$, $P = 0.012$; contributed 51.26%), again with no spatial autocorrelation in the residuals (Table 4.5). This result indicates that high aboveground biomass is associated with high functional evenness where most of understorey tree species' basal area distribution is homogeneous across the multivariate-trait space, and located on soils with low soil nutrients (Fig. 4.8B). The optimal joint model showed that aboveground biomass ($R^2 = 0.20$) was best predicted by overstorey functional evenness ($\beta = -0.32$, $P < 0.001$; contributed 57.81%), understorey functional evenness ($\beta = 0.15$, $P = 0.085$; contributed 18.95%) and soil nutrients ($\beta = -0.19$, $P = 0.024$; contributed 23.24%), without spatial autocorrelation in the residuals (Table 4.5). This result indicates that aboveground biomass is high in plots with low functional evenness of overstorey tree species and high functional evenness of understorey tree species, and located on soils with low soil nutrients (Fig. 4.8C).

A) Overstorey optimal model



B) Understorey optimal model



C) Joint optimal model for vegetation strata

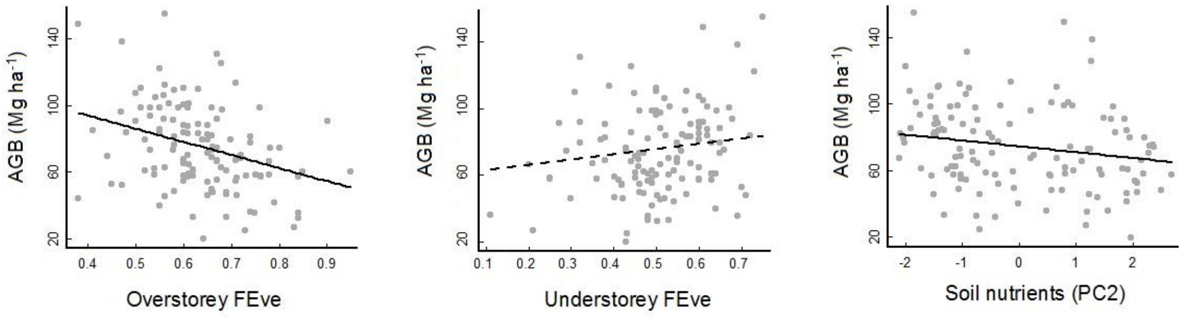


Fig. 4.8. The response of whole-community aboveground biomass to the retained predictors in the forest strata optimal models (see Table 4.5 for statistics). (A) Overstorey optimal model; aboveground biomass (AGB; Mg ha^{-1}) as a function of overstorey functional evenness (FEve) and soil nutrients (soil PC2), (B) understorey optimal model, AGB as a function of understorey FEve and soil nutrients; and (C) joint optimal model for overstorey and understorey strata, AGB as a function of overstorey FEve, understorey FEve and soil nutrients. 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 and dashed lines represent non-significant relationships ($P > 0.05$). See Figs 4.4, 4.5 and 4.7 for bivariate relationships.

Table 4.5. The forest strata optimal models (i.e. overstorey, understorey, and joint models) obtained from a series of multiple regression analyses for aboveground biomass and 12 predictors (4 FTD indices for each of overstorey and understorey, and 4 environmental factors axes) using linear model. Relative contribution (RC in %), standardized regression coefficient, *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. *P* values < 0.05 are given in bold. Moran's *I* test was conducted on the residuals for optimal linear model, and *P* value > 0.05 indicates no spatial autocorrelation in the residuals of the model. The gray portion in the table represents that variables were not included in the given model, whereas blank cells represent that variables were not retained in the selected optimal model.

Predictors	*Overstorey FTD model*				*Understorey FTD model*				*Joint model (overstorey + understorey)*			
	RC	Beta	*t*	*P*	RC	Beta	*t*	*P*	RC	Beta	*t*	*P*
Constant	----	0.00	9.77	**<0.001**	----	0.00	5.25	**<0.001**	----	0.00	6.07	**<0.001**
Overstorey strata FTD												
Functional divergence												
Functional richness												
Functional evenness	71.99	–0.35	–4.20	**<0.001**					57.81	–0.32	–3.76	**<0.001**
Functional dispersion												
Understorey strata FTD												
Functional divergence												
Functional richness												
Functional evenness					48.74	0.21	2.49	**0.014**	18.95	0.15	1.74	0.085
Functional dispersion												
Environmental factors												
Soil PC1												
Soil PC2	28.01	–0.20	–2.44	**0.016**	51.26	–0.22	–2.56	**0.012**	23.24	–0.19	–2.28	**0.024**
Topography PC1												

Topography PC2			
Model statistics			
F-test (P-value)	13.36 (<**0.001**)	7.24 (**0.001**)	10.10 (<**0.001**)
R^2	0.18	0.11	0.20
AICc	1149.8	1160.5	1148.9
Moran's I- test (P-value)	0.04 (0.310)	0.07 (0.113)	0.05 (0.288)

The joint optimal model showed that the direct effect of understorey functional evenness on aboveground biomass is no longer significant (Table 4.5; Fig. 4.8C), possibly weakened by the strong effect of overstorey functional evenness. The SEM showed that overstorey functional evenness had a strong direct negative effect on understorey functional evenness (β = –0.23, P = 0.008), and weakened the positive relationship between understorey functional evenness and aboveground biomass (β = 0.15, P = 0.076). Indirect effect of overstorey functional evenness via understorey functional evenness on aboveground biomass was non-significant (β = –0.04, P = 0.117), while total effect (direct + indirect effects) of overstorey functional evenness was significantly negative (β = –0.37, P <0.001; Fig. 4.9).

In comparison, the optimal whole-community model showed that aboveground biomass (R^2 = 0.20) was best predicted by functional dispersion (β = −0.20, P = 0.024; contributed 32.05%) and soil nutrients (β = −0.27, P = 0.002; contributed 67.95%), with no spatial autocorrelation in the residuals (Table 4.6). This result indicates that aboveground biomass is high in plots with low functional dispersion, represents functionally similar average distance species to the basal-area weighted centroid of all species in community trait space, and located on soils with low soil nutrients (Fig. 4.10).

Table 4.6. The whole-community optimal model obtained from a series of multiple regression analyses for aboveground biomass and 8 predictors (4 whole-community FTD indices, and 4 environmental factors axes) using linear model. Relative contribution (RC in %), standardized regression coefficient, *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. *P* values < 0.05 are given in bold. Moran's *I* test was conducted on the residuals for optimal linear model, and *P* value > 0.05 indicates no spatial autocorrelation in the residuals of the model. Blank cells represent that variables were not retained in the selected optimal model.

Predictor	RC	Beta	*t*	*P*
Constant	----	0.00	7.71	**0.043**
Whole-community level FTD				
Functional divergence				
Functional richness				
Functional evenness				
Functional dispersion	32.05	–0.20	–2.28	**0.024**
Environmental factors				
Soil PC1				
Soil PC2	67.95	–0.27	–3.12	**0.002**
Topography PC1				
Topography PC2				

Model statistics	
F-test (*P*-value)	6.72 (**0.002**)
R^2	0.10
AICc	1154.0
Moran's *I*- test (*P*-value)	0.06 (0.183)

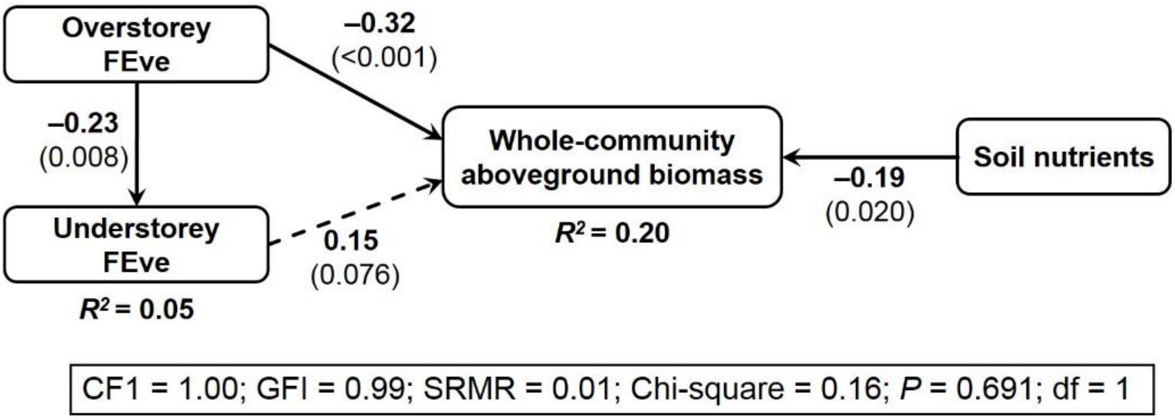


Fig. 4.9. Structural equation model linking functional trait diversity (i.e. functional evenness) of overstorey and understorey strata, and soil nutrients (soil PC2) with whole-community aboveground biomass. Solid arrows represent significant ($P < 0.05$) paths and dashed arrows represent non-significant paths ($P > 0.05$). For each path the standardized regression coefficient and *P*-value in bracket 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. The variables in model were selected based on final joint optimal model obtained from a series of multiple regressions (see Table 4.5). Abbreviations: FEve, functional evenness; CFI, comparative fit index; GFI, goodness of fit index; SRMR, standardized root mean square residual; df, degree of freedom.

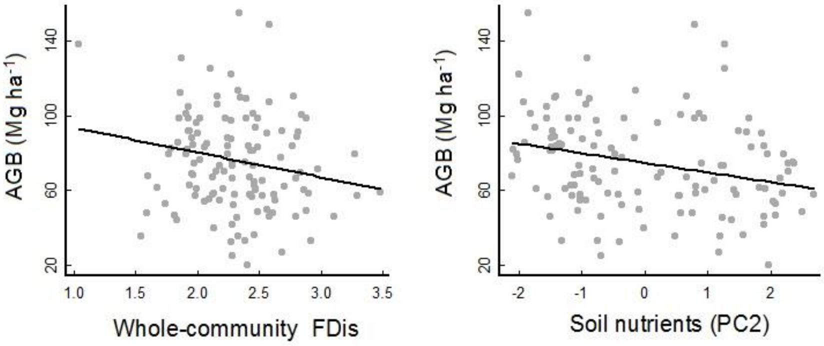


Fig. 4.10. The response of whole-community aboveground biomass to the retained predictors in the whole-community optimal models (see Table 4.6 for statistics). Aboveground biomass (AGB; Mg ha^{-1}) as a function of whole-community functional dispersion (FDis) and soil nutrients. See Figs 4.6 and 4.7 for bivariate relationships.

4.4. Discussion

This study highlights that separating functional trait diversity of overstorey and understorey strata improves predictions of aboveground biomass in a subtropical forest because overstorey and understorey strata have differential effects on aboveground biomass. Our results are in support of our hypotheses that high functional trait diversity of understorey strata has positive effect on aboveground biomass due to the niche complementarity, while functional evenness of overstorey strata has negative influence on aboveground biomass due to the strong effect of a few dominant and functionally-similar species in the canopy of the studied forest. The main finding of this study is that high aboveground biomass in a community is associated to different mechanisms where both niche complementarity (in terms of high functional trait diversity of understorey) and functionally-similar big trees effects (in terms of low functional trait diversity of overstorey) are at play (Figs 4.1 and 4.9). Since the overstorey is the main contributor to aboveground biomass probably due to their large stem volumes, low functional trait diversity and high functional dominance (i.e. functional identity of tree height), and hence supporting the mass ratio rather than the niche complementarity effect (Ali & Yan 2017b, Fotis *et al.* 2017, Prado-Junior *et al.* 2016). We also show that the explained variance by overstorey strata is higher compared to the explained variance by understorey strata, probably due to the strong effects of stand structural attributes, mass ratio and soil nutrients rather than the niche complementarity (Ali & Yan 2017c, b, Fotis *et al.* 2017). As such, understorey functional trait diversity has a weak positive effect on aboveground biomass probably due to the complementarity among slow-growing conservative species rather than fast-growing acquisitive species in the studied forest (Ali & Yan 2017b), and hence also supporting the niche complementarity effect.

The negative relationship between overstorey functional evenness and aboveground biomass indicates that aboveground biomass is high in plots with low functional evenness where most of overstorey trees' basal area is concentrated in a constrained area of the multivariate-trait space, contrary to predictions by the niche complementarity hypothesis. Indeed the few productive species dominating the canopy contribute to most of the aboveground biomass in the forest, as shown previously (Ali & Yan 2017b, Balvanera *et al.* 2005, Lohbeck *et al.* 2016). Actually, the negative relationship between overstorey functional evenness and aboveground biomass substantiates the fact that high biomass can be built up by few dominant species with functional similarity through the process of niche overlap (species redundancy) and/or the mass ratio effect (e.g., Ali & Yan 2017b, Fotis *et al.* 2017, Prado-Junior *et al.* 2016). This is likely the result of decades of environmental filtering that trees need to pass through to be able to occupy the overstorey, combined with the fact that only a subset of the species are able to become tall enough to occupy the overstorey (see Ali & Yan 2017c, Ali & Yan 2017b). Strong effects of environmental filtering will narrow down the range and diversity of functional strategies that becomes abundant to drive biomass (Keddy 1992).

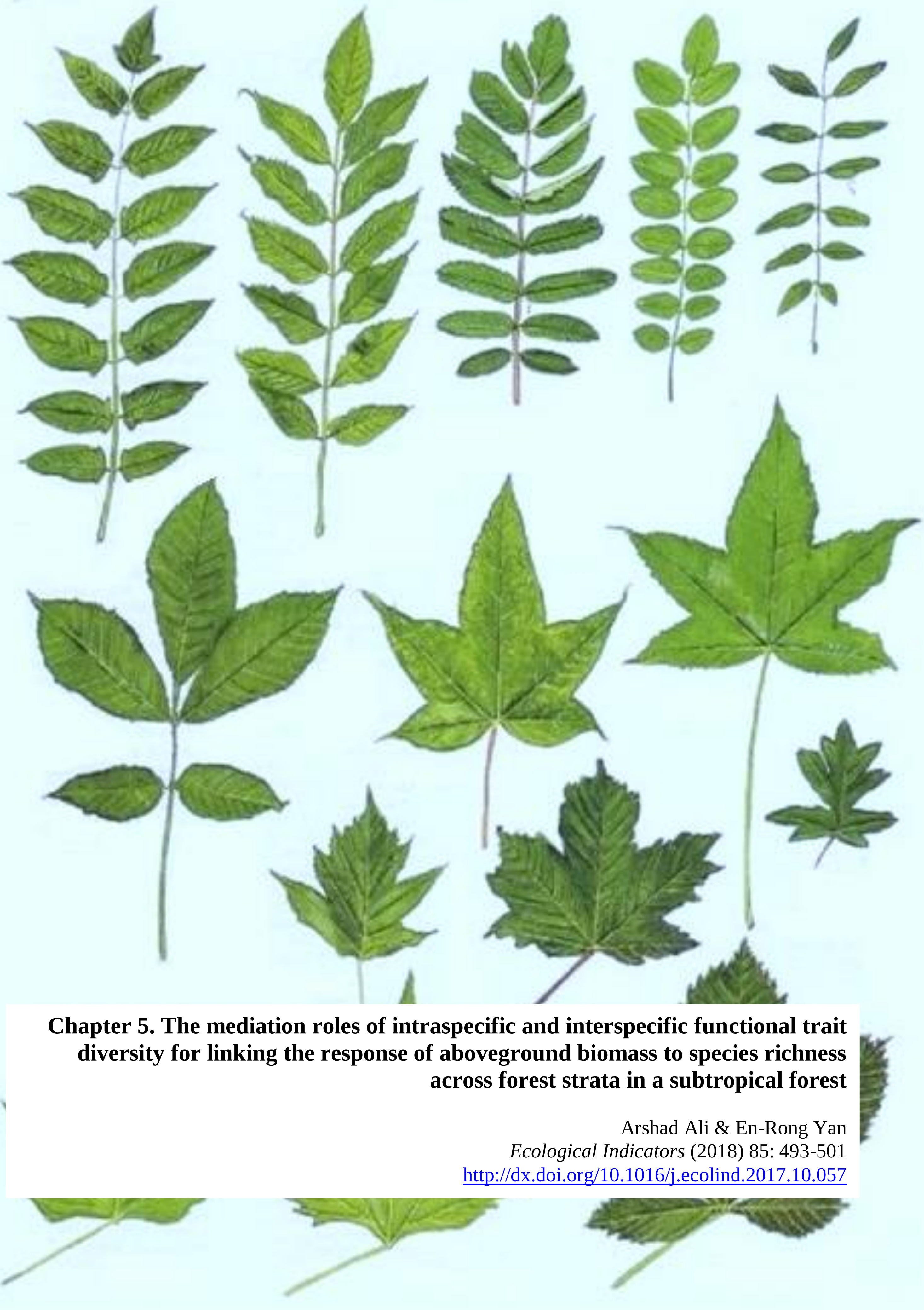
In the understorey, the mechanism seems to be very different: we found that high functional evenness of understorey species enhances aboveground biomass, supporting the niche complementarity hypothesis (Díaz *et al.* 2011a, Tilman 1999). Our findings confirm that resource-use complementarity, the ability of functionally diverse co-occurring species to more efficiently utilize a pool of limiting resources, manifests under resource-limiting environments – in our case the understorey strata of a subtropical forest (Grime 1973, Hardin 1960). The major resources needed for plant growth and survival are light, water and nutrients. It is well-known that light is limiting in the understorey strata of (sub-) tropical forests (Brenes-Arguedas *et al.* 2011, Canham *et al.* 1990, Wright 2002). Whether water and nutrients are more plentiful for the overstorey because they have large root systems that efficiently absorb these resources, or for the understory that is characterized by a less extreme environment is less well-known. Some studies point at the vulnerability of big trees for drought (Lindenmayer & Laurance 2017) while understorey trees are protected against extreme drought (Qiu *et al.* 2012). This difference in knowledge on the effects of light *versus* those of nutrients and water also points to the relative ease of studying aboveground plant strategies and environmental conditions compared to the difficulty of studying belowground strategies and environmental conditions. We thus cannot exclude the effects of water and nutrients on our findings but suggest the differential effect of functional trait diversity of understorey and overstorey strata on aboveground biomass is likely driven by light, in line with previous research (Ali & Yan 2017b, Bartels & Chen 2010, Rüger *et al.* 2012). Further research testing the influence of functional traits related to the uptake of water and soil nutrients across different forest strata will have to elucidate their effects on aboveground biomass and other functions in natural forests (but see Ali & Yan 2017c, Ali & Yan 2017b).

Overstorey strata impose competitive constraints on understorey because of their large stem volumes (Zhang *et al.* 2016a), and hence altering resource availability such as light, water and space (Gilliam 2007, Gilliam *et al.* 1995, Mason *et al.* 2011). In the SEM analysis (Fig. 4.9), this was strongly evident by the negative direct effect of overstorey functional evenness on understorey functional evenness, and as a consequence negative indirect effect on aboveground biomass via understorey functional evenness. Interestingly, we found that understorey functional evenness had non-significant positive effect on aboveground biomass, which might be resulted due to the dominant role of overstorey strata on available resources (Ali & Yan 2017b, Zhang *et al.* 2016a). Resource filtering, caused by the overstorey strata (Bartels & Chen 2010), likely reduced the strength of the effect of understorey diversity on increased resource utilization in the resource-limited understorey environment (Hooper *et al.*

2005). This result supports the general notion that niche overlap reveals the effects of competition and contrasting assembly processes (Mason *et al.* 2011), which is true for woody species groups with overlapping niches such as overstorey strata (Zhang *et al.* 2016a). This indicates that in complex (sub-) tropical forest, combining data across forest strata may swamp these relationships and that to better understand the mechanisms of biodiversity – ecosystem function it is worth to analyse the understorey and overstorey strata separately. In addition, the observed negative relationships between aboveground biomass and soil nutrients are not driven by a higher productivity with poor soils in the studied forest. However, this may be attributable to species adaptations to the local soil conditions that increase longevity at the species level, and hence biomass retention and the storage of higher aboveground biomass at the stand level (see Ali & Yan 2017c, b, Prado-Junior *et al.* 2016).

4.5. Concluding remarks

We found support for the presence of two main ecological mechanisms explaining aboveground biomass in a subtropical forest: niche complementarity effect for understorey strata and functionally-similar big trees effect for overstorey strata. The strong negative relationship between overstorey functional trait diversity and aboveground biomass suggests that functional dominance of certain trait(s), niche overlap and/or stand structural attributes rather than niche complementarity (based on functional traits) may better explain aboveground biomass. The weak positive effect of understorey functional trait diversity on aboveground biomass suggests the complementarity mechanism among slow-growing conservative species rather than fast-growing acquisitive species of understorey in the studied forest, and hence supporting the niche complementarity effect. Given that we found contrasting mechanisms to explain aboveground biomass in a community, ecological models for predicting aboveground biomass in subtropical forests can be improved by including separate effects of functional trait diversity of overstorey and understorey strata.



Chapter 5. The mediation roles of intraspecific and interspecific functional trait diversity for linking the response of aboveground biomass to species richness across forest strata in a subtropical forest

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5.1. Introduction

Substantial evidences exist for the positive relationship between species richness and aboveground biomass or productivity in forest ecosystems (Poorter *et al.* 2015), and such relationship is thus a potential ecological indicator for biodiversity conservation and carbon storage (Chisholm *et al.* 2013, Poorter *et al.* 2015, Zhang *et al.* 2016a). However, increasing species richness may also lead to niche overlap and species redundancy (functionally similar species that make use of the same resources) instead of niche complementarity (Prado-Junior *et al.* 2016, Walker 1992). Therefore, the positive relationship between species richness and aboveground biomass does not always hold true in forest ecosystems (Szwagrzyk & Gazda 2007, Vilà *et al.* 2003). The direction of this relationship depends on the resource-use complementarity of co-occurring individuals within and between or among species, and functional traits can be used as indicators for the ecological mechanisms (e.g., Paquette & Messier 2011, Vilà *et al.* 2007). However, in the past empirical studies, mean values of the functional traits have been generally used for relating functional trait diversity (FTD) with aboveground biomass or productivity in forest ecosystems. Intraspecific FTD was considered to be negligible for explaining variation in aboveground biomass (Ali *et al.* 2017, Conti & Díaz 2013, Yuan *et al.* 2016) or productivity (Finegan *et al.* 2015, Prado-Junior *et al.* 2016). It is insufficient to use only interspecific FTD to represent total FTD of a forest community (de Bello *et al.* 2011, Mao *et al.* 2017). For instance, considering mean trait values per species can underestimates the ability of a species to endure the presence of others in a community, and ultimately underestimates the degree of niche differentiation and facilitation among species (e.g. Violle *et al.* 2012).

Intraspecific FTD has been recognized as a critical driver for maintaining individuals within species, co-occurring species dynamics, total FTD and functioning of communities (e.g. Chesson 2000, Chu *et al.* 2009, Clark 2010, Kichenin *et al.* 2013, Siefert *et al.* 2015). In fact, some plant species are tolerant and perform well for a diverse array of environmental heterogeneity by adjusting its phenotypic plasticity (Via *et al.* 1995), hence maintaining high level of intraspecific FTD (Clark 2010, Kichenin *et al.* 2013, Siefert *et al.* 2015). At the global scale, intraspecific trait variability can explain about 25% of the total trait variation on average within communities (Siefert & Ritchie 2016). In a given community, species richness maintains total FTD that directly influences ecosystem function (e.g. Clark 2010, Flynn *et al.* 2011, Siefert *et al.* 2015). As such, both intraspecific and interspecific FTD may evoke or mediate the effects of species richness on aboveground biomass (Fig. 5.1). Interspecific FTD is the primary mechanism underlying the effect of species richness on the community level productivity or aboveground biomass (Loreau 2010). At the same time, intraspecific FTD allows individual plants to adjust in response to environmental fluctuation (Clark 2010, Ravenscroft *et al.* 2014, Spasojevic *et al.* 2016) and modifies their traits in response to the activity of their closest neighbors (Le Bagousse-Pinguet *et al.* 2015, Uriarte *et al.* 2010, Violle *et al.* 2012), thus modulating the stabilizing effect of species diversity on the aboveground biomass of coexisting species.

Natural forests are always structurally and functionally complex due to the life-history and resource allocation strategies of different tree species (Rüger *et al.* 2012, Wright 2002). To consider the functional strategies and trade-offs underlying different life-history strategies (Wright *et al.* 2004, Zhao *et al.* 2017), it is therefore essential to gain insights into the relationship between species richness and aboveground biomass across forest strata (i.e. overstorey and understorey). Species compositions and thus functional strategies generally differ across overstorey and understorey strata (Ali & Yan 2017b). In addition, understorey strata account for the majority of species richness but less quantities of aboveground biomass, whereas overstorey strata maintain few dominant species but large quantities of aboveground biomass due to their large wood volumes in subtropical forests (Ali & Yan 2017c). As such, environmental conditions that influence plant performance vary with forest strata, and important resources such as light is often limiting in the understorey while abundant in overstorey strata of forests (e.g., Brenes-Arguedas *et al.* 2011, Wright 2002). In this context, the mechanisms behind the relationship between species richness and aboveground biomass may be forest strata-specific.

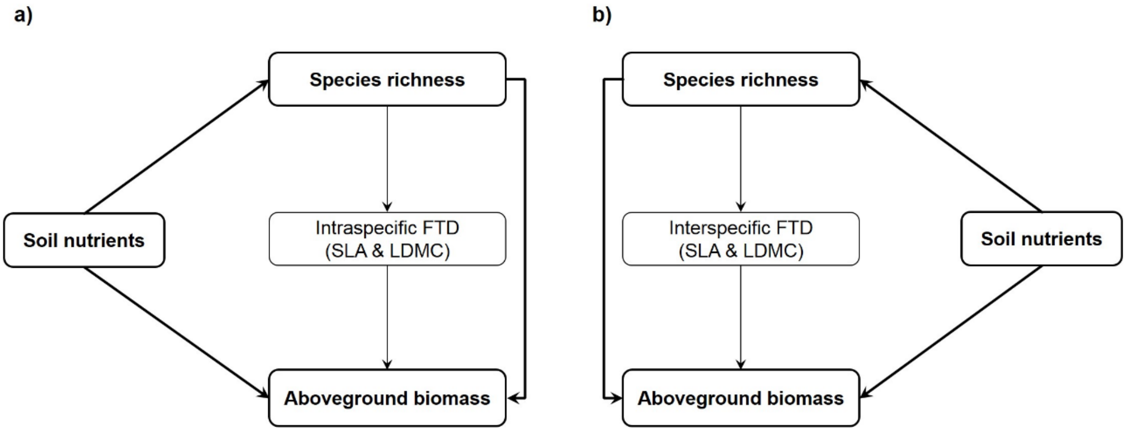


Fig. 5.1. Conceptual model showing how functional trait diversity mediates the response of aboveground biomass to species richness, in addition to the effects of soil nutrients. Conceptual model was constructed based on two theoretical frameworks, including a) intraspecific functional trait diversity and b) interspecific functional trait diversity, for each of the overstorey and understorey strata, and whole-community. Functional trait diversity is characterized by the variation in functional trait (e.g. SLA and LDMC) using Rao's quadratic entropy.

The niche complementarity hypothesis predicts that communities with a variety of species (Tilman 1999) or functional traits (Díaz *et al.* 2011a) are therefore able to use available resources more efficiently, thus enhancing the magnitude of ecosystem functions in natural forests (Zhang *et al.* 2012b). As shown by the niche-based model, the functional similarity or dissimilarity within and among coexisting species or functional groups indicates how the available resources are distributed among species within the community (de Bello *et al.* 2011, Mao *et al.* 2017, Mason *et al.* 2011, Tilman 1997). In a given forest, an increase of species richness may contribute to aboveground biomass through both the niche overlap of functionally similar species, and the niche complementarity across functionally dissimilar species (Prado-Junior *et al.* 2016, Walker 1992). Indeed, the niche overlap effect may be more important in productive environment of the overstorey due to the presence of a few large tree species, while niche complementarity effect may be a main driver of aboveground biomass in the light-stressful understorey strata as a result of a larger number of small tree species. As such, we have previously reported that high aboveground biomass was potentially driven by functional identity of tree height through making use of plentiful soil nutrients at overstorey strata, whereas by conservative strategy at understorey strata through enduring nutrient-poor soils (Ali & Yan 2017b).

Intraspecific FTD, due to the predominantly uneven abundances of dominant species, may largely determine community trait space and the ability of species to acquire resources (Johnson *et al.* 2015), and consequently influencing aboveground biomass (Li *et al.* 2017). As such, traits of dominant species have been shown to produce high aboveground biomass at community level through opposing strategies in different (sub-) tropical forests (Ali *et al.* 2017, Finegan *et al.* 2015, Lin *et al.* 2016, Prado-Junior *et al.* 2016). For instance, high specific leaf area (SLA) is positively related with relative growth rate, photosynthetic efficiency and leaf net carbon assimilation rate, i.e. acquisitive strategy of a plant, while high leaf dry matter content (LDMC) is associated with low leaf water and nutrient retention, i.e. conservative strategy of a plant (Finegan *et al.* 2015, Poorter & Markesteijn 2008, Reich 2014, Wright *et al.* 2010). Environmentally and taxonomically driven changes of some key traits such as SLA and LDMC may very well scale up to forest strata, community and ecosystem levels. In this case, the trait(s) weighted by the species' relative basal area or abundance will improve the scaling of individual responses to community and ecosystem functions (Ali *et al.* 2017, de Bello *et al.* 2011, Mao *et al.* 2017, Prado-Junior *et al.* 2016). Previous studies have shown that the few productive species dominating at the canopy contribute to most of the aboveground biomass in forests (Balvanera *et al.* 2005, Lohbeck *et al.* 2016). High aboveground biomass or productivity can be built up by few dominant species with functional similarity through the niche overlap (species redundancy) or intraspecific FTD, rather than interspecific FTD (e.g., Prado-Junior *et al.* 2016). In this context, we addressed whether intraspecific and/ or interspecific FTD mediate the response of aboveground biomass to species richness across forest strata and at whole-community in a subtropical forest (Fig. 5.1).

We present biophysical data including functional traits (SLA and LDMC) weighted by species' relative basal area for the quantification of intraspecific and interspecific FTD, species identity, soil nutrients and aboveground biomass from 125 plots inside a 5-ha natural subtropical forest in Eastern China. In order to unravel the mediation role of intraspecific and interspecific FTD for the response of aboveground biomass to species richness, we construct two separate theoretical frameworks based on conceptual model for each of overstorey and understorey strata, and whole-community level in a subtropical forest (Fig. 5.1). We hypothesized that intraspecific and interspecific FTD mediate the response of aboveground biomass to species richness in understorey strata through niche complementarity, whereas only intraspecific FTD would mediate this response in overstorey strata or whole-community due to the presence of a few large trees occupying larger niche space in a community. This hypothesis leads to three key predictions: 1) positive direct relationship between species richness and aboveground biomass at each of forest strata and whole-community level; 2) intraspecific and interspecific FTD will strongly affect aboveground biomass in understorey strata; and 3) intraspecific rather than interspecific FTD will strongly affect aboveground biomass in overstorey strata or whole-community. We tested the proposed hypothesis and predictions after accounting for the main effects of soil nutrients on species richness and aboveground biomass because soil nutrients may strongly influence species adaptation and aboveground biomass in (sub-) tropical forests (Ali & Yan 2017b, Prado-Junior *et al.* 2016).

5.2. Materials and methods

5.2.1. Quantification of intraspecific and interspecific functional trait diversity

Overstorey strata were defined as all individuals with DBH ≥ 10 cm in each forest plot, and understorey strata included trees with 1 ≤ DBH < 10 cm. This resulted in a total of 3,224 stems belonging to 75 species, 51 genera and 29 families in the overstorey strata, and a total of 17,004 stems belonging to 103 species, 65 genera and 37 families in the understorey strata across 125 plots in a 5-ha subtropical forest (Ali & Yan 2017c, b).

For calculation of intra- and interspecific FTD of overstorey (75), understorey (103), and whole-community species (108 species in total), we used two functional traits that are important for plant growth and survival (Poorter & Markesteijn 2008, Wright *et al.* 2010), and hence for standing aboveground biomass, biomass productivity and carbon storage (Finegan *et al.* 2015, Prado-Junior *et al.* 2016). We used five measures of diversity that were quantified for the overstorey and understory strata separately: species richness, intra- and interspecific FTD (single trait) based on SLA and LDMC. This resulted in ten diversity measures per plot for forest strata level analyses, while five measures per plot for whole-community level analyses.

We used Rao's quadratic entropy approach for the partitioning of total FTD into between species and within species components for each plot (de Bello *et al.* 2011). This approach is similar to the partitioning of total regional species diversity into between communities (β-diversity) and within communities (α-diversity). The species' relative basal area (relative to the whole-community or understorey/ overstorey basal area) was used to weight the traits of species within each plot, because basal area is a better indicator of plant performance than abundance (Prado-Junior *et al.* 2016).

Table 5.1. Summary of the variables used in analyses, from 125 subtropical forest plots across forest strata and whole-community level. Abbreviations: AGB, aboveground biomass; SR, species richness; FTD, functional trait diversity; FTD_{SLA}, functional trait diversity based on specific leaf area; FTD_{LDMC}, functional trait diversity based on leaf dry matter content; SN: soil nutrients (PC 2).

Variable	Mean	S.E.	Minimum	Maximum
Overstorey strata				
Intraspecific FTD_{SLA}	1305.22	334.33	2.50	38754.94
Interspecific FTD_{SLA}	3777.64	314.50	48.18	16459.00
Intraspecific FTD_{LDMC}	2715.23	292.27	88.59	24395.58
Interspecific FTD_{LDMC}	5856.17	373.09	769.04	31637.62
SR	11.93	0.27	4.00	19.00
AGB (Mg ha^{-1})	69.53	2.26	17.59	149.56
Understorey strata				
Intraspecific FTD_{SLA}	2129.25	164.98	275.85	10209.17
Interspecific FTD_{SLA}	4161.38	206.18	1239.21	14799.80
Intraspecific FTD_{LDMC}	4062.62	350.76	1056.24	32034.08
Interspecific FTD_{LDMC}	6051.17	277.15	2166.58	26257.01
SR	20.40	0.54	10.00	43.00
AGB (Mg ha^{-1})	5.01	0.15	1.25	9.34
Whole-community level				

Intraspecific FTD$_{SLA}$	1230.92	95.54	216.86	5680.19
Interspecific FTD$_{SLA}$	1399.32	78.72	281.09	5060.08
Intraspecific FTD$_{LDMC}$	2597.54	232.85	785.37	22542.60
Interspecific FTD$_{LDMC}$	2604.22	148.20	1076.85	15355.18
SR	26.59	0.55	14.00	47.00
AGB (Mg ha^{-1})	74.54	2.29	21.93	154.79
Soil nutrients				
SN (soil PC2)	0.00	0.12	-2.11	2.69

Note: Natural-logarithm transformed and standardized data were used in statistical analyses

The intraspecific FTD at the plot-level (whole community, understorey or overstorey) is represented by the average trait dissimilarity between each pair of individuals within a species weighted by the relative basal area of that same species and averaged for all the species within the plot. It thus reflects the community-weighted mean intraspecific trait variation. The interspecific FTD at the plot-level (whole community, understorey or overstorey) is represented by the average trait dissimilarity between each pair of species weighted by their relative basal area within plot. An example R function used in this study for partitioning of the total FTD into inter- and intraspecific FTD is available in de Bello *et al.* (2011). The calculations on the Rao diversity indices were performed using the *ade4* and *cati* packages (Dray 2016, Taudiere & Violle 2015).

The descriptions about the measurements of functional traits, estimation of aboveground biomass and measurement of soil nutrients are provided in Chapter 2. Summary of intraspecific and interspecific FTD, species richness aboveground biomass across forest strata and whole-community, and soil nutrients (soil PC2) is provided in Table 5.1.

5.2.2. Statistical analyses

All numerical variables including aboveground biomass, species richness, intraspecific and interspecific FTD indices were natural-logarithm transformed and standardized in order to meet the assumptions of normality and linearity, and to allow comparisons among multiple predictors and models (Zuur *et al.* 2009). We first tested a structural equation model (SEM) for the relationship between species richness and aboveground biomass without including FTD (intraspecific and interspecific) as a mediator, in addition to the effects of soil nutrients at each of the overstorey and understorey strata, and whole-community in a natural subtropical forest (Fig. 5.1). To test our proposed hypothesis and predictions, we further constructed two SEMs based on known theoretical multivariate causes of FTD and aboveground biomass, i.e., intraspecific FTD model and interspecific FTD model, at each of the overstorey and understorey strata, and whole-community level, after accounting for the effects of species richness on FTD and aboveground biomass (Fig. 5.1). The direct effects of soil nutrients were only considered on species richness and aboveground biomass, but not on FTD indices because we were only interested whether and how intraspecific and interspecific FTD act as mediators for linking species richness with aboveground biomass. See conceptual model or SEM of Flynn *et al.* (2011) for known theoretical paths for linking species richness, FTD and aboveground biomass. Several tests were used to assess the goodness of fit for SEMs (Malaeb *et al.* 2000), i.e., the Chi-square (χ^2) test, goodness-of-fit index (GFI), comparative fit index (CFI), standardized root mean square residual (SRMR) and Akaike information criterion (AIC). We critically used χ^2 test, representing the maximum likelihood estimation, to assess how well the hypothesized SEM fits the data (Ali & Yan 2017c). The SEMs were implemented using the *lavaan* package (Rosseel 2012).

Our study design may confound statistical results when there is spatial autocorrelation in the variables of interest. To account for this we performed generalized least-squares (GLS) models (Pinheiro & Bates 2016), accounting for subplots spatial autocorrelation (including subplots X and Y coordinates as a spatial effect), and without spatial autocorrelation (no reference to subplots X and Y coordinates) among subplots for each of the relationships between predictors and aboveground biomass. The goodness of fit of spatial and non-spatial GLS models was evaluated by the AIC, and we found that models without spatial autocorrelation always had the lower AIC values (Table 5.2), which is similar to the recent observations in forest ecosystems (Ali & Yan 2017c, b, Chiang *et al.* 2016, Yuan *et al.* 2016).

Table 5.2. Summary of the generalized least-squares (GLS) models of aboveground biomass on predictors at forest strata and whole-community level. Bold numbers indicate significant correlations (P < 0.05). All the abbreviations for variables are explained in Table 5.1.

GLS model	GLS model	Coefficient	*t*-value	*P*-value	AIC	R^2_{pseudo}
Forest strata						
AGB ~ SR	Non-spatial	0.38	6.42	<0.001	665.36	0.151
	Spatial	0.39	6.39	<0.001	675.05	0.151
AGB ~ Intraspecific FTD_{SLA}	Non-spatial	0.07	1.21	0.229	702.13	0.004
	Spatial	0.07	1.06	0.291	711.47	0.004
AGB ~ Intraspecific FTD_{LDMC}	Non-spatial	0.13	2.01	0.046	699.50	0.017
	Spatial	0.12	1.95	0.053	708.82	0.017
AGB ~ Interspecific FTD_{SLA}	Non-spatial	0.11	1.73	0.085	700.61	0.008

	Spatial	0.09	1.40	0.164	710.65	0.008
AGB ~ Interspecific FTD$_{\text{LDMC}}$	Non-spatial	0.11	1.74	0.084	700.52	0.006
	Spatial	0.08	1.30	0.195	710.85	0.006
AGB ~ SN	Non-spatial	-0.28	-5.69	<0.001	675.07	0.148
	Spatial	-0.28	-5.90	<0.001	682.49	0.148
Whole-community level						
AGB ~ SR	Non-spatial	0.29	3.37	0.001	354.86	0.084
	Spatial	0.29	3.36	0.001	368.81	0.084
AGB ~ Intraspecific FTD$_{\text{SLA}}$	Non-spatial	-0.11	-1.24	0.217	364.17	0.012
	Spatial	-0.11	-1.23	0.221	368.14	0.012
AGB ~ Intraspecific FTD$_{\text{LDMC}}$	Non-spatial	0.07	0.80	0.428	365.07	0.005
	Spatial	0.07	0.79	0.433	369.03	0.005
AGB ~ Interspecific FTD$_{\text{SLA}}$	Non-spatial	-0.14	-1.56	0.122	363.30	0.019
	Spatial	-0.14	-1.55	0.125	367.29	0.019
AGB ~ Interspecific FTD$_{\text{LDMC}}$	Non-spatial	-0.10	-1.06	0.291	364.58	0.009
	Spatial	-0.09	-1.04	0.299	368.56	0.009
AGB ~ SN	Non-spatial	-0.17	-2.68	0.008	359.35	0.055
	Spatial	-0.17	-2.68	0.008	363.35	0.055

For the interpretation of SEM results, we conducted the bivariate relationships indicating each hypothesized path according to the conceptual model in Fig. 5.1, using Pearson’s correlation and regression analyses. The complementary Pearson’s correlations and bivariate relationships to the SEMs are provided in Table 5.3 and Figs 5.2-5.4, respectively. For all statistical and ecological analyses R 3.2.2 was used (R Development Core Team 2015). Dataset used in the analyses can be found at http://dx.doi.org/10.1016/j.ecolind.2017.10.057.

Table 5.3. Pearson’s correlation coefficient between predictors used in the structural equation models (Figs. 5.5 and 5.6). Bold numbers indicate significant correlations ($P < 0.05$). All the abbreviations for variables are explained in Table 5.1.

	Predictors in intraspecific FTD model				Predictors in interspecific FTD model			
	FTD$_{\text{SLA}}$	FTD$_{\text{LDMC}}$	SR	SN	FTD$_{\text{SLA}}$	FTD$_{\text{LDMC}}$	SR	SN
Overstorey strata								
FTD$_{\text{SLA}}$	---				---			
FTD$_{\text{LDMC}}$	**0.57**	---			**0.38**	---		
SR	**0.19**	0.15	---		**0.22**	0.09	---	
SN	**-0.24**	**-0.22**	**-0.45**	---	0.14	0.12	**-0.45**	---
Understorey strata								
FTD$_{\text{SLA}}$	---				---			
FTD$_{\text{LDMC}}$	**0.36**	---			**0.69**	---		

SR	**0.18**	0.14	---		**0.59**	**0.55**	---	
SN	0.05	0.06	**-0.24**	---	-0.05	-0.01	**-0.24**	---
Whole-community								
FTD_{SLA}	---				---			
FTD_{LDMC}	**0.32**	---			**0.44**	---		
SR	**0.18**	0.07	---		**0.29**	0.14	---	
SN	0.07	0.02	**-0.31**	---	0.11	0.17	**-0.31**	---

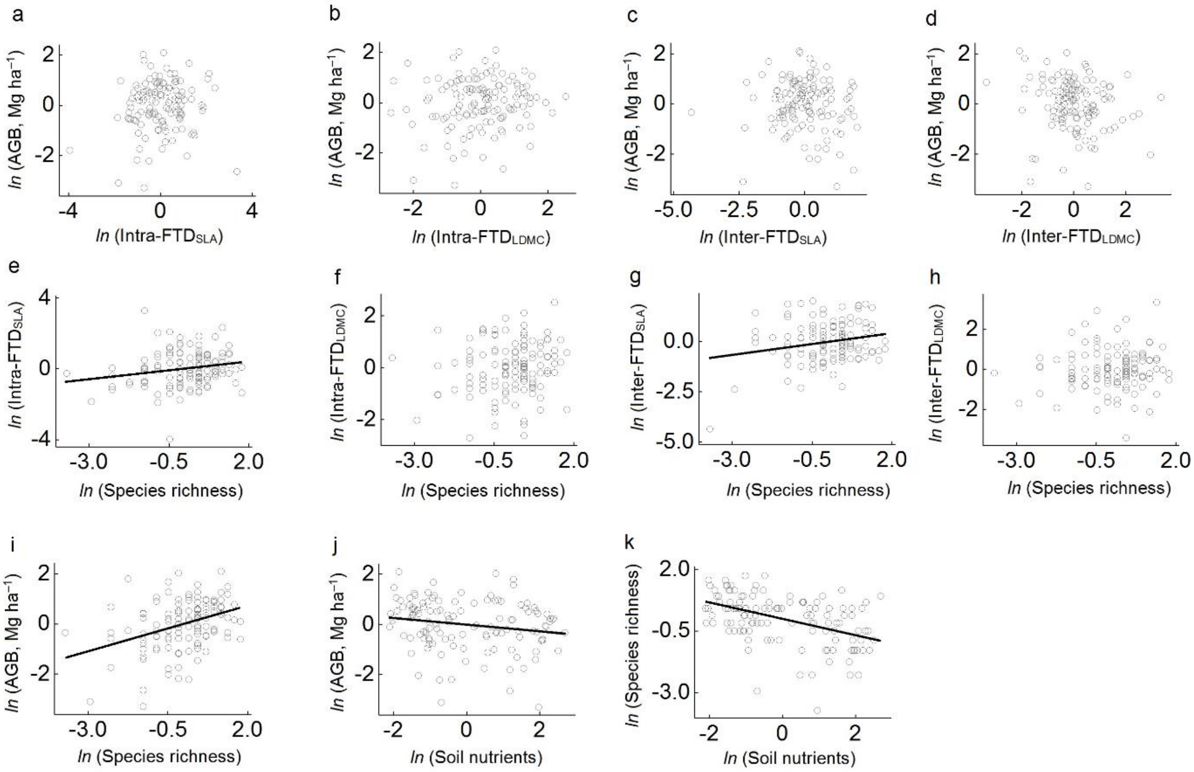


Fig. 5.2. The bivariate relationships between endogenous and exogenous variables (n = 125) for hypothesized causal paths in the SEMs at overstorey strata in a subtropical evergreen broadleaf forest in Eastern China. Fitted regressions are significant at $P < 0.05$. All the abbreviations for variables are explained in Table 5.1.

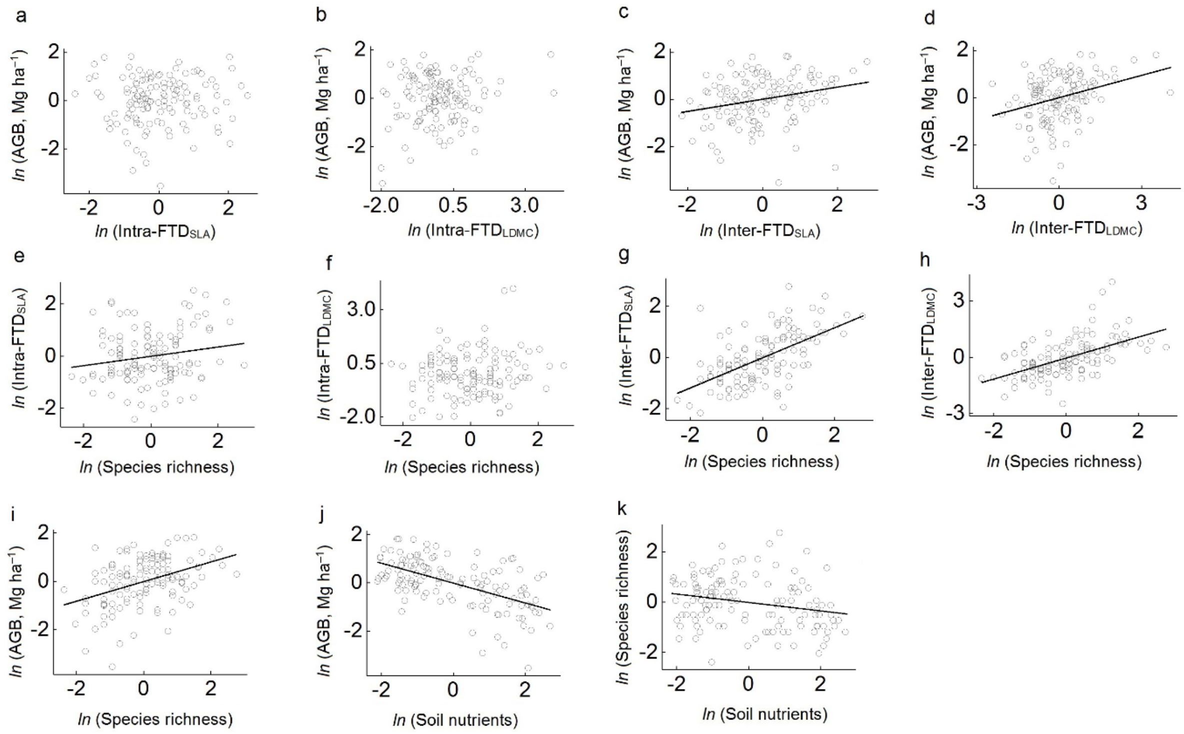


Fig. 5.3. The bivariate relationships between endogenous and exogenous variables (n = 125) for hypothesized causal paths in the SEMs at understorey strata in a subtropical evergreen broadleaf forest in Eastern China. Fitted regressions are significant at $P < 0.05$. All the abbreviations for variables are explained in Table 5.1.

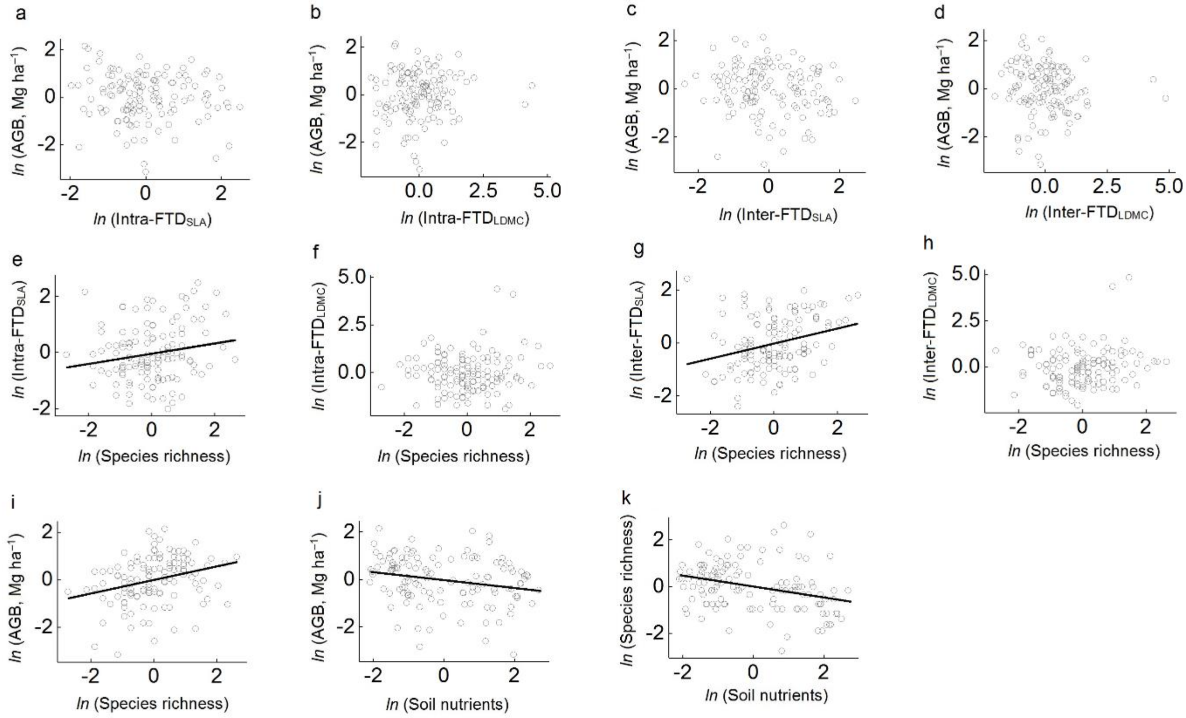


Fig. 5.4. The bivariate relationships between endogenous and exogenous variables (n = 125) for hypothesized causal paths in the SEMs at whole-community level in a subtropical evergreen broadleaf forest in Eastern China. Fitted regressions are significant at $P < 0.05$. All the abbreviations for variables are explained in Table 5.1.

5.3. Results

5.3.1. Performance of intraspecific and interspecific FTD to aboveground biomass

According to the χ^2 test, the model without considered FTD as a mediator was saturated ($\chi^2 = 0.00$, $P = 0$) at each of the overstorey and understorey strata, and whole-community level (Table 5.4). Therefore, it was not possible to accept the goodness of fit for prediction of aboveground biomass. The intraspecific FTD model was well fit to the data at each of the overstorey ($\chi^2 = 5.15$, $P = 0.076$) and understorey strata ($\chi^2 = 1.71$, $P = 0.426$), as well as at the whole-community level ($\chi^2 = 2.30$, $P = 0.317$). The interspecific FTD model at understorey strata was also well fit to the data ($\chi^2 = 2.91$, $P = 0.233$) whereas model at each of the overstorey strata ($\chi^2 = 10.95$, $P = 0.004$) and whole-community level ($\chi^2 = 8.87$, $P = 0.012$) was rejected (Table 5.4). In conclusion, this result indicates that both intraspecific and interspecific FTD mediate the response of aboveground biomass to species richness at understorey strata, whereas only intraspecific FTD mediates the response of aboveground biomass to species richness at overstorey strata and whole-community level (Figs 5.5 and 5.6).

5.3.2. Intraspecific FTD mediates the response of aboveground biomass to species richness at forest strata and whole-community level

With respect to the overstorey strata, the intraspecific FTD model explained 14, 20, 4, and 2% of variation in aboveground biomass, species richness, intraspecific FTD_{SLA}, and intraspecific FTD_{LDMC}, respectively (Fig. 5.5a). Species richness had the strongest positive direct effect on aboveground biomass ($\beta = 0.35$, $P < 0.001$), whereas intraspecific FTD_{SLA} ($\beta = 0.00$, $P = 0.997$), intraspecific FTD_{LDMC} ($\beta = 0.04$, $P = 0.495$) and soil nutrients ($\beta = –0.03$, $P = 0.712$) had negligible direct effects on aboveground biomass (Table 5.5). There was a significant positive direct effect of species richness on intraspecific FTD_{SLA} ($\beta = 0.19$, $P = 0.028$), but a non-significant positive direct effect on intraspecific FTD_{LDMC} ($\beta = 0.15$, $P = 0.097$; Fig. 5.5a).

When testing the role of intraspecific FTD at understorey strata, the model accounted for 44, 6, 3, and 2 % of the variation in aboveground biomass, species richness, intraspecific FTD_{SLA}, and intraspecific FTD_{LDMC}, respectively (Fig. 5.5b). Soil nutrients had the strongest positive direct effect on aboveground biomass ($\beta = –0.51$, $P < 0.001$), followed by the positive direct effect of species richness had ($\beta = 0.27$, $P < 0.001$), positive direct effect of intraspecific FTD_{LDMC} ($\beta = 0.18$, $P = 0.014$), and a negligible direct effect of intraspecific FTD_{SLA} ($\beta = –0.06$, $P = 0.402$; Table 5.5). There was a significant positive direct effect of species richness on intraspecific FTD_{SLA} ($\beta = 0.18$, $P = 0.042$), but a non-significant positive direct effect on intraspecific FTD_{LDMC} ($\beta = 0.14$, $P = 0.125$, Fig. 5.5b).

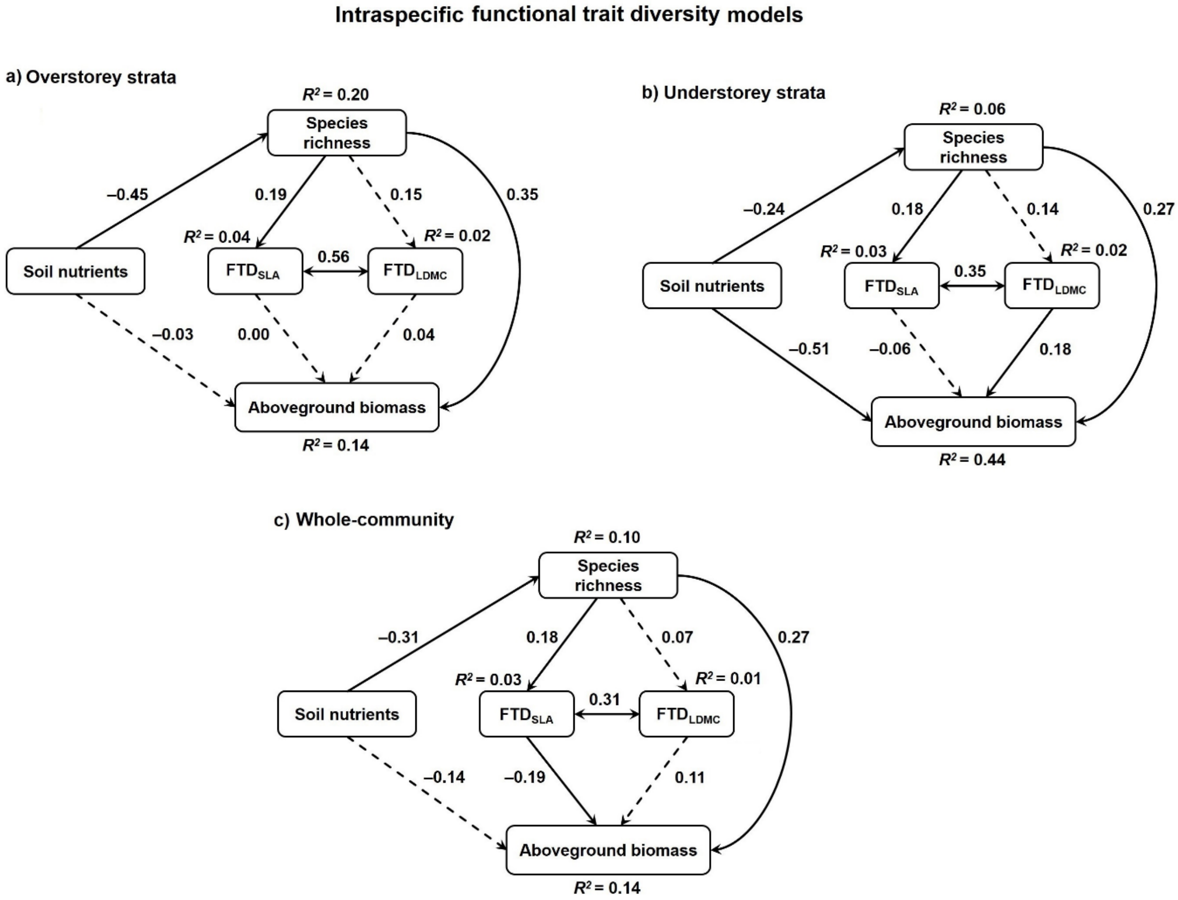


Fig. 5.5. The best-fit structural equation models of intraspecific functional trait diversity relating aboveground biomass to species richness, in addition to the effects of soil nutrients, at overstorey and understorey strata, and whole-community level. Solid arrows represent significant ($P < 0.05$) paths and dashed arrows represent non-significant paths ($P > 0.05$). For each path the standardized regression 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 shown in Table 5.4. For abbreviations, see Table 5.5.

At whole-community level, the intraspecific FTD model accounted for 14, 10, 3, and 1% of the variation in aboveground biomass, species richness, intraspecific FTD$_{SLA}$, and intraspecific FTD$_{LDMC}$, respectively (Fig. 5.5c). Species richness had the strongest positive direct effect on aboveground biomass (β = 0.27, P = 0.002), followed by the negative direct effect of intraspecific FTD$_{SLA}$ (β = –0.19, P = 0.035), non-significant negative direct effect of soil nutrients (β = –0.14, P = 0.113), and positive direct effect of intraspecific FTD$_{LDMC}$ (β = 0.11, P = 0.195; Table 5.5). There was a significant positive direct effect of species richness on intraspecific FTD$_{SLA}$ (β = 0.18, P = 0.038), but a non-significant positive direct effect on intraspecific FTD$_{LDMC}$ (β = 0.07, P = 0.410; Fig. 5.5c).

Table 5.4. Model selection of good-fit structural equation model (SEM) for aboveground biomass (AGB). Models were accepted, rejected and saturated based on χ^2 test. Only accepted models were considered in this study (see Table 5.5; and Figs 5.5 and 5.6). Abbreviations: FTD, functional trait diversity; df, degrees of freedom; CFI, comparative fit index; GFI, goodness of fit index; SRMR, standardized root mean square residual; AIC, Akaike information criterion; χ^2, Chi-square test; R^2 indicates the total variation in aboveground biomass that is explained by the combined independent variables.

Ecosystem functions	Hypothesized model	df	Model fit statistics summary						Model remarks	SEM
			CFI	GFI	SRMR	AIC	R^2	χ^2 (*P*-value)		
Overstorey AGB	No FTD mediation model	0	1.00	1.00	0.000	1104.72	0.14	0.00 (0)	Saturated	Not shown
	Intraspecific FTD model	2	0.97	0.98	0.057	1771.62	0.14	5.15 (0.076)	Accepted	Fig. 5.5a
	Interspecific FTD model	2	0.90	0.97	0.077	1793.17	0.19	10.95 (0.004)	Rejected	Not shown
Understorey AGB	No FTD mediation model	0	1.00	1.00	0.000	1079.34	0.40	0.00 (0)	Saturated	Not shown
	Intraspecific FTD model	2	1.00	0.99	0.038	1772.41	0.44	1.71 (0.426)	Accepted	Fig. 5.5b
	Interspecific FTD model	2	0.99	0.99	0.045	1650.86	0.45	2.91 (0.233)	Accepted	Fig. 5.6
Whole-community AGB	No FTD mediation model	0	1.00	1.00	0.000	1124.13	0.11	0.00 (0)	Saturated	Not shown
	Intraspecific FTD model	2	0.99	0.99	0.035	1823.23	0.14	2.30 (0.317)	Accepted	Fig. 5.5c
	Interspecific FTD model	2	0.90	0.97	0.076	1801.00	0.14	8.87 (0.012)	Rejected	Not shown

Note: df is based on the number of ‘knowns’ minus the number of free parameters in the model, not on the sample size.

Table 5.5. The direct, indirect, and total standardized effects of soil nutrients, species richness and functional trait diversity (intra- and interspecific) on aboveground biomass based on structural equation models (SEMs). Effects values of accepted SEMs are shown here (see Table 5.4 for model fit statistics, and Figs 5.5 and 5.6 for accepted SEMs). Significant effects are indicted in bold ($P < 0.05$). All the abbreviations for variables are explained in Table 5.1.

		Intraspecific FTD models						*Interspecific FTD model*	
Predictor	Pathway to aboveground biomass	Overstorey strata model in Fig. 5.5a		Understorey strata model in Fig. 5.5b		Whole-community model in Fig. 5.5c		Understorey strata model in Fig. 5.6	
		Effect	*P*-value	Effect	*P*-value	Effect	*P*-value	Effect	*P*-value
Soil nutrients	Direct effect	−0.03	0.712	−0.51	**<0.001**	−0.14	0.113	−0.52	**<0.001**
	Indirect effect via species richness	−0.16	**0.002**	−0.07	**0.026**	−0.09	**0.018**	−0.04	0.107
	Total effect	−0.19	0.031	−0.57	**<0.001**	−0.22	**0.009**	−0.56	**<0.001**
Species richness	Direct effect	0.35	**<0.001**	0.27	**<0.001**	0.27	**0.002**	0.17	**0.045**
	Indirect effect via FD$_{SLA}$	0.00	0.997	−0.01	0.438	−0.03	0.138	−0.02	0.764
	Indirect effect via FD$_{LDMC}$	0.01	0.703	0.02	0.192	0.01	0.486	0.13	**0.023**
	Total effect	0.35	**<0.001**	0.29	**<0.001**	0.25	**0.005**	0.28	**<0.001**
FTD$_{SLA}$	Direct effect	0.00	0.997	−0.06	0.402	−0.19	**0.035**	−0.03	0.764
FTD$_{LDMC}$	Direct effect	0.04	0.495	0.18	**0.014**	0.11	0.195	0.23	**0.017**

In all intraspecific FTD models (Fig. 5.5), soil nutrients had the significant negative direct effect on species richness but the strength of the effect varies at overstorey (β = –0.45, P < 0.001), understorey (β = –0.24, P = 0.007) and whole-community (β = –0.31, P < 0.001). Soil nutrients had a significant indirect negative effect via species richness on aboveground biomass at overstorey (β = –0.16, P = 0.002), understorey (β = –0.07, P = 0.026) and whole-community (β = –0.09, P = 0.018; Table 5.5). There were negligible indirect effect of species richness on aboveground biomass via intraspecific FTD_{SLA} and intraspecific FTD_{LDMC} at forest strata and whole-community. The total (direct + indirect) effect of soil nutrients on aboveground biomass was quite similar at overstorey strata (β = –0.19, P = 0.031) and whole-community (β = –0.22, P = 0.009), but relatively high at understorey strata (β = –0.57, P < 0.001; Table 5.5). The total effect of species richness on aboveground biomass was quite similar at overstorey strata (β = 0.35, P < 0.001), understorey strata (β = 0.29, P < 0.001) and whole-community (β = 0.25, P = 0.005; Table 5.5).

5.3.3. Interspecific FTD mediates the response of aboveground biomass to species richness at understorey strata

At understorey strata, the interspecific FTD model accounted for 44, 6, 3, and 2 % of the variation in aboveground biomass, species richness, interspecific FTD_{SLA}, and interspecific FTD_{LDMC}, respectively (Fig. 5.6). Soil nutrients had the strong negative direct effect on aboveground biomass (β = –0.52, P < 0.001), followed by the significant positive direct effect of species richness (β = 0.17, P = 0.045), positive direct effect of interspecific FTD_{LDMC} (β = 0.23, P = 0.017), and a negligible direct effect of interspecific FTD_{SLA} (β = –0.03, P = 0.764; Table 2). There was a significant positive direct effect of species richness on interspecific FTD_{SLA} (β = 0.59, P < 0.001) and interspecific FTD_{LDMC} (β = 0.55, P < 0.034, Fig. 5.6). Soil nutrients had the significant negative direct effect on species richness (β = –0.24, P < 0.001), but a negligible indirect effect via species richness on aboveground biomass (β = –0.04, P = 0.107). Species richness had the significant positive indirect effect via interspecific FTD_{LDMC} (β = 0.13, P = 0.023), but a negligible indirect effect via interspecific FTD_{SLA} (β = –0.02, P = 0.764). The total effect of soil nutrients and species richness on understorey aboveground biomass was –0.56 (P < 0.001) and 0.28 (P < 0.001), respectively (Table 5.5).

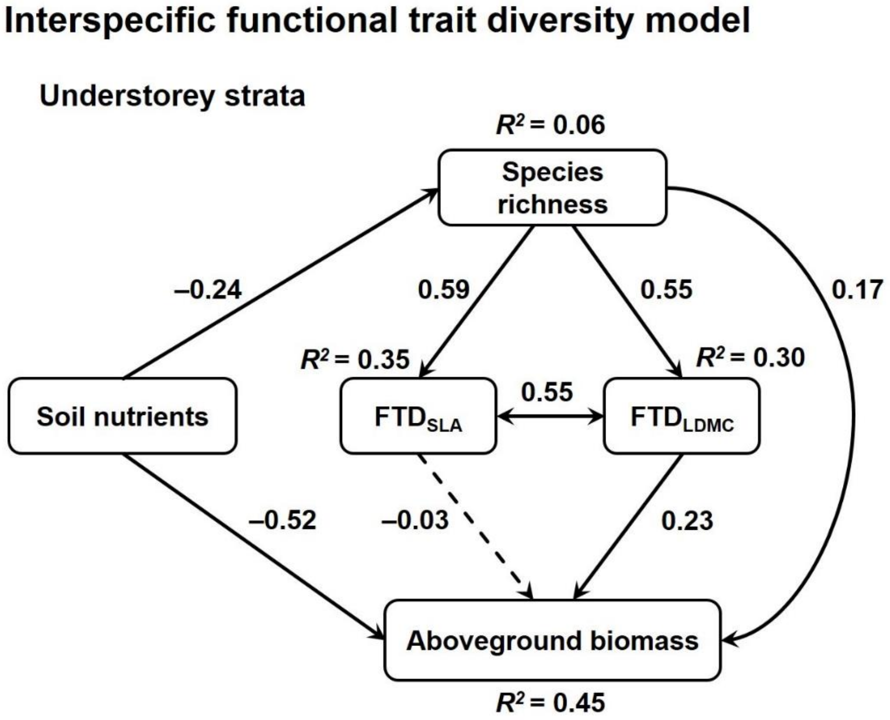


Fig. 5.6. The best-fit structural equation models of interspecific functional trait diversity relating aboveground biomass to species richness, in addition to the effects of soil nutrients, at understorey strata. Solid arrows represent significant ($P < 0.05$) paths and dashed arrows represent non-significant paths ($P > 0.05$). For each path the standardized regression 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 shown in Table 5.4. For abbreviations, see Table 5.5.

5.4. Discussion

This study highlights the mediation role of intraspecific and interspecific FTD for linking the response of aboveground biomass to species richness, after accounting for the effects of soil nutrients, in a subtropical forest. In agreement with our hypothesis, this study showed that intraspecific and interspecific FTD mediate the response of aboveground biomass to species richness at understorey strata, whereas only intraspecific FTD did so at overstorey strata and whole-community level. The main novelty of this study is determining that high aboveground biomass in a subtropical forest is shaped by high intraspecific and interspecific FTD at understorey strata, whereas high intraspecific FTD has negligible or negative relationships with aboveground biomass at overstorey strata and whole-community, respectively.

At overstorey strata, the negligible mediation role of intraspecific FTD and no role of interspecific FTD for linking the response of aboveground biomass to species richness may be due to the intraspecific variation of few dominant species which largely determine community trait space and the ability to obtain resources. In line with the previous studies, these findings suggest that aboveground biomass or productivity likely depends to a great extent on the functional traits of the dominant species or functional groups within communities due to the mass ratio effect rather than niche complementarity effect (Ali & Yan 2017b, Chiang *et al.* 2016, Conti & Díaz 2013, Finegan *et al.* 2015). This is likely the result of decades of environmental filtering that trees need to pass through to be able to occupy the overstorey, combined with the fact that only a subset of the species, and hence individuals of those few species, are able to become tall enough to occupy the overstorey strata. Strong effects of environmental filtering will narrow down the range and diversity of functional strategies (hence low FTD) that becomes abundant to drive aboveground biomass (Keddy 1992).

Interestingly, at the whole-community level, the strong negative association of intraspecific FTD_{SLA} with aboveground biomass implies the presence of few large trees having low intraspecific differentiation towards a more light acquisitive strategy within studied species in a community. Therefore, low intraspecific FTD_{SLA} tends to have high aboveground biomass at whole-community level. This result indicates intraspecific-level carbon gain but the presence of few large trees occupying larger niche space makes this relationship negative, and hence high functioning (Ali & Yan 2017b, Johnson *et al.* 2015, Siefert *et al.* 2015). Alternately, this result may be attributable to complex vertical structures of the studied forest having a lot of unshaded leaves, which result mainly from the few dominant canopy species that are effective in light acquisition (Ali *et al.* 2017, Fotis *et al.* 2017).

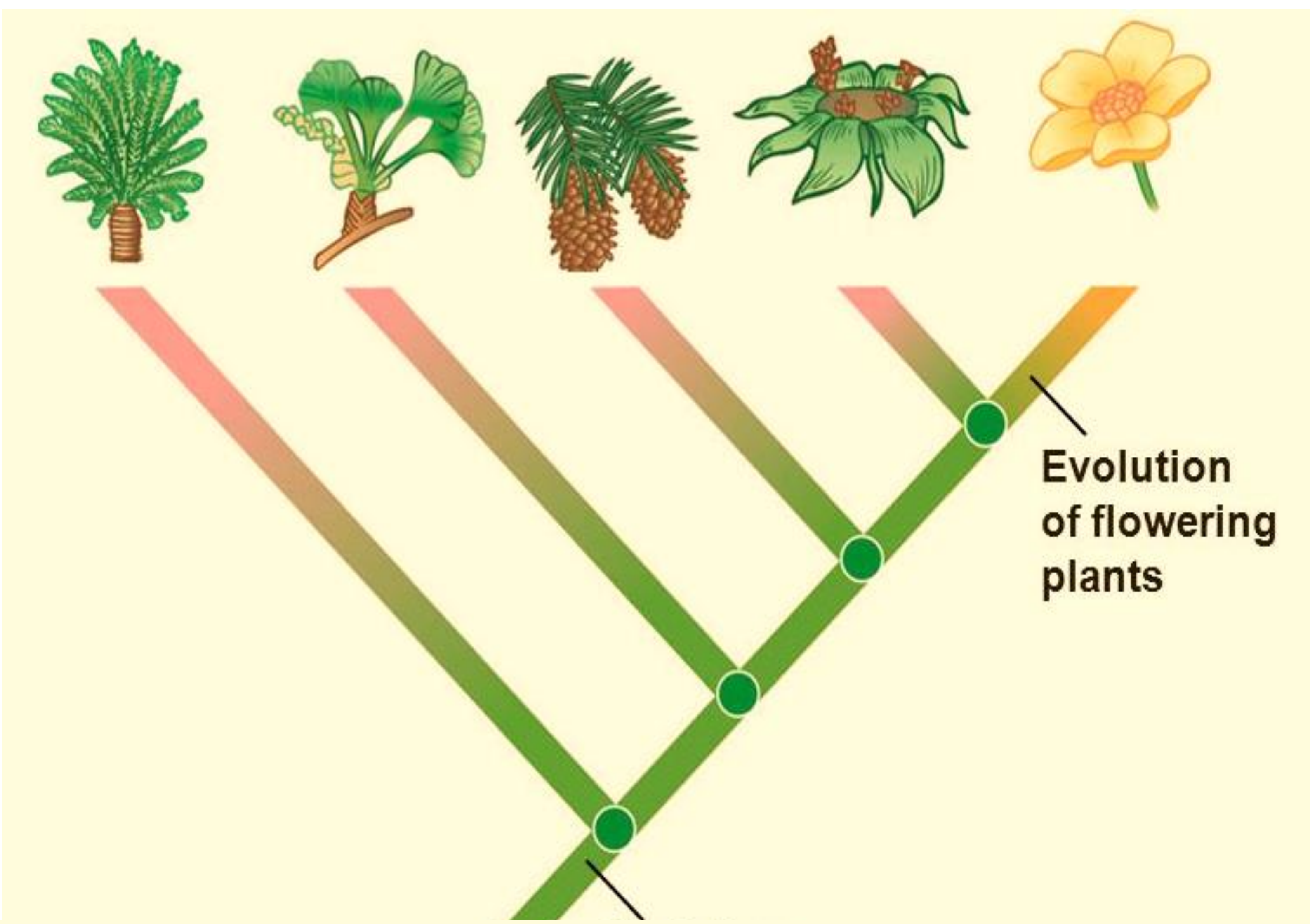
At understorey strata, the strong positive associations of intraspecific and interspecific FTD_{LDMC} with aboveground biomass indicate the niche differentiation between and within species towards a more resource conservative strategy, supporting the niche complementarity hypothesis (Ali & Yan 2017b, Díaz *et al.* 2011a, Tilman 1999). Our findings confirm that resource-use complementarity, the ability of functionally diverse co-occurring species or individuals within species to more efficiently utilize a pool of limiting resources, manifests under resource-limiting environments – in our case the understorey strata of a subtropical forest (Grime 1973, Hardin 1960). At structurally complex forests, overstorey trees have dominant effect over understorey trees by effectively intercept light to the understorey trees (Bartels & Chen 2010, Lohbeck *et al.* 2016, Oberle *et al.* 2009). Consequently, few dominant overstorey trees with a high proportion of unshaded leaves within species have high aboveground biomass through low intraspecific niche differentiation towards light acquisitive strategy. This may be attributable to the greater effect of large woody trees on overall functioning of forest ecosystems, in contrast to that of small woody trees (Ali & Yan 2017c, Liang *et al.* 2015). These results implies that expectations derived from intraspecific niche similarity at overstorey strata will scale up to the whole-community level due to the superior role of overstorey trees on understorey trees in terms of canopy properties and ecosystem function (Siefert *et al.* 2015). Further, this result indicates that in a complex subtropical forest, combining data across forest strata may swamp these relationships and that to better understand the mechanisms of intraspecific FTD – aboveground biomass it is worth to analyse the understorey and overstorey strata separately.

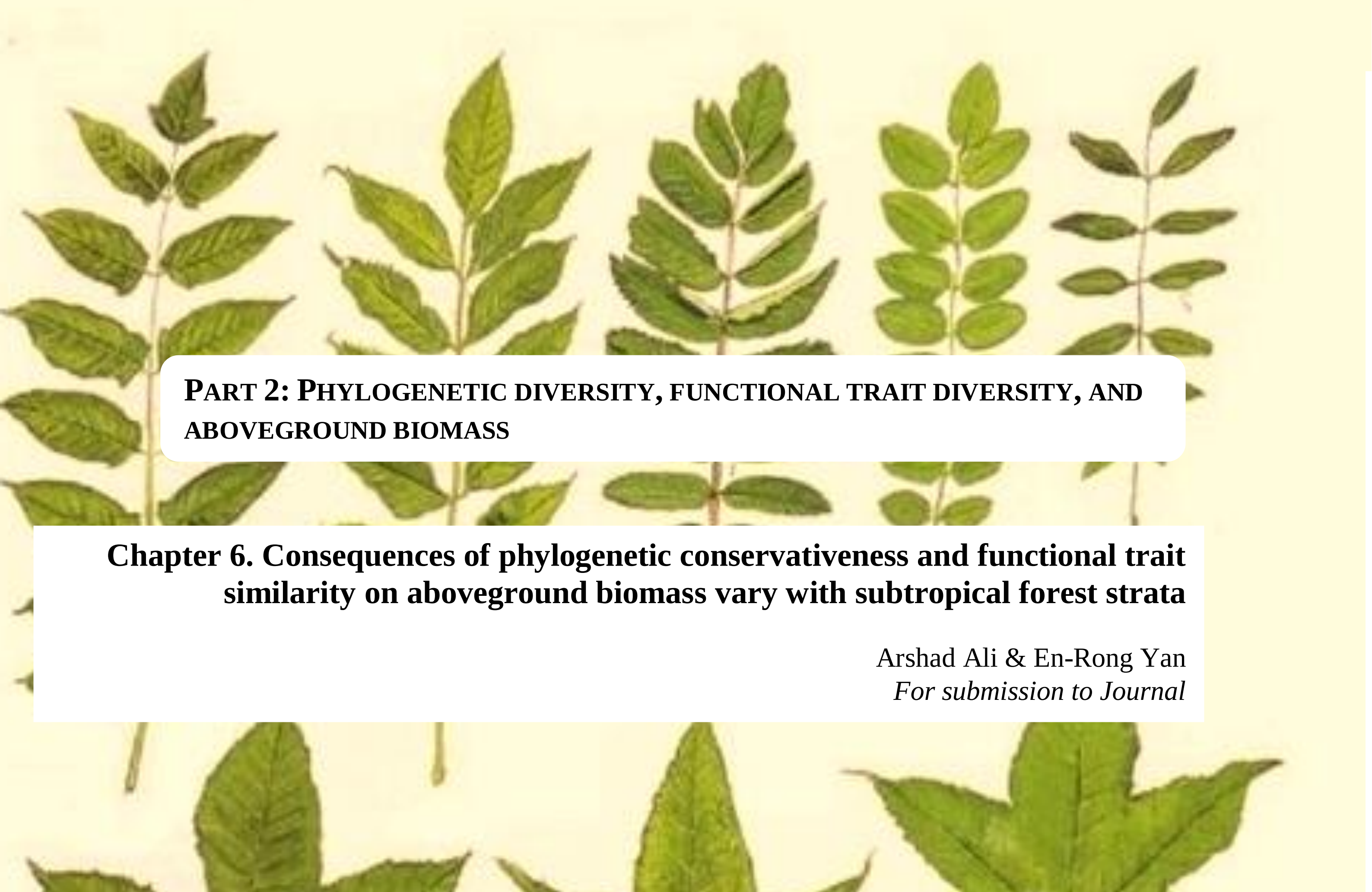
The contrasting relationships of aboveground biomass with intraspecific FTD_{SLA} and FTD_{LDMC} may be related to the plant's leaf economics spectrum (e.g., Garnier *et al.* 2004), at different forest strata as well as at whole-community. These results indicate that extensive intraspecific variation in leaf economic traits arising from plastic responses to light, nutrients and other environmental factors (Mao *et al.* 2017, Rozendaal *et al.* 2006), as well as genetic variability and ontogenetic variation (Mason *et al.* 2013, Siefert *et al.* 2015, Vasseur *et al.* 2012). Our findings that leaf economic traits consistently represent intraspecific FTD at different forest strata in the studied forest have important implications in the individual plant strategies, community assembly and ecosystem function (Reich 2014, Siefert *et al.* 2015). For instance, this study showed that, on the one hand, exploitative plants characterized by high SLA and fast nutrient acquisition and turnover, thus being conducive to fast growth and high aboveground biomass at overstorey strata. On the other hand, conservative plants with high LDMC, nutrient-poor leaves and slower growth associated with slow nutrient and biomass turnover at understorey strata (Wright *et al.* 2004, Zhao *et al.* 2017).

The observed negative relationships of soil nutrients with species richness and aboveground biomass at forest strata and whole-community are not driven by a higher productivity with poor soils in the studied forests. However, this may be attributable to species adaptations to the local soil conditions through increasing longevity and stand biomass retention (Ali & Yan 2017c, b, Poorter *et al.* 2015, Prado-Junior *et al.* 2016). As such, we have previously reported that nutrient-poor soils tend to be dominated by species with conservative strategy, whereas nutrient-rich soils tend to be dominated by species with acquisitive strategy in the studied forest (Ali & Yan 2017b).

5.5. Concluding remarks

We conclude that the mediation role of intraspecific and interspecific FTD for the response of aboveground biomass to species richness along soil nutrients gradients depends on the forest strata of a community. For example, intraspecific and interspecific FTD mediate the response of aboveground biomass to species richness at understorey strata, whereas only intraspecific FTD mediates the response of aboveground biomass to species richness at whole-community and overstorey strata. Intraspecific and interspecific FTD_{LDMC} had strong direct positive effect on aboveground biomass at understorey strata representing niche differentiation. Intraspecific FTD_{SLA} had strong direct negative effect on aboveground biomass at whole-community level, probably due to the presence of a few large trees occupying larger niche space in a community. Intraspecific FTD had negligible mediation role, whereas interspecific FTD had no role, for linking the response of aboveground biomass to species richness at overstorey strata indicating that only dominant species may largely determine community trait space and the ability to obtain resources. Clearly, this study shows that intraspecific versus interspecific FTD plays a central role for linking the response of aboveground biomass to species richness. Lastly, this study suggests that trait variability within species need to be separately or explicitly considered in the theoretical development for linking biodiversity and ecosystem function across forest strata in a subtropical forest.





PART 2: PHYLOGENETIC DIVERSITY, FUNCTIONAL TRAIT DIVERSITY, AND ABOVEGROUND BIOMASS

Chapter 6. Consequences of phylogenetic conservativeness and functional trait similarity on aboveground biomass vary with subtropical forest strata

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6.1. 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 & 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. More recently, this 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 diversity are frequently considered as the main drivers of aboveground biomass or productivity in both experimental and natural environments, including forests (Cadotte *et al.* 2009, Flynn *et al.* 2011, Paquette & 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 diversity drive aboveground biomass across forest strata (i.e. overstorey and understorey).

Functional trait diversity and phylogenetic or evolutionary 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. 6.1A and 6.1B) (Wiens & Graham 2005). For instance, on the one hand, phylogenetically close species are likely to assemble due to environmental filtering, and hence patterns of evolutionary relatedness and/or functional trait similarity are expected if traits are phylogenetically conserved (Fig. 6.1A) (Webb 2000). On the other hand, it is possible that niche differentiation or ecological fitting mediates community assembly, and hence patterns of phylogenetic overdispersion and/or functional trait dissimilarity are generally expected (Fig. 6.1B) (Cavender-Bares *et al.* 2009). Competition or facilitation among species can leads to overdispersion under expectation of phylogenetically conserved traits, or environmental filtering can leads overdispersion due to the dominate convergence role of ecologically important traits (Cavender-Bares *et al.* 2009, Mayfield & Levine 2010).

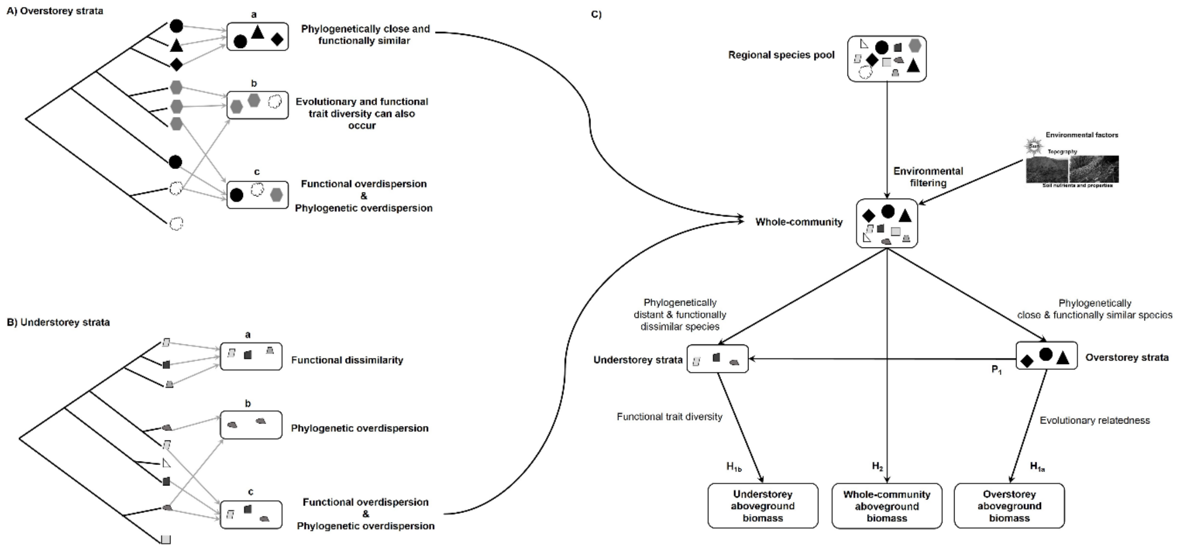


Fig. 6.1. An example patterns for functional trait diversity and evolutionary diversity when traits are conserved or labile on the phylogeny. A) Individual species are represented by the shapes of symbols at the tips of the phylogenetic tree, the colors of the symbols indicate different traits, and rectangles represent species assemblage within a strata. In this example (Fig. 6.1A), 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. 6.1A) 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. 6.1A), such that less phylogenetically close and functionally similar species. Interspecific competition limits similarity between co-occurring species resulting in different traits (c in Fig. 6.1A) causing functional or phylogenetic overdispersion. B) Functional dissimilarity in a strata where variety of traits are conserved on the phylogeny (a in Fig. 6.1B), such that phylogenetically close species tend to have the different traits (colors). Phylogenetic overdispersion (b in Fig. 6.1B) could be clustered in functional trait diversity, such that phylogenetically distant species tend to have the same traits. Both phylogenetic and functional overdisperison can also be expected (c in Fig. 6.1B), such that phylogenetically distant species tend to have the different traits. Note that these patterns (shown in Fig. 6.1B and 6.1B) 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 size of the symbols represent 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).

It is therefore possible that functional, evolutionary and ecological similarities of trees might be fundamentally different across forest strata (i.e. overstorey and understorey). 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, natural forests are always structurally complex and trees with different functional strategies are generally assembled in different vertical layers (Rüger *et al.* 2012). For instance, it is expected that evolutionary relatedness would drive aboveground biomass at overstorey strata, probably due to environmental filtering of phylogenetically close species with similar physiological or functional tolerances (Webb *et al.* 2002). Phylogenetic overdispersion can result from competition causing limiting similarity of phylogenetically conserved traits, environmental filtering acting on convergent traits, or other processes such as complementarity and facilitation among phylogenetically distant species (Cavender-Bares *et al.* 2009). Therefore, it is expected that functional dissimilarity would drive aboveground biomass at understorey strata, probably due to the niche complementarity in the resource-limited environment. As such, we have previously reported that high aboveground biomass was potentially driven by functional identity of tree height through making use of plentiful soil nutrients at overstorey strata, whereas by conservative strategy at understorey strata through enduring nutrient-poor soils (Ali & Yan 2017b).

In this study, we hypothesize that phylogenetically close and functionally similar species drive high aboveground biomass in overstorey strata due to the evolutionary relatedness (H_{1a}), while phylogenetically distant and functionally dissimilar species drive high aboveground biomass in understorey strata due to the functional dissimilarity (H_{1b}) (Fig. 6.1C). Our proposed hypothesis (H_1) leads to the following two key predictions: 1) based on the less stringent conditions for influencing species interactions at overstorey strata, we predict that evolutionary relatedness would drive aboveground biomass better than functional similarity; and 2) based on the dominant effect of overstorey strata on understorey (P_1), we predict that functional dissimilarity would drive aboveground biomass better than phylogenetic overdispersion. If the above predictions are true, we therefore 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. 6.1C).

6.2. Materials and methods

6.2.1. Quantification of functional trait diversity and evolutionary diversity

Overstorey strata were defined as all individuals with DBH ≥ 10 cm in each subplot, and understorey strata included trees with 1 ≤ DBH < 10 cm (Barrufol *et al.* 2013). This resulted in a total of 3,213 stems belonging to 71 species, 47 genera and 27 families in the overstorey, and a total of 17,004 stems belonging to 94 species, 57 genera and 33 families in the understorey across 125 plots in a 5-ha subtropical forest.

Two attributes of biodiversity were used to test the strength of the relationships between forest diversity and aboveground biomass at overstorey and understorey strata as well as at whole-community level in a subtropical forest. This framework distinguishes two different generic attributes of forest diversity in a community, 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 & Díaz 2013, Finegan *et al.* 2015, Potter & Woodall 2014). For calculation of functional trait diversity of overstorey, understorey and whole-community, we used eight functional traits that are important for plant growth and survival (Poorter & Markesteijn 2008, Wright *et al.* 2010), and hence for standing aboveground biomass, biomass productivity and carbon storage (Finegan *et al.* 2015, Prado-Junior *et al.* 2016).

We used four complementary indices to measure multivariate functional trait diversity: functional evenness, functional richness, functional divergence and functional dispersion. Functional richness is the amount of multivariate trait space filled by the community. Functional evenness indicates how species' basal area is spread over multivariate-trait space, being higher when basal area distribution is homogeneous across this space. Functional divergence is the degree of divergence from the center that most dominant species occupy in multivariate-trait space and it is higher when most of basal area is concentrated in the extremes of the multivariate-trait space. Functional dispersion is the average distance of the species to the basal-area weighted centroid of all species in community trait space (Laliberté & Legendre 2010, Mason *et al.* 2005, Villéger *et al.* 2008). The species' relative basal area (relative to the total understory/ overstorey basal area) was used to weight the trait(s) of overstorey and understorey species at each plot, because basal area is a better indicator of plant performance than abundance (Prado-Junior *et al.* 2016). Trait values were standardized before the calculation of four functional trait diversity indices. All functional trait diversity indices were calculated using the *vegan* (Oksanen *et al.* 2015), and *FD*, *dbFD* packages (Laliberté & Legendre 2010).

For the quantifications of evolutionary diversity indices, we first constructed phylogenetic supertree of all species, for each of overstorey (Fig. 6.2), understorey (Fig. 6.3) and whole-community (Fig. 6.4), based on the 'R20120829 phylomatic tree for plants' in Phylomatic v3 (Webb & Donoghue 2005). This is an online interface that supplies a phylogeny based on taxonomic names of plant species (http://phylodiversity.net/phylomatic/). This supertree was then assigned branch lengths estimated from multi-gene molecular and fossil data implemented in Phylomatic, which is the largest and most updated standardized species-level phylogeny of seed plants (Zanne *et al.* 2014). We then calculated five evolutionary diversity indices – including 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, which is the minimum spanning distance (sum of all branch lengths) of a phylogenetic tree representing all the species from a given plot, measured in millions of years of evolutionary time (Faith 1992). The other four evolutionary diversity indices are the part of an integrated and relatively easy-to-understand package of phylogenetic measures of species richness, evenness, variability and clustering, with well-defined statistical properties (Helmus *et al.* 2007). Phylogenetic species variability is a measure of the deviation from a star phylogeny, and has a maximum value of 1 when species are less closely related, declining to a minimum of zero as species are more closely related. Phylogenetic species evenness which is similar to phylogenetic species variability but this index incorporates relative species abundances, and has a maximum value of 1 when abundances of the highly-unrelated species are equal, and declining to 0 as closely-related species have highly different abundances. 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., value is maximum at the species richness, and decreases towards 0 as relatedness increases. Phylogenetic species clustering quantifies the branch-tip clustering of species across the phylogenetic tree, and when approaches to a maximum value of 1 as species are less related to one another at the tips of the phylogenetic tree. All evolutionary diversity indices were calculated using the *picante* package (Kembel *et al.* 2010).

Phylogenetic species richness, was not included in our statistical analysis because of its similarity to and 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 measures of diversity that were quantified for the overstorey and understorey strata, and whole-community, separately: four complementary functional trait diversity and four evolutionary diversity indices.

The descriptions about the measurement of functional traits, estimation of aboveground biomass and measurement of environmental factors are provided in Chapter 2. Summary of evolutionary diversity and aboveground biomass across forest strata and whole-community is provided in Table 6.1.

Table 6.1. Descriptive statistics for evolutionary diversity and aboveground biomass, from 125 subtropical forest plots used for analysis of biodiversity – aboveground biomass. See Table 4.1 for summary of functional trait diversity across forest strata and whole-community level, and environmental factors axes.

Variable	Unit	Mean	S.E.	Minimum	Maximum
Overstorey strata					
Phylogenetic diversity (PD)	unitless	37.79	0.65	11.00	55.00
Phylogenetic species variability (PSV)	unitless	0.64	0.00	0.52	0.83

Phylogenetic species richness (PSR)	unitless	7.48	0.17	2.23	12.49
Phylogenetic species evenness (PSE)	unitless	0.55	0.01	0.32	0.77
Phylogenetic species clustering (PSC)	unitless	0.71	0.01	0.28	0.82
Aboveground biomass (AGB)	Mg ha^{-1}	69.34	2.27	15.38	149.56
Understorey strata					
Phylogenetic diversity (PD)	unitless	49.01	0.96	26.00	86.00
Phylogenetic species variability (PSV)	unitless	0.61	0.00	0.47	0.71
Phylogenetic species richness (PSR)	unitless	12.21	0.30	6.29	25.04
Phylogenetic species evenness (PSE)	unitless	0.51	0.01	0.25	0.71
Phylogenetic species clustering (PSC)	unitless	0.76	0.00	0.63	0.85
Aboveground biomass (AGB)	Mg ha^{-1}	4.98	0.16	1.22	9.72
Whole-community level					
Phylogenetic diversity (PD)	unitless	60.39	0.85	39.00	92.00
Phylogenetic species variability (PSV)	unitless	0.62	0.00	0.54	0.69
Phylogenetic species richness (PSR)	unitless	16.09	0.30	8.19	27.20
Phylogenetic species evenness (PSE)	unitless	0.52	0.01	0.32	0.71
Phylogenetic species clustering (PSC)	unitless	0.78	0.00	0.67	0.86
Aboveground biomass (AGB)	Mg ha^{-1}	74.32	2.31	19.64	154.84

Note: natural-logarithm transformed and standardized data were used in statistical analyses

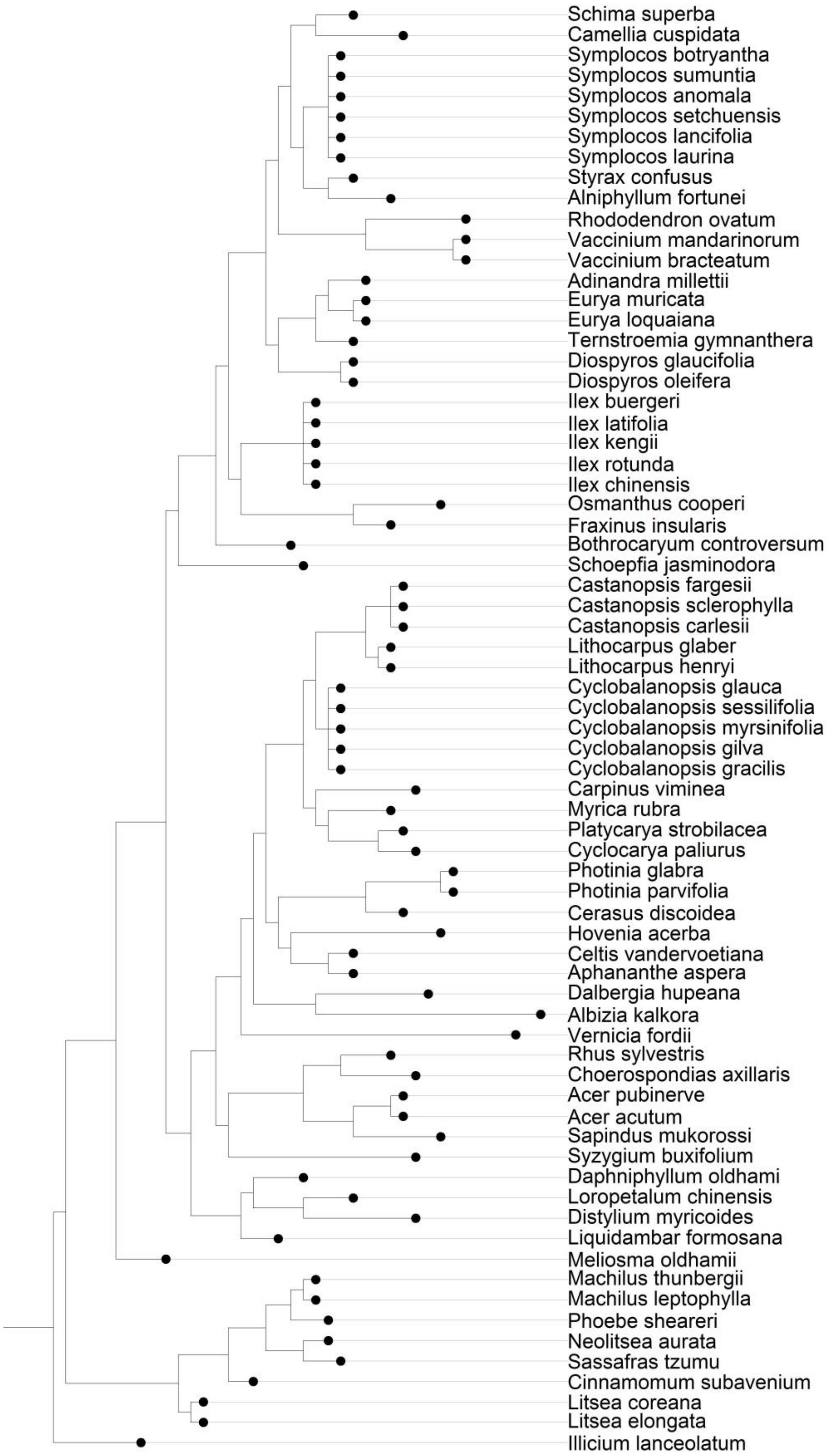


Fig. 6.2. Phylogenetic tree of tree species in overstorey strata in a subtropical forest.

Fig. 6.3. Phylogenetic tree of tree species in understorey strata in a subtropical forest.

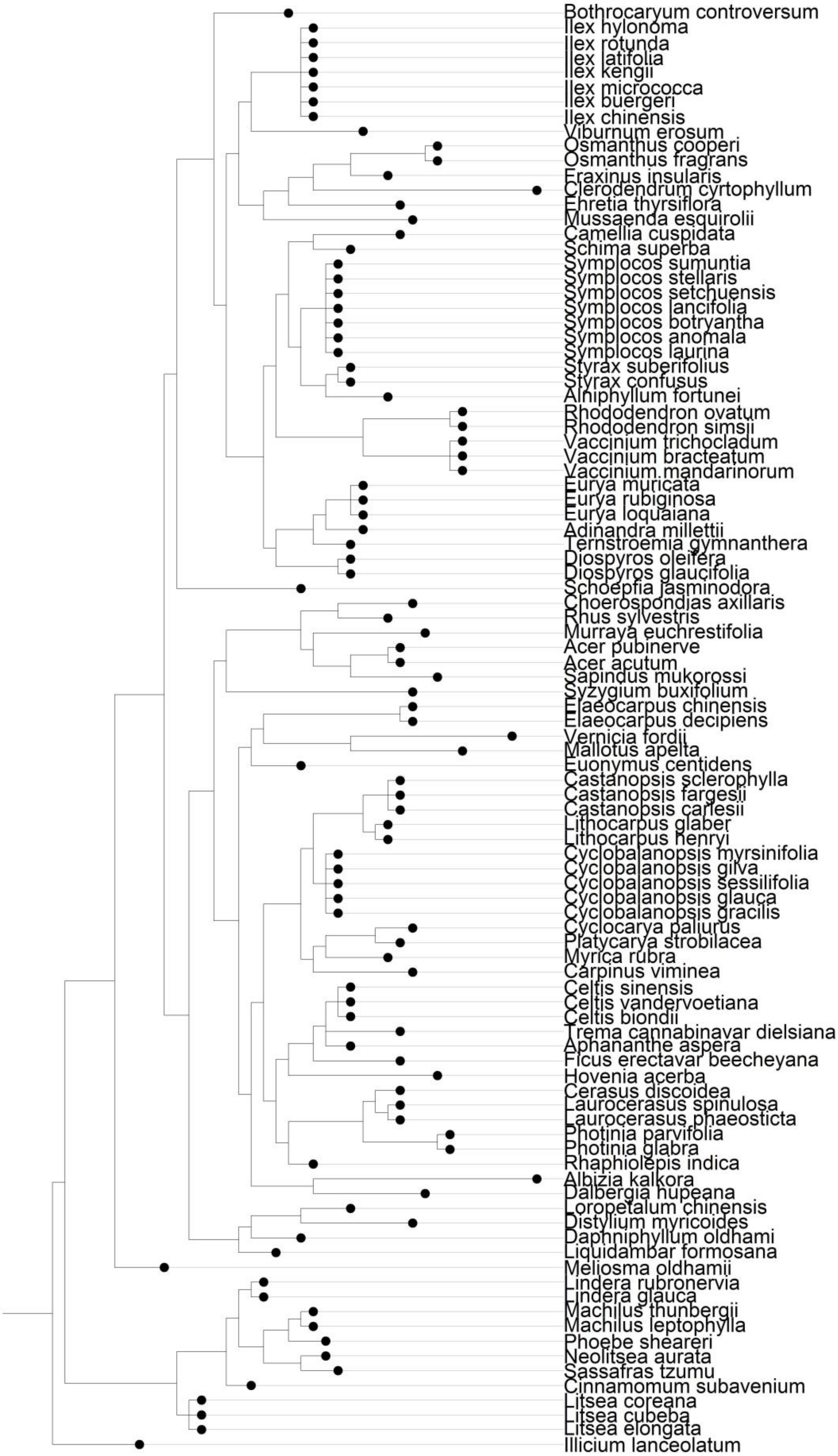


Fig. 6.4. Phylogenetic tree of tree species in whole-community in a subtropical forest.

6.2.2. Statistical analyses

We performed multiple linear regressions models (i.e. general linear models) to evaluate how aboveground biomass was driven by functional trait diversity and evolutionary diversity at each of overstorey and understorey strata across local environmental conditions. More specifically, we jointly included all indices of functional trait diversity (4 indices) and evolutionary diversity (4 indices) in order to test the effects of evolutionary diversity and functional trait diversity on aboveground biomass across forest strata._ENREF_3 For comparison, we also evaluated how aboveground biomass was driven by functional trait diversity and evolutionary diversity at whole-community level across local environmental conditions. In all models, we included local environmental factors, i.e. soil PC1, soil PC2, topography PC1 and PC2, as covariates. We used all subsets regression analysis and selected the optimal model that had lowest AICc (i.e. Akaike Information Criterion adjusted for small sample sizes). Models were considered to be equally supported if the difference in AICc was less than two units (Bartoń 2016). When models were equally supported, we selected the most parsimonious model by considering the lowest number of predictors. General linear models were performed using the *stats* package and all subsets regression analyses using the *MuMIn* package (Bartoń 2016). We plotted a bivariate model's response (optimal linear model) against each predictor's marginal effect (i.e. while holding all other predictors constant), by using the *plotmo* package (Milborrow 2015).

We tested spatial autocorrelation on the relationship between each predictor and response variable (i.e. aboveground biomass) by using generalized least-squares (GLS) model. Spatial autocorrelation may only affects tests of correlation between response and predictor variables when both variables are spatially autocorrelated (Legendre *et al.* 2002). We therefore performed GLS models, using the *nlme* package (Pinheiro & Bates 2016), with and without spatial autocorrelation among subplots for each of the relationships between predictors and aboveground biomass, as recommended by previous studies (Chisholm *et al.* 2013, Yuan *et al.* 2016). The goodness-of-fit of spatial and non-spatial models was evaluated by the AIC (e.g. Chisholm *et al.* 2013). We found that models without spatial autocorrelation always had the lower AIC values (Table 6.2), which is similar to the recent observations in forest ecosystems (Ali & Yan 2017c, b, Yuan *et al.* 2016). In addition, we applied the Moran's I test for spatial autocorrelation in the selected optimal linear model residuals, while assessing the range and type of spatial autocorrelation in lag classes by plotting the correlograms (Fig. 6.5), using the *spdep* package (Bivand 2016). The complementary Pearson's correlations and bivariate relationships to the general linear models are shown in Tables 6.3, 6.4 and 6.5, and Figs 6.6-6.8 (also see Table 6.6), respectively.

Table 6.2. Summary of the generalized least-squares (GLS) models of aboveground biomass on predictors at forest strata and whole-community level in a subtropical forest. 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; Topo, topography; PC1 and PC2, PCA axes.

GLS model	Model	Coefficient	*t*-value	*P*-value	AIC	R^2_{pseudo}
Forest strata						
AGB ~ FRic	Non-spatial	0.20	3.31	0.001	692.08	0.057
	Spatial	0.22	3.43	<0.001	699.97	0.057
AGB ~ FEve	Non-spatial	-0.13	-2.19	0.030	698.07	0.020
	Spatial	-0.15	-2.39	0.018	705.84	0.020
AGB ~ FDis	Non-spatial	-0.11	-1.82	0.071	699.55	0.005
	Spatial	-0.15	-2.39	0.018	706.20	0.005
AGB ~ FDiv	Non-spatial	-0.12	-2.09	0.038	698.54	0.012
	Spatial	-0.13	-2.15	0.032	706.93	0.012
AGB ~ PD	Non-spatial	0.34	5.56	<0.001	673.62	0.126
	Spatial	0.34	5.65	<0.001	681.69	0.126
AGB ~ PSE	Non-spatial	-0.13	-2.18	0.030	698.05	0.021
	Spatial	-0.19	-3.04	0.003	702.69	0.021
AGB ~ PSC	Non-spatial	0.36	6.17	<0.001	669.24	0.168
	Spatial	0.38	6.45	<0.001	675.40	0.168
AGB ~ PSV	Non-spatial	-0.28	-4.56	<0.001	684.01	0.111
	Spatial	-0.31	-4.92	<0.001	688.75	0.111
AGB ~ Soil PC1	Non-spatial	-0.09	-2.27	0.024	698.59	0.032
	Spatial	-0.09	-2.49	0.013	706.34	0.032
AGB ~ Soil PC2	Non-spatial	-0.28	-5.87	<0.001	672.62	0.156
	Spatial	-0.29	-6.06	<0.001	679.75	0.156
AGB ~ Topo PC1	Non-spatial	0.32	6.66	<0.001	664.50	0.186
	Spatial	0.33	6.89	<0.001	670.70	0.186
AGB ~ Topo PC2	Non-spatial	-0.10	-1.30	0.195	700.57	0.007
	Spatial	-0.08	-1.07	0.284	709.89	0.007
Whole-community level						
AGB ~ FRic	Non-spatial	0.30	3.44	<0.001	354.34	0.088
	Spatial	0.30	3.44	<0.001	358.28	0.088
AGB ~ FEve	Non-spatial	-0.12	-1.34	0.182	363.87	0.014
	Spatial	-0.12	-1.34	0.183	367.83	0.014
AGB ~ FDis	Non-spatial	-0.15	-1.68	0.095	362.86	0.022
	Spatial	-0.15	-1.70	0.091	366.75	0.022
AGB ~ FDiv	Non-spatial	0.08	0.94	0.348	364.78	0.007
	Spatial	0.09	1.01	0.317	368.62	0.007

AGB ~ PD	Non-spatial	0.31	3.64	<0.001	353.06	0.097
	Spatial	0.31	3.64	<0.001	357.02	0.097
AGB ~ PSE	Non-spatial	-0.27	-3.17	0.002	356.00	0.075
	Spatial	-0.28	-3.17	0.002	359.95	0.075
AGB ~ PSC	Non-spatial	0.20	2.22	0.028	360.83	0.038
	Spatial	0.20	2.22	0.028	364.83	0.038
AGB ~ PSV	Non-spatial	-0.16	-1.84	0.068	362.32	0.027
	Spatial	-0.16	-1.84	0.068	366.32	0.027
AGB ~ Soil PC1	Non-spatial	-0.04	-0.90	0.370	366.09	0.007
	Spatial	-0.04	-0.88	0.382	370.05	0.007
AGB ~ Soil PC2	Non-spatial	-0.18	-2.85	0.005	358.42	0.062
	Spatial	-0.18	-2.85	0.005	362.42	0.062
AGB ~ Topo PC1	Non-spatial	0.18	2.72	0.007	359.02	0.057
	Spatial	0.18	2.72	0.007	363.02	0.057
AGB ~ Topo PC2	Non-spatial	-0.17	-1.64	0.103	362.68	0.021
	Spatial	-0.17	-1.63	0.105	366.67	0.021

In addition, we employed structural equation model (SEM) in order to evaluate whether functional trait diversity and evolutionary diversity of overstorey strata affect understorey strata and its relationship with aboveground biomass. Here, we selected best predictors for aboveground biomass which were retained in the selected optimal model for overstorey and understorey strata. In order to keep possible consistency with the optimal linear model and to test our second prediction, we critically selected the best-fit SEM based on the following three hypothesized paths: 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 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 strata on understorey aboveground biomass. Best-fit SEM was assessed through several tests (Malaeb *et al.* 2000), i.e., the Chi-square (χ^2) test, goodness-of-fit index (GFI), comparative fit index (CFI) and standardized root mean square residual (SRMR). The SEM was implemented using the *lavaan* package (Rosseel 2012).

All numerical variables including aboveground biomass, functional trait diversity and evolutionary diversity indices were natural-logarithm transformed and standardized. Transformations of the variables were conducted for the purpose to meet the assumptions of normality and linearity, and to reduce the effect of outliers and to account for possible nonlinear relationships between variables, and to allow comparisons among multiple predictors and models (Zuur *et al.* 2009). For all statistical analyses R 3.2.2 was used (R Development Core Team 2015).

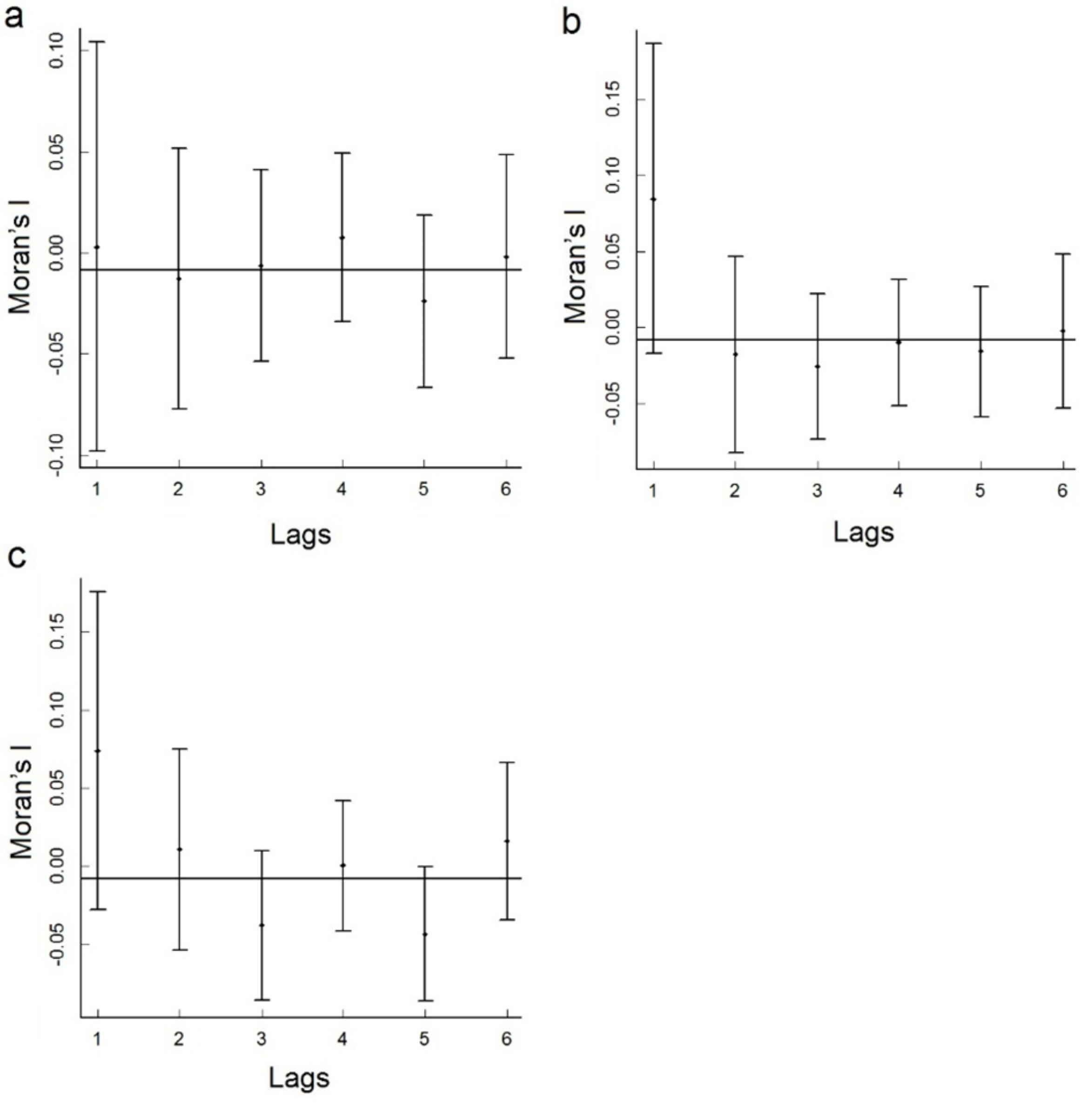


Fig. 6.5. Correlograms plots of the Moran's I test on the residuals of linear multiple models in order to check the range and type of autocorrelation in lag classes. a) Overstorey optimal model, b) understorey optimal model, and c) whole-community optimal model (Table 6.7).

Table 6.3. Pearson's correlation coefficient between pairs of all tested predictors at overstorey strata. Bold numbers indicate significant correlations ($P < 0.05$). All the abbreviations for variables are explained in Table 6.2.

	FRic	FEve	FDiv	FDis	PD	PSV	PSR	PSE	PSC	Soil PC1	Soil PC2	Topo PC1	Topo PC2
FRic	---												
FEve	-0.02	---											
FDiv	-0.13	**0.21**	---										
FDis	-0.04	**0.24**	**0.72**	---									
PD	0.11	**-0.21**	**-0.24**	0.06	---								
PSV	-0.16	0.08	0.10	-0.01	**-0.18**	---							
PSR	**0.18**	-0.14	**-0.21**	0.13	**0.90**	-0.02	---						
PSE	0.06	**0.23**	0.04	**0.36**	0.06	**0.44**	0.20	---					
PSC	-0.05	-0.12	-0.16	0.05	**0.46**	**-0.68**	**0.43**	**-0.30**	---				
Soil PC1	-0.12	0.10	**0.24**	0.17	**-0.18**	**0.28**	-0.14	**0.18**	**-0.25**	---			
Soil PC2	-0.13	0.10	0.10	-0.14	**-0.44**	**0.36**	**-0.39**	0.01	**-0.30**	0.00	---		
Topo PC1	0.12	-0.11	-0.16	0.04	**0.46**	**-0.34**	**0.41**	-0.07	**0.35**	**-0.47**	**-0.69**	---	
Topo PC2	-0.04	0.01	0.17	0.04	-0.03	0.12	-0.08	-0.04	-0.07	0.16	0.03	-0.00	---

Table 6.4. Pearson's correlation coefficient between pairs of all tested predictors at understorey strata. Bold numbers indicate significant correlations ($P < 0.05$). All the abbreviations for variables are explained in Table 6.2.

	FRic	FEve	FDiv	FDis	PD	PSV	PSR	PSE	PSC	Soil PC1	Soil PC2	Topo PC1	Topo PC2
FRic	---												
FEve	0.05	---											
FDiv	-0.01	**0.22**	---										
FDis	0.30	**0.24**	**0.72**	---									
PD	**0.87**	0.05	-0.12	0.17	---								
PSV	**-0.36**	-0.04	-0.09	-0.14	**-0.23**	---							
PSR	**0.89**	0.04	-0.13	**0.19**	**0.94**	-0.09	---						

PSE	**0.27**	0.15	0.14	**0.46**	**0.24**	0.08	**0.28**	---					
PSC	**0.69**	0.00	0.01	**0.23**	**0.58**	**-0.74**	**0.53**	0.08	---				
Soil PC1	**-0.31**	-0.04	**-0.23**	-0.09	**-0.27**	0.13	**-0.22**	0.08	**-0.24**	---			
Soil PC2	**-0.26**	-0.14	-0.16	**-0.23**	**-0.23**	**0.57**	-0.12	-0.09	**-0.45**	0.00	---		
Topo PC1	**0.36**	-0.02	**0.25**	**0.28**	**0.31**	**-0.48**	**0.23**	0.07	**0.51**	**-0.47**	**-0.69**		
Topo PC2	-0.06	-0.10	-0.09	0.02	-0.01	-0.03	-0.05	-0.07	-0.04	0.16	0.03	-0.00	---

Table 6.5. Pearson's correlation coefficient between pairs of all tested predictors at whole-community level. Bold numbers indicate significant correlations ($P < 0.05$). All the abbreviations for variables are explained in Table 6.2.

	FRic	FEve	FDiv	FDis	PD	PSV	PSR	PSE	PSC	Soil PC1	Soil PC2	Topo PC1	Topo PC2
FRic	---												
FEve	-0.06	---											
FDiv	-0.01	0.06	---										
FDis	-0.01	0.13	**0.59**	---									
PD	**0.88**	-0.10	-0.09	-0.09	---								
PSV	**-0.50**	-0.12	-0.10	**-0.24**	**-0.44**	---							
PSR	**0.89**	-0.06	-0.08	-0.06	**0.94**	**-0.35**	---						
PSE	**-0.19**	0.02	-0.13	0.03	**-0.20**	**0.38**	**-0.14**	---					
PSC	**0.65**	0.09	0.03	**0.18**	**0.60**	**-0.85**	**0.60**	**-0.30**	---				
Soil PC1	**-0.31**	-0.02	0.05	0.11	**-0.28**	**0.25**	**-0.24**	0.04	**-0.29**	---			
Soil PC2	**-0.30**	-0.09	0.09	-0.15	**-0.27**	**0.61**	**-0.24**	**0.30**	**-0.57**	0.00	---		
Topo PC1	**0.39**	0.12	0.04	0.13	0.32	**-0.59**	**0.30**	**-0.25**	0.60	**-0.47**	**-0.69**	---	
Topo PC2	-0.03	0.01	0.11	0.08	-0.03	-0.04	-0.07	-0.19	0.00	0.16	0.03	-0.00	---

Table 6.6. Summary of the simple linear models for bivariate relationships of functional trait diversity, evolutionary diversity indices and environmental factors axes with aboveground biomass at each of the forest strata and whole-community level of subtropical forests.

Abbreviations: Beta, standardized regression coefficient; *P*, significance level; R^2, coefficient of determination; PMSE, predictive mean squared error; all other abbreviations for variables are explained in Table 6.2. *P* values < 0.05 are given in bold.

Predictor	*Understorey strata*				*Overstorey strata*				*Whole-community level*			
	Beta	*P*	PMSE	R^2	Beta	*P*	PMSE	R^2	Beta	*P*	PMSE	R^2
Functional trait diversity indices												
FRic	0.42	**<0.001**	0.86	0.18	0.05	0.543	1.04	0.00	0.30	**0.001**	0.95	0.09
FEve	0.06	0.521	1.04	0.00	-0.34	**<0.001**	0.92	0.12	-0.12	0.182	1.03	0.01
FDiv	-0.01	0.939	1.05	0.00	-0.22	**0.016**	1.00	0.05	0.08	0.348	1.03	0.01
FDis	0.05	0.566	1.04	0.00	-0.20	**0.027**	1.00	0.04	-0.15	0.095	1.02	0.02
Evolutionary diversity indices												
PD	0.37	**<0.001**	0.90	0.14	0.34	**<0.001**	0.94	0.11	0.31	**<0.001**	0.94	0.10
PSV	-0.43	**<0.001**	0.85	0.18	-0.24	**0.007**	0.99	0.06	-0.16	0.068	1.01	0.03
PSE	0.01	0.883	1.05	0.00	-0.30	**<0.001**	0.94	0.09	-0.27	**0.002**	0.96	0.08
PSC	0.49	**<0.001**	0.80	0.24	0.33	**<0.001**	0.92	0.11	0.20	**0.028**	1.00	0.04
Environmental factors axes												
Soil PC1	-0.16	**0.001**	0.95	0.09	-0.03	0.499	1.03	0.00	-0.04	0.370	1.03	0.01
Soil PC2	-0.42	**<0.001**	0.70	0.33	-0.15	**0.018**	0.99	0.04	-0.18	**0.005**	0.97	0.06
Topo PC1	0.50	**<0.001**	0.58	0.45	0.15	**0.030**	0.99	0.04	0.18	**0.007**	0.98	0.06
Topo PC2	-0.03	0.811	1.05	0.00	-0.17	0.097	1.02	0.02	-0.17	0.103	1.02	0.02

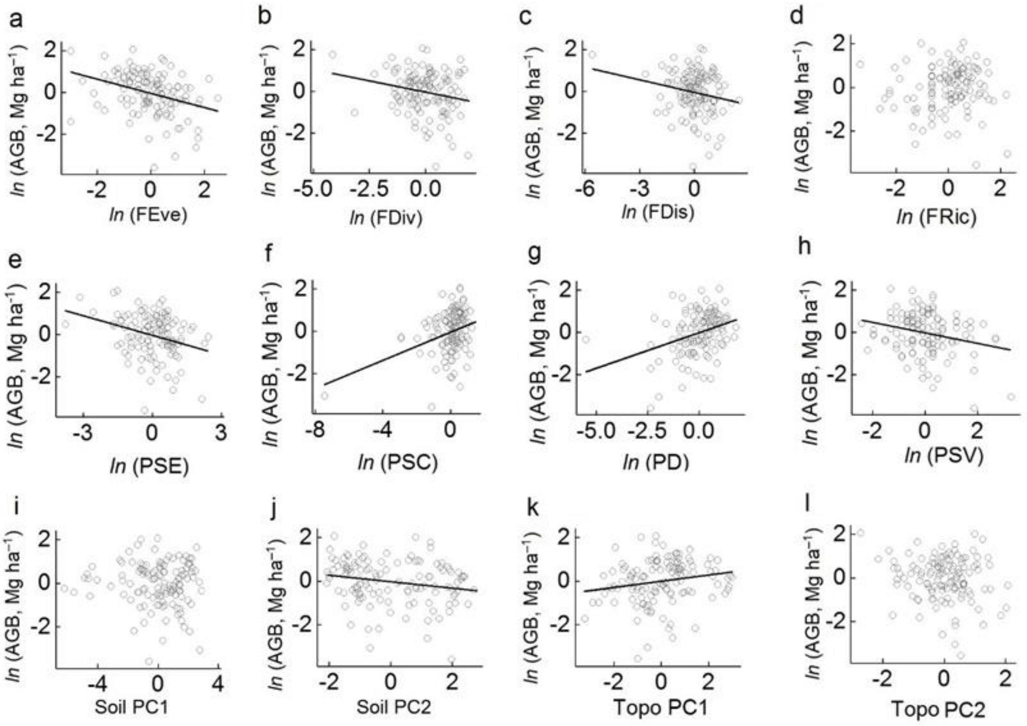


Fig. 6.6. The bivariate relationships between aboveground biomass (AGB) and predictors (a-d, functional trait diversity indices; e-h, evolutionary diversity indices; and i-l, environmental factors axes; *n* = 125) at overstorey strata in subtropical evergreen broadleaf forests in Eastern China. Fitted regressions are significant at $P < 0.05$. All the abbreviations for variables are explained in Table 6.2, and summary of statistics for each bivariate relationships are provided in Table 6.6.

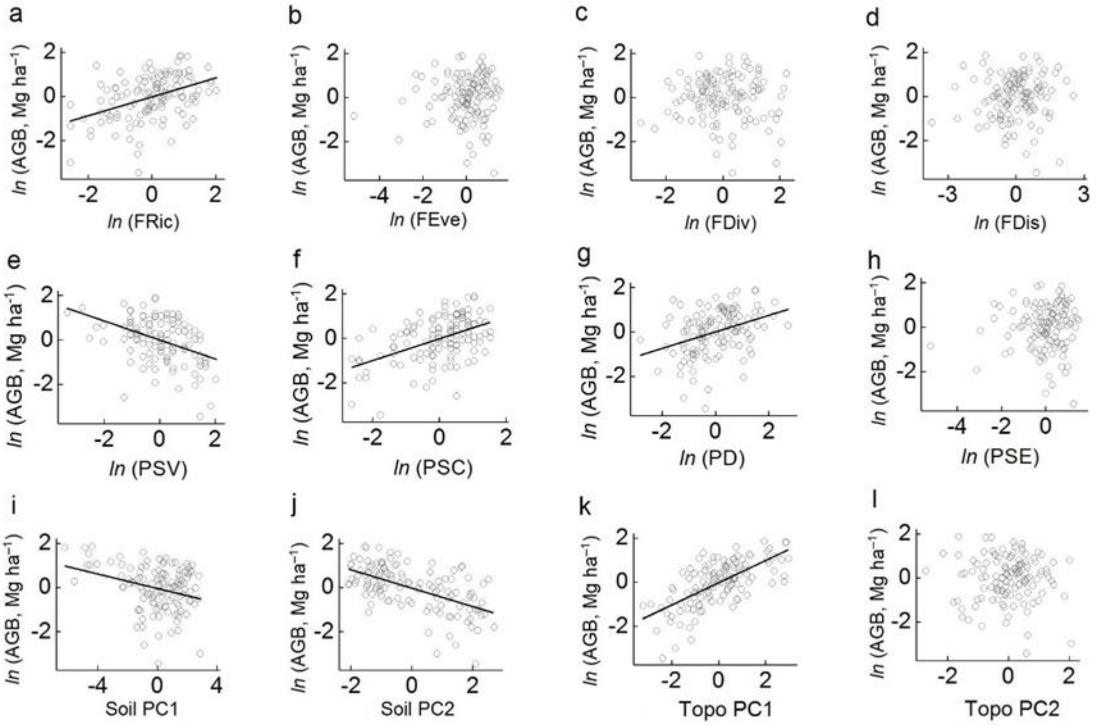


Fig. 6.7. The bivariate relationships between aboveground biomass (AGB) and predictors (a-d, functional trait diversity indices; e-h, evolutionary diversity indices; and i-l, environmental factors axes; *n* = 125) at understorey strata in subtropical evergreen broadleaf forests in Eastern China. Fitted regressions are significant at $P < 0.05$. All the abbreviations for variables are explained in Table 6.2, and summary of statistics for each bivariate relationships are provided in Table 6.6.

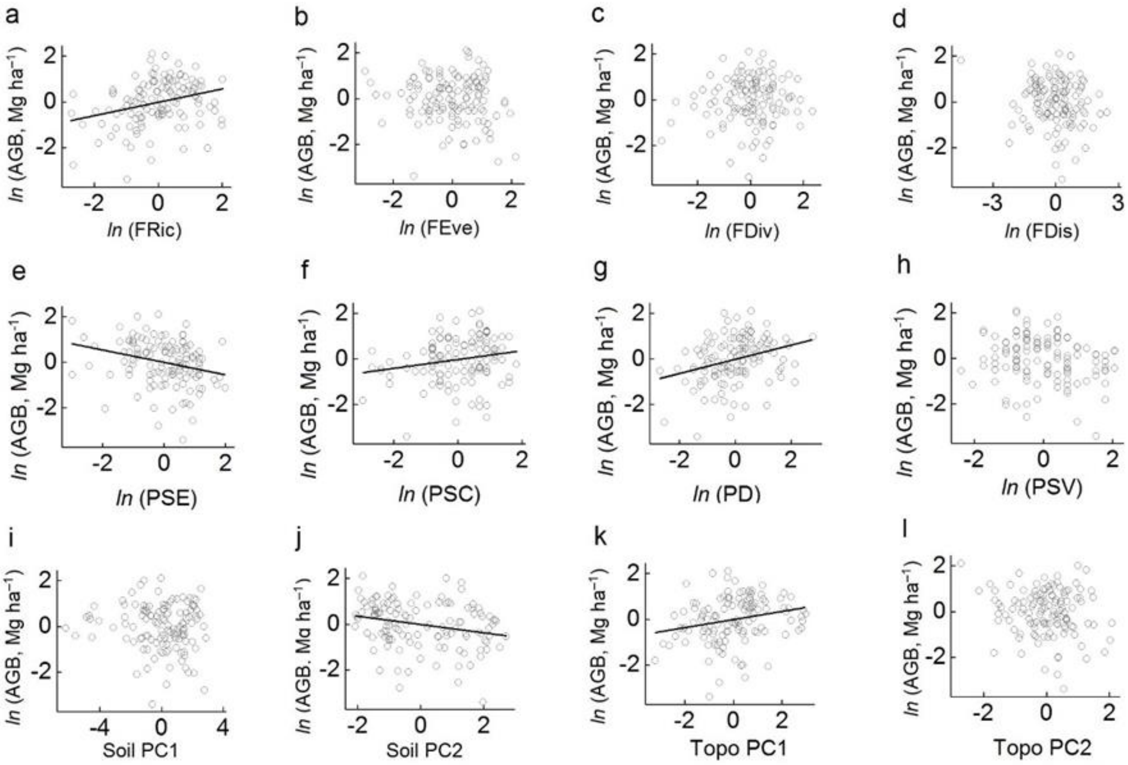


Fig. 6.8. The bivariate relationships between aboveground biomass (AGB) and predictors (a-d, functional trait diversity indices; e-h, evolutionary diversity indices; and i-l, environmental factors axes; n = 125) at whole-community level in subtropical evergreen broadleaf forests in Eastern China. Fitted regressions are significant at $P < 0.05$. All the abbreviations for variables are explained in Table 6.2, and summary of statistics for each bivariate relationships are provided in Table 6.6.

6.3. Results

The overstorey strata optimal model showed that 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 ($\beta = 0.31$, $P < 0.001$) at overstorey strata, with no spatial autocorrelation in the residuals (Table 6.7). This result indicates that overstorey strata have high aboveground biomass when phylogeny is occupied by high closely-related species having highly different abundances, and low functional evenness where most of species' basal area is concentrated in a constrained area of the multivariate-trait space (Fig. 6.9A). The understorey strata optimal model showed that 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 ($\beta = 0.36$, $P < 0.001$) at understorey strata, with no spatial autocorrelation in the residuals (Table 6.7). This finding indicates that understorey strata have high aboveground biomass when they are occupied by high functional richness and low functional dispersion. This result implies that multivariate trait space is filled by most of understorey species' basal area having similar average distances to the basal-area weighted centroid of all species in community trait space, and located on soils with low soil nutrients and high topography (Fig. 6.9B).

Table 6.7. The overstorey strata, understorey strata 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 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 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. Abbreviations for variables are explained in Table 6.2.

Predictors	*Overstorey strata model*			*Understorey strata model*			*Whole-community model*		
	Beta	*t*	*P*	Beta	*t*	*P*	Beta	*t*	*P*
Constant	0.00	0.00	0.997	0.00	–0.01	0.995	0.00	–0.01	0.996
Niche complementarity hypothesis (multivariate functional trait diversity)									
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**
Niche complementarity hypothesis (Evolutionary diversity)									
PD	0.31	3.85	**<0.001**				0.24	2.81	**0.006**
PSE	–0.27	–3.37	**<0.001**						
PSV									
PSC									
Environmental factors effects (soil nutrients, properties and topography axes)									
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									
Model statistics									
F-test (*P*-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*- test (*P*-value)	0.00 (0.826)			0.08 (0.068)			0.07 (0.107)		

In comparison, the whole-community optimal model showed that aboveground biomass (R^2 = 0.23) was best predicted by functional divergence (β = 0.36, P < 0.001), functional dispersion (β = –0.38, P < 0.001), phylogenetic diversity (β = 0.24, P = 0.006) and soil nutrients

($\beta = -0.20$, $P = 0.002$) at whole-community level, with no spatial autocorrelation in the residuals (Table 6.7). This result indicates that whole-community have 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 where most of species basal area having similar average distances is concentrated in the extremes of the multivariate-trait space, and located on soils with low soil nutrients (Fig. 6.9C).

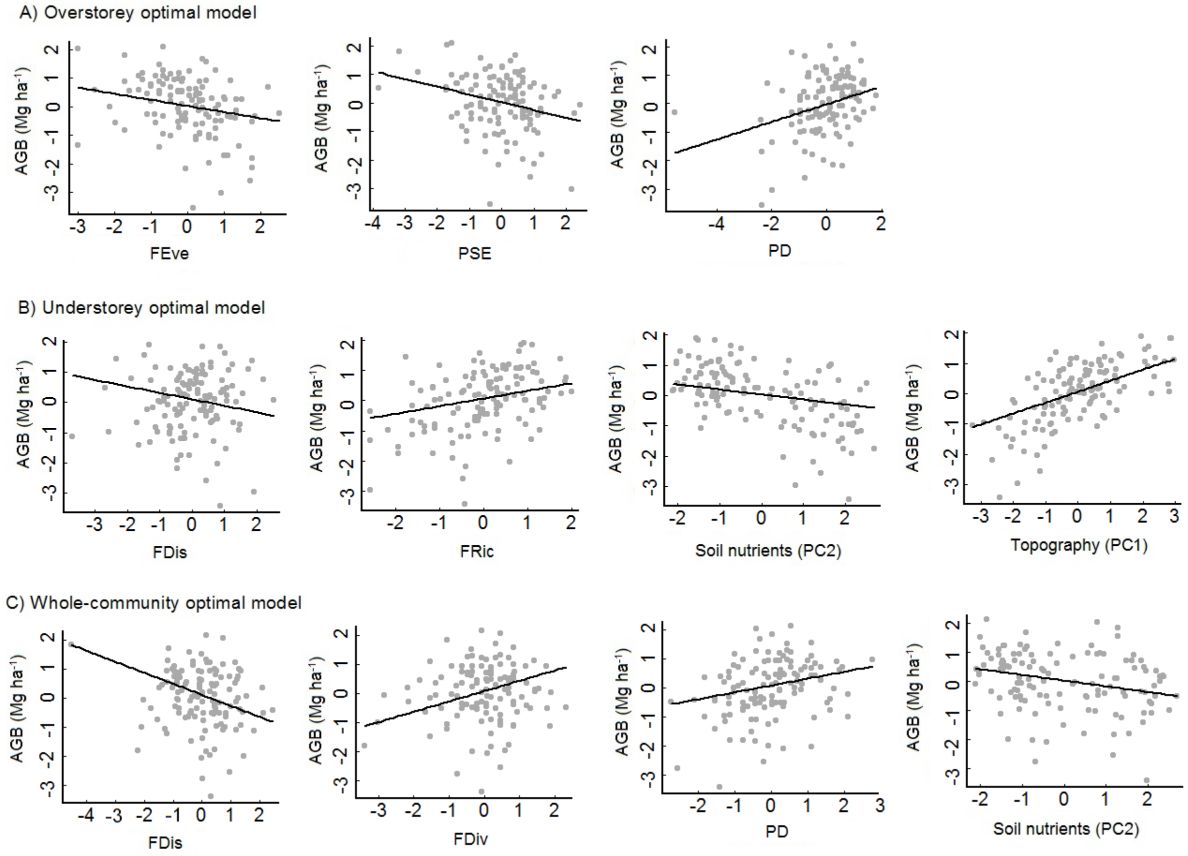


Fig. 6.9. The response of aboveground biomass to the retained predictors in the overstorey strata, understorey strata and whole-community level optimal models (see Table 1 for statistics). (A) Overstorey strata optimal model, aboveground biomass (AGB; Mg ha^{-1}) as a function of functional evenness (FEve), phylogenetic evenness (PSE) and soil phylogenetic diversity (PD); (B) understorey strata optimal model, AGB as a function of functional dispersion (FDis), functional richness (FRic), soil nutrients and topography (PC1); and (C) whole-community level optimal model, AGB as a function of FDis, functional divergence (FDiv), PD and soil nutrients. 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 Figs. 6.6, 6.7 and 6.8 for bivariate relationships.

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 diversity of overstorey species had a significant direct positive effect on understorey functional trait diversity (*β* = 0.55, *P* < 0.001), and as a result indirect positive effect on understorey aboveground biomass (*β* = 0.36, *P* < 0.001; Fig. 6.10). Understorey functional trait diversity (as a latent variable of functional richness and dispersion) had a significant positive direct effect on understorey aboveground biomass (*β* = 0.66, *P* < 0.001; Fig. 6.10). This results indicates that low evolutionary diversity (high phylogenetic diversity and low phylogenetic species evenness) of overstorey strata is the cause for positive functional trait diversity and aboveground biomass at understorey strata, probably due to the resource heterogeneity and big trees effect. For instance, on the one hand, this result indicates that high phylogenetic diversity of overstorey species are promoting understorey functional trait diversity (Fig. 6.10), and hence positive relationship between functional richness and aboveground biomass at understorey strata probably due to the resource heterogeneity (Table 6.7). On the other hand, high phylogenetic species evenness rather than functional evenness are reducing understorey functional trait diversity (Fig. 6.10), and hence negative relationship between functional dispersion and aboveground biomass at understorey strata (Table 6.7), probably due to the high phylogenetic dominance of closely-related overstorey tree species which may consume additional resources, i.e. the big trees effect.

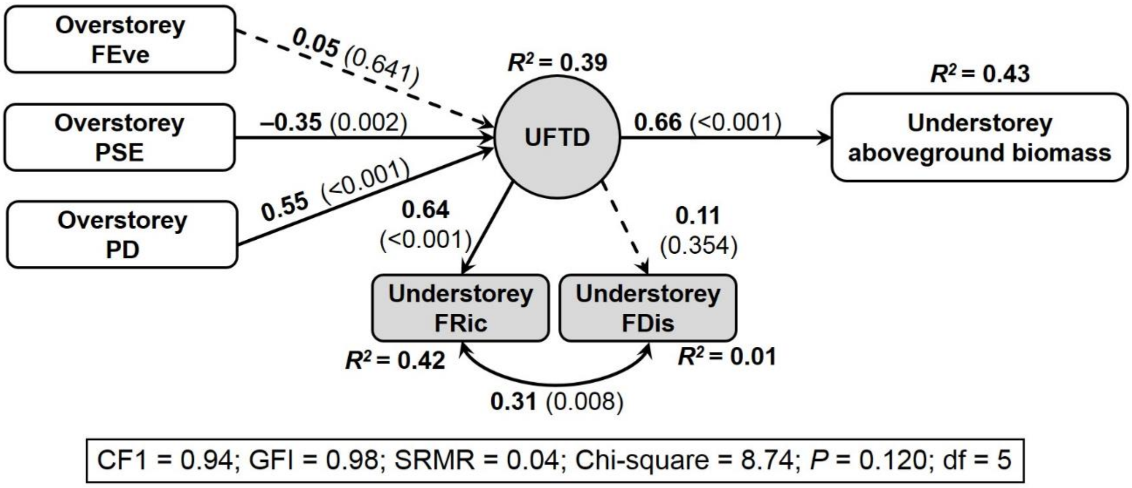


Fig. 6.10. Best-fit structural equation model (SEM) linking evolutionary and functional trait diversity of overstorey (i.e. PD, PSE and FEve) and functional trait diversity of understorey (UFTD as a latent variable for FRic and FDis) with understorey aboveground biomass. Solid arrows represent significant (*P* < 0.05) paths and dashed arrows represent non-significant paths (*P* > 0.05). For each path the standardized regression coefficient and associated *P*-value in bracket 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. The diversity indices of overstorey and understorey strata in SEM were selected based on selected optimal models for overstorey and understorey strata obtained from a series of multiple regressions (see Table 6.7). Abbreviations: FEve, functional evenness; FRic, functional richness; FDis, functional dispersion; PD, phylogenetic diversity; PSE, phylogenetic species evenness; CFI, comparative fit index; GFI, goodness of fit index; SRMR, standardized root mean square residual; df, degree of freedom.

6.4. Discussion

Evolutionary relatedness indicates the ecological uniqueness of species and a predictor of patterns of competitive coexistence (Cahill *et al.* 2008, Valiente-Banuet & Verdú 2007, Webb 2000). For instance, it has been anticipated that ecological differentiation among species is related to evolutionary diversity within a given habitat type (e.g. Cadotte *et al.* 2008). Greater ecological differentiation allowing species to stably coexist together due to the efficient utilisation of resources by co-occurring species (e.g., niche partitioning). These ecologically differentiated species could potentially complement each other in their resource use by differentially capturing resources in space and/or time. Greater niche and trait differences could, in turn, drive high aboveground biomass or productivity (Heemsbergen *et al.* 2004, Hooper *et al.* 2005, Petchey *et al.* 2004). As such, we found that overstorey aboveground biomass are greater for groups of phylogenetically close species having low functional trait variation than for groups of phylogenetically distant species having high functional trait variation. At understorey strata, our results showed that high aboveground biomass is related with functional trait diversity, after accounting for the effects of overstorey functional and evolutionary diversity. Therefore, the main novelty of this study is determining that high aboveground biomass in natural forests is greatly dependent on the species coexistence based on their ecological similarity and biotic interactions as well as partitioning of limiting resources (e.g. Cahill *et al.* 2008, Valiente-Banuet & Verdú 2007, Webb 2000).

In this study, our optimal models suggest that evolutionary diversity indices compared to functional trait diversity indices are important predictors for best explaining variation in aboveground biomass at overstorey strata, not at understorey strata, while a bit similarly important at whole-community level in a subtropical forest. This result is not surprising because evolutionary diversity has been hypothesized as the proxy of functional trait diversity (Cadotte *et al.* 2008, Cadotte *et al.* 2009, Flynn *et al.* 2011, Paquette & Messier 2011, Yuan *et al.* 2016), and therefore as significant predictors of aboveground biomass at overstorey strata and whole-community level. Additionally, we also expected functional trait diversity indices to better explain variation in aboveground biomass at understorey strata, since trait differences should drive ecological differences – regardless of patterns of shared ancestry on the traits (e.g. Cadotte *et al.* 2009). Consequently, we found that evolutionary diversity and functional trait diversity have underpinned similar ecological mechanisms for driving high aboveground biomass at overstorey and understorey strata, as well as at whole-community level, in a subtropical forest. However, the ecological mechanisms at overstorey and understorey strata seem to be very different, which could be the results of biotic interactions, resource availability and heterogeneity at each individual strata (Ali & Yan 2017c, Zhang *et al.* 2016a).

As hypothesized we found that overstorey strata dominated by phylogenetically close and functionally similar species had high aboveground biomass in the studied forest. On the one hand, low phylogenetic species evenness and high phylogenetic diversity of overstorey strata interpret the co-occurrence of phylogenetically close species, and as indication for environmental filtering on phylogenetically conserved traits (Cavender-Bares *et al.* 2009, Kembel & Hubbell 2006, Webb 2000). On the other hand, low functional evenness of overstorey species indicates that most of the species' basal area is concentrated in a restricted part of the multivariate-trait space, and hence contrary to the prediction of niche complementarity hypothesis (Villéger *et al.* 2008). In addition, the bivariate relationships suggest that overstorey strata 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 & Woodall 2014). In combination, our results suggest that phylogenetically close overstorey species have high aboveground biomass due to ecological similarity and hence absence of strong biotic interactions among functionally similar species, which leads phylogenetically close anf functionally similar species to use similar resources (e.g. Cavender-Bares *et al.* 2009, Wiens & Graham 2005).

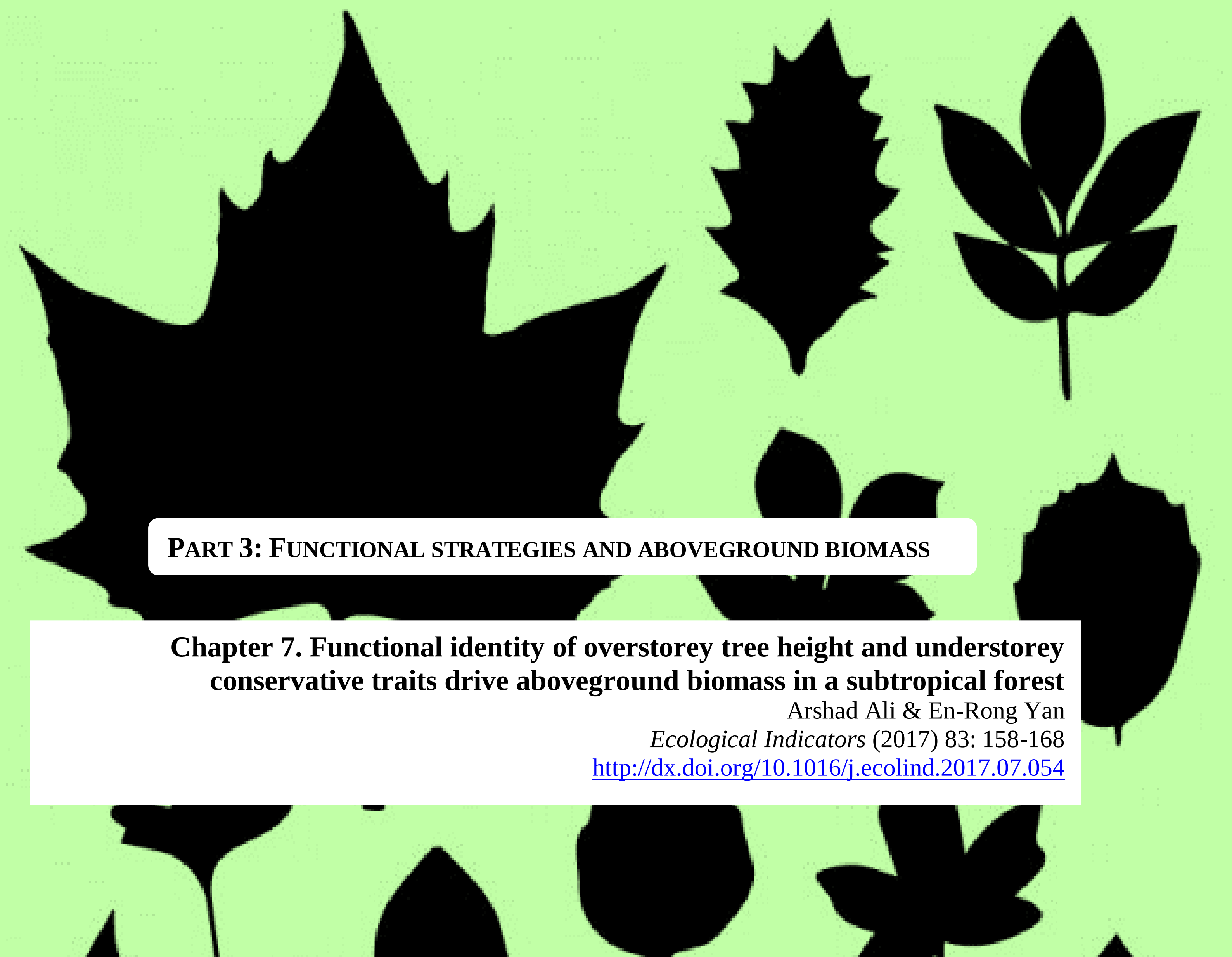
At understorey strata, high aboveground biomass is driven by species having variety of functional traits with similar average functional distances for efficient ultilisation of resources under resource limited environments (Valiente-Banuet & Verdú 2007). High functional richness indicates that multivariate trait space is filled by most of species' basal area (Villéger *et al.* 2008), and hence supporting the niche complementarity hypothesis (Heemsbergen *et al.* 2004, Hooper *et al.* 2005). 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 complementarity among species with different traits (Loreau *et al.* 2001). Consequently, SEM result showed that functional richness and dispersion were positively correlated for driving high aboveground biomass under the niche complementarity mechanism, where functional dispersion had negligible positive contribution. This result indicates that the selection effect was strongest when functional richness was low, while complementarity was greatest with high functional richness (Villéger *et al.* 2008). These opposing mechanism might be happen due to the effects of overstorey strata. As such, we found that high evolutionary relatedness (low phylogenetic species evenness and high phylogenetic diversity) of overstorey strata has modulated the positive relationship between functional trait diversity (a latent variable of functional dispersion and richness) and aboveground biomass at understorey strata. It is plausible that the niche complementarity effect may be less important in stable and productive environments, where competition is often the most common form of species interaction, than in unstable and stressful environments (Paquette & Messier 2011).

Although functional richness and functional dispersion were significant best predictors of aboveground biomass at understorey strata, 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 having almost similar hypothetical trait (i.e. functional strategy) shared by all the species (Cavender-Bares *et al.* 2009), and as indication for conservative strategy (Ali & Yan 2017b). This could result either from competition causing overdispersion of conserved traits or environmental filtering on ecologically important convergent traits, due to partitioning of limiting resources (Kembel & Hubbell 2006, Valiente-Banuet & Verdú 2007, Webb 2000). 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 (Cadotte *et al.* 2008, Cavender-Bares *et al.* 2009, Simberloff 1970, Valiente-Banuet & Verdú 2007, Webb 2000). Taken together, our results suggest that understorey strata have high aboveground biomass when they are occupied by high clustering of phylogenetically distant species having high functional richness with similar average functional distances or a specific functional strategy (Ali & Yan 2017b). These results might be happened due to the partitioning of limiting resources and absence of strong biotic interactions, which leads the coexistence of phylogenetically distant species under the niche complementarity mechanism (Heemsbergen *et al.* 2004, Hooper *et al.* 2005, Valiente-Banuet & Verdú 2007).

In comparison, the whole-community optimal model showed that high aboveground biomass is strongly driven by high phylogenetic diversity, high functional divergence and low functional dispersion. However, the bivariate relationships suggest that overstorey strata have high aboveground biomass when they are occupied by 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 & Woodall 2014). As hypothesized, this mechanism at the whole-community level might be resulted due to 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 & Yan 2017b).

6.5. Concluding remarks

We conclude that evolutionary diversity indices compared to functional trait diversity indices within a plot are important predictors for best explaining variation in aboveground biomass at overstorey strata, not at understorey strata, while a bit similarly important at whole-community level in a subtropical forest. Evolutionary diversity serves as a useful proxy for functional trait diversity, and therefore evolutionary diversity and functional trait diversity have underpinned similar ecological mechanisms for driving high aboveground biomass across forest strata and whole-community level. The ecological mechanisms at overstorey and understorey strata compared to whole-community level seem to be very different, which could be the results of biotic interactions, resource availability and heterogeneity at each individual strata. For example, understorey aboveground biomass are greater for groups of phylogenetically distant species having high functional trait diversity, while high overstorey aboveground biomass are related with groups of phylogenetically close species having low functional trait diversity. High evolutionary relatedness of overstorey strata has modulated the positive relationship between functional trait diversity and aboveground biomass at understorey strata. 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.



PART 3: FUNCTIONAL STRATEGIES AND ABOVEGROUND BIOMASS

Chapter 7. Functional identity of overstorey tree height and understorey conservative traits drive aboveground biomass in a subtropical forest

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7.1. Introduction

One of the biggest challenges in functional ecology is to explain the underlying mechanisms for the relationships between functional attributes of biodiversity (i.e. functional trait diversity and identity) and ecosystem functions in forest ecosystems. Although the niche complementarity and mass ratio hypotheses have been put forward to explain the relationships between functional attributes of biodiversity and ecosystem functions (e.g. Ali *et al.* 2017, Conti & Díaz 2013, Finegan *et al.* 2015, Lin *et al.* 2016, Prado-Junior *et al.* 2016), few studies have tested these relationships across forest strata (i.e. overstorey and understorey). The niche complementarity hypothesis based on species richness has received some empirical support across forest strata (e.g. Zhang *et al.* 2016a), but species differ in functional strategies for their contribution to ecosystem functions (Rüger *et al.* 2012) as predicted by the mass ratio hypothesis (Grime 1998). As such, the relationships between functional attributes of biodiversity and aboveground biomass, especially the associated mechanisms might be fundamentally different across forest strata. To date, few studies have teased apart the contributions of functional attributes of trees with either conservative or acquisitive strategies at overstorey and understorey strata to aboveground biomass in forests.

The mass ratio hypothesis predicts that ecosystem function is driven by the (traits of the) most abundant species in plant communities (Grime 1998). Aboveground biomass ought to closely relate to community-weighted mean (CWM) of a trait values, i.e., functional identity (Díaz *et al.* 2007, Garnier *et al.* 2004, Tobner *et al.* 2016). With respect to the plant trait syndromes, high CWM of specific leaf area, leaf nitrogen and phosphorus concentrations in plant communities associate with high productivity or aboveground biomass due to fast-growing of acquisitive species (Chiang *et al.* 2016, Finegan *et al.* 2015). In contrast, high CWM of leaf dry matter content and wood density indicate a low productivity in communities dominated by conservative species (Garnier *et al.* 2004, Wright *et al.* 2010). Additionally, tree species present in overstorey strata are tall stature whereas tree species in understorey strata are short stature. Therefore, tree height and diameter relate to the investment of structure per unit of stem volume, and hence directly influencing its aboveground biomass (Conti & Díaz 2013, Moles *et al.* 2009). In some extent, the potential maximum plant height or maximum diameter of a given species reflects its adult stature for growth and survival (Poorter & Bongers 2006, Poorter *et al.* 2008), and positively relates with productivity or aboveground biomass through functionally dominant strategy (i.e. CWM of plant maximum height or diameter) (Cavanaugh *et al.* 2014, Finegan *et al.* 2015, Prado-Junior *et al.* 2016).

Since light condition is more stressful in understorey than in overstorey in complex natural forests (e.g. Brenes-Arguedas *et al.* 2011), trees in understorey tend to employ conservative strategy whereas acquisitive strategy may be more apparent in overstorey strata (Bartels & Chen 2010, Zhang *et al.* 2016a). Previous studies suggest that conservative strategy is crucial for plant species to cope with more stressful environments (i.e., dry forests) (Prado-Junior *et al.* 2016), whereas acquisitive strategy is advantageous for plant species in more favorable conditions such as in wet and moist forests (Finegan *et al.* 2015, Malhi *et al.* 2004). Under the mass ratio hypothesis, high aboveground biomass or productivity is strongly driven by functional identity with either conservative strategy in dry forests (Prado-Junior *et al.* 2016) or acquisitive strategy in wet and moist forests (Finegan *et al.* 2015). When the data have been combined across dry and moist tropical forests, Cavanaugh *et al.* (2014) found that only functional identity matters for high aboveground biomass. Insightfully, these findings provide strong evidence for the presence of big trees effect on available resources for shaping community structure, assemblage and functions. However, as a coin has two sides, big trees in overstorey strata can positively contribute to ecosystem functions through large stem volumes and consumption of resources, but at the same time, they may also slow down the ecosystem functioning rates in understorey strata in forests by reducing light and soil nutrients availabilities (Poorter *et al.* 2015, Slik *et al.* 2013, Zhang *et al.* 2016a).

In this study, we tested how aboveground biomass was driven by functional identity with either conservative or acquisitive strategies of tree species at overstorey and understorey strata separately, in addition to the whole-community level in a subtropical forest. Considering the mass ratio effect in overstorey strata where light condition is favorable, we hypothesize (H_{1a}) the positive relationships of aboveground biomass with CWM of acquisitive traits, especially with functional identity of potential maximum tree height, while the negative relationships of aboveground biomass with CWM of conservative traits. With regard to the mass ratio effect in light-stressful understorey, we hypothesize (H_{1b}) the positive relationships of aboveground biomass with CWM of conservative traits, while negative relationships of aboveground biomass with CWM of acquisitive traits. In addition, due to the dominant role of big trees on available resources, we hypothesize (H_{1c}) that functional identity of overstorey strata negatively relates with functional identity and aboveground biomass of understorey strata. For the comparison to whole-community level, we hypothesize (H_2) that high aboveground biomass is potentially driven by high CWM of acquisitive traits due to the dominant role of big trees on the available resources (Fig. 7.1).

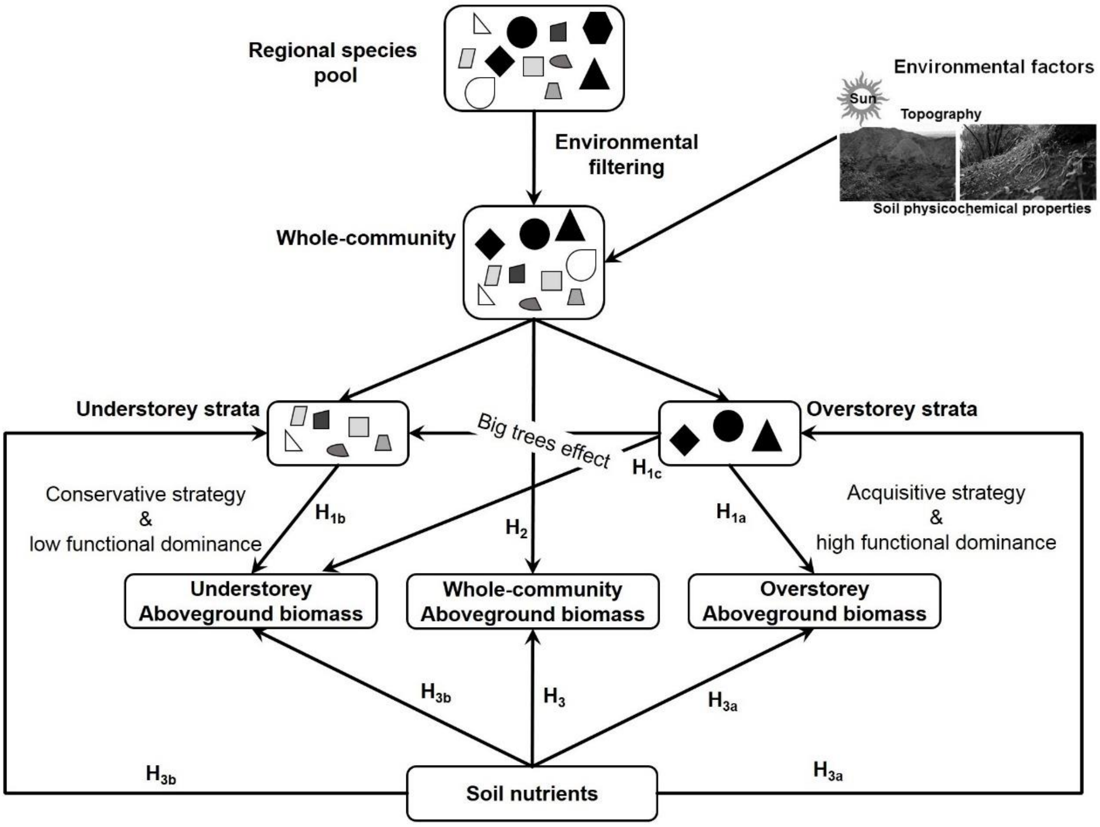


Fig. 7.1. Conceptual framework showing how changes in aboveground biomass are determined by the mass ratio mechanism. The acquisitive traits were CWM of specific leaf area, mean leaf area, leaf nitrogen and phosphorus concentrations, and ratio of leaf nitrogen to phosphorus concentrations. The conservative traits were CWM of leaf dry matter content and stem wood density. Functional dominance strategy of plant species was represented by CWM of tree maximum height, i.e., functional identity of tree height. Species pool having different symbols represent different species, colors represent different traits such as black color for acquisitive and high functional dominance while white to gray colors for conservative and low functional dominance, and size of the symbols represent the overstorey (big size) and understorey (small size) species. H_{1a}, H_{1b}, H_{1c}, H_2, and H_3 indicate proposed hypotheses, prediction or questions (see introduction section).

Studies in tropical forests have revealed that soil physicochemical properties should be included when testing multivariate relationships between biodiversity and aboveground biomass because it determines nutrients availability that may strongly influence the relationships between functional traits and aboveground biomass (Chiang *et al.* 2016, Lin *et al.* 2016, Prado-Junior *et al.* 2016). Soil fertility hypothesis predicts that aboveground biomass or productivity increases with increase in soil nutrients availability, and plants can grow faster when resource availability is high (Quesada *et al.* 2012, Wright *et al.* 2011). However, high nutrients availability may also lead to increased competition, and hence high mortality and biomass turnover rates of plant species (Prado-Junior *et al.* 2016). Consequently, high aboveground biomass or productivity in (sub-) tropical forests associates often with nutrient-poor soils (Chiang *et al.* 2016, Poorter *et al.* 2015, Prado-Junior *et al.* 2016). In this case, we hypothesize (H_3) that high CWM of acquisitive trait values relates to nutrient-rich soils (H_{3a}) while high CWM of conservative trait values of understorey associates with nutrient-poor soils (H_{3b}) in driving high aboveground biomass across forest strata (Fig. 7.1).

We tested the above hypotheses by using multiple linear models and structural equation model (SEM) based on the biophysical data from 125 plots inside a 5-ha natural subtropical forest in Eastern China. Specifically, we asked the following two questions: 1) which functional strategy – conservative or acquisitive drives high aboveground biomass across forest strata, while accounting for the effects of soil nutrients? and 2) whether functional identity of overstorey strata affects functional identity and aboveground biomass of understorey strata?

7.2. Materials and methods

7.2.1. Quantification of community-weighted mean of trait values

Overstorey strata were defined as all tree individuals with DBH ≥ 10 cm in each forest plot, and understorey strata included individuals with 1 ≤ DBH < 10 cm (Barrufol *et al.* 2013). This resulted in a total of 3,213 stems belonging to 71 species, 47 genera and 27 families in the overstorey, and a total of 17,004 stems belonging to 94 species, 57 genera and 33 families in the understorey across 125 plots.

For calculation of CWM indices, we used eight functional traits that are important for plant growth and survival (Poorter & Markesteijn 2008, Wright *et al.* 2010), and hence for standing aboveground biomass (Finegan *et al.* 2015, Prado-Junior *et al.* 2016). We used eight measures of functional identity (8 CWM indices based on a single-trait) that were quantified for the overstorey and understory strata, and whole-community level, separately. The CWM of a single trait (Eq. 7.1) was calculated as the mean trait value in the overstorey strata, understorey strata and whole-community level, weighted by the species' relative basal area (Garnier *et al.* 2004). This metric represents the expected functional trait value of a specific strata or community (Díaz *et al.* 2007).

$$\mathrm{CWM_x} = \sum_{\mathrm{i}=1}^{\mathrm{s}} \mathrm{p_i t_i} \qquad (7.1)$$

where CWM_x is the CWM for trait x, s is the number of species in the strata or community, p_i is the relative basal area of the ith species in the strata or community and t_i is the trait value for the ith species.

The CWM indices were calculated using the *vegan* (Oksanen *et al.* 2015), *FD, dbFD* and *functcomp* packages (Laliberté & Legendre 2010). The descriptions about the measurement of functional traits, estimation of aboveground biomass and measurement of environmental factors are provided in Chapter 2. Summary of functional identity and aboveground biomass across forest strata and whole-community is provided in Table 7.1.

Table 7.1. Descriptive statistics for functional identity and aboveground biomass, from 125 subtropical forest plots used for analysis of biodiversity – aboveground biomass. See Table 4.1 for summary of soil physicochemical properties axes. Note that natural-logarithm transformed and standardize data was used in statistical analyses.

Variable	Unit	Mean	S.E.	Minimum	Maximum
Overstorey strata					
Community-weighted mean of height (CWM H)	m	20.69	0.23	14.37	28.72
CWM of mean leaf area (CWM MLA)	cm^2	52.92	2.21	19.70	153.11
CWM of specific leaf area (CWM SLA)	$cm^2 g^{-1}$	131.04	1.98	88.17	207.31
CWM of leaf dry matter content (CWM LDMC)	$mg g^{-1}$	395.98	2.61	328.12	455.48
CWM of leaf nitrogen concentration (CWM LNC)	$mg g^{-1}$	19.21	0.15	15.13	23.34
CWM of leaf phosphorus concentration (CWM LPC)	$mg g^{-1}$	0.56	0.00	0.42	0.87
CWM of leaf nitrogen to phosphorus concentration ratio (CWM LNC:LPC)	unitless	37.08	0.39	28.24	51.64
CWM of stem wood density (CWM SWD)	$g cm^{-3}$	0.54	0.00	0.45	0.59
Aboveground biomass	$Mg ha^{-1}$	69.34	2.27	15.38	149.56
Understorey strata					
Community-weighted mean of height (CWM H)	m	11.49	0.16	7.43	19.19
CWM of mean leaf area (CWM MLA)	cm^2	19.92	0.68	10.35	55.01
CWM of specific leaf area (CWM SLA)	$cm^2 g^{-1}$	131.37	1.43	95.98	178.34
CWM of leaf dry matter content (CWM LDMC)	$mg g^{-1}$	407.70	1.76	365.31	460.48
CWM of leaf nitrogen concentration (CWM LNC)	$mg g^{-1}$	17.15	0.10	14.95	20.04
CWM of leaf phosphorus concentration (CWM LPC)	$mg g^{-1}$	0.56	0.00	0.48	0.69
CWM of leaf nitrogen to phosphorus concentration ratio (CWM LNC:LPC)	unitless	32.64	0.19	26.58	40.20
CWM of stem wood density (CWM SWD)	$g cm^{-3}$	0.55	0.00	0.50	0.65
Aboveground biomass	$Mg ha^{-1}$	4.98	0.16	1.22	9.72
Whole-community level					
Community-weighted mean of height (CWM H)	m	19.40	0.22	12.89	26.73
CWM of mean leaf area (CWM MLA)	cm^2	47.94	1.97	19.36	134.83
CWM of specific leaf area (CWM SLA)	$cm^2 g^{-1}$	132.32	1.78	89.43	192.04
CWM of leaf dry matter content (CWM LDMC)	$mg g^{-1}$	396.97	2.38	341.44	451.55
CWM of leaf nitrogen concentration (CWM LNC)	$mg g^{-1}$	18.92	0.14	15.18	23.00
CWM of leaf phosphorus concentration (CWM LPC)	$mg g^{-1}$	0.55	0.00	0.44	0.84
CWM of leaf nitrogen to phosphorus concentration ratio (CWM LNC:LPC)	unitless	36.48	0.34	28.96	49.00
CWM of stem wood density (CWM SWD)	$g cm^{-3}$	0.54	0.00	0.46	0.60
Aboveground biomass	$Mg ha^{-1}$	74.32	2.31	19.64	154.84

7.2.2. Statistical analyses

Our study design may confound statistical results when there is spatial autocorrelation in the variables of interest. To account for this we performed generalized least-squares (GLS) models (Pinheiro & Bates 2016), with (accounted for the spatial location of each subplot, i.e. local X and Y coordinates within a 5-ha plot) and without spatial autocorrelation among subplots for each of the relationships between predictors and aboveground biomass, as recommended by previous studies (Chisholm *et al.* 2013, Yuan *et al.* 2016). In addition, forest strata may also confound the spatial autocorrelation in the variables of interest, as overstorey and understorey strata within a plot have similar spatial location (X and Y coordinates). We therefore explicitly accounted for the effect of forest strata (overstorey and understorey), using grouping variable, on the relationship between predictor and aboveground biomass in both spatial and non-spatial GLS models. GLS model is a reliable method for testing whether subplots sharing the same abiotic conditions are independent from each other within a forest (Zuur *et al.* 2009). The goodness of fit of spatial and non-spatial GLS models was evaluated by AIC, and we found that models without spatial autocorrelation always had the lower AIC values (Tables 7.2 and 7.3), which is similar to the recent observations in 25-ha broad-leaved Korean pine mixed forest and 5-ha secondary poplar-birch forest in northeastern China (Yuan *et al.* 2016).

Table 7.2. Summary of the generalized least-squares (GLS) models of aboveground biomass on predictors at forest strata. All the abbreviations for variables are explained in Table 7.1; PC1 (soil physicochemical properties) and PC2 (soil nutrients), PCA axes.

GLS model	Model	Coefficient	*t*-value	*P*-value	AIC	R^2_{pseudo}
AGB ~ CWM H	Non-spatial	0.02	0.24	0.810	702.56	0.003
	Spatial	0.02	0.30	0.766	711.27	0.003
AGB ~ CWM MLA	Non-spatial	-0.12	-1.91	0.057	699.57	0.046
	Spatial	-0.16	-2.51	0.013	705.45	0.046
AGB ~ CWM SLA	Non-spatial	-0.19	-3.00	0.003	694.47	0.063
	Spatial	-0.22	-3.34	0.001	700.72	0.063
AGB ~ CWM LDMC	Non-spatial	0.17	2.67	0.008	695.93	0.049
	Spatial	0.19	3.03	0.003	702.49	0.049
AGB ~ CWM LNC	Non-spatial	-0.24	-3.77	<0.001	690.85	0.093
	Spatial	-0.26	-4.09	<0.001	697.16	0.093
AGB ~ CWM LPC	Non-spatial	-0.02	-0.36	0.722	702.59	0.002
	Spatial	-0.03	-0.52	0.606	711.17	0.002
AGB ~ CWM LNC:LPC	Non-spatial	-0.09	-1.38	0.167	700.92	0.026
	Spatial	-0.11	-1.69	0.093	708.74	0.026
AGB ~ CWM SWD	Non-spatial	0.23	3.63	<0.001	691.17	0.086

	Spatial	0.25	3.84	<0.001	698.49	0.086
AGB ~ Soil PC1	Non-spatial	-0.09	-2.27	0.024	698.59	0.032
	Spatial	-0.09	-2.49	0.013	706.34	0.032
AGB ~ Soil PC2	Non-spatial	-0.28	-5.87	<0.001	672.62	0.156
	Spatial	-0.29	-6.06	<0.001	679.75	0.156

Table 7.3. Summary of the generalized least-squares (GLS) models of aboveground biomass on predictors at whole-community level. All the abbreviations for variables are explained in Table 7.1; PC1 (soil physicochemical properties) and PC2 (soil nutrients), PCA axes.

GLS model	Model	Coefficient	*t*-value	*P*-value	AIC	R^2_{pseudo}
AGB ~ CWM H	Non-spatial	0.39	4.69	<0.001	345.43	0.152
	Spatial	0.42	4.91	<0.001	348.14	0.152
AGB ~ CWM MLA	Non-spatial	-0.02	-0.27	0.784	365.58	0.001
	Spatial	-0.02	-0.21	0.834	369.54	0.001
AGB ~ CWM SLA	Non-spatial	-0.12	-1.31	0.191	363.94	0.014
	Spatial	-0.12	-1.31	0.193	367.94	0.014
AGB ~ CWM LDMC	Non-spatial	0.18	2.05	0.043	361.53	0.033
	Spatial	0.18	2.05	0.043	365.53	0.033
AGB ~ CWM LNC	Non-spatial	-0.05	-0.54	0.590	365.37	0.002
	Spatial	-0.05	-0.50	0.617	369.35	0.002
AGB ~ CWM LPC	Non-spatial	0.01	0.12	0.905	365.64	0.000
	Spatial	0.01	0.08	0.935	369.60	0.000
AGB ~ CWM LNC:LPC	Non-spatial	-0.08	-0.89	0.374	364.86	0.006
	Spatial	-0.08	-0.89	0.374	368.86	0.006
AGB ~ CWM SWD	Non-spatial	0.06	0.72	0.473	365.14	0.004
	Spatial	0.06	0.72	0.473	369.14	0.004
AGB ~ Soil PC1	Non-spatial	-0.04	-0.90	0.370	366.09	0.007
	Spatial	-0.04	-0.88	0.382	370.05	0.007
AGB ~ Soil PC2	Non-spatial	-0.18	-2.85	0.005	358.42	0.062
	Spatial	-0.18	-2.85	0.005	362.42	0.062

Having found no strong evidences for spatial autocorrelation, we then performed multiple linear regressions models (i.e., general linear models) to evaluate how aboveground biomass related to CWM of trait values at each of overstorey and understorey strata across a range of local soil conditions. More specifically, we included all CWM of trait values (8 indices) in order to test for the joint effects of the functional identity of conservative and acquisitive strategies of studied trees on aboveground biomass at each of the overstorey and understorey strata, and whole-community level. In all models, we included local soil factors, i.e., soil PC1 and soil PC2, as covariates. We used all subsets regression analysis and selected the optimal model that had lowest AICc (i.e. AIC adjusted for small sample sizes). Models were considered to be equally supported if the difference in AICc was less than two units (Bartoń 2016). When models were equally supported, we selected the most parsimonious model by considering the lowest number of predictors. General linear models were performed using the *stats* package and all subsets regression analyses using the *MuMIn* package (Bartoń 2016). We plotted a bivariate model's response (optimal linear model) against each predictor's marginal effect (i.e. holding all other predictors in constant), by using the *plotmo* package (Milborrow 2015). In addition, we applied the Moran's I test for spatial autocorrelation in the selected optimal linear model residuals, while assessing the range and type of spatial autocorrelation in lag classes by plotting the correlograms (Fig. 7.2), by using the *spdep* package (Bivand 2016). The complementary Pearson's correlations between all tested predictors at each of the overstorey and understorey strata, and whole-community level are shown in Tables 7.4, 7.5 and 7.6, respectively.

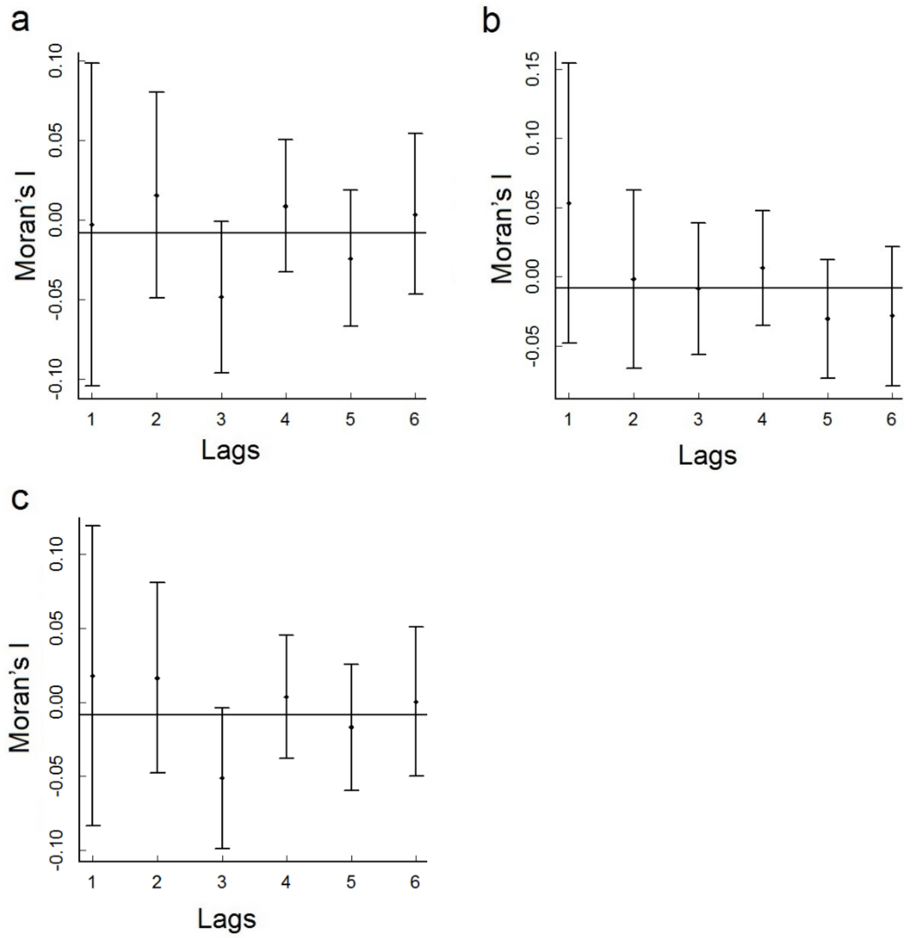


Fig. 7.2. Correlograms plots of the Moran's I test on the residuals of linear multiple models in order to check the range and type of autocorrelation in lag classes. a) Overstorey optimal model, b) understorey optimal model, and c) whole-community optimal model (Table 7.9).

Table 7.4. Pearson's correlation coefficient between all tested predictors for aboveground biomass at overstorey strata (see Table 7.9). Bold numbers indicate significant correlations ($P < 0.05$). All the abbreviations for variables are explained in Table 7.1.

	CWM H	CWM MLA	CWM SLA	CWM LDMC	CWM LNC	CWM LPC	CWM LNC:LPC	CWM SWD	Soil PC1	Soil PC2
CWM H	---									
CWM MLA	0.10	---								
CWM SLA	0.14	**0.52**	---							
CWM LDMC	-0.06	**-0.62**	**-0.70**	---						
CWM LNC	0.12	**0.78**	**0.55**	**-0.60**	---					
CWM LPC	0.03	-0.07	**0.32**	-0.06	**0.23**	---				
CWM LNC:LPC	-0.09	**0.58**	0.10	**-0.40**	**0.45**	**-0.61**	---			
CWM SWD	-0.17	**-0.71**	**-0.38**	**0.52**	**-0.63**	**0.22**	**-0.55**	---		
Soil PC1	-0.13	**0.24**	**0.23**	**-0.30**	**0.38**	0.07	0.13	-0.14	---	
Soil PC2	**0.21**	**0.53**	**0.29**	**-0.38**	**0.56**	0.03	**0.36**	**-0.55**	0.00	---

Table 7.5. Pearson's correlation coefficient between all tested predictors for aboveground biomass at understorey strata (see Table 7.9). Bold numbers indicate significant correlations ($P < 0.05$). All the abbreviations for variables are explained in Table 7.1.

	CWM H	CWM MLA	CWM SLA	CWM LDMC	CWM LNC	CWM LPC	CWM LNC:LPC	CWM SWD	Soil PC1	Soil PC2
CWM H	---									
CWM MLA	**0.74**	---								
CWM SLA	**0.49**	**0.47**	---							
CWM LDMC	**-0.27**	**-0.28**	**-0.69**	---						
CWM LNC	**0.71**	**0.74**	**0.67**	**-0.30**	---					
CWM LPC	0.15	**0.39**	0.06	0.09	**0.34**	---				
CWM LNC:LPC	**0.42**	**0.25**	**0.29**	**-0.19**	**0.28**	**-0.53**	---			
CWM SWD	**-0.48**	**-0.42**	**-0.73**	**0.46**	**-0.74**	0.05	**-0.38**	---		
Soil PC1	0.15	0.09	**0.58**	**-0.56**	**0.28**	**-0.27**	0.09	**-0.48**	---	
Soil PC2	**0.53**	**0.56**	**0.44**	-0.15	**0.76**	**0.26**	**0.24**	**-0.56**	0.00	---

Table 7.6. Pearson's correlation coefficient between all tested predictors for aboveground biomass at whole-community level (see Table 7.9). Bold numbers indicate significant correlations ($P < 0.05$). All the abbreviations for variables are explained in Table 7.1.

	CWM H	CWM MLA	CWM SLA	CWM LDMC	CWM LNC	CWM LPC	CWM LNC:LPC	CWM SWD	Soil PC1	Soil PC2
CWM H	---									
CWM MLA	**0.19**	---								
CWM SLA	0.13	**0.56**	---							
CWM LDMC	-0.11	**-0.62**	**-0.74**	---						
CWM LNC	**0.21**	**0.79**	**0.60**	**-0.64**	---					

CWM LPC	0.05	-0.05	**0.32**	-0.08	**0.24**	---				
CWM LNC:LPC	-0.03	**0.58**	0.15	**-0.41**	**0.47**	**-0.57**	---			
CWM SWD	-0.20	**-0.74**	**-0.46**	**0.55**	**-0.68**	**0.18**	**-0.55**	---		
Soil PC1	-0.09	**0.24**	**0.32**	**-0.37**	**0.38**	0.05	0.14	**-0.19**	---	
Soil PC2	**0.26**	**0.55**	**0.34**	**-0.38**	**0.61**	0.06	**0.38**	**-0.59**	0.00	---

Finally, we employed SEM in order to evaluate whether CWM of trait values of overstorey strata affect CWM of trait values of at understorey strata and its relationship with aboveground biomass, by simultaneously accounting for the effects of soil nutrients and physicochemical properties. Here, we selected the best predictors for aboveground biomass which were retained in the selected optimal model for overstorey and understorey strata. In order to keep possible consistency with the optimal linear model and to answer our question, we constructed SEM based on the following three paths: 1) direct effects of overstorey CWM of trait values on understorey's CWM of trait values and aboveground biomass, after accounting for the effects of soil factors (PC1 and PC2); 2) indirect effects of overstorey CWM of trait values on understorey aboveground biomass via understorey CWM of trait values; and 3) direct effects of soil factors and understorey CWM of trait values on understorey aboveground biomass. Best-fit SEM was assessed through several tests (Malaeb *et al.* 2000), including the Chi-square (χ^2) test, goodness-of-fit index (GFI), comparative fit index (CFI) and standardized root mean square residual (SRMR). The SEM was implemented using the *lavaan* package (Rosseel 2012).

Prior to the statistical analyses, Shapiro-Wilk goodness-of-fit test was used to assess the normality for all variables. All numerical variables including aboveground biomass and CWM of trait values were natural-logarithm transformed and standardized. Transformations of the variables were conducted for the purpose to meet the assumptions of normality and linearity, and to reduce the effect of outliers and to account for possible nonlinear relationships between variables, and to allow comparisons among multiple predictors and models (Zuur *et al.* 2009). For all statistical analyses R 3.2.2 was used (R Development Core Team 2015). Dataset used in the analyses can be found at http://dx.doi.org/10.1016/j.ecolind.2017.07.054.

7.3. Results

7.3.1. Bivariate relationships between aboveground biomass and each of CWM of trait values and soil properties

Bivariate relationships showed that, in overstorey strata, aboveground biomass significantly increased with increasing CWM of tree height (i.e. functional identity of tree height) only (Fig.

7.3). In understorey strata, aboveground biomass significantly increased with increasing CWM of leaf dry matter content and stem wood density, but significantly decreased with increasing CWM of mean leaf area, specific leaf area, leaf nitrogen concentration and LNC:LPC, as well as with increasing CWM of tree height (Fig. 7.3). At the whole-community level, aboveground biomass significantly increased with increasing CWM of tree height and leaf dry matter content (Fig. 7.5). The CWM of other trait values did not significantly relate to aboveground biomass in overstorey and understorey strata, and whole-community level (Table 7.7). In addition, aboveground biomass in overstorey and understorey strata, as well as in whole-community level was consistently negative related to soil nutrients (PC2 axis), while soil physiochemical properties (PC1 axis) only negatively related to aboveground biomass of understorey strata (Figs. 7.3, 7.4 and 7.5).

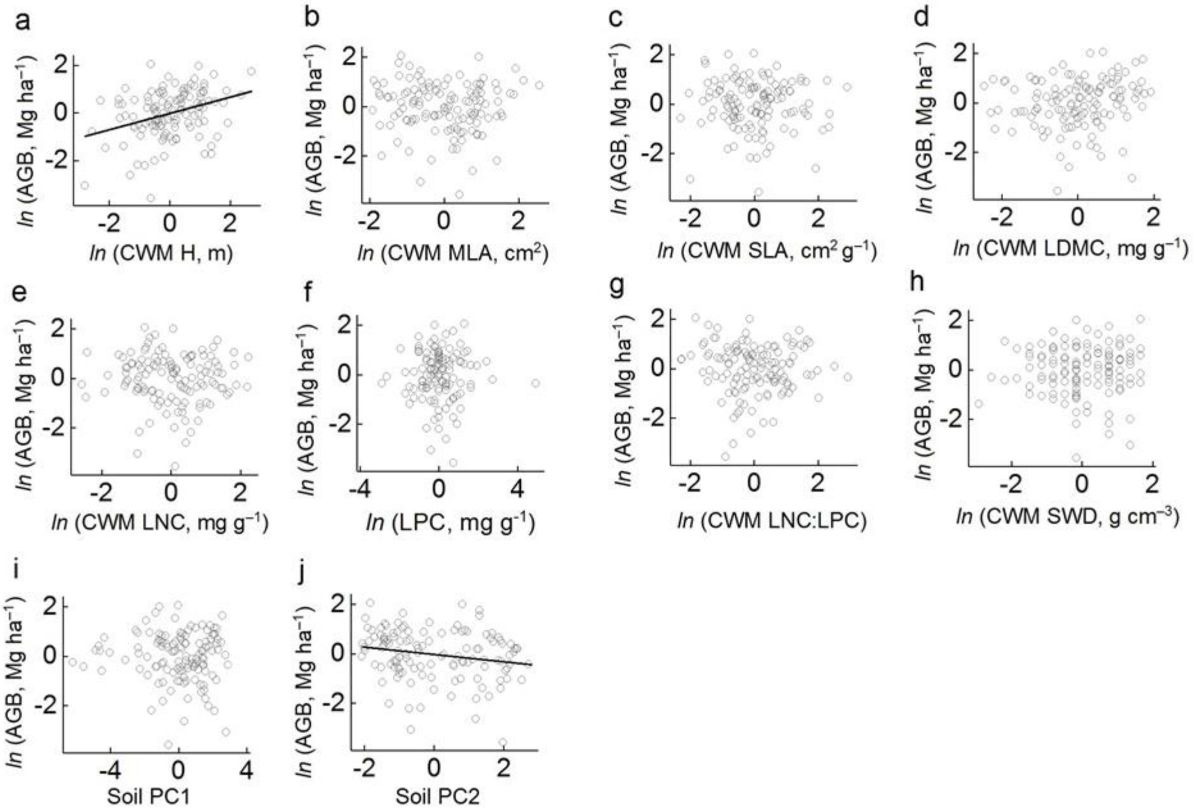


Fig. 7.3. The bivariate relationships between aboveground biomass (AGB) and predictors (a-h, CWM of trait values; and i-j, soil physiochemical properties axes; $n = 125$) at overstorey strata in subtropical evergreen broadleaf forests in Eastern China. Fitted regressions are significant at $P < 0.05$. All the abbreviations for variables are explained in Table 7.1.

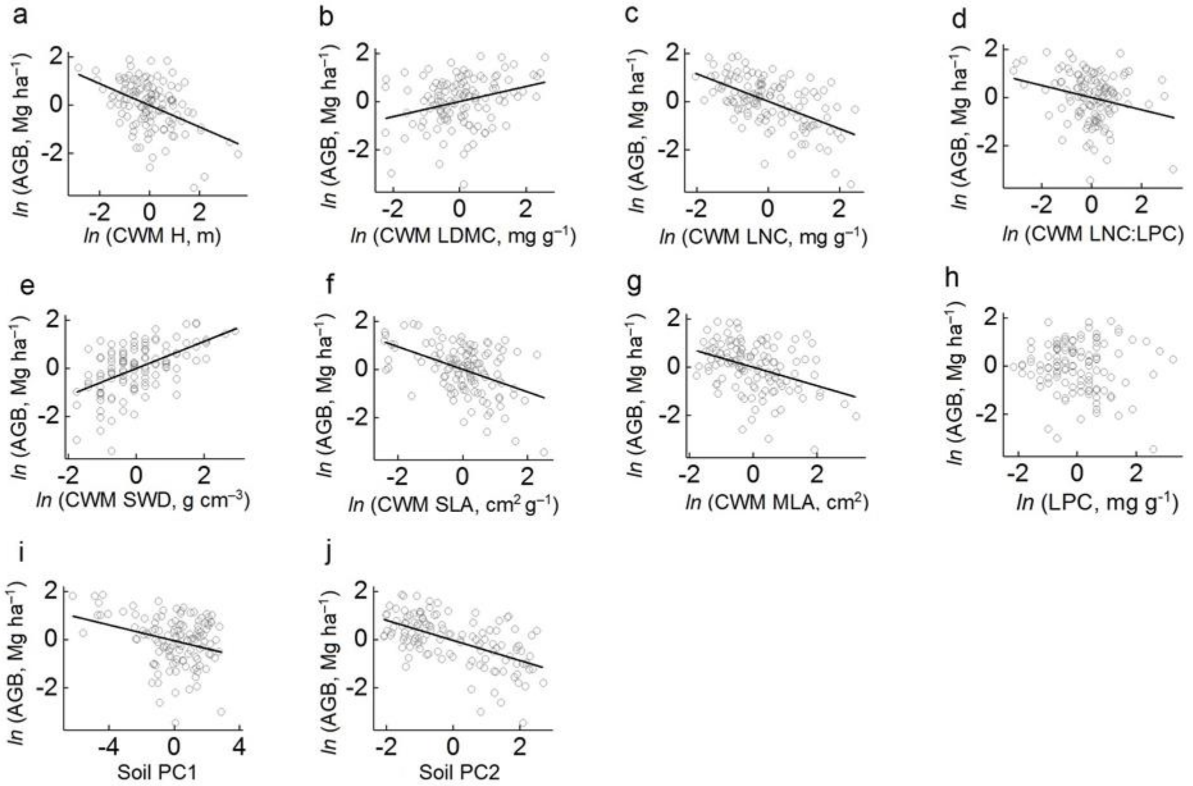


Fig. 7.4. The bivariate relationships between aboveground biomass (AGB) and predictors (a-h, CWM of trait values; and i-j, soil physiochemical properties axes; *n* = 125) at understorey strata in subtropical evergreen broadleaf forests in Eastern China. Fitted regressions are significant at $P < 0.05$. All the abbreviations for variables are explained in Table 7.1.

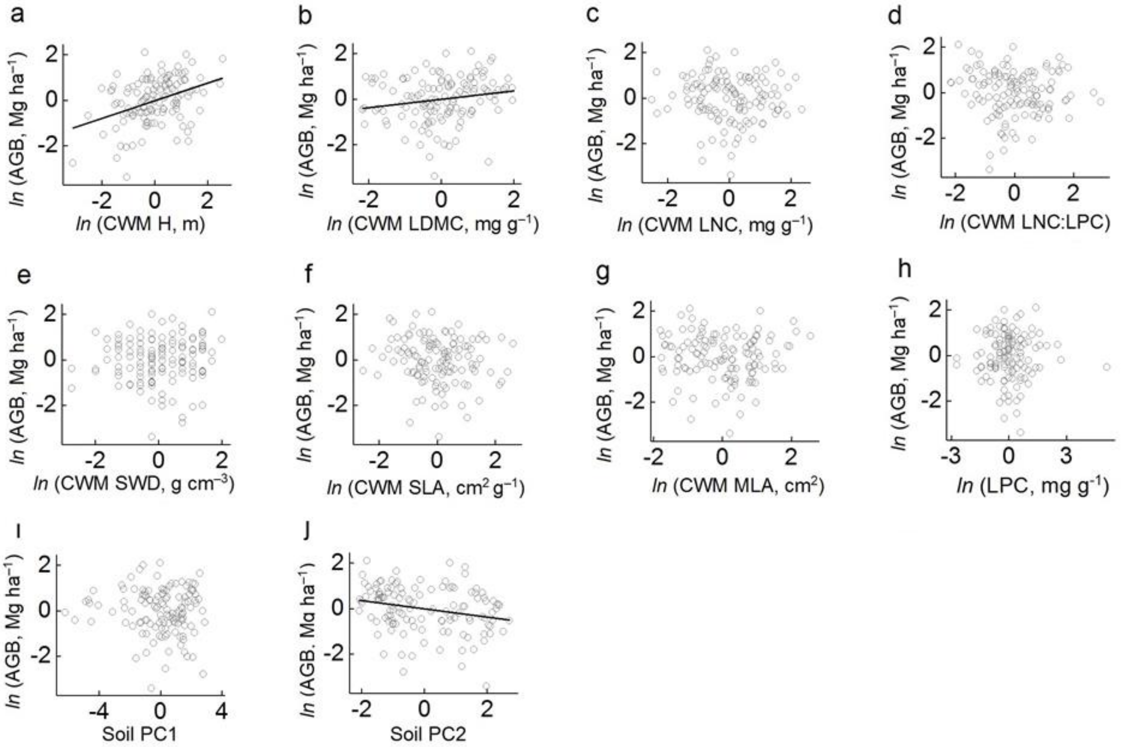


Fig. 7.5. The bivariate relationships between aboveground biomass (AGB) and predictors (a-h, CWM of trait values; and i-j, soil physiochemical properties axes; *n* = 125) at whole-community level in subtropical evergreen broadleaf forests in Eastern China. Fitted regressions are significant at $P < 0.05$. All the abbreviations for variables are explained in Table 7.1.

Table 7.7. Summary of the simple linear models for bivariate relationships of CWM of trait values and soil physicochemical properties (PC1 and PC2) with aboveground biomass at forest strata and whole-community level in subtropical forests. P values < 0.05 are given in bold. All the abbreviations for variables are explained in Table 7.1.

	Understorey strata				Overstorey strata				Whole-community level			
Predictors	Beta	P	PMSE	R^2	Beta	P	PMSE	R^2	Beta	P	PMSE	R^2
CWM indices												
CWM H	-0.45	**<0.001**	0.83	0.20	0.34	**<0.001**	0.92	0.12	0.39	**<0.001**	0.89	0.15
CWM MLA	-0.39	**<0.001**	0.89	0.15	-0.04	0.635	1.04	0.00	-0.02	0.784	1.04	0.00
CWM SLA	-0.47	**<0.001**	0.82	0.22	-0.04	0.692	1.04	0.00	-0.12	0.191	1.02	0.01
CWM LDMC	0.32	**<0.001**	0.94	0.10	0.13	0.163	1.02	0.02	0.18	**0.043**	1.00	0.03
CWM LNC	-0.57	**<0.001**	0.71	0.33	-0.04	0.671	1.03	0.00	-0.05	0.590	1.03	0.00
CWM LPC	-0.08	0.404	1.04	0.01	0.00	0.981	1.03	0.00	0.01	0.905	1.03	0.00
CWM LNC:LPC	-0.26	**0.004**	0.98	0.07	-0.06	0.471	1.03	0.00	-0.08	0.374	1.03	0.01
CWM SWD	0.57	**<0.001**	0.71	0.32	0.02	0.825	1.04	0.00	0.06	0.473	1.03	0.00
Soil physicochemical properties												
Soil PC1	-0.16	**0.001**	0.95	0.09	-0.03	0.499	1.03	0.00	-0.04	0.370	1.03	0.01
Soil PC2	-0.42	**<0.001**	0.7	0.33	-0.15	**0.018**	0.99	0.04	-0.18	**0.005**	0.97	0.06

Table 7.8. Top best models (having ΔAICcs < two units) obtained from a series of multiple regression analyses for aboveground biomass and 10 predictors (8 CWM indices, and 2 soil PCA axes within each model) using linear model for each of the overstorey, understorey and whole-community level. Standardized regression coefficient (Beta) for each predictor is given. P values < 0.05 are given in bold. Abbreviations: *df*, number of model parameters; LL, maximum log-likelihood; AICc, the information-theoretic Akaike's information criterion corrected for small samples; ΔAICc, change in AICc relative to the top-ranked model; *wi*, model probability; all other variables are abbreviated in Table 7.1.

CWM H	CWM LDMC	CWM LNC	CWM LPC	CWM MLA	CWM LNC:LPC	CWM SLA	CWM SWD	Soil PC1	Soil PC2	*df*	LL	AICc	ΔAICc	*wi*	Remarks
Overstorey strata models															
0.41									**-0.22**	4	-162.60	333.50	0.00	0.04	**Selected**
0.41		0.12							**-0.26**	5	-161.88	334.30	0.72	0.03	---

0.40						-0.11		**-0.26**	5	-161.93	334.40	0.82	0.03	---
0.41				0.10				**-0.25**	5	-162.02	334.50	1.00	0.03	---
0.42					0.09			**-0.24**	5	-162.02	334.60	1.01	0.03	---
0.40	0.13	0.19						**-0.26**	6	-161.04	334.80	1.26	0.02	---
0.41	0.13			0.17				**-0.25**	6	-161.23	335.20	1.63	0.02	---
0.40	0.10					-0.16		**-0.25**	6	-161.37	335.50	1.91	0.02	---
0.41	0.04							**-0.20**	5	-162.48	335.50	1.93	0.02	---
Understorey strata models														
						0.22	**-0.10**	**-0.33**	5	-140.33	291.20	0.00	0.04	**Selected**
-0.11						0.19	**-0.10**	**-0.30**	6	-139.39	291.50	0.33	0.04	---
					-0.06	0.19	**-0.11**	**-0.33**	6	-140.03	292.80	1.60	0.02	---
	0.06					**0.21**	-0.09	**-0.33**	6	-140.06	292.80	1.66	0.02	---
-0.14							**-0.15**	**-0.36**	5	-141.18	292.90	1.70	0.02	---
Whole-community level models														
0.48	**0.24**			**0.27**				**-0.31**	6	-151.85	316.40	0.00	0.05	**Selected**
0.48	**0.25**	**0.29**						**-0.33**	6	-151.89	316.50	0.08	0.04	---
0.47	**0.28**	0.18		0.17				**-0.34**	7	-150.95	316.80	0.44	0.04	---
0.49	**0.27**	**0.26**			0.10			**-0.34**	7	-151.17	317.30	0.89	0.03	---
0.47	**0.27**	**0.24**				-0.11		**-0.35**	7	-151.40	317.70	1.34	0.02	---
0.47	**0.23**	**0.32**					-0.04	**-0.35**	7	-151.50	318.00	1.55	0.02	---
0.50	**0.28**		0.16	0.20	0.20			**-0.34**	8	-150.45	318.10	1.74	0.02	---
0.49	**0.24**			**0.23**	0.06			**-0.32**	7	-151.61	318.20	1.76	0.02	---
0.48	**0.25**			0.23		-0.07		**-0.33**	7	-151.68	318.30	1.91	0.02	---
0.47	**0.24**		0.04	**0.28**				**-0.32**	7	-151.68	318.30	1.91	0.02	---

7.3.2. Effects of functional identity of conservative and acquisitive strategies on aboveground biomass

The overstorey strata optimal model showed that aboveground biomass of overstorey strata was best predicted ($R^2 = 0.20$) by CWM of tree height ($\beta = 0.41$, $P < 0.001$) and soil nutrients ($\beta = -0.22$, $P < 0.001$) (Tables 7.8 and 7.9; Fig. 7.6A). The understorey strata optimal model showed that aboveground biomass of understorey strata was best predicted ($R^2 = 0.44$) by CWM of stem wood density ($\beta = 0.22$, $P = 0.032$), soil nutrients ($\beta = -0.33$, $P < 0.001$) and physicochemical properties ($\beta = -0.10$, $P = 0.023$) (Tables 7.8 and 7.9; Fig. 7.6B). In comparison, the whole-community optimal model showed that aboveground biomass was best predicted ($R^2 = 0.32$) by CWM of tree height ($\beta = 0.48$, $P < 0.001$), leaf dry matter content ($\beta = 0.24$, $P = 0.014$), mean leaf area ($\beta = 0.27$, $P = 0.013$) and soil nutrients ($\beta = -0.31$, $P < 0.001$) (Tables 7.8 and 7.9; Fig. 7.6C).

Table 7.9. The overstorey strata, understorey strata and whole-community level optimal models obtained from a series of multiple regression analyses for aboveground biomass and 10 predictors (8 CWM indices, and 2 soil PCA axes within each model) using 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. *P* values < 0.05 are given in bold. Moran's *I* test was conducted on the residuals for optimal linear model ($P > 0.05$ indicates no spatial autocorrelation). The blank cells represent that predictor variables were not retained in the selected optimal model. Model selection table is shown in Table 7.8. All the abbreviations for variables are explained in Table 7.1.

Predictors	*Overstorey strata model*			*Understorey strata model*			*Whole-community model*		
	Beta	*t*	*P*	Beta	*t*	*P*	Beta	*t*	*P*
Constant	0.00	0.00	0.998	0.00	–0.01	0.992	0.00	0.00	0.999
Mass ratio hypothesis (community-weighted mean of a trait)									
CWM H	0.41	4.92	**<0.001**				0.48	6.15	**<0.001**
CWM SLA									
CWM LDMC							0.24	2.49	**0.014**
CWM MLA							0.27	2.52	**0.013**
CWM LNC									
CWM LPC									
CWM LNC:LPC									
CWM SWD				0.22	2.17	**0.032**			
Soil physicochemical properties axes									
Soil PC1				–0.10	–2.31	**0.023**			
Soil PC2	–0.22	–3.59	**<0.001**	–0.33	–5.16	**<0.001**	–0.31	–4.72	**<0.001**
Model statistics									

F-test (*P*-value)	15.52	32.13	14.75
	(<0.001)	**(<0.001)**	**(<0.001)**
R^2	0.20	0.44	0.32
AICc	333.5	291.2	316.4
Moran's *I*- test	–0.003	0.05	0.02
(*P*-value)	(0.917)	(0.225)	(0.608)

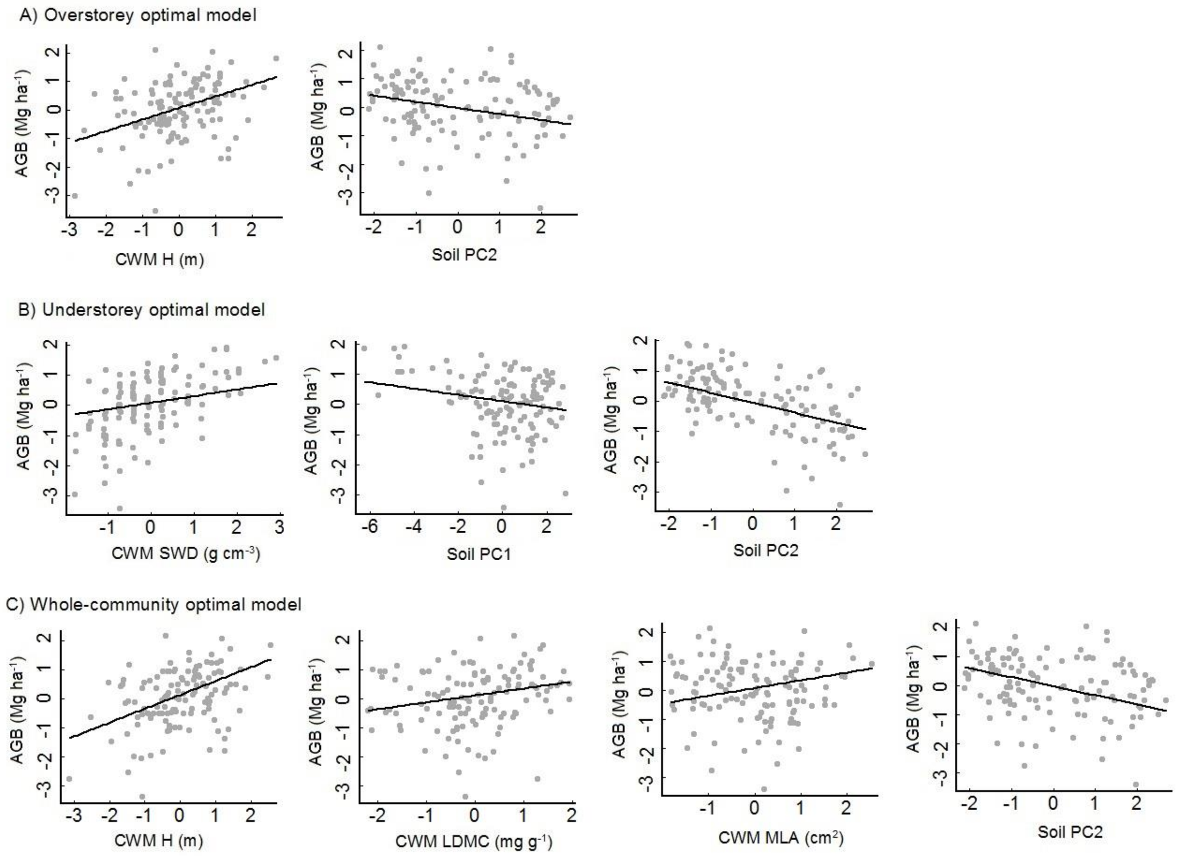


Fig. 7.6. The response of aboveground biomass to the retained predictors in the overstorey strata (A), understorey strata (B) and whole-community level (C) optimal models (see Table 7.9 for statistics). The partial dependence plots represent an optimal linear model's response when varying predictor while holding the other predictors constant (i.e. marginal effect of a predictor). Solid lines represent significant ($P < 0.05$) relationships. See Figs. 2, 4 and 4 for bivariate relationships. All the abbreviations for variables are explained in Table 7.1.

7.3.3. The big trees effect on functional identity and aboveground biomass in understorey

The best-fit SEM (Fig. 7.7) showed that CWM of overstorey tree height did not directly affect both CWM of stem wood density (β = –0.04, *P* = 0.549) and aboveground biomass (β = –0.07, *P* = 0.286) of understorey strata. Also, CWM of overstorey tree height had the non-significant negative indirect effect on understorey aboveground biomass via CWM of stem wood density of understorey, and hence the total (direct + indirect effects) negative effect was not significant (Table 7.10). Interestingly, soil nutrients had the direct positive effect on CWM of overstorey tree height ($\beta = 0.21$, $P = 0.017$). In contrast, soil nutrients and physicochemical properties had direct negative effects on the CWM of stem wood density ($\beta = –0.55$ and –0.49, $P < 0.001$) and aboveground biomass ($\beta = –0.44$ and –0.20, $P < 0.001$ and 0.013; Fig. 7.7) in understorey strata. Soil nutrients had indirect negative effects on understorey aboveground biomass via CWM of understorey's stem wood density but non-significant via CWM of overstorey tree height. The total effect of soil nutrients on understorey aboveground biomass was significantly negative ($\beta = –0.57$, $P < 0.001$; Table 7.10).

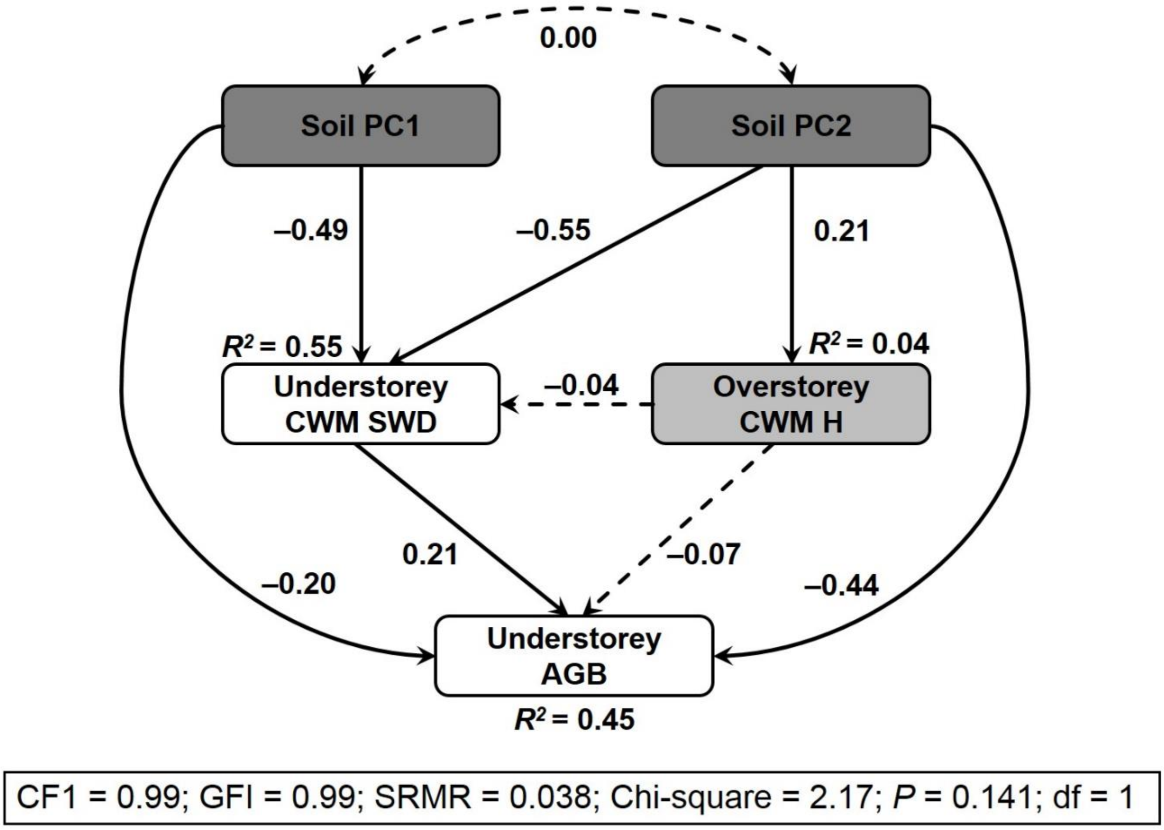


Fig. 7.7. Best-fit structural equation model (SEM) linking functional identity of overstorey (i.e. CWM H) and understorey strata (i.e. CWM SWD), and soil physicochemical properties (i.e. soil PC1 and PC2) with understorey aboveground biomass. Solid arrows represent significant ($P < 0.05$) paths and dashed arrows represent non-significant paths ($P > 0.05$). For each path the standardized regression 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. The variables in SEM were selected based on selected optimal models for overstorey and understorey strata obtained from a series of multiple regressions (see Table 7.9). Abbreviations: AGB, aboveground biomass; CWM H, community-weighted mean of tree height; CWM SWD, community-weighted mean of stem wood density; CFI, comparative fit index; GFI, goodness of fit index; SRMR, standardized root mean square residual; df, degree of freedom.

Table 7.10. The direct, indirect, and total standardized effects of soil nutrients, overstorey and understorey functional identity (i.e. CWM of a trait values) on understorey aboveground biomass based on structural equation model (SEM). Significant effects are indicated in bold ($P < 0.05$). All the abbreviations for variables are explained in Table 7.1.

Predictor	Pathway to understorey aboveground biomass	Model in Fig. 7.7	
		Effect	*P*-value
Soil properties (PC1)	Direct effect	–0.20	**0.013**
	Indirect effect via understorey CWM SWD	–0.10	**0.037**
	Total effect	–0.31	**<0.001**
Soil nutrients (PC2)	Direct effect	–0.44	**<0.001**
	Indirect effect via overstorey CWM H	–0.02	0.330
	Indirect effect via understorey CWM SWD	–0.12	**0.036**
	Total effect	–0.57	**<0.001**
Overstorey CWM H	Direct effect	–0.07	0.286
	Indirect effect via understorey CWM SWD	–0.01	0.563
	Total effect	–0.08	0.245
Understorey CWM SWD	Direct effect	0.21	**0.031**

7.4. Discussion

In partial agreement with our specific hypothesis (H_1), we found that high aboveground biomass is potentially driven by functional identity of tall trees in overstorey strata, whereas by dense-wooded conservative trees in understorey strata, respectively. In comparison, high aboveground biomass is associated with high CWM of tree height, leaf dry matter content and mean leaf area at whole-community level. These results provide strong evidence to the functional strategy-dependent mass ratio mechanisms driving aboveground biomass across forest strata within a subtropical forest. This study highlights the fundamental roles of forest strata where overstorey and understorey strata contribute to their corresponding aboveground biomass with contrasting strategies based on functional identity across a range of local soil nutrients and physicochemical properties.

7.4.1. Functional identity of tree height drives high aboveground biomass in overstorey strata

It is plausible that tall and big trees with positive allometric relationship between height and diameter have large stem volumes, thus substantially contributing to the aboveground biomass (Chave *et al.* 2009), due to the big trees effect on the available resources (e.g. Slik *et al.* 2013). This result agrees with previous studies that the relative abundance, stand basal area and functional identity of tall and big trees have a large effect on aboveground biomass (Balvanera *et al.* 2005, Cavanaugh *et al.* 2014, Lohbeck *et al.* 2016, Slik *et al.* 2013) and productivity (Prado-Junior *et al.* 2016). Our result as well as those from previous studies, collectively support the selection effect hypothesis or the mass ratio hypothesis, which highlights the importance of dominant species in maintaining ecosystem function (Cardinale *et al.* 2012, Loreau & Hector 2001).

Interestingly, the CWM of wood density and leaf traits appeared to be unimportant for driving aboveground biomass at the overstorey strata, and hence no any clear or significant evidence for the effects of the conservative or acquisitive strategy of trees on aboveground biomass in overstorey strata. This result suggests that the functional identity of tree height, and to a lesser extent wood density and leaf traits, with a narrow range of functional trait variation best explain aboveground biomass in natural forests (Conti & Díaz 2013). However, our result and those of previous studies (Cavanaugh *et al.* 2014, Conti & Díaz 2013) argue against the general hypotheses that aboveground biomass is related to the high stature trees with either dense-wooded or light-wooded species (e.g. Stegen *et al.* 2009), and either with nutrient-rich and nutrient-poor leaves species (Finegan *et al.* 2015, Prado-Junior *et al.* 2016). Our results suggest that an increase of the functional identity of tree height of overstorey trees, rather than conservative or acquisitive strategy, may enhance aboveground biomass or productivity (Cavanaugh *et al.* 2014, Conti & Díaz 2013), probably due to their better response to environmental filtering (Lasky *et al.* 2014, Zhang *et al.* 2016a). Our study was local in its spatial extent, and therefore our results indicate that the positive relationship between functional identity of tree height and aboveground biomass is consistent across a variety of scales, i.e. local, regional, continent and global scales (Baker *et al.* 2009, Cavanaugh *et al.* 2014, Conti & Díaz 2013, Slik *et al.* 2013).

7.4.2. Conservative strategy drives high aboveground biomass in understorey strata

Surprisingly, as hypothesized we found that understorey strata dominated by slow-growing conservative species (i.e. low leaf nitrogen and phosphorus concentrations, low specific leaf area, and high wood density and leaf dry matter content) had high aboveground biomass (Table 7.9; Fig. 7.4). Our results suggest that slow-growing conservative species driving high aboveground biomass in the resource-limited environments (e.g. understorey strata in our study) (Chave *et al.* 2009, Prado-Junior *et al.* 2016). We found that functional identity of tree height was not the most important variable for aboveground biomass in understorey strata. The negative bivariate relationship between CWM of tree height and aboveground biomass might relate to the various underlying demographic processes in understorey strata (Poorter & Markesteijn 2008, Russo *et al.* 2008). Further research is needed to disentangle how different drivers affect different demographic processes, and hence net aboveground biomass change

(Prado-Junior *et al.* 2016). However, this negative relationship might happen due to the slow growth of understorey species, as a result of the strong light limitation in understorey strata (Rüger *et al.* 2012).

Our study showed that the acquisitive-conservative trait spectrum has different consequences for overstorey and understorey strata. The major resources needed for plant growth and survival are light, water and nutrients (Jucker *et al.* 2014, Sterck *et al.* 2011). It has been hypothesized that the niche complementarity effect may be less important in stable and productive environments, where competition is often the most common form of species interaction, than in unstable and stressful environments (Paquette & Messier 2011). Our findings confirm that resource-use complementarity of the conservative strategy of the species manifests under resource-limiting environments (Prado-Junior *et al.* 2016, Sterck *et al.* 2011) – in our case the understorey strata of a subtropical forest.

7.4.3. The big trees effect on understorey functional identity and aboveground biomass

Overstorey strata with great tree size consume a plenty of resources such as light and water, thus remaining few resources to the trees in understorey strata (Bartels & Chen 2010, 2013). The dominant filtering role of overstorey strata on the available resources may therefore impose negative influence on the aboveground biomass in understorey strata probably due to the limited resources availability (Bartels & Chen 2013, Hooper *et al.* 2005, Zhang *et al.* 2016a). This pattern can be clearly evidenced by the positive effect of soil nutrients on CWM of overstorey tree height and the negative effect of soil nutrients on CWM of understorey stem wood density (Fig. 7.7). Water and nutrients are more plentiful for trees in overstorey strata because they have large root systems that efficiently absorb these resources. Hence, the positive response of overstorey functional identity of tree height to soil nutrients has probably indirectly reduced resources in understorey strata. However, the big trees effect does not work directly on functional identity and aboveground biomass of understorey strata in this study (Fig. 7.7). This might happen due to the resource heterogeneity in understorey strata caused by overstorey stand structure, which in turn affects species diversity and thus functional identity of understorey (Bartels & Chen 2013, Zhang *et al.* 2016a).

In comparison, the whole-community optimal model showed that high aboveground biomass is strongly driven by functional identity of tall and big trees with high leaf dry matter content (conservative strategy) and mean leaf area (acquisitive strategy). This result may be attributable to the selection effect, i.e., diverse communities are more likely to by chance include certain productive, high-functioning species and traits (Loreau & Hector 2001), and hence high aboveground biomass (Cavanaugh *et al.* 2014).

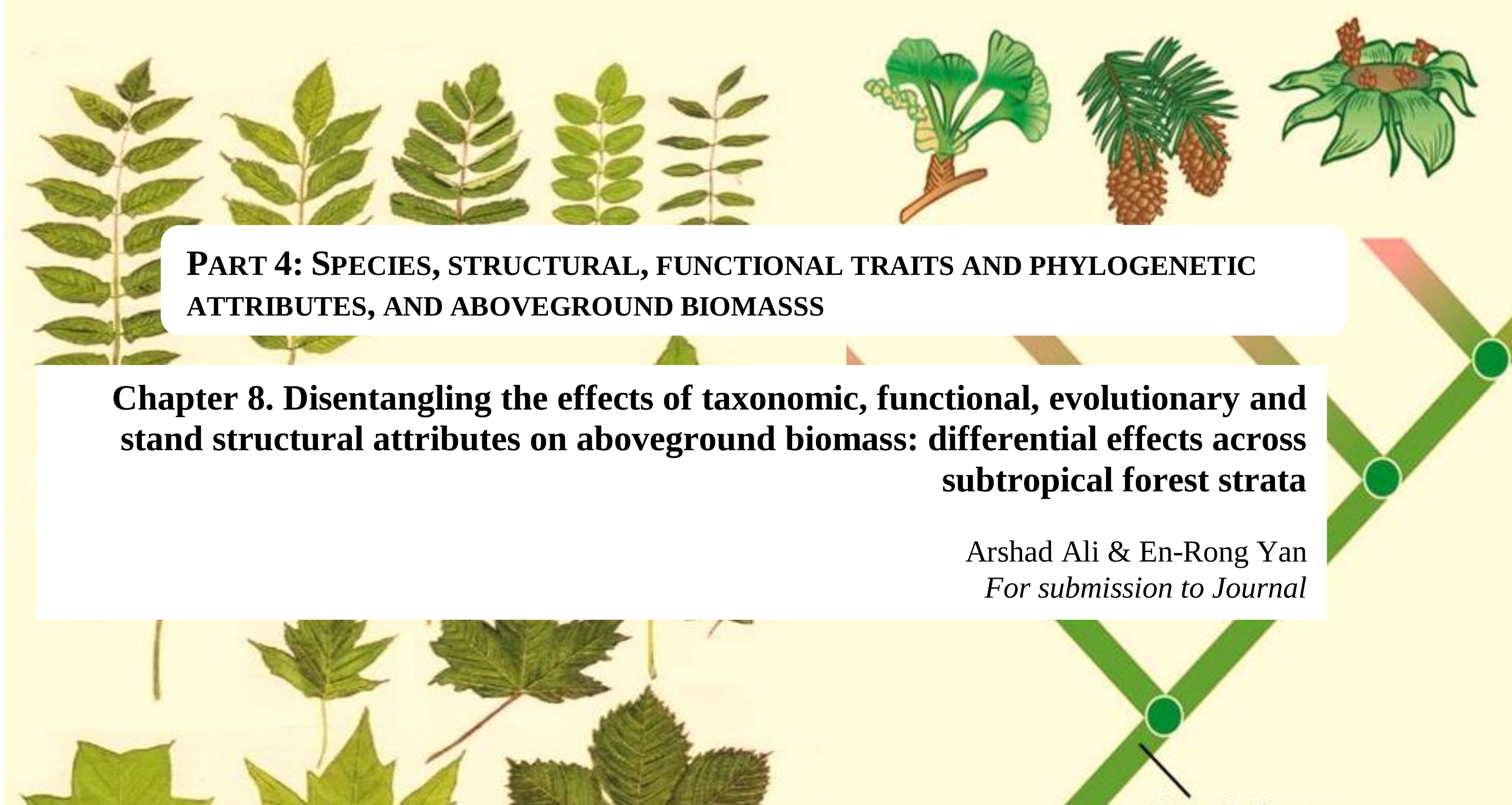
7.4.4. Soil nutrients modulate functional strategies for driving high aboveground biomass across forest strata

In contrary to the soil fertility hypothesis, we found that soil nutrients had negative effect on aboveground biomass at each of overstorey and understorey strata, and whole-community level. These negative relationships may be attributable to species adaptations to the local soil conditions through increasing longevity and stand biomass retention (Jucker *et al.* 2016, Poorter *et al.* 2015, Prado-Junior *et al.* 2016). Besides the direct effects, soil nutrients can also indirectly affect aboveground biomass via edaphic filtering (Jucker *et al.* 2016, Reich 2014). Nutrient-poor soils tend to be dominated by species with conservative strategy, whereas nutrient-rich soils tend to be dominated by species with acquisitive strategy (Fortunel *et al.* 2014, Poorter & Bongers 2006, Reich 2014).

As expected, we found that, on the one hand, soil nutrients positively affect functional identity of tree height in overstorey strata but negatively affect the overstorey aboveground biomass, indicating a fast-growing strategy for overstorey trees. On the other hand, strong negative direct effects of soil nutrients and physicochemical on understorey functional identity and aboveground biomass indicate a slow-growing conservative strategy for nutrient-tolerant trees in understorey strata. It is plausible that trees with conservative trait values (e.g. high wood density) dominate on nutrient-poor soils because dense-wooded trees enhance nutrient residence time in the trees (e.g. Prado-Junior *et al.* 2016). In our studied forest, the same conservative trait values are important to deal with nutrient-limited environment (i.e. understorey strata), and hence enhances aboveground biomass through conservative strategy. In addition, our results showed that direct effect of overstorey functional identity of tree height had no significant effects on the understorey's functional identity and aboveground biomass. In combination, our study suggests that in understorey strata of the forest, soil nutrients (i.e. the big trees effect on the available resources) may be a stronger driver of aboveground biomass than light availability in a subtropical forest.

7.5. Concluding remarks

We conclude that the roles of functional identity of conservative and acquisitive strategies based on the mass ratio hypothesis for predicting aboveground biomass depend on the individual strata of concern. The big trees effect on the available resources has probably caused reduction in resources in the understorey strata, and hence trees in understorey tended to employ conservative strategy for driving high aboveground biomass. High aboveground biomass was potentially driven by tall stature or functional identity of tree height through making use of plentiful soil nutrients at overstorey strata, whereas by conservative strategy at understorey strata through enduring nutrient-poor soils, simultaneously both strategies do so at the whole-community level. Our study suggests that in complex subtropical forest, combining data across forest strata may swamp the contrasting observed relationships at overstorey and understorey strata. Therefore, to better understand the roles of functional identity of conservative and acquisitive strategies in driving ecosystem functions, it is worth to analyse the overstorey and understorey strata separately.



PART 4: SPECIES, STRUCTURAL, FUNCTIONAL TRAITS AND PHYLOGENETIC ATTRIBUTES, AND ABOVEGROUND BIOMASSS

Chapter 8. Disentangling the effects of taxonomic, functional, evolutionary and stand structural attributes on aboveground biomass: differential effects across subtropical forest strata

Arshad Ali & En-Rong Yan

For submission to Journal

8.1. Introduction

Biodiversity is a multifaceted concept, and hence quantified in many different ways, e.g., taxonomic diversity, functional trait diversity and identity, and evolutionary diversity (Purvis & Hector 2000). Biodiversity as such is not an ecosystem function but is important to many ecosystem functions such as aboveground biomass and productivity (Cadotte *et al.* 2008, Finegan *et al.* 2015, Prado-Junior *et al.* 2016, Yuan *et al.* 2016). In addition, stand structural diversity or attributes have been recognized as the coupling factors with some of the above metrics of biodiversity for explaining variation in ecosystem functions (Ali *et al.* 2016b, Chiang *et al.* 2016, Poorter *et al.* 2015, Zhang & Chen 2015). Recently, some empirical studies have suggested that the relationship between biodiversity (including stand structure) and aboveground biomass is greatly dependent on forest strata (i.e. overstorey and understorey) (Ali & Yan 2017c, Zhang *et al.* 2016a). Therefore, it is insightful to assess the effects of multiple metrics of biodiversity and stand structural attributes on aboveground biomass across forest strata alone or combined, since light limits plant performance in different vertical layers (e.g., Brenes-Arguedas *et al.* 2011, Wright 2002).

Several ecological hypotheses or theories have been put forward to explain the relationships between biodiversity and aboveground biomass or productivity. The most prominent hypotheses are the niche complementarity and mass ratio. The niche complementarity hypothesis may measure based on taxonomic diversity and the multivariate-trait space, i.e., functional richness, evenness, divergence and dispersion (Laliberté & Legendre 2010, Villéger *et al.* 2008). The niche complementarity hypothesis predicts that communities with a higher diversity of species (Tilman 1999) or functional traits (Díaz *et al.* 2011a) use available resources more efficiently, thereby increasing the magnitude of ecosystem functions in natural forests (Zhang *et al.* 2012b). In addition, longer evolutionary differentiation has been theorized to generate greater functional trait variation related to ecological niches and provides evidence for the niche complementarity hypothesis (Cadotte *et al.* 2008, Flynn *et al.* 2011, Zuppinger-Dingley *et al.* 2014). Therefore, evolutionary diversity is the alternative approach for testing the niche complementarity hypothesis based on phylogenetic distances of the species within a community (Cadotte *et al.* 2008). Evolutionary diversity can be quantified as phylogenetic diversity, phylogenetic species richness, evenness, clustering and variability (Faith 1992, Helmus *et al.* 2007). The mass ratio hypothesis predicts that ecosystem processes are driven by the (traits of the) most abundant species in plant communities (Grime 1998), and therefore aboveground biomass should be closely related to CWM of trait values (Conti & Díaz 2013, Díaz *et al.* 2007, Garnier *et al.* 2004). Traits that are associated with the growth rate of individual plants are expected to be mechanistically associated to primary productivity of the vegetation (Finegan *et al.* 2015, Garnier *et al.* 2004).

Aboveground biomass or productivity may be determined not only by multiple metrics of biodiversity but also by several stand structural attributes including tree size inequality, mean stem diameter and stand structural diversity (Ali *et al.* 2016b, Poorter *et al.* 2015, Zhang & Chen 2015). Stand structural attributes (i.e. mean diameter, stand density and wood density) contribute directly to aboveground biomass (Ali *et al.* 2016b, Poorter *et al.* 2015). Therefore, variation in stand structure (i.e. individual tree size inequality) also enhances light capture, and as a consequence increases aboveground biomass gain (Ali & Yan 2017c, Zhang & Chen 2015). Similarly, multiple metrics of biodiversity and stand structure attributes could also increase aboveground biomass through their feedbacks or interactions, because high stand densities are driven by biodiversity which leads to more light interception (Ali *et al.* 2016b, Dănescu *et al.* 2016, Zhang & Chen 2015). For instance, high species diversity may have indirect positive effects on aboveground biomass (Ali *et al.* 2016b, Zhang & Chen 2015) and productivity (Dănescu *et al.* 2016) by increasing stand structural attributes. Moreover, variation in big-diameter trees and functional identity of maximum tree height have strong positive relationships with aboveground biomass (Ali & Yan 2017c, b, Chiang *et al.* 2016). It is also clear that taxonomic diversity has explained additional variation in aboveground biomass, once the role of stand structural attributes has explicitly been taken into account in natural forests (Poorter *et al.* 2015). Therefore, any study attempting to address the effects of multiple metrics of biodiversity and stand structure attributes on aboveground biomass must account for these important feedbacks among biotic factors for better understanding of ecological mechanisms.

Studies in forests also reveal that local environmental or abiotic factors, such as topographic factors (elevation, slope and convexity) and soil physicochemical properties, have both direct and indirect (via biodiversity and/ or stand structural attributes) effects on aboveground biomass or productivity in natural forests (Chiang *et al.* 2016, Jucker *et al.* 2016, Poorter *et al.* 2015, Zhang & Chen 2015). The relative importance of some of these multiple metrics of biodiversity and stand structural attributes (i.e. biotic factors), and environmental factors (i.e. abiotic factors) have recently been acknowledged for explaining net biomass change in natural forests (van der Sande *et al.* 2017). However, it is poorly understood how taxonomic diversity, functional trait diversity and identity, evolutionary diversity and stand structural attributes, are affecting aboveground biomass while accounting for the effects of local environmental factors across forest strata and at whole-community level in natural forests (Fig. 8. 1). Since light condition is more stressful in understorey strata than in overstorey strata in the complex natural forests (e.g., Brenes-Arguedas *et al.* 2011, Wright 2002). It is therefore plausible that plant species in understorey strata tend to employ complementarity or conservative strategy whereas functional dominance (adult stature) or the big trees effect may more apparent in overstorey strata for driving high aboveground biomass (Ali & Yan 2017b, Bartels & Chen 2010).

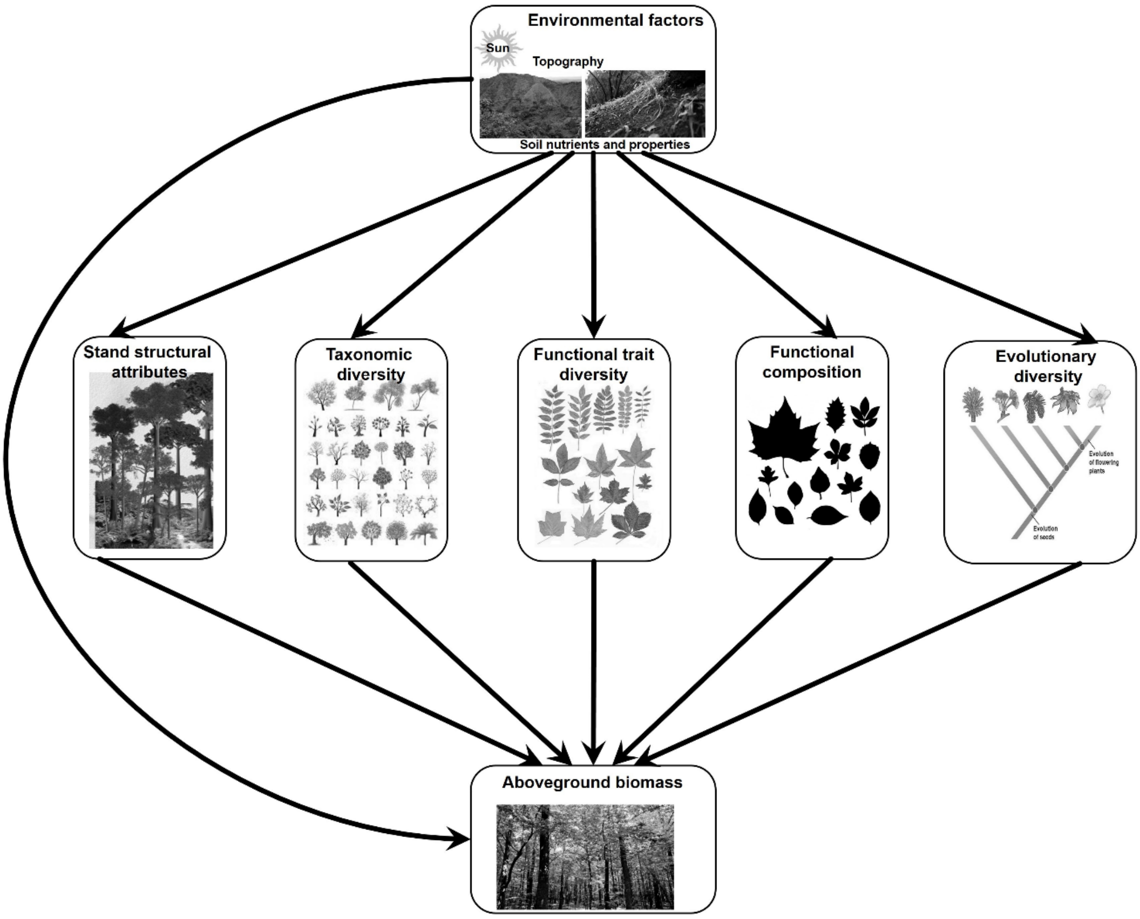


Fig. 8.1. Conceptual model for the prediction of aboveground biomass in a subtropical forest of Eastern China. Model showing hypothesized relationships of how environmental factors affect forest diversity, and how environmental factors and forest diversity concomitantly affect aboveground biomass across forest strata (overstorey and understorey) and whole-community level. Pictures for forest diversity attributes are shown for the purpose of visual exhibition only.

In this study, we address two major questions by analyzing biophysical data from 125 plots inside a 5-ha natural subtropical forest in Eastern China. First, what are the relative effects of taxonomic diversity, functional trait diversity, functional identity, evolutionary diversity and stand structural attributes on aboveground biomass across forest strata, and at whole-community level? We hypothesize that taxonomic diversity, functional trait diversity and evolutionary diversity have positive effects on aboveground biomass at understorey strata (through the niche complementarity effect) whereas the negative effect at overstorey strata (due to the presence of few dominant and functionally-similar big trees). Under the mass ratio hypothesis, we hypothesize: 1) the positive relationships of aboveground biomass with CWM of acquisitive traits and tree height while negative relationships with conservative traits at overstorey strata; and 2) the positive relationships of aboveground biomass with conservative traits while negative relationships with CWM of acquisitive traits at understorey strata. At whole-community level, we expect almost the same relationships as hypothesized for the overstorey strata due to the dominant role of overstorey strata on understorey, and hence may be obscured the role of understorey when mixed data across forest strata (Ali & Yan 2017b). Under the niche complementarity hypothesis based on the stand structural attributes, we hypothesize that as stand structural attributes increase there will be greater aboveground biomass across forest strata and at whole-community level, and that they have stronger effects on aboveground biomass than individual effect of each biodiversity attributes. The second question is, what are the direct effects of local environmental factors on aboveground biomass, multiple metrics of biodiversity and stand structural attributes across forest strata and at whole-community in a subtropical forest? Under the soil fertility hypothesis (Quesada *et al.* 2012, Wright *et al.* 2011), we hypothesize that with an increase in soil nutrients there will be an increase in aboveground biomass, biodiversity and stand structure.

8.2. Materials and methods

8.2.1. Quantification of forest diversity attributes

Overstorey strata were defined as all individuals with DBH ≥ 10 cm in each forest plot, and understorey strata included individuals with 1 ≤ DBH < 10 cm (Barrufol *et al.* 2013). This resulted in a total of 3,213 stems belonging to 71 species, 47 genera and 27 families in the overstorey, and a total of 17,004 stems belonging to 94 species, 57 genera and 33 families in the understorey across 125 plots in a 5-ha subtropical forest (Ali & Yan 2017b).

Stand structural attributes and four metrics of biodiversity (hereafter collectively called as ‘forest diversity attributes’) were used to test the relative effect of the relationship between forest diversity and aboveground biomass at each of the overstorey and understorey strata, and whole-community level in a subtropical forest. This framework distinguishes five different generic attributes of forest diversity in a community, i.e. the structural variation, the variation in component species based on taxonomic features, the dominant (most abundant) trait values, functional trait diversity based on multivariate-trait space, evolutionary diversity based on plant species phylogeny or supertree (e.g., Ali *et al.* 2017, Conti & Díaz 2013, Finegan *et al.* 2015, Poorter *et al.* 2015, Zhang & Chen 2015). It is therefore not a question of whether these forest diversity attributes are related to aboveground biomass, but what their relative effects is in determining aboveground biomass across forest strata and whole-community level.

Three stand structural attributes were calculated that are relevant to the aboveground biomass: stand density (number of trees per hectare), mean tree DBH (in cm) and coefficient of variance of DBH (expressed as percentage) at each of overstorey and understorey, and whole-community level within each plot. To describe taxonomic diversity, we calculated three diversity indices at each of overstorey and understorey, and whole-community level within each plot: species richness, Pielou's species evenness and Shannon-Wiener species diversity. The calculations on the coefficient of variation was performed using *cv* function of *raster* package. The calculations on the taxonomic diversity indices were performed using the *vegan* package (Oksanen *et al.* 2015).

For calculation of functional trait diversity indices and CWM of trait values, we used eight functional traits that are important for plant growth and survival (Poorter & Markesteijn 2008), and hence for standing aboveground biomass, biomass productivity and carbon storage (Finegan *et al.* 2015, Prado-Junior *et al.* 2016). The CWM of a single trait was calculated as the mean trait value in the overstorey strata, understorey strata and whole-community level, weighted by the species' relative basal area (Garnier *et al.* 2004). We used four complementary indices to measure multivariate functional trait diversity: functional evenness, functional richness, functional divergence and functional dispersion (Laliberté & Legendre 2010, Mason *et al.* 2005, Villéger *et al.* 2008). The species' relative basal area (relative to the total understorey, overstorey or whole-community basal area) was used to weight the trait(s) of overstorey, understorey and whole-community species within each plot, because basal area is a better indicator of plant performance than abundance (Prado-Junior *et al.* 2016). Trait values were standardized before the calculation of four functional trait diversity indices. All functional trait diversity indices and CWM values were calculated using the *vegan* (Oksanen *et al.* 2015), *FD, dbFD* and *functcomp* packages (Laliberté & Legendre 2010).

For the quantifications of evolutionary diversity indices, we first constructed phylogenetic supertree of all species, for each of overstorey, understorey and whole-community, based on the 'R20120829 phylomatic tree for plants' in Phylomatic v3 (Webb & Donoghue 2005). This is an online interface that supplies a phylogeny based on taxonomic names of plant species (http://phylodiversity.net/phylomatic/). This supertree was then assigned branch lengths estimated from multi-gene molecular and fossil data implemented in Phylomatic, which is the largest and most updated standardized species-level phylogeny of seed plants (Zanne *et al.* 2014). We then calculated five evolutionary diversity indices – including phylogenetic diversity, phylogenetic species richness, phylogenetic species evenness, phylogenetic species variability and phylogenetic species clustering (Faith 1992, Helmus *et al.* 2007). All evolutionary diversity indices were calculated using the *picante* package (Kembel *et al.* 2010).

The descriptions about the measurement of functional traits, estimation of aboveground biomass and measurement of environmental factors are provided in Chapter 2.

Table 8.1. Summary of the stand structural attributes, multiple metrics of biodiversity indices, aboveground biomass across forest strata and whole-community (*n* = 125) in a subtropical evergreen broadleaf forest in Eastern China. Summary for environmental factors axes (PCA) is also provided.

Abbreviations: DBH, diameter at breast height; CV DBH, individual tree size inequality (coefficient of variance); SR, species richness; SE, species evenness; Hs, species diversity; FRic, functional richness; FEve, functional evenness; FDiv, functional divergence; FDis, functional dispersion; FDiv, functional divergence; CWM, community-weighted mean; H, plant maximum potential height; SLA, specific leaf area; LDMC, leaf dry matter content; MLA, mean leaf area; LNC, leaf nitrogen concentration; LPC, leaf phosphorus concentration; LNC:LPC leaf nitrogen to phosphorus ratio; SWD, stem wood density; PSC, phylogenetic species clustering; PSE, phylogenetic species evenness; PSV, phylogenetic species variability; PD, phylogenetic diversity; PSR, phylogenetic species richness; AGB, aboveground biomass; PC1 and PC2, PCA axes; Topo, topography.

Variable	Unit	Overstorey strata				Understorey strata				Whole-community			
		Mean	S.E.	Min	Max	Mean	S.E.	Min	Max	Mean	S.E.	Min	Max
Stand structural attributes													
Mean DBH	cm	20.59	0.26	14.35	31.56	3.36	0.05	2.42	4.95	6.18	0.12	3.81	12.14
CV DBH	%	49.55	1.12	21.15	89.41	63.54	0.52	49.26	84.34	126.82	2.02	82.84	183.74
Stand density	trees/ha	642.60	19.42	200.00	1200.00	3400.80	110.34	775.00	8475.00	4043.40	111.96	1075.00	9275.00
Taxonomic diversity indices													
SR	unitless	11.84	0.28	4.00	19.00	20.24	0.53	10.00	42.00	26.35	0.54	12.00	46.00
SE	unitless	0.79	0.01	0.44	0.99	0.72	0.01	0.44	0.90	0.68	0.01	0.40	0.81
Hs	unitless	1.92	0.03	0.85	2.52	2.14	0.04	1.18	3.24	2.22	0.03	1.31	2.92
Multivariate functional trait diversity indices													
FRic	unitless	0.22	0.06	0.00	5.03	2.23	0.32	0.01	21.94	4.94	0.50	0.12	27.83
FEve	unitless	0.63	0.01	0.38	0.95	0.50	0.01	0.11	0.75	0.42	0.01	0.20	0.69
FDiv	unitless	0.77	0.01	0.45	0.97	0.64	0.01	0.42	0.86	0.77	0.01	0.55	0.96
FDis	unitless	2.28	0.03	0.83	3.46	1.92	0.03	1.07	2.80	2.31	0.03	1.04	3.48
Community-weighted mean (functional identity of a single trait) indices													
CWM H	m	20.69	0.23	14.37	28.72	11.49	0.16	7.43	19.19	19.40	0.22	12.89	26.73
CWM MLA	cm^2	52.92	2.21	19.70	153.11	19.92	0.68	10.35	55.01	47.94	1.97	19.36	134.83
CWM SLA	$cm^2\ g^{-1}$	131.04	1.98	88.17	207.31	131.37	1.43	95.98	178.34	132.32	1.78	89.43	192.04
CWM LDMC	$mg\ g^{-1}$	395.98	2.61	328.12	455.48	407.70	1.76	365.31	460.48	396.97	2.38	341.44	451.55
CWM LNC	$mg\ g^{-1}$	19.21	0.15	15.13	23.34	17.15	0.10	14.95	20.04	18.92	0.14	15.18	23.00

CWM LPC	mg g^{-1}	0.56	0.00	0.42	0.87	0.56	0.00	0.48	0.69	0.55	0.00	0.44	0.84
CWM LNC:LPC	unitless	37.08	0.39	28.24	51.64	32.64	0.19	26.58	40.20	36.48	0.34	28.96	49.00
CWM SWD	g cm^{-3}	0.54	0.00	0.45	0.59	0.55	0.00	0.50	0.65	0.54	0.00	0.46	0.60
Evolutionary diversity indices													
PD	unitless	37.79	0.65	11.00	55.00	49.01	0.96	26.00	86.00	60.39	0.85	39.00	92.00
PSV	unitless	0.64	0.00	0.52	0.83	0.61	0.00	0.47	0.71	0.62	0.00	0.54	0.69
PSR	unitless	7.48	0.17	2.23	12.49	12.21	0.30	6.29	25.04	16.09	0.30	8.19	27.20
PSE	unitless	0.55	0.01	0.32	0.77	0.51	0.01	0.25	0.71	0.52	0.01	0.32	0.71
PSC	unitless	0.71	0.01	0.28	0.82	0.76	0.00	0.63	0.85	0.78	0.00	0.67	0.86
Response variable (Strata or community function)													
AGB	Mg ha^{-1}	69.34	2.27	15.38	149.56	4.98	0.16	1.22	9.72	74.32	2.31	19.64	154.84
Environmental factors axes (PCA)													
PCA	Unit	Mean	S.E.	Min	Max	PCA	Unit	Mean	S.E.	Min	Max		
Topo PC1	unitless	0.00	0.12	-3.25	2.97	Soil PC1	unitless	0.00	0.17	-6.25	2.87		
Topo PC2	unitless	0.00	0.08	-2.75	2.06	Soil PC2	unitless	0.00	0.12	-2.11	2.69		

Note: Natural-logarithm transformed and standardized data was used in the statistical analyses.

8.2.2. Statistical analyses

We employed structural equation model (SEM) to examine the relationships of stand structural attributes and multiple metrics of biodiversity with aboveground biomass, in addition to the effects of environmental factors, at each of overstorey, understorey and whole-community level (Fig. 8.1). For this purpose, we selected only one important variable per forest diversity group in order to avoid complexity in SEM and correlations between pairs of predictors within each group as we had numerous indices per group, by following the standard statistical procedures of previous studies (Ali *et al.* 2017, Conti & Díaz 2013, Díaz *et al.* 2007, Poorter *et al.* 2015, van der Sande *et al.* 2017). However, our study design may confound statistical results when there is spatial autocorrelation in the variables of interest. To account for this we first performed generalized least-squares (GLS) models, as shown in our previous studies (Ali & Yan 2017c, b). _ENREF_18We found that models without spatial autocorrelation always had the lower AIC values (Table 8.2), which is similar to the recent observations in natural forests (Ali & Yan 2017c, b, Yuan *et al.* 2016).

Table 8.2. Summary of the generalized least-squares (GLS) models of aboveground biomass on predictors at forest strata and whole-community level, used in the structural equation models (Figs 8.3, 8.5 and 8.7). Only main results are shown here because of 54 models at each of forest strata and whole-community level (in total 108 models). All the abbreviations for variables are explained in Table 8.1.

GLS model	Model	Coefficient	*t*-value	*P*-value	AIC	R^2_{pseudo}
Forest strata						
AGB ~ mean DBH	Non-spatial	0.57	10.82	<0.001	606.99	0.308
	Spatial	0.58	11.07	<0.001	613.27	0.308
AGB ~ stand density	Non-spatial	0.46	7.80	<0.001	648.21	0.195
	Spatial	0.45	7.65	<0.001	658.94	0.195
AGB ~ species diversity	Non-spatial	0.17	2.68	0.008	695.64	0.041
	Spatial	0.15	2.31	0.022	706.56	0.041
AGB ~ species richness	Non-spatial	0.41	6.94	<0.001	658.70	0.174
	Spatial	0.41	6.92	<0.001	668.11	0.174
AGB ~ FRic	Non-spatial	0.20	3.31	0.001	692.08	0.057
	Spatial	0.22	3.43	<0.001	699.97	0.057
AGB ~ FEve	Non-spatial	-0.13	-2.19	0.030	698.07	0.020
	Spatial	-0.15	-2.39	0.018	705.84	0.020
AGB ~ CWM H	Non-spatial	0.02	0.24	0.810	702.56	0.003
	Spatial	0.02	0.30	0.766	711.27	0.003
AGB ~ CWM SWD	Non-spatial	0.23	3.63	<0.001	691.17	0.086
	Spatial	0.25	3.84	<0.001	698.49	0.086
AGB ~ PSR	Non-spatial	0.35	5.82	<0.001	670.92	0.121

	Spatial	0.34	5.62	<0.001	681.84	0.121
AGB ~ Soil PC2	Non-spatial	-0.28	-5.87	<0.001	672.62	0.156
	Spatial	-0.29	-6.06	<0.001	679.75	0.156
Whole-community level						
AGB ~ CV DBH	Non-spatial	0.32	3.69	<0.001	352.75	0.100
	Spatial	0.43	4.76	<0.001	352.24	0.100
AGB ~ species evenness	Non-spatial	-0.23	-2.66	0.009	358.78	0.054
	Spatial	-0.27	-2.98	0.004	361.68	0.054
AGB ~ FDis	Non-spatial	-0.15	-1.68	0.095	362.86	0.022
	Spatial	-0.15	-1.70	0.091	366.75	0.022
AGB ~ CWM H	Non-spatial	0.39	4.69	<0.001	345.43	0.152
	Spatial	0.42	4.91	<0.001	348.14	0.152
AGB ~ PSE	Non-spatial	-0.27	-3.17	0.002	356.00	0.075
	Spatial	-0.28	-3.17	0.002	359.95	0.075
AGB ~ Soil PC2	Non-spatial	-0.18	-2.85	0.005	358.42	0.062
	Spatial	-0.18	-2.85	0.005	362.42	0.062

For the selection of one important and strong predictor variable within each group, we therefore performed multiple linear regressions models (i.e. general linear models) to evaluate how aboveground biomass was driven by stand structural attributes, taxonomic diversity, functional trait diversity, functional identity and evolutionary diversity across local environmental conditions. More specifically, we tested five series of multiple linear regressions models in order to find best subset of predictor(s) within each group for explaining variation in aboveground biomass at each of the overstorey and understorey strata, and whole-community level. The five series of multiple linear regressions models were: 1) stand structural attributes (3 variables; Table 8.3), taxonomic diversity (3 variables; Table 8.4), functional trait diversity (4 variables; Table 8.5), functional identity (8 variables; Table 8.6) and evolutionary diversity (5 variables; Table 8.7). In all five series of models, we included local environmental factors, i.e. topography PC1, topography PC2, soil PC1 and soil PC2, as covariates. We used all subsets regression analyses and selected the optimal model that had lowest AICc (i.e. AIC adjusted for small sample sizes) within each series of multiple linear regressions models (Tables 8.3-8.7). Models were considered to be equally supported if the difference in AICc was less than two units (Bartoń 2016). When models were equally supported, we selected the most parsimonious model by considering the lowest number of predictors, but preferred the optimal model having at least one forest diversity index over the model having only environmental factors, if any. In addition, multicollinearity diagnosis was performed in multiple linear regressions models using the variance inflation factor (VIF), as multicollinearity larger than 10 could cause inaccurate model parameterization and decrease statistical power, and exclude significant predictor variables (Graham 2003). If any warning for the confounding effect of multicollinearity among predictor variables (i.e. indices), we then separately tested the multiple linear regressions models by including one predictor variable per group in addition to environmental factors as covariates, and selected the optimal model that had lowest AICc across all individual models.

Table 8.3. Top best models (having ΔAICcs < two units) obtained from a series of multiple regression analyses for aboveground biomass and 7 predictors (3 stand structural attributes, and 4 environmental factors axes within each model) using linear model for each of the overstorey, understorey and whole-community level. Standardized regression coefficient (Beta) for each predictor is given. *P* values < 0.05 are given in bold, and selected optimal models are highlighted in gray color. For whole-community level models, combinations of CV DBH, mean DBH (mean DBH) and stand density with environmental factors were separately tested in order to avoid the confounding effect of multicollinearity among stand structural attributes for aboveground biomass, and then selected the optimal model having lowest AICs across all models.
Abbreviations: *df*, number of model parameters; LL, maximum log-likelihood; AICc, the information-theoretic Akaike's information criterion corrected for small samples; ΔAICc, change in AICc relative to the top-ranked model; *wi*, model probability. All the abbreviations for variables are explained in Table 8.1.

CV DBH	Mean DBH	Stand density	Soil PC1	Soil PC2	Topo PC1	Topo PC2	*df*	LL	AICc	ΔAICc	*wi*
Overstorey strata											
0.38	**0.80**	**0.85**	-0.02	**-0.04**			7	52.51	-90.10	0.00	0.30
0.38	**0.80**	**0.85**	**-0.02**	**-0.04**		0.02	8	52.99	-88.70	1.34	0.15
0.38	**0.80**	**0.86**		**-0.03**			6	50.57	-88.40	1.65	0.13
Understorey strata											
0.25	**0.91**	**0.91**	**-0.03**	**-0.04**	**0.04**	**-0.03**	9	107.46	-195.40	0.00	0.83
Whole-community level											
CV DBH and environmental factors models											
0.75			-0.09	**-0.27**	**0.24**	**-0.23**	7	-139.68	294.30	0.00	0.52
0.72				**-0.19**	**0.34**	**-0.26**	6	-141.25	295.20	0.90	0.33
Mean DBH and environmental factors models											
	0.32			-0.11			4	-166.23	340.80	0.00	0.19
	0.37						3	-167.72	341.60	0.86	0.12
	0.32				0.09		4	-166.76	341.80	1.06	0.11
	0.30			-0.11		-0.08	5	-165.88	342.30	1.47	0.09
Stand density and environmental factors models											
		0.20		**-0.14**		-0.17	5	-169.09	348.70	0.00	0.14
		0.20			0.14	**-0.18**	5	-169.29	349.10	0.40	0.11
		0.19		**-0.14**			4	-170.64	349.60	0.93	0.09
		0.19		-0.09	0.08	-0.18	6	-168.73	350.20	1.49	0.06
		0.19			**0.14**		4	-170.96	350.30	1.57	0.06
		0.20	-0.03	**-0.14**		-0.16	6	-168.85	350.40	1.73	0.06

Table 8.4. Top best models (having ΔAICcs < two units) obtained from a series of multiple regression analyses for aboveground biomass and 7 predictors (3 taxonomic diversity indices, and 4 environmental factors axes within each model) using linear model for each of the overstorey, understorey and whole-community level. Standardized regression coefficient (Beta) for each predictor is given. *P* values < 0.05 are given in bold, and selected optimal models are highlighted in gray color. All the abbreviations for variables are explained in Table 8.1.

Hs	SR	SE	Soil PC1	Soil PC2	Topo PC1	Topo PC2	*df*	LL	AICc	ΔAICc	*wi*
Overstorey strata											
-0.66	**0.88**					-0.15	5	-150.49	311.50	0.00	0.08
-0.68	**0.92**		0.05			-0.17	6	-149.72	312.20	0.67	0.06
-0.65	**0.89**						4	-152.05	312.40	0.96	0.05
-0.67	**0.85**			-0.07		-0.15	6	-149.88	312.50	0.98	0.05
	0.41	-0.41				-0.15	5	-151.25	313.00	1.53	0.04
-0.69	**0.88**		0.05	-0.06		-0.17	7	-149.23	313.40	1.94	0.03
Understorey strata											
0.63		**-0.61**		**-0.16**	**0.36**		6	-127.30	267.30	0.00	0.18
	0.30	**-0.18**		**-0.16**	**0.36**		6	-127.62	267.90	0.63	0.13
-0.26	**0.43**			**-0.17**	**0.36**		6	-127.80	268.30	0.99	0.11
Whole-community level											
0.44		**-0.74**		**-0.23**		-0.17	6	-158.56	329.80	0.00	0.09
	0.21	**-0.37**		**-0.23**		-0.17	6	-158.92	330.60	0.80	0.06
0.45		**-0.74**		**-0.23**			5	-160.29	331.10	1.25	0.05
0.39		**-0.71**		**-0.18**	0.08	-0.17	7	-158.12	331.20	1.37	0.04
-0.43	**0.42**			**-0.23**		-0.17	6	-159.34	331.40	1.56	0.04

Table 8.5. Top best models (having ΔAICcs < two units) obtained from a series of multiple regression analyses for aboveground biomass and 8 predictors (4 functional trait diversity indices, and 4 environmental factors axes within each model) using linear model for each of the overstorey, understorey and whole-community level. Standardized regression coefficient (Beta) for each predictor is given. *P* values < 0.05 are given in bold, and selected optimal models are highlighted in gray color. All the abbreviations for variables are explained in Table 8.1.

FDis	FDiv	FEve	FRic	Soil PC1	Soil PC2	Topo PC1	Topo PC2	*df*	LL	AICc	ΔAICc	*wi*
Overstorey strata												
-0.15		**-0.29**			**-0.15**		-0.15	6	-163.52	339.70	0.00	0.06
-0.16		**-0.29**			**-0.15**			5	-164.85	340.20	0.46	0.05
		-0.32			**-0.13**		-0.16	5	-165.16	340.80	1.08	0.03
	-0.14	**-0.30**			**-0.12**			5	-165.30	341.10	1.35	0.03
	-0.12	**-0.30**			**-0.12**		-0.14	6	-164.23	341.20	1.42	0.03
-0.13		**-0.29**				**0.13**	-0.16	6	-164.41	341.50	1.79	0.02
		-0.33			**-0.13**			4	-166.61	341.50	1.80	0.02
		-0.32				0.12	-0.17	5	-165.60	341.70	1.96	0.02

Understorey strata											
-0.21			**0.25**	**-0.17**	**0.36**		6	-127.63	268.00	0.00	0.18
-0.23		0.08	**0.25**	**-0.15**	**0.38**		7	-126.79	268.50	0.56	0.14
Whole-community level											
-0.39	**0.36**		**0.21**	**-0.20**		-0.16	7	-159.77	334.50	0.00	0.15
-0.38	**0.36**	-0.10	**0.20**	**-0.20**		-0.16	8	-158.88	335.00	0.52	0.12
-0.39	**0.34**		**0.22**	**-0.20**			6	-161.34	335.40	0.90	0.10
-0.38	**0.34**	-0.11	**0.21**	**-0.20**			7	-160.48	335.90	1.42	0.07

Table 8.6. Top best models (having ΔAICcs < two units) obtained from a series of multiple regression analyses for aboveground biomass and 12 predictors (8 CWM indices, and 4 environmental factors axes within each model) using linear model for each of the overstorey, understorey and whole-community level. Standardized regression coefficient (Beta) for each predictor is given. *P* values < 0.05 are given in bold, and selected optimal models are highlighted in gray color. All the abbreviations for variables are explained in Table 8.1.

CWM H	CWM LDMC	CWM LNC	CWM LPC	CWM MLA	CWM LNC:LPC	CWM SLA	CWM SWD	Soil PC1	Soil PC2	Topo PC1	Topo PC2	*df*	LL	AICc	ΔAICc	*wi*
Overstorey strata																
0.41									**-0.22**			4	-162.60	333.50	0.00	0.02
0.41		0.12							**-0.26**			5	-161.88	334.30	0.72	0.01
0.40							-0.11		**-0.26**			5	-161.93	334.40	0.82	0.01
0.41				0.10					**-0.25**			5	-162.02	334.50	1.00	0.01
0.42					0.09				**-0.24**			5	-162.02	334.60	1.01	0.01
0.40	0.13	0.19							**-0.26**			6	-161.04	334.80	1.26	0.01
0.40		0.16							**-0.21**	0.11		6	-161.13	335.00	1.44	0.01
0.41									**-0.17**	0.06		5	-162.31	335.10	1.59	0.01
0.41	0.13			0.17					**-0.25**			6	-161.23	335.20	1.63	0.01
0.40	0.10						-0.16		**-0.25**			6	-161.37	335.50	1.91	0.01
0.41	0.04								**-0.20**			5	-162.48	335.50	1.93	0.01
0.40									**-0.21**		-0.05	5	-162.50	335.50	1.95	0.01
Understorey strata																
							0.16		**-0.14**	**0.32**		5	-135.79	282.10	0.00	0.01

					-0.11				**-0.14**	**0.39**	5	-135.79	282.10	0.01	0.01
-0.17		0.25					**0.20**		**-0.17**	**0.36**	7	-133.78	282.50	0.43	0.01
-0.21				0.17					**-0.15**	**0.39**	6	-134.92	282.50	0.47	0.01
									-0.16	**0.39**	4	-137.23	282.80	0.71	0.01
					-0.08		0.12		**-0.14**	**0.33**	6	-135.07	282.80	0.77	0.01
-0.09							0.14		-0.12	**0.31**	6	-135.16	283.00	0.95	0.01
-0.11									-0.13	**0.37**	5	-136.27	283.00	0.95	0.01
-0.18				0.15			0.12		**-0.14**	**0.33**	7	-134.09	283.10	1.05	0.01
					-0.11			-0.04	**-0.18**	**0.33**	6	-135.34	283.40	1.32	0.01
-0.17				0.15	-0.08				**-0.14**	**0.39**	7	-134.26	283.50	1.40	0.01
-0.07					-0.09				-0.13	**0.37**	6	-135.43	283.60	1.48	0.01
		0.11					0.19		**-0.17**	**0.34**	6	-135.45	283.60	1.53	0.01
	0.06				-0.10				**-0.16**	**0.36**	6	-135.45	283.60	1.53	0.01
								-0.05	**-0.20**	**0.32**	5	-136.64	283.80	1.70	0.01
	0.08								**-0.18**	**0.35**	5	-136.65	283.80	1.71	0.01
				0.06	-0.12				**-0.16**	**0.40**	6	-135.55	283.80	1.72	0.01
-0.20	0.07			0.17					**-0.17**	**0.36**	7	-134.43	283.80	1.73	0.00
			0.07						**-0.17**	**0.39**	5	-136.67	283.80	1.76	0.00
	0.05						0.14		**-0.16**	**0.30**	6	-135.58	283.90	1.79	0.00

			0.04				0.14		**-0.16**	**0.32**	6	-135.60	283.90	1.83	0.00
-0.21		0.19		0.10			0.18		**-0.17**	**0.36**	8	-133.38	284.00	1.92	0.00
							0.14	-0.03	**-0.17**	**0.29**	6	-135.65	284.00	1.93	0.00
						0.05	0.19		**-0.14**	**0.33**	6	-135.65	284.00	1.93	0.00
-0.11			0.07						**-0.15**	**0.37**	6	-135.66	284.00	1.96	0.00
Whole-community level															
0.48	**0.22**	**0.33**							**-0.27**	0.13	7	-150.59	316.10	0.00	0.02
0.48	**0.24**			**0.27**					**-0.31**		6	-151.85	316.40	0.27	0.02
0.48	**0.25**	**0.29**							**-0.33**		6	-151.89	316.50	0.36	0.02
0.47	**0.25**	0.23		0.16					**-0.28**	0.13	8	-149.80	316.80	0.70	0.02
0.47	**0.28**	0.18		0.17					**-0.34**		7	-150.95	316.80	0.71	0.02
0.49	**0.27**	**0.26**			0.10				**-0.34**		7	-151.17	317.30	1.16	0.01
0.48	**0.21**			0.27					**-0.26**	0.09	7	-151.19	317.30	1.19	0.01
0.47	**0.24**	**0.29**					-0.11		**-0.29**	0.13	8	-150.07	317.40	1.24	0.01
0.49	**0.24**	**0.30**			0.08				**-0.28**	0.12	8	-150.12	317.50	1.34	0.01
0.47	**0.27**	**0.24**					-0.11		**-0.35**		7	-151.40	317.70	1.61	0.01
0.47	**0.23**	**0.32**						-0.04	**-0.35**		7	-151.50	318.00	1.83	0.01

Table 8.7. Top best models (having ΔAICcs < two units) obtained from a series of multiple regression analyses for aboveground biomass and 9 predictors (5 evolutionary diversity indices, and 4 environmental factors axes within each model) using linear model for each of the overstorey, understorey and whole-community level. Standardized regression coefficient (Beta) for each predictor is given. *P* values < 0.05 are given in bold, and selected optimal models are highlighted in gray color. All the abbreviations for variables are explained in Table 8.1.

PSC	PSE	PSV	PD	PSR	Soil PC1	Soil PC2	Topo PC1	Topo PC2	*df*	LL	AICc	ΔAICc	*wi*
Overstorey strata													
	-0.39			**0.40**				-0.16	5	-156.84	324.20	0.00	0.07
	-0.41			**0.42**	0.05			-0.17	6	-156.13	325.00	0.79	0.05
	-0.38			**0.41**					4	-158.35	325.00	0.84	0.05
	-0.36	-0.06		**0.40**				-0.15	6	-156.60	325.90	1.74	0.03
	-0.38			**0.38**		-0.04		-0.16	6	-156.61	325.90	1.74	0.03
0.05	**-0.37**			**0.38**				-0.15	6	-156.69	326.10	1.91	0.03
Understorey strata													
	-0.13		**-0.39**	**0.62**		**-0.20**	**0.35**		7	-127.36	269.70	0.00	0.09
	-0.11	-0.11	**-0.47**	**0.69**		**-0.17**	**0.34**		8	-126.30	269.80	0.18	0.08
		-0.13	**-0.44**	**0.64**		**-0.16**	**0.34**		7	-127.91	270.80	1.11	0.05
	-0.12		**-0.42**	**0.64**	-0.04	**-0.24**	**0.30**		8	-127.01	271.30	1.59	0.04
			-0.35	**0.55**		**-0.19**	**0.35**		6	-129.35	271.40	1.73	0.04
	-0.11	-0.11	**-0.49**	**0.71**	-0.04	**-0.20**	**0.29**		9	-125.95	271.50	1.80	0.04
-0.10	-0.11	-0.19	**-0.49**	**0.76**		**-0.17**	**0.35**		9	-125.99	271.50	1.87	0.03
0.05	-0.12		**-0.40**	**0.61**		**-0.20**	**0.34**		8	-127.18	271.60	1.93	0.03
Whole-community level													
	-0.28			**0.25**				**-0.21**	5	-164.49	339.50	0.00	0.03
	-0.26		**0.25**					**-0.22**	5	-164.52	339.50	0.05	0.03
-0.18	**-0.26**			**0.32**		-0.14		**-0.19**	7	-162.43	339.80	0.34	0.02
	-0.24			**0.23**		-0.08		**-0.20**	6	-163.58	339.90	0.39	0.02
	-0.26	0.17	**0.28**			-0.14		**-0.21**	7	-162.53	340.00	0.54	0.02
	-0.23		**0.23**			-0.08		**-0.21**	6	-163.68	340.10	0.58	0.02
	-0.25			**0.22**			0.08	**-0.21**	6	-163.73	340.20	0.69	0.02
	-0.24		**0.23**				0.08	**-0.22**	6	-163.79	340.30	0.80	0.02
-0.18	**-0.27**			**0.31**			0.14	**-0.21**	7	-162.67	340.30	0.82	0.02
-0.16	**-0.24**		**0.31**			-0.13		**-0.21**	7	-162.74	340.40	0.94	0.02
	-0.27	0.14		**0.26**		-0.13		**-0.20**	7	-162.80	340.60	1.08	0.02
	-0.27	0.15	**0.26**				0.13	**-0.22**	7	-162.81	340.60	1.09	0.02
-0.16	**-0.26**		**0.30**				0.13	**-0.22**	7	-162.87	340.70	1.21	0.02
	-0.28	0.12		**0.25**			0.12	**-0.21**	7	-163.10	341.20	1.68	0.01
-0.22	**-0.26**			**0.32**		-0.10	0.08	**-0.20**	8	-162.00	341.20	1.75	0.01
-0.06	**-0.29**			**0.29**				**-0.21**	6	-164.31	341.30	1.84	0.01
	-0.28	0.06	**0.28**					**-0.22**	6	-164.34	341.40	1.90	0.01

	-0.27	0.13	0.14			**-0.22**	6	-164.35	341.40	1.92	0.01
-0.06	**-0.27**	**0.29**				**-0.22**	6	-164.37	341.40	1.96	0.01
	-0.23	**0.24**		0.05	0.11	**-0.23**	7	-163.26	341.50	1.99	0.01

Finally, we selected the most important or strong predictor from optimal model per group or series having highest standardized effect (β) on the variable of interest (i.e. aboveground biomass) (Tables 8.3-8.7). In order to avoid complexity in SEM, we used soil PC2 as the main local environmental factor because it basically represents soil nutrients gradients, and also retained in most of the optimal models across five series of multiple regressions models for explaining variation in aboveground biomass (Tables 8.3-8.7), and also significantly correlated with topography PC1 and soil PC1 (Tables 8.8-8.12). In addition, a modeling averaging approach (synthetic model) for each group of forest diversity was developed to evaluate which predictor variable (or index) contributed consistently across all models for explaining variation in aboveground biomass. For this, regression coefficients of each predictor were averaged across all possible models, weighted by their Akaike Information Criterion weight (AICc-wi), which represents the likelihood of a given best fit model relative to all other models (Wagenmakers & Farrell 2004). An importance value was calculated by adding the AICc-wi values of the models in which the variables were present (e.g., Ali *et al.* 2017, Finegan *et al.* 2015). We found the same important or strong predictor variable for each group or series, as suggest by optimal model (Tables 8.3-8.7).

General linear models were performed using the *stats* package and all subsets regression analyses using the *MuMIn* package (Bartoń 2016). Top best models (having ΔAICcs < two units) obtained from a series of multiple regression analyses for each of the stand structural attributes, taxonomic diversity, functional trait diversity, functional identity (CWM indices) and evolutionary diversity effects on aboveground biomass at overstorey, understorey and whole-community level, are shown in Table 8.3, 8.4, 8.5, 8.6 and 8.7, respectively. The complementary Pearson's correlations between all tested predictors at each of the overstorey and understorey strata, and whole-community level are shown in Tables 8.8-8.12.

Several tests were used to assess the goodness of fit for SEMs, as suggested by previous studies (Ali & Yan 2017c, Jucker *et al.* 2016, Zhang & Chen 2015). We included all significant covariance between pairs of best predictors in order to test that whether stand structural attributes and biodiversity metrics provide any feedback to each other for driving variation in aboveground biomass (Ali *et al.* 2016b, Durán *et al.* 2015, Jucker *et al.* 2016). The SEMs were employed using the *lavaan* package (Rosseel 2012). Prior to the statistical analyses, all numerical variables including aboveground biomass, stand structural attributes and multiple metrics of biodiversity values were natural-logarithm transformed and standardized for the purpose of normality and linearity (Zuur *et al.* 2009). The summary of variables is provided in Table 8.1. For all statistical analyses R 3.2.2 was used (R Development Core Team 2015).

Table 8.8. Pearson's correlation coefficient between all tested stand structural attributes for aboveground biomass at each of the overstorey, understorey and whole-community level. Significant correlations are indicated in bold ($P < 0.05$). All the abbreviations for variables are explained in Table 8.1.

	Mean DBH	CV DBH	Stand density	Topo PC1	Topo PC2	Soil PC1	Soil PC2
Overstorey strata							
Mean DBH	---						
CV DBH	**0.52**	---					
Stand density	**-0.43**	**-0.45**	---				
Topo PC1	**-0.31**	**-0.44**	**0.65**	---			
Topo PC2	0.00	0.08	**-0.22**	0.00	---		
Soil PC1	**0.24**	0.16	**-0.33**	**-0.47**	0.16	---	
Soil PC2	**0.24**	**0.38**	**-0.58**	**-0.69**	0.03	0.00	---
Understorey strata							
Mean DBH	---						
CV DBH	**-0.28**	---					
Stand density	**-0.45**	0.00	---				
Topo PC1	**0.49**	-0.11	0.15	---			
Topo PC2	-0.08	-0.02	0.10	0.00	---		
Soil PC1	**-0.36**	0.16	0.08	**-0.47**	0.16	---	
Soil PC2	**-0.39**	0.02	-0.15	**-0.69**	0.03	0.00	---
Whole-community level							
Mean DBH	---						
CV DBH	**-0.55**	---					
Stand density	**-0.56**	0.17	---				
Topo PC1	**0.35**	**-0.56**	**0.28**	---			
Topo PC2	**-0.23**	0.12	0.04	0.00	---		
Soil PC1	**-0.27**	**0.35**	0.00	**-0.47**	0.16	---	
Soil PC2	**-0.31**	**0.47**	**-0.27**	**-0.69**	0.03	0.00	---

Table 8.9. Pearson's correlation coefficient between all tested taxonomic diversity indices for aboveground biomass at each of the overstorey, understorey and whole-community level. Significant correlations are indicated in bold ($P < 0.05$). All the abbreviations for variables are explained in Table 8.1.

	SR	Hs	SE	Topo PC1	Topo PC2	Soil PC1	Soil PC2
Overstorey strata							
SR	---						
Hs	**0.77**	---					

SE	0.09	**0.70**	---				
Topo PC1	**0.49**	**0.37**	0.04	---			
Topo PC2	-0.11	-0.11	-0.07	0.00	---		
Soil PC2	**-0.21**	-0.10	0.08	**-0.47**	0.16	---	
Soil PC2	**-0.48**	**-0.43**	-0.15	**-0.69**	0.03	0.00	---
Understorey strata							
SR	---						
Hs	**0.79**	---					
SE	**0.44**	**0.90**	---				
Topo PC1	**0.34**	**0.44**	**0.39**	---			
Topo PC2	-0.04	-0.03	-0.03	0.00	---		
Soil PC2	**-0.25**	-0.16	-0.06	**-0.47**	0.16	---	
Soil PC2	**-0.25**	**-0.35**	**-0.32**	**-0.69**	0.03	0.00	---
Whole-community strata							
SR	---						
Hs	**0.54**	---					
SE	0.05	**0.87**	---				
Topo PC1	**0.40**	**0.47**	**0.32**	---			
Topo PC2	-0.05	-0.06	-0.05	0.00	---		
Soil PC2	**-0.27**	-0.13	0.01	**-0.47**	0.16	---	
Soil PC2	**-0.34**	**-0.50**	**-0.38**	**-0.69**	0.03	0.00	---

Table 8.10. Pearson's correlation coefficient between all tested functional trait diversity indices for aboveground biomass at each of the overstorey, understorey and whole-community level. Significant correlations are indicated in bold ($P < 0.05$). All the abbreviations for variables are explained in Table 8.1.

	FRic	FEve	FDiv	FDis	Topo PC1	Topo PC2	Soil PC1	Soil PC2
Overstorey strata								
FRic	---							
FEve	-0.02	---						
FDiv	-0.13	**0.21**	---					
FDis	-0.04	**0.24**	**0.72**	---				
Topo PC1	0.12	-0.11	-0.16	0.04	---			
Topo PC2	-0.04	0.01	0.17	0.04	0.00	---		
Soil PC1	-0.12	0.10	**0.24**	0.17	**-0.47**	0.16	---	
Soil PC2	-0.13	0.10	0.10	-0.14	**-0.69**	0.03	0.00	---
Understorey strata								
FRic	---							
FEve	0.05	---						
FDiv	-0.01	**0.22**	---					
FDis	**0.30**	**0.24**	**0.72**	---				

Topo PC1	**0.36**	-0.02	0.25	**0.28**	---			
Topo PC2	-0.06	-0.10	-0.09	0.02	0.00	---		
Soil PC1	-0.31	-0.04	**-0.23**	-0.09	**-0.47**	0.16	---	
Soil PC2	**-0.26**	-0.14	**-0.16**	**-0.23**	**-0.69**	0.03	0.00	---
Whole-community level								
FRic	---							
FEve	-0.06	---						
FDiv	-0.01	0.06	---					
FDis	-0.01	0.13	**0.59**	---				
Topo PC1	**0.39**	0.12	0.04	0.13	---			
Topo PC2	-0.03	0.01	0.11	0.08	0.00	---		
Soil PC1	**-0.31**	-0.02	0.05	0.11	**-0.47**	0.16	---	
Soil PC2	**-0.30**	-0.09	0.09	-0.15	**-0.69**	0.03	0.00	---

Table 8.11. Pearson's correlation coefficient between all tested CWM indices for aboveground biomass at each of the overstorey, understorey and whole-community level. Significant correlations are indicated in bold ($P < 0.05$). All the abbreviations for variables are explained in Table 8.1.

	CWM H	CWM MLA	CWM SLA	CWM LDMC	CWM LNC	CWM LPC	CWM LNC:LPC	CWM SWD	Topo PC1	Topo PC2	Soil PC1	Soil PC2
Overstorey strata												
CWM H	---											
CWM MLA	0.10	---										
CWM SLA	0.14	**0.52**	---									
CWM LDMC	-0.06	**-0.62**	**-0.70**	---								
CWM LNC	0.12	**0.78**	**0.55**	**-0.60**	---							
CWM LPC	0.03	-0.07	**0.32**	-0.06	**0.23**	---						
CWM LNC:LPC	-0.09	**0.58**	0.10	**-0.40**	**0.45**	**-0.61**	---					
CWM SWD	-0.17	**-0.71**	**-0.38**	**0.52**	**-0.63**	**0.22**	**-0.55**	---				
Topo PC1	-0.14	**-0.48**	**-0.35**	**0.41**	**-0.58**	-0.13	**-0.25**	**0.47**	---			
Topo PC2	**-0.26**	0.06	0.13	-0.13	0.06	0.13	0.01	0.01	0.00	---		
Soil PC1	-0.13	**0.24**	**0.23**	**-0.30**	**0.38**	0.07	0.13	-0.14	**-0.47**	0.16	---	
Soil PC2	**0.21**	**0.53**	**0.29**	**-0.38**	**0.56**	0.03	**0.36**	**-0.55**	**-0.69**	0.03	0.00	---
Understorey strata												
CWM H	---											
CWM MLA	**0.74**	---										
CWM SLA	**0.49**	**0.47**	---									
CWM LDMC	**-0.27**	**-0.28**	**-0.69**	---								
CWM LNC	**0.71**	**0.74**	**0.67**	**-0.30**	---							
CWM LPC	0.15	**0.39**	0.06	0.09	**0.34**	---						
CWM LNC:LPC	**0.42**	**0.25**	**0.29**	**-0.19**	**0.28**	**-0.53**	---					
CWM SWD	**-0.48**	**-0.42**	**-0.73**	**0.46**	**-0.74**	0.05	**-0.38**	---				

Topo PC1	**-0.50**	**-0.55**	**-0.68**	**0.43**	**-0.79**	-0.16	**-0.19**	**0.71**	---			
Topo PC2	0.06	-0.04	**0.23**	**-0.25**	0.05	**-0.29**	**0.28**	**-0.22**	0.00	---		
Soil PC1	0.15	0.09	**0.58**	**-0.56**	**0.28**	**-0.27**	0.09	**-0.48**	**-0.47**	0.16	---	
Soil PC2	**0.53**	**0.56**	**0.44**	-0.15	**0.76**	**0.26**	**0.24**	**-0.56**	**-0.69**	0.03	0.00	---
Whole-community level												
CWM H	**---**											
CWM MLA	**0.19**	---										
CWM SLA	0.13	**0.56**	---									
CWM LDMC	-0.11	**-0.62**	**-0.74**	---								
CWM LNC	**0.21**	**0.79**	**0.60**	**-0.64**	---							
CWM LPC	0.05	-0.05	**0.32**	-0.08	**0.24**	---						
CWM LNC:LPC	-0.03	**0.58**	0.15	**-0.41**	**0.47**	**-0.57**	---					
CWM SWD	-0.20	**-0.74**	**-0.46**	**0.55**	**-0.68**	**0.18**	**-0.55**	---				
Topo PC1	**-0.20**	**-0.51**	**-0.46**	**0.47**	**-0.63**	-0.15	**-0.27**	**0.54**	---			
Topo PC2	**-0.26**	0.03	0.14	-0.13	0.05	0.09	0.03	0.00	0.00	---		
Soil PC1	-0.09	**0.24**	**0.32**	**-0.37**	**0.38**	0.05	0.14	**-0.19**	**-0.47**	0.16	---	
Soil PC2	**0.26**	**0.55**	**0.34**	**-0.38**	**0.61**	0.06	**0.38**	**-0.59**	**-0.69**	0.03	0.00	---

Table 8.12. Pearson's correlation coefficient between all tested evolutionary diversity indices for aboveground biomass at each of the overstorey, understorey and whole-community level. Significant correlations are indicated in bold (*P* < 0.05). All the abbreviations for variables are explained in Table 8.1.

	PD	PSV	PSR	PSE	PSC	Soil PC1	Soil PC2	Topo PC1	Topo PC2
Overstorey strata									
PD	---								
PSV	**-0.18**	---							
PSR	**0.90**	-0.02	---						
PSE	0.06	**0.44**	0.20	---					
PSC	**0.46**	**-0.68**	**0.43**	**-0.30**	---				
Soil PC1	**-0.18**	**0.28**	-0.14	**0.18**	**-0.25**	---			
Soil PC2	**-0.44**	**0.36**	**-0.39**	0.01	**-0.30**	0.00	---		
Topo PC1	**0.46**	**-0.34**	**0.41**	-0.07	**0.35**	**-0.47**	**-0.69**	---	
Topo PC2	-0.03	0.12	-0.08	-0.04	-0.07	0.16	0.03	-0.00	---
Understorey strata									
PD	---								
PSV	**-0.23**	---							
PSR	**0.94**	-0.09	---						
PSE	**0.24**	0.08	**0.28**	---					
PSC	**0.58**	**-0.74**	**0.53**	0.08	---				
Soil PC1	**-0.27**	0.13	**-0.22**	0.08	**-0.24**	---			
Soil PC2	**-0.23**	**0.57**	-0.12	-0.09	**-0.45**	0.00	---		
Topo PC1	**0.31**	**-0.48**	**0.23**	0.07	**0.51**	**-0.47**	**-0.69**		
Topo PC2	-0.01	-0.03	-0.05	-0.07	-0.04	0.16	0.03	-0.00	---
Whole-community level									
PD	---								
PSV	**-0.44**	---							
PSR	**0.94**	**-0.35**	---						
PSE	**-0.20**	**0.38**	**-0.14**	---					
PSC	**0.60**	**-0.85**	**0.60**	**-0.30**	---				
Soil PC1	**-0.28**	**0.25**	**-0.24**	0.04	**-0.29**	---			
Soil PC2	**-0.27**	**0.61**	**-0.24**	**0.30**	**-0.57**	0.00	---		
Topo PC1	0.32	**-0.59**	**0.30**	**-0.25**	0.60	**-0.47**	**-0.69**	---	
Topo PC2	-0.03	-0.04	-0.07	-0.19	0.00	0.16	0.03	-0.00	---

8.3. Results

8.3.1. Overstorey aboveground biomass is mainly driven by functional identity of tree height, stand density and functional evenness

The bivariate relationships showed that overstorey aboveground biomass was significantly increased with increasing stand structural attributes, species richness, functional identity of tree height, phylogenetic diversity, phylogenetic species clustering, phylogenetic species richness and topography (PC1). Aboveground biomass of overstorey strata was significantly decreased with increasing species evenness, functional evenness, functional divergence, functional dispersion, phylogenetic species evenness, phylogenetic species variability and soil nutrients (PC2), whereas all other relationships were non-significant (Fig. 8.2, Table 8.13).

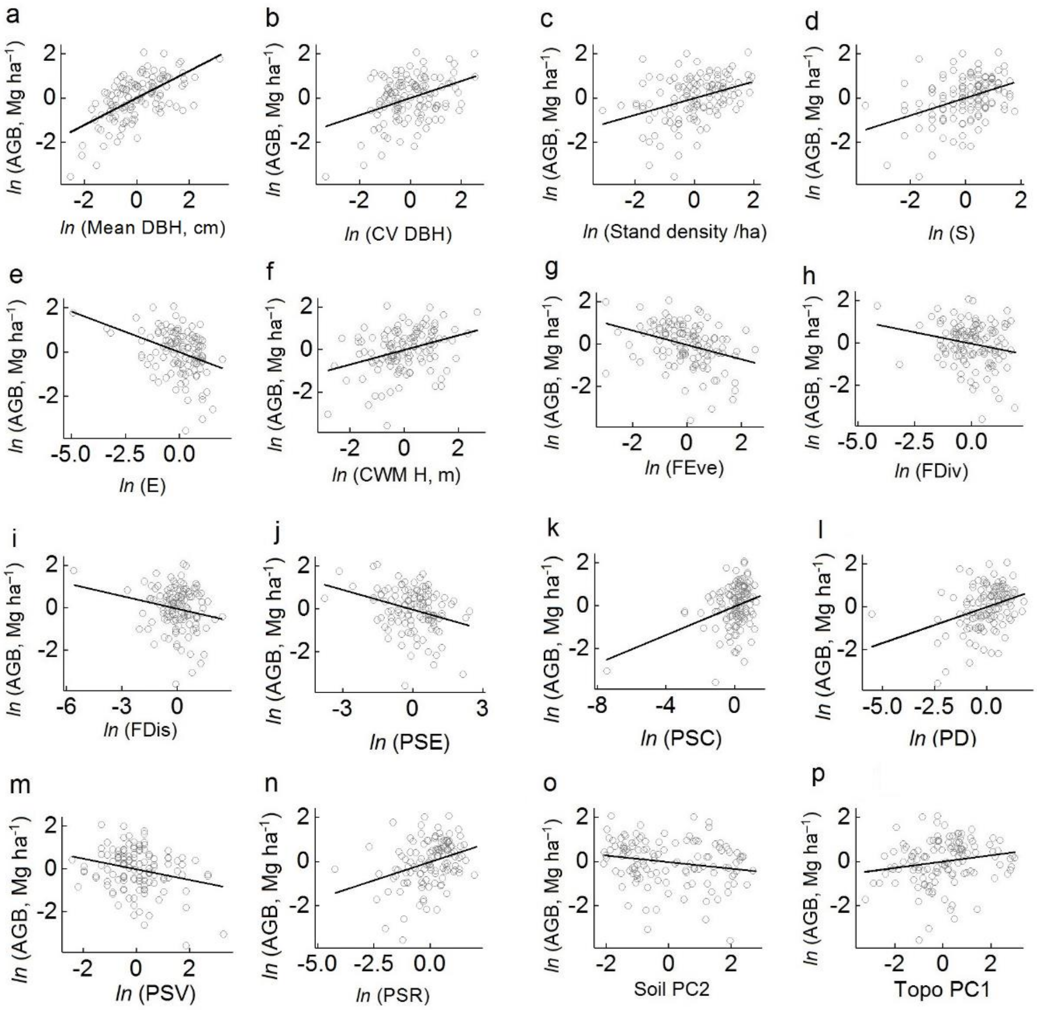


Fig. 8.2. The bivariate relationships between aboveground biomass (AGB) and predictors (a-c, stand structural attributes; d-e, taxonomic diversity indices; f, CWM of trait values; g-i, functional trait diversity indices; j-n, evolutionary diversity indices; and o-p, environmental factors axes; *n* = 125) at overstorey strata. Only significant relationships ($P < 0.05$) are shown here (see Table 8.13). All the abbreviations for variables are explained in Table 8.1.

Table 8.13. Summary of the simple linear models for bivariate relationships of stand structural attributes, multiple metrics of biodiversity indices and environmental factors with aboveground biomass at forest strata and whole-community level in subtropical forests. Significant relationships are indicted in bold ($P < 0.05$). All the abbreviations for variables are explained in Table 8.1.

Predictors	Overstorey strata				Understorey strata				Whole-community level			
	Beta	*P*	PMSE	R^2	Beta	*P*	PMSE	R^2	Beta	*P*	PMSE	R^2
Stand structural attributes												
Mean DBH	0.61	**<0.001**	0.65	0.38	0.50	**<0.001**	0.79	0.25	0.37	**<0.001**	0.90	0.14
CV DBH	0.38	**<0.001**	0.90	0.15	-0.01	0.876	1.05	0.00	0.32	**<0.001**	0.94	0.10
Stand density	0.38	**<0.001**	0.89	0.15	0.50	**<0.001**	0.78	0.25	0.24	**0.007**	0.98	0.06
Taxonomic diversity indices												
Hs	0.04	0.695	1.05	0.00	0.37	**<0.001**	0.90	0.14	-0.04	0.663	1.04	0.00
SR	0.39	**<0.001**	0.89	0.15	0.44	**<0.001**	0.84	0.19	0.30	**0.001**	0.95	0.09
SE	-0.37	**<0.001**	0.89	0.14	0.21	**0.019**	1.00	0.04	-0.23	**0.009**	0.98	0.05
Community-weighted mean (CWM) indices												
CWM H	0.34	**<0.001**	0.92	0.12	-0.45	**<0.001**	0.83	0.20	0.39	**<0.001**	0.89	0.15
CWM MLA	-0.04	0.635	1.04	0.00	-0.39	**<0.001**	0.89	0.15	-0.02	0.784	1.04	0.00
CWM SLA	-0.04	0.692	1.04	0.00	-0.47	**<0.001**	0.82	0.22	-0.12	0.191	1.02	0.01
CWM LDMC	0.13	0.163	1.02	0.02	0.32	**<0.001**	0.94	0.10	0.18	**0.043**	1.00	0.03
CWM LNC	-0.04	0.671	1.03	0.00	-0.57	**<0.001**	0.71	0.33	-0.05	0.590	1.03	0.00
CWM LPC	0.00	0.981	1.03	0.00	-0.08	0.404	1.04	0.01	0.01	0.905	1.03	0.00
CWM LNC:LPC	-0.06	0.471	1.03	0.00	-0.26	**0.004**	0.98	0.07	-0.08	0.374	1.03	0.01
CWM SWD	0.02	0.825	1.04	0.00	0.57	**<0.001**	0.71	0.32	0.06	0.473	1.03	0.00
Functional trait diversity indices												
FRic	0.05	0.543	1.04	0.00	0.42	**<0.001**	0.86	0.18	0.30	**0.001**	0.95	0.09
FEve	-0.34	**<0.001**	0.92	0.12	0.06	0.521	1.04	0.00	-0.12	0.182	1.03	0.01
FDiv	-0.22	**0.016**	1.00	0.05	-0.01	0.939	1.05	0.00	0.08	0.348	1.03	0.01
FDis	-0.20	**0.027**	1.00	0.04	0.05	0.566	1.04	0.00	-0.15	0.095	1.02	0.02

Evolutionary diversity indices												
PD	0.34	**<0.001**	0.94	0.11	0.37	**<0.001**	0.90	0.14	0.31	**<0.001**	0.94	0.10
PSV	-0.24	**0.007**	0.99	0.06	-0.43	**<0.001**	0.85	0.18	-0.16	0.068	1.01	0.03
PSE	-0.30	**<0.001**	0.94	0.09	0.01	0.883	1.05	0.00	-0.27	**0.002**	0.96	0.08
PSC	0.33	**<0.001**	0.92	0.11	0.49	**<0.001**	0.80	0.24	0.20	**0.028**	1.00	0.04
PD	0.34	**<0.001**	0.94	0.11	0.37	**<0.001**	0.90	0.14	0.31	**<0.001**	0.94	0.10
Environmental factors												
Soil PC1	-0.03	0.499	1.03	0.00	-0.16	**0.001**	0.95	0.09	-0.04	0.370	1.03	0.01
Soil PC2	-0.15	**0.018**	0.99	0.04	-0.42	**<0.001**	0.7	0.33	-0.18	**0.005**	0.97	0.06
Topo PC1	0.15	**0.030**	0.99	0.04	0.50	**<0.001**	0.58	0.45	0.18	**0.007**	0.98	0.06
Topo PC2	-0.17	0.097	1.02	0.02	-0.03	0.811	1.05	0.00	-0.17	0.103	1.02	0.02

The overstorey SEM (Fig. 8.3) showed that CWM of plant height had the strong positive direct effect on overstorey aboveground biomass ($\beta = 0.35$, $P < 0.001$), followed by the significant positive direct effect of stand density ($\beta = 0.24$, $P = 0.040$) and negative direct effect of functional evenness ($\beta = –0.24$, $P = 0.001$) while non-significant direct effects of taxonomic and phylogenetic species richness. Soil nutrients had non-significant direct effect on overstorey aboveground biomass, but significant negative direct effects on stand density ($\beta = –0.58$, $P < 0.001$), species richness ($\beta = –0.48$, $P < 0.001$) and phylogenetic species richness ($\beta = –0.39$, $P < 0.001$). Soil nutrients had the significant positive direct effect on CWM of plant height ($\beta = 0.21$, $P = 0.017$), and non-significant direct effect on functional evenness. Soil nutrients had an indirect negative effect via stand density ($\beta = –0.14$, $P = 0.047$) while positive indirect effect via CWM of plant height ($\beta = 0.07$, $P = 0.035$) on overstorey aboveground biomass. The total effect of soil nutrients on overstorey aboveground biomass was significantly negative ($\beta = –0.22$, $P = 0.013$; Table 8.14).

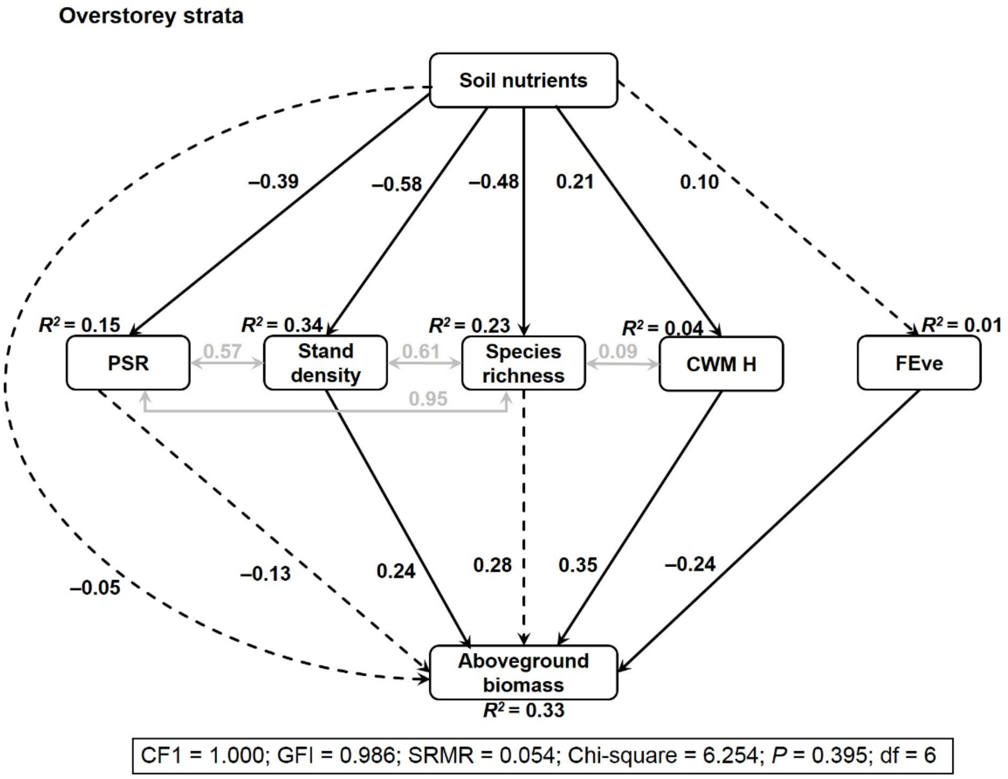


Fig. 8.3. Best-fit structural equation model for the effects of stand structural attribute and multiple metrics of biodiversity on aboveground biomass at overstorey strata in a subtropical forest, after accounting for the effects of soil nutrients. One-sided black arrow represents regression path or 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; all other abbreviations for variables are explained in Table 8.1.

Table 8.14. The direct, indirect, and total standardized effects of soil nutrients, stand structural attribute and multiple metrics of biodiversity on aboveground biomass at overstorey strata, based on structural equation model (SEM; Fig. 8.3). The direct, indirect and total standardized effects (beta) are shown with associated *z*-values and *P*-values. The indirect effect of soil nutrients was calculated by multiplying (*) the standardized effects of all paths on one route, from soil nutrients to mediator, and then to aboveground biomass, while the total effect was calculated by adding standardized direct and indirect effects of soil nutrients. Covariance coefficients between pairs of predictors are shown in the lower section of the Table. Significant effects and covariance are indicated in bold ($P < 0.05$). All the abbreviations for variables are explained in Table 8.1.

Response variable	Predictor variable	Effect	Path label	Beta	z-value	P-value
Regressions						
AGB	Soil nutrients (PC2)	Direct	a	-0.05	-0.47	0.638
Stand density	Soil nutrients (PC2)	Direct	b	-0.58	-7.95	**<0.001**
AGB	Stand density	Direct	c	0.24	2.05	**0.040**
AGB	Soil nutrients (PC2)	Indirect	b*c	-0.14	-1.99	**0.047**
CWM H	Soil nutrients (PC2)	Direct	d	0.21	2.40	**0.017**
AGB	CWM H	Direct	e	0.35	4.45	**<0.001**
AGB	Soil nutrients (PC2)	Indirect	d*e	0.07	2.11	**0.035**
FEve	Soil nutrients (PC2)	Direct	f	0.10	1.12	0.264
AGB	FEve	Direct	g	-0.24	-3.27	**0.001**
AGB	Soil nutrients (PC2)	Indirect	f*g	-0.02	-1.06	0.290
PSR	Soil nutrients (PC2)	Direct	h	-0.39	-4.78	**<0.001**
AGB	PSR	Direct	i	-0.13	-0.45	0.650
AGB	Soil nutrients (PC2)	Indirect	h*i	0.05	0.45	0.651
Species richness	Soil nutrients (PC2)	Direct	j	-0.48	-6.07	**<0.001**
AGB	Species richness	Direct	k	0.28	0.93	0.352
AGB	Soil nutrients (PC2)	Indirect	j*k	-0.14	-0.92	0.358
AGB	Soil nutrients (PC2)	Total	a+(b*c)+(d*e)+(f*g)+(h*i)+(j*k)	-0.22	-2.49	**0.013**
Covariance						
Stand density	Species richness			0.61	5.85	**<0.001**
Stand density	PSR			0.57	5.52	**<0.001**
CWM H	Species richness			0.09	3.38	**0.001**
PSR	Species richness			0.95	7.73	**<0.001**

8.3.2. Understorey aboveground biomass is mainly driven by biodiversity, stand structure and soil nutrients

The bivariate relationships showed that understorey aboveground biomass was significantly increased with increasing stand structural attributes, taxonomic indices, functional richness, CWM of conservative traits, evolutionary diversity indices (with exception of phylogenetic species variability) and topography (PC1). Aboveground biomass of understorey strata was significantly decreased with increasing CWM of acquisitive traits and tree height, phylogenetic species variability, and soil properties and nutrients (PC1 and PC2), whereas all other relationships were non-significant (Fig. 8.4, Table 8.15).

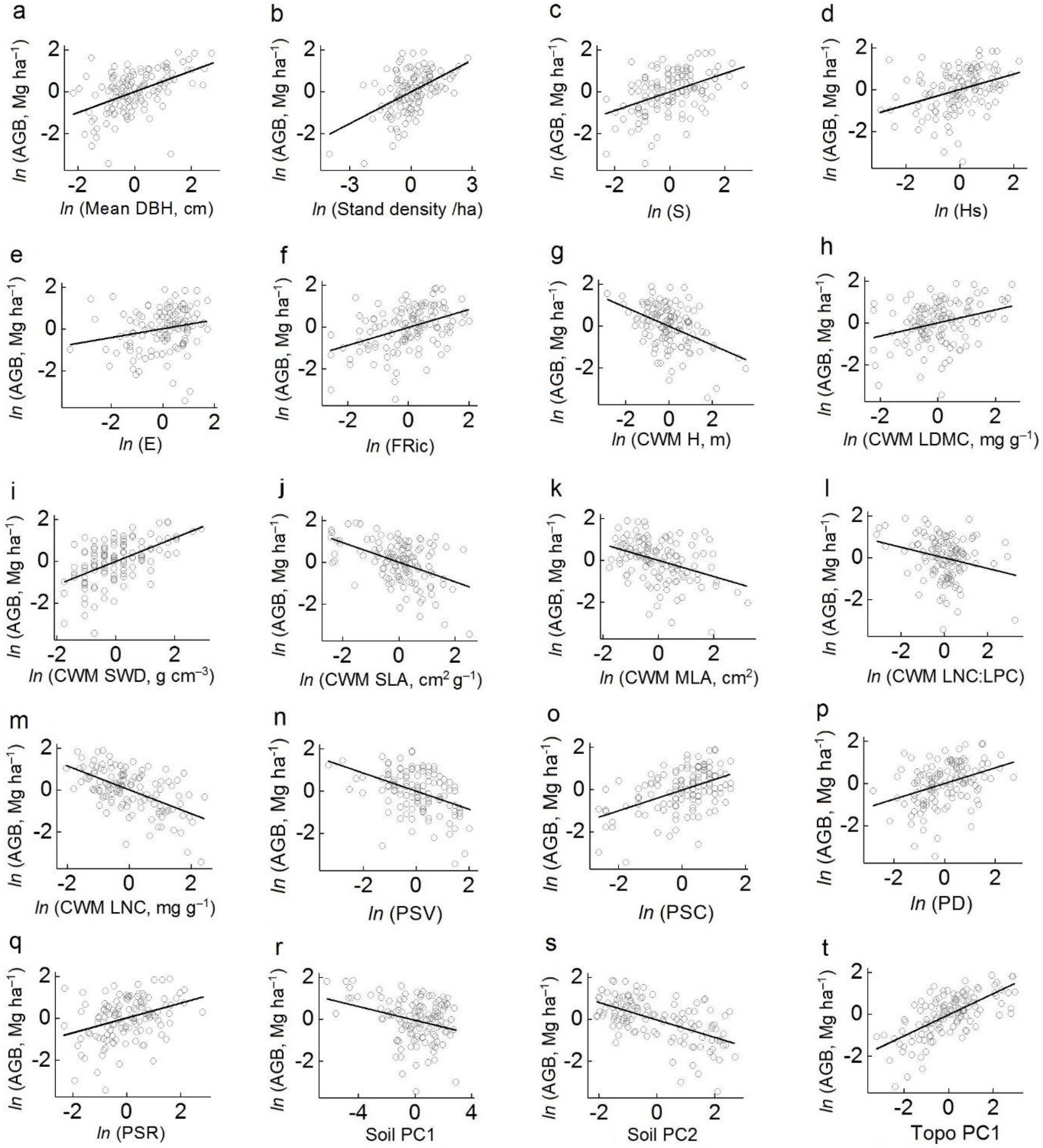


Fig. 8.4. The bivariate relationships between aboveground biomass (AGB) and predictors (a-b, stand structural attributes; c-e, taxonomic diversity indices; f, functional trait diversity index; g-m, CWM of trait values; n-q, evolutionary diversity indices; and s-t, environmental factors axes; n = 125) at understorey strata. Only significant relationships ($P < 0.05$) are shown here (see Table 8.15). All the abbreviations for variables are explained in Table 8.1.

The understorey SEM (Fig. 8.5) showed that phylogenetic species richness had the strong positive direct effect on understorey aboveground biomass (β = 0.40, P = 0.006), followed by the significant negative direct effect of soil nutrients (β = –0.35, P < 0.001), positive direct effect of mean DBH (β = 0.34, P < 0.001), negative direct effect of species diversity (β = –0.33, P = 0.001), positive direct effect of CWM of stem wood density (β = 0.22, P = 0.007) and non-significant direct effect of functional richness. Soil nutrients had significant negative direct effects on CWM of stem wood density (β = –0.56, P < 0.001), mean DBH (β = –0.39, P < 0.001), species diversity (β = –0.36, P < 0.001), functional richness (β = –0.26, P = 0.002) but non-significant effect on phylogenetic species richness. Soil nutrients had the indirect negative effect via CWM of mean DBH (β = –0.13, P = 0.001), stem wood density (β = –0.12, P = 0.011) but positive indirect effect via species diversity (β = 0.12, P = 0.010) on understorey aboveground biomass. The total effect of soil nutrients on understorey aboveground biomass was significantly negative (β = –0.58, P < 0.001; Table 8.15).

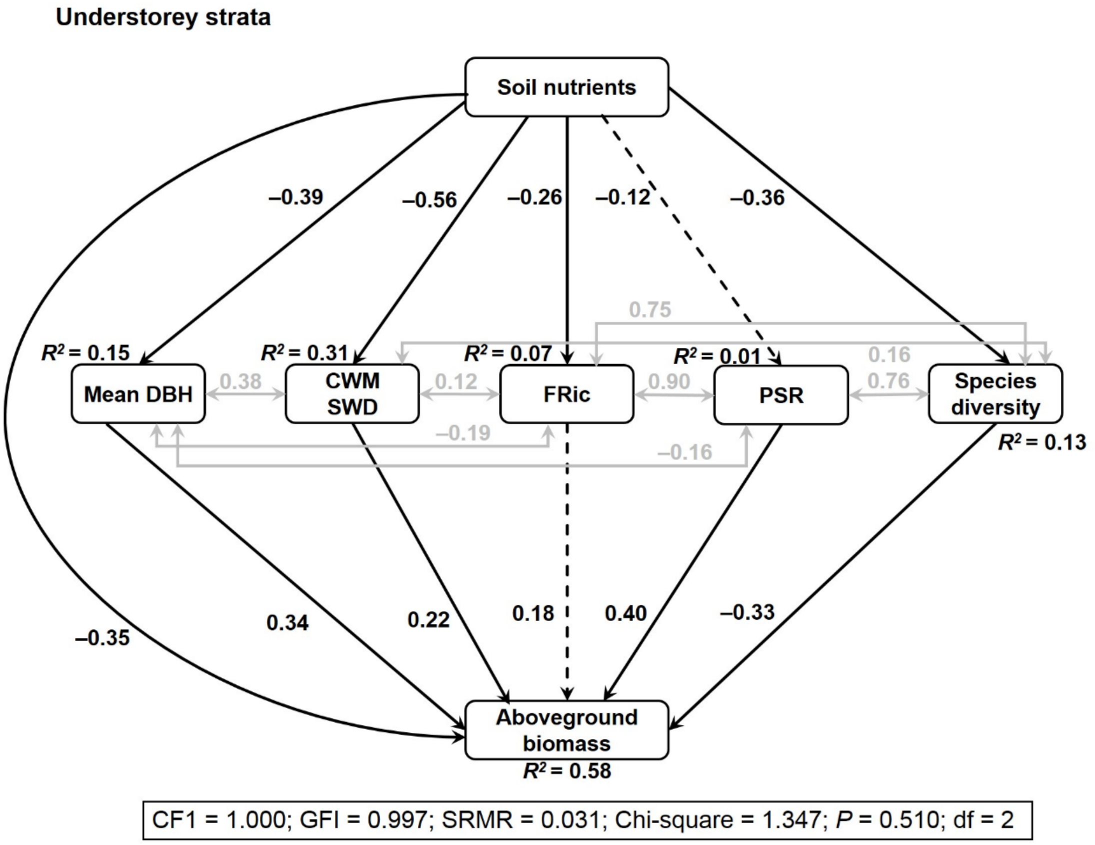


Fig. 8.5. Best-fit structural equation model for the effects of stand structural attribute and multiple metrics of biodiversity on aboveground biomass at understorey strata in subtropical forests, after accounting for the effects of soil nutrients. All the abbreviations for variables are explained in Table 8.1, and explanations are provided in Fig. 8.3.

Table 8.15. The direct, indirect, and total standardized effects of soil nutrients, stand structural attribute and multiple metrics of biodiversity on aboveground biomass at understorey strata, based on structural equation model (SEM; Fig. 8.5). The direct, indirect and total standardized effects (beta) are shown with associated *z*-values and *P*-values. Covariance coefficients between pairs of predictors are shown in the lower section of the Table. Significant effects and covariance are indicated in bold ($P < 0.05$). All the abbreviations for variables are explained in Table 8.1.

Response variable	Predictor variable	Effect	Path label	Beta	*z*-value	*P*-value
Regressions						
AGB	Soil nutrients (PC2)	Direct	a	-0.35	-4.73	**<0.001**
Mean DBH	Soil nutrients (PC2)	Direct	b	-0.39	-4.74	**<0.001**
AGB	Mean DBH	Direct	c	0.34	4.73	**<0.001**
AGB	Soil nutrients (PC2)	Indirect	b*c	-0.13	-3.35	**0.001**
CWM SWD	Soil nutrients (PC2)	Direct	d	-0.56	-7.57	**<0.001**
AGB	CWM SWD	Direct	e	0.22	2.68	**0.007**
AGB	Soil nutrients (PC2)	Indirect	d*e	-0.12	-2.53	**0.011**
FRic	Soil nutrients (PC2)	Direct	f	-0.26	-3.04	**0.002**
AGB	FRic	Direct	g	0.18	1.19	0.235
AGB	Soil nutrients (PC2)	Indirect	f*g	-0.05	-1.11	0.269
PSR	Soil nutrients (PC2)	Direct	h	-0.12	-1.33	0.183
AGB	PSR	Direct	i	0.40	2.74	**0.006**
AGB	Soil nutrients (PC2)	Indirect	h*i	-0.05	-1.20	0.231
Species diversity	Soil nutrients (PC2)	Direct	j	-0.36	-4.27	**<0.001**
AGB	Species diversity	Direct	k	-0.33	-3.25	**0.001**
AGB	Soil nutrients (PC2)	Indirect	j*k	0.12	2.58	**0.010**
AGB	Soil nutrients (PC2)	Total	a+(b*c)+(d*e)+(f*g)+(h*i)+(j*k)	-0.58	-7.99	**<0.001**
Covariance						
Mean DBH	CWM SWD			0.38	4.11	**<0.001**
Mean DBH	PSR			-0.16	-2.82	**0.005**
Mean DBH	FRic			-0.19	-3.18	**0.001**
CWM SWD	FRic			0.12	2.82	**0.005**
FRic	PSR			0.90	7.70	**<0.001**
FRic	Species diversity			0.75	7.00	**<0.001**
PSR	Species diversity			0.76	6.90	**<0.001**
CWM SWD	Species diversity			0.16	2.83	**0.005**

8.3.3. Whole-community aboveground biomass is mainly driven by functional identity of tree height, individual tree size inequality and soil nutrients

The bivariate relationships showed that whole-community aboveground biomass was significantly increased with increasing stand structural attributes, species richness, functional identity of tree height and leaf dry matter content, functional richness, phylogenetic diversity, phylogenetic species richness, phylogenetic species clustering and topography (PC1).

Aboveground biomass of whole-community was significantly decreased with increasing taxonomic and phylogenetic species evenness, and soil nutrients (PC2), whereas all other relationships were non-significant (Fig. 8.6, Table 8.16).

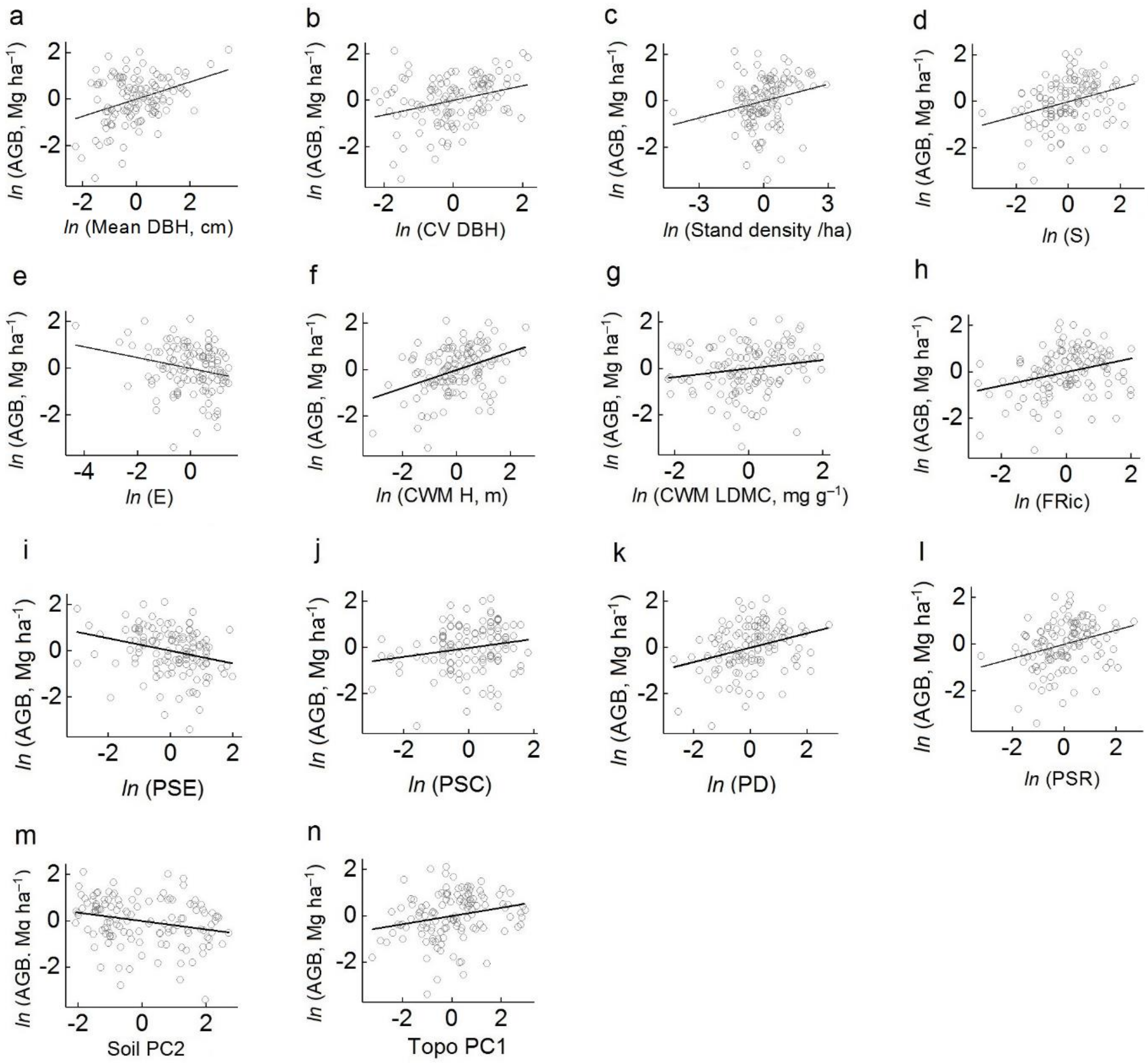


Fig. 8.6. The bivariate relationships between aboveground biomass (AGB) and predictors (a-c, stand structural attributes; d-e, taxonomic diversity indices; f-g, CWM of trait values; h, functional trait diversity index; i-l, evolutionary diversity indices; and m-n, environmental factors axes; *n* = 125) at whole-community level. Only significant relationships ($P < 0.05$) are shown here (see Table 8.16). All the abbreviations for variables are explained in Table 8.1.

The whole-community SEM (Fig. 8.7) showed that soil nutrients had the strong negative direct effect on whole-community aboveground biomass ($\beta = –0.49$, $P < 0.001$), followed by the significant positive direct effects of individual tree size inequality (CV of DBH) ($\beta = 0.37$, $P < 0.001$) and CWM of plant height ($\beta = 0.33$, $P < 0.001$), while non-significant negative direct effects of phylogenetic species evenness, functional dispersion and taxonomic species evenness. Soil nutrients had significant positive direct effects on CV of DBH ($\beta = 0.47$, $P < 0.001$), phylogenetic species evenness ($\beta = 0.30$, $P = 0.001$) and CWM of plant height ($\beta = 0.26$, $P = 0.002$), whereas negative direct effect on species evenness ($\beta = –0.39$, $P < 0.001$) but non-significant effect on functional dispersion. Soil nutrients had the indirect positive effect via CV of DBH ($\beta = 0.18$, $P = 0.001$) and CWM of plant height ($\beta = 0.09$, $P = 0.015$) on whole-community aboveground biomass. The total effect of soil nutrients on whole-community aboveground biomass was significantly negative ($\beta = –0.25$, $P = 0.004$; Table 8.16).

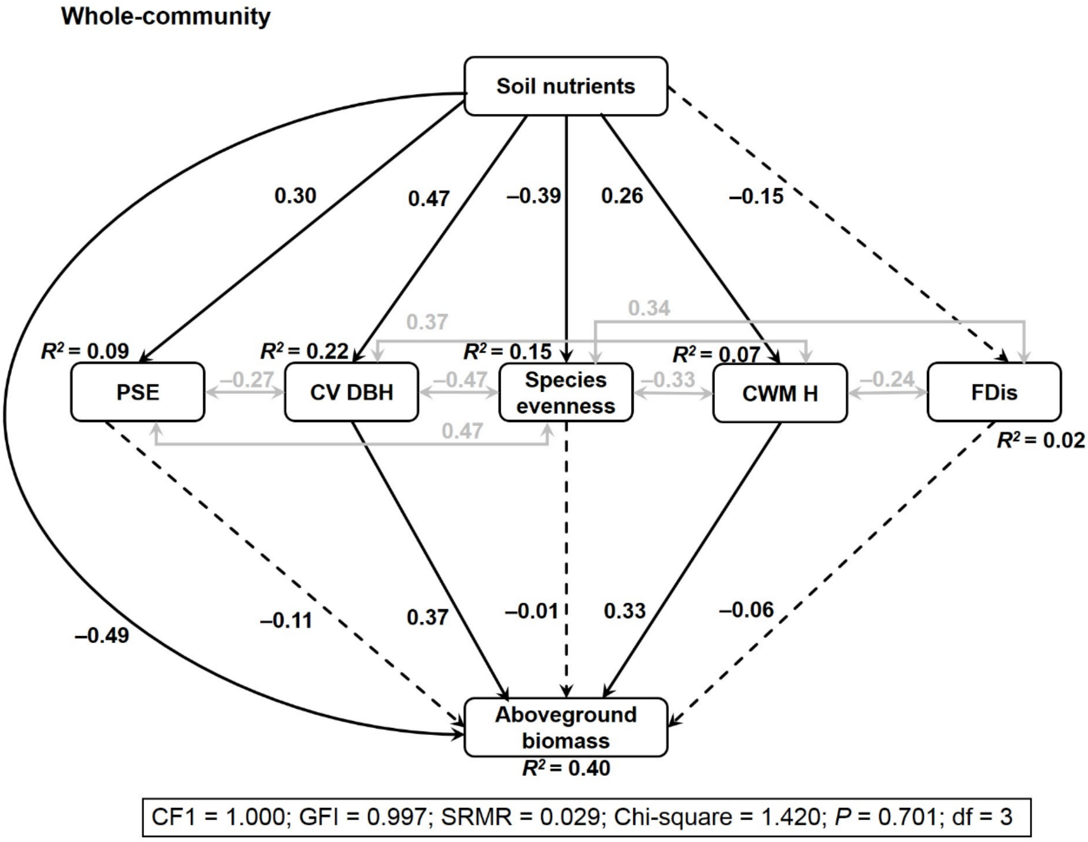


Fig. 8.7. Best-fit structural equation model for the effects of stand structural attribute and multiple metrics of biodiversity on whole-community aboveground biomass in a subtropical forests, after accounting for the effects of soil nutrients. All the abbreviations for variables are explained in Table 8.1, and explanations are provided in Fig. 8.3.

Table 8.16. The direct, indirect, and total standardized effects of soil nutrients, stand structural attribute and multiple metrics of biodiversity on aboveground biomass at whole-community level, based on structural equation model (SEM; Fig. 8.7). The direct, indirect and total standardized effects (beta) are shown with associated *z*-values and *P*-values. Covariance coefficients between pairs of predictors are shown in the lower section of the Table. Significant effects and covariance are indicated in bold ($P < 0.05$). All the abbreviations for variables are explained in Table 8.1.

Response variable	Predictor variable	Effect	Path label	Beta	*z*-value	*P*-value
Regressions						
AGB	Soil nutrients (PC2)	Direct	a	-0.49	-5.49	**<0.001**

CV DBH	Soil nutrients (PC2)	Direct	b	0.47	5.97	**<0.001**
AGB	CV DBH	Direct	c	0.37	3.88	**<0.001**
AGB	Soil nutrients (PC2)	Indirect	b*c	0.18	3.25	**0.001**
CWM H	Soil nutrients (PC2)	Direct	d	0.26	3.05	**0.002**
AGB	CWM H	Direct	e	0.33	4.06	**<0.001**
AGB	Soil nutrients (PC2)	Indirect	d*e	0.09	2.44	**0.015**
FDis	Soil nutrients (PC2)	Direct	f	-0.15	-1.64	0.101
AGB	FDis	Direct	g	-0.06	-0.77	0.441
AGB	Soil nutrients (PC2)	Indirect	f*g	0.01	0.70	0.485
PSE	Soil nutrients (PC2)	Direct	h	0.30	3.45	**0.001**
AGB	PSE	Direct	i	-0.11	-1.29	0.198
AGB	Soil nutrients (PC2)	Indirect	h*i	-0.03	-1.21	0.228
Species evenness	Soil nutrients (PC2)	Direct	j	-0.39	-4.75	**<0.001**
AGB	Species evenness	Direct	k	-0.01	-0.12	0.906
AGB	Soil nutrients (PC2)	Indirect	j*k	0.01	0.12	0.906
AGB	Soil nutrients (PC2)	Total	a+(b*c)+(d*e)+(f*g)+(h*i)+(j*k)	-0.25	-2.90	**0.004**
Covariance						
CV DBH	PSE			-0.27	-3.13	**0.002**
CV DBH	Species evenness			-0.47	-5.17	**<0.001**
CV DBH	CWM H			0.37	4.15	**<0.001**
FDis	Species evenness			0.34	4.37	**<0.001**
CWM H	FDis			-0.24	-2.84	**0.004**
PSE	Species evenness			0.47	5.13	**<0.001**
CWM H	Species evenness			-0.33	-3.96	**<0.001**

8.4. Discussion

We assessed the effects of taxonomic diversity, functional trait diversity and identity, evolutionary diversity and stand structural attributes on aboveground biomass in a subtropical forest, after accounting for the effects of local environmental factors. To better understand the ecological mechanisms, we disentangled the effects of these multiple drivers on aboveground biomass at each of overstorey and understorey strata, and whole-community level. At overstorey strata, we mainly found strong support for the mass ratio effect in term of functional identity of tree height having low functional evenness in a dense stand or closed canopy system for driving high aboveground biomass at overstorey strata. At understorey strata, our results mainly support the niche complementarity effect in terms of high phylogenetic species richness and mean DBH, and the mass ratio effect based on conservative strategy in term of high dominance of dense-wooded species. In addition, competitive exclusion in term of low species diversity was also found as the associated mechanism for driving high aboveground biomass at the understorey strata. We mainly support the mass ratio and stand structure effects based on the functional identity of tree height and individual tree size inequality for driving whole-community aboveground biomass in the studied subtropical forest.

8.4.1. Functional identity of overstorey tree height drives high aboveground biomass at overstorey strata

As hypothesized we found the evidence that overstorey strata dominated by tall trees or high adult stature plant species having low functional evenness with an increase in stand density (canopy packing) had high aboveground biomass in the studied forest. The positive relationship between CWM of plant maximum height, a measure of functional dominance, and aboveground biomass suggests that characteristics of the dominant mature trees (specifically their maximum potential height) do influence aboveground biomass in overstorey strata of the forests (Ali & Yan 2017b, Cavanaugh *et al.* 2014). This result agrees with previous studies that the dominant tree species have a large effect on aboveground biomass (Balvanera *et al.* 2005, Lohbeck *et al.* 2016) and productivity (Prado-Junior *et al.* 2016). In addition, relative abundance of big trees is shown to be positively correlated with aboveground biomass in the Brazilian Amazon (Brown & Lugo 1992), further indicating the importance of big trees for variation of aboveground biomass within a plot, sites and across the tropics (Cavanaugh *et al.* 2014, Slik *et al.* 2013). This result indicates that overstorey strata have high aboveground biomass when they are dominated by tall tree species with low functional evenness where most of overstorey tree species' basal area is concentrated in a constrained area of the multivariate-trait space (Villéger *et al.* 2008).

Interestingly, evolutionary and taxonomic diversity appeared to be unimportant for strongly affecting aboveground biomass at the overstorey strata. Assuming that niche differentiation based on functional traits, phylogenetic distances and species identity underlies the niche complementarity hypothesis. Therefore functional trait diversity, evolutionary diversity and taxonomic diversity indices should outperform each other in predicting aboveground biomass (Laliberté & Legendre 2010, Mason *et al.* 2005, Villéger *et al.* 2008, Webb & Donoghue 2005). In our analysis, we strongly observed positive feedback between taxonomic and phylogenetic species richness, but functional evenness was found to be independent (Fig. 8.3). Functional traits provide a more mechanistic link between species identity and ecosystem functioning from ecological perspectives than to taxonomic diversity, suggesting that greater trait variation is related to ecological niches and provides evidence for the niche complementarity hypothesis (Díaz *et al.* 2011a). If the niche complementarity drives ecosystem function, then aboveground biomass should increase with increasing functional trait diversity. Alternatively, if mass ratio drives ecosystem function, then aboveground biomass should be more strongly affected by CWM of a trait values and negatively related to functional trait diversity and evolutionary diversity, as the dominant trait value (not the variety of traits) drives aboveground biomass (Chiang *et al.* 2016).

In addition, it is plausible that the niche complementarity and mass ratio effects on ecosystem function are maintained by stand density (canopy packing), because greater stand density is related with both high diversity and more aboveground biomass and productivity (Chisholm *et al.* 2013, Jucker *et al.* 2016). We strongly observed positive feedback between stand density and species richness (taxonomic and phylogenetic), and hence strong direct effect on aboveground biomass whereas species richness had non-significant effect (Fig. 8.3). Moreover, taxonomic species richness and functional dominance had provided weak positive feedback to each other, whereas functional evenness was observed as an independent driver. Therefore, our results suggest that an increase in the dominance of overstorey species with certain traits (e.g. plant maximum height in this study) and low functional trait diversity (e.g. functional evenness in this study) in a complex stand structure (e.g. high stand density), may enhance aboveground biomass or productivity (Chiang *et al.* 2016, Prado-Junior *et al.* 2016) due to their better response to environmental filtering (Lasky *et al.* 2014, Zhang *et al.* 2016a). These findings strongly support the mass ratio hypothesis, rather than the niche complementarity hypothesis, which highlights the importance of dominant species in maintaining ecosystem function (Cardinale *et al.* 2012, Loreau & Hector 2001).

8.4.2. Conservative and complementarity understorey species drive high aboveground biomass at understorey strata

Surprisingly, as hypothesized we found that understorey strata dominated by dense-wooded and phylogenetically-rich species having almost similar mean tree DBH had high aboveground biomass. We found that understorey trees were slow-growing as CWM of wood density and mean DBH provide positive feedback to each other, and hence positive direct effects on aboveground biomass (Fig. 8.5). Although aboveground biomass or productivity may increase with species richness and evenness (Zhang *et al.* 2012b), the lack of positive effects of Shannon’s species diversity on aboveground biomass might be attributable to competitive exclusion, for example, high stand biomass may exclude weak competitors (Ali *et al.* 2016b, Grace *et al.* 2016). However, the multi-model comparative approach (ΔAICc < 2 units; Table 8.4) showed that high aboveground biomass was consistently related to high species richness and low species evenness but the directions of the effect of species diversity changed with the single combination of species evenness or richness, in addition to the consistent effects of environmental factors, at understorey strata. Therefore, the dominance of certain productive species with a specific strategy (i.e. slow-growing conservative strategy, CWM of wood density and mean DBH, in this study) has a potent effect on aboveground biomass, carbon storage or productivity (Ali & Yan 2017b, Prado-Junior *et al.* 2016, Tobner *et al.* 2016).

Moreover, we found that functional richness had the non-significant positive effect on aboveground biomass at understorey strata. As explained in the above section, the phylogenetic species richness may outperform functional richness because measurements of evolutionary history within a set of co-occurring species are assumed to represent the functional trait diversity within a given community (Faith 2002). In our analyses, strong positive feedbacks among phylogenetic species richness, functional richness and species diversity were observed (Fig. 8.5). In combination, our results mainly suggest that slow-growing conservative species in a phylogenetically-rich system driving high aboveground biomass in the resource-limited environments (e.g. understorey strata in our study) (Chave *et al.* 2009, Prado-Junior *et al.* 2016), and hence support both the niche complementarity and mass ratio hypotheses. In addition, we found that the main 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 also to functional richness, but mean DBH had negative feedbacks with phylogenetic species richness and functional richness (Fig. 8.5). This indicates that understorey strata was species-rich (phylogenetically, functionally and taxonomically) but employed a conservative and equal slow-growing strategy among the individuals of dense-wooded species for efficient utilization of resources (Ali & Yan 2017b). In our analysis, it was strongly observed that functional identity of tree height had negative effect on aboveground biomass at understorey strata (Table 8.6). Lastly, the slow growth of understorey tree species might be happened due to the strong resource limitation in the understorey strata within a closed canopy forests (Ali & Yan 2017c, b, Bartels & Chen 2010, Rüger *et al.* 2012).

8.4.3. Functional identity of tree height and individual tree size inequality drive high aboveground biomass at whole-community level

As expected we found the evidence that communities dominated by high adult stature tree species having low functional dispersion and species evenness (taxonomic and phylogenetic) with an increase in individual tree size inequality (complex stand structure) had high aboveground biomass in the studied forests. This result suggests that observed relationships for stand structure and multiple metrics of biodiversity with aboveground biomass at understorey strata are obscured due to the dominant effect of overstorey trees in the complex natural forests. In other words, the dominant effect of overstorey trees have likely weaken the strength and magnitude of understorey trees (Zhang *et al.* 2016a), and hence the relationships observed at whole-community level are almost similar to the observed relationships at overstorey strata. In addition, overstorey strata with high aboveground biomass, dominant tree species and greater tree size may consume additional resources (such as light and water), resulting in the reduction of resources that remain available for understorey trees (Bartels & Chen 2010, 2013). In our analyses, we strongly observed the significant positive effect of adult stature tree species having low functional evenness on aboveground biomass at overstorey strata (Fig. 8.3), i.e., we call the functional dominance effect of big trees (Prado-Junior *et al.* 2016), whereas the slow-growing conservative strategy at the understorey strata (Fig. 8.5), i.e., we call the conservative strategy of small trees.

We did not found any evidence for the positive effects of taxonomic, functional trait and evolutionary diversity on aboveground biomass at whole-community level. Therefore, in combination, our results suggest that high functional dominance of adult stature trees having individual tree size inequality (probably more towards big trees and less towards small trees) had strongly driven high aboveground biomass at the whole-community level. In addition, we strongly observed that functional dominance of adult stature trees and individual tree size inequality provide positive feedback to each other, but both of them 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. dominance of species with particular traits), which further impose negative influences on species having variety of traits, phylogenetic distances and different taxonomies (Loreau *et al.* 2001). These results may be attributable to the selection effect, i.e., diverse communities are more likely to by chance include certain productive, high-functioning species and traits (Loreau & Hector 2001), and hence high aboveground biomass (Cavanaugh *et al.* 2014).

8.4.4. Soil nutrients availability modulates the effects of biodiversity and stand structural attributes on aboveground biomass

At overstorey strata, the species complementarity effect occurred at low-nutrients soils while functional dominance effect of big trees occurred at high-nutrients soils for driving high aboveground biomass at overstorey strata. In contrary, at understorey strata, the species complementarity effect with conservative strategy strongly occurred at low-nutrients soils for driving high aboveground biomass, probably due to the resource heterogeneity caused by the dominant effect of overstorey trees on the available resources (Ali & Yan 2017b, Bartels & Chen 2010, Zhang *et al.* 2016a). At whole-community, the contrasting observed relationships for overstorey and understorey strata were obscured where high functional dominance of adult stature trees having high individual tree size inequality were found on nutrient-rich soils for driving high aboveground biomass. Therefore, the observed negative direct and total effects of soil nutrients on aboveground biomass may be attributable to species adaptations to the local soil conditions that increase longevity at the species level, and hence biomass retention and the storage of high aboveground biomass at the stand level (Jucker *et al.* 2016, Poorter *et al.* 2015).

Besides the direct effects, soil nutrients can also indirectly affect aboveground biomass via species filtering along edaphic gradients (Jucker *et al.* 2016, Reich 2014, Russo *et al.* 2005). For instance, nutrient-poor soils tend to be dominated by conservative strategy of plant species, whereas nutrient-rich soils tend to be dominated by acquisitive strategy which depends on fast growth of relatively cheap plant tissues to escape shaded understories (Coomes *et al.* 2009, Fortunel *et al.* 2014, Holdaway *et al.* 2011, Poorter & Bongers 2006, Reich 2014). Under these expectations, at overstorey strata, we found the positive indirect effect of soil nutrients on aboveground biomass via adult stature tree species but negative effect via stand density, and hence indicates fast-growing strategy for high aboveground biomass on nutrient-rich soils. At understorey strata, we observed strong negative indirect effect of soil nutrients on aboveground biomass via CWM of stem wood density and mean DBH but positive indirect effect via species diversity. This result indicates slow-growing strategy for high understorey aboveground biomass on nutrient-poor soils in the studied forests (Ali & Yan 2017b). At whole-community level, soil nutrients had positive indirect effects on aboveground biomass via functional dominance of adult stature tree species and individual tree size inequality. This finding indicates the fast-growing strategy for high aboveground biomass on nutrient-rich soils, probably due to the dominant effect of overstorey trees on the available resources, and what is left available for understorey trees (Ali & Yan 2017b, Bartels & Chen 2010).

8.5. Concluding remarks

To best of our knowledge, this is the first empirical study to disentangle the effects of multiple metrics of biodiversity (taxonomic, functional trait and evolutionary diversity, and functional identity) and stand structural attributes in addition to local environmental factors on aboveground biomass across forest strata and at whole-community level in a species-rich and structurally-complex subtropical forest. At overstorey strata, aboveground biomass is mainly driven by adult stature tree species (functional dominance), followed by stand density and functional evenness. At understorey strata, aboveground biomass is mainly driven by phylogenetic species richness followed by soil nutrients, mean DBH, species diversity and CWM of stem wood density. At whole-community level, aboveground biomass is mainly driven by soil nutrients followed by individual tree size inequality and functional dominance of adult stature tree species. At overstorey strata, functional dominance effect of big trees occurs at high-nutrients soils while species complementarity effect occurs at low-nutrients soils for driving high aboveground biomass. In contrary, at understorey strata, the species complementarity effect with conservative strategy strongly occurs at low-nutrients soils for driving high aboveground biomass. At whole-community level, the big trees effect occurs on nutrient-rich soils for driving high aboveground biomass. This study highlights that simultaneously testing the effects of multiple metrics of biodiversity and stand structural attributes in addition to local environmental factors on aboveground biomass across forest strata will provide better understandings of observations into mechanisms for the carbon sequestration and mitigation potential of natural ecosystems. Hence, conserving biodiversity and maintaining stand structure at both overstorey and understorey strata are sustainable ecological strategies because high biodiversity with productive stand structure is crucial for effective functioning of the forest ecosystems.

Chapter 9. General discussion and concluding remarks

9.1. Introduction

The research presented here links environment, multiple metrics of biodiversity, stand structural attributes and aboveground biomass in order to explores theory or hypotheses and applications dealing with variation among tree individuals, species, functional traits, phylogeny and its consequences for driving high aboveground biomass across forest strata (overstorey and understorey) and whole-community level, and predicts how local environmental factors (soil physicochemical properties and/ or topography) affect these relationships in a subtropical forest. In this last chapter (chapter 9), I synthesize the results of this thesis in order to generally discuss my research questions and hypotheses. I also discuss the role of science and its research significances for conservation of biodiversity, maintenance of stand structure and enhancement of aboveground biomass of a subtropical forest, and elaborate on the role that policy and society should have in assuring diverse and productive subtropical forests for the long-term.

9.2. A matter of forest strata: understanding biodiversity – aboveground biomass relationships across forest strata in a subtropical forest

In forest ecosystems, overstorey strata store large quantities of aboveground biomass due to their high wood volumes and disproportionate contribution of large trees to the whole-community level aboveground biomass (Slik *et al.* 2013). Understorey strata contribute much to the majority of biodiversity, and thus influence soil carbon storage and nutrient cycling through their higher turn-over rates (Barbier *et al.* 2008, Gilliam 2007, Nilsson & Wardle 2005). Moreover, local environmental conditions affecting plant performance can strongly differ between forest strata in natural forests (Barbier *et al.* 2008, Bartels & Chen 2010, 2013), which may further influence species diversity and tree size variation across forest strata. Light, being one of the most important plant resources, is often limiting in the understorey of forests, while light is abundant in the overstorey strata (Brenes-Arguedas *et al.* 2011, Wright 2002). Indeed the niche complementarity effect may be less important in stable and productive environments of the overstorey, while competition may be driving species interactions in a more stressful understorey environment (Paquette & Messier 2011).

In the review of chapter 3, we mainly found support for the presence of the niche complementarity effect in addition to the big trees effect on the available resources for driving positive relationships of species diversity and tree size variation with aboveground biomass at overstorey strata. At the same time, overstorey species diversity promotes the understorey species diversity through resource heterogeneity in the understorey strata in a subtropical forest. In other words, high species diversity of overstorey strata was found at nutrient-poor soils while high tree size variation of overstorey strata was found at nutrient-rich soils for driving high overstorey aboveground biomass and understorey species diversity. Hence, the contrary responses of overstorey species diversity and tree size variation to soil nutrients indicate the niche complementarity effect with the addition of big trees effect on available resources for driving high aboveground biomass and promoting understorey species diversity rather than tree size variation and aboveground biomass of understorey strata.

In the conclusion of chapter 4, we found support for the presence of two main ecological mechanisms explaining whole-community aboveground biomass in subtropical forest: niche complementarity effect for understorey strata and functionally-similar big trees effect for overstorey strata. In the summary of chapter 5, we conclude that the mediation roles of intraspecific and interspecific functional trait diversity for driving the response of aboveground biomass to species richness along soil nutrients gradients depends on the forest strata of a community. For example, intraspecific and interspecific functional trait diversity mediate the response of aboveground biomass to species richness at understorey strata, whereas only intraspecific functional trait diversity mediates the response of aboveground biomass to species richness at whole-community and overstorey strata. Second, to understand changes in aboveground biomass, it is important to measure intraspecific functional trait diversity based on different functional traits, in order to represent both the conservative and acquisitive strategies of a plant. Third, from a theoretical point of view, we conclude that: 1) intraspecific and interspecific functional trait diversity based on leaf dry matter content had strong direct positive effect on aboveground biomass at understorey strata representing niche differentiation; 2) intraspecific functional trait diversity based on specific leaf area had strong direct negative effect on aboveground biomass at whole-community level representing low intraspecific niche differentiation probably due to the dominant effect of few large overstorey trees; and 3) both intraspecific functional trait diversity based on specific leaf area and leaf dry matter content had negligible effects on aboveground biomass at overstorey strata indicating that low trait diversity within species driving high aboveground biomass, probably due to the presence of few large trees. Clearly, intraspecific versus interspecific functional trait diversity plays a central role for prediction of aboveground biomass, suggesting that trait variability within species need to be separately or explicitly considered in the theoretical development and relationship of biodiversity and ecosystem functioning at different forest strata of a forest.

In chapter 6, we found that evolutionary diversity indices compared to functional trait diversity indices within a plot are important predictors for best explaining variation in aboveground biomass at overstorey strata, not at understorey strata, while a bit similarly important at whole-community level in subtropical forests. Although functional trait diversity indices are the best significant predictors of aboveground biomass at the understorey strata, evolutionary diversity indices are also important for understorey aboveground biomass. Evolutionary diversity serves as a useful proxy for functional trait diversity, and therefore evolutionary diversity and functional trait diversity have underpinned similar ecological mechanisms for driving higher aboveground biomass at each of forest strata and whole-community level. The ecological mechanisms at overstorey and understorey strata compared to whole-community level seem to be very different, which could be the results of biotic interactions, resource availability and heterogeneity at each individual strata. For example, understorey aboveground biomass are greater for groups of phylogenetically distantly-related plant species having high functional trait diversity, while higher overstorey aboveground biomass are related with groups of closely related plant species having low functional trait diversity. High phylogenetic relatedness of overstorey species could be the cause of positive functional trait diversity and aboveground biomass relationship at understorey strata.

In the concluding remarks of chapter 7, we found that high aboveground biomass was potentially driven by high adult stature at overstorey strata while by conservative strategy at understorey strata, whereas all the three strategies did so at the whole-community level. Overstorey strata dominated by adult stature plant species rather than the acquisitive or conservative strategy of plant species while understorey strata dominated by conservative strategy of plant species have high aboveground biomass in subtropical forests.

In the concluding review of chapter 8, we found that at overstorey strata, aboveground biomass is mainly driven by adult stature tree species (functional dominance), followed by stand density and functional evenness. At understorey strata, aboveground biomass is mainly driven by phylogenetic species richness followed by soil nutrients, mean DBH, species diversity and CWM of stem wood density. At whole-community level, aboveground biomass is mainly driven by soil nutrients followed by individual tree size inequality and functional dominance of adult stature tree species. At overstorey strata, functional dominance effect of big trees occurs at high-nutrients soils while species complementarity effect occurs at low-nutrients soils for driving high aboveground biomass. In contrary, at understorey strata, the species complementarity effect with conservative strategy strongly occurs at low-nutrients soils for driving high aboveground biomass at understorey strata. At whole-community level, the big trees effect occurs on nutrient-rich soils for driving high aboveground biomass.

Given that we found contrasting mechanisms to affect aboveground biomass for different strata in a community, ecological models for predicting aboveground biomass in a subtropical forest can improve by including separate effects of biodiversity and stand structure of overstorey and understorey strata.

9.3. Wrapping up: what determines aboveground biomass?

The simplest metric, taxonomic diversity (species diversity, richness and evenness), has repeatedly been shown to relate with aboveground biomass or productivity in natural forests (e.g. Ali & Yan 2017a, Zhang *et al.* 2012b). In the past decade, there have been two important advances to move beyond taxonomic diversity for explaining variation in ecosystem functions (Cadotte *et al.* 2008, Díaz *et al.* 2007): 1) functional traits based approach and 2) phylogenetic distances based approach. In addition, functional trait composition (measured as the community-weighted mean of a trait values, CWM) has been found to be closely related with ecosystem functions in natural forests (Ali *et al.* 2017, Chiang *et al.* 2016, Finegan *et al.* 2015, Prado-Junior *et al.* 2016). Forest functioning may be determined not only by multiple metrics of biodiversity (i.e. taxonomic, functional and evolutionary diversity) of the vegetation but also by several stand structural attributes including tree size inequality, mean stem diameter, stand structural diversity (Ali *et al.* 2016b, Poorter *et al.* 2015, Zhang & Chen 2015). Studies in natural tropical forests also reveal that local environmental factors, such as topography and soil nutrients or physicochemical properties, have both direct and indirect (via biodiversity and/ or stand structural attributes) on aboveground biomass or productivity in natural forests (Chiang *et al.* 2016, Jucker *et al.* 2016, Poorter *et al.* 2015, Zhang & Chen 2015).

In chapter 8, we disentangled the effects of taxonomic diversity, functional trait diversity and composition, evolutionary diversity and stand structural attributes on aboveground biomass in a subtropical forest, after accounting for the effects of local environmental factors. To better understand the effects of these multiple drivers with associated ecological mechanisms, we tested the relative effect of these multiple drivers on aboveground biomass at each of overstorey and understorey strata, and whole-community level. At overstorey strata, we mainly found strong support for the mass ratio effect in term of high functional dominance of adult stature tree species having low functional evenness in a dense stand or closed canopy system for driving high aboveground biomass at overstorey strata. At understorey strata, our results mainly support the niche complementarity effect in terms of high phylogenetic species richness and mean DBH, and the mass ratio effect based on conservative strategy in term of high dominance of dense-wooded species. In addition, competitive exclusion in term of low species diversity was also found as the associated mechanism for driving high aboveground biomass at the understorey strata. With respect to the whole-community level, we mainly support the mass ratio and stand structure effects based on the functional identity of tree height and individual tree size inequality for driving whole-community aboveground biomass in the studied subtropical forest.

9.4. Wrapping up: how do overstorey strata influence the diversity, composition, structure and aboveground biomass of understorey?

A dense forest with great aboveground biomass can positively contribute to ecosystem functions through large stem volumes of overstorey trees, but slows down ecosystem functioning rates in understorey due to low light availabilities (Poorter *et al.* 2015, Slik *et al.* 2013, Zhang *et al.* 2016a). Additionally, species diversity of overstorey strata may promote species diversity in understorey strata as a result of reduced interspecific competition (Bartels & Chen 2013, Zhang *et al.* 2016a). In chapter 3, we show that the magnitude of the effects of species diversity and individual tree size variation on aboveground biomass in understorey strata is relatively weaker compared to the observations at overstorey strata. The non-significant relationships between biodiversity and aboveground biomass in understorey strata might be attributable to developmental effect of tree species. Understorey strata include both shrub species and regeneration of canopy tree species, which are functionally different in coping with biotic interaction and resource competition. Regeneration of trees could have a different ecology than developed trees, as trees grow they may experience varying biomechanical burdens and environmental conditions, or pre-programmed ontogenetic switch, which can induce concomitant changes in tree structure and function (Meinzer *et al.* 2011). Therefore, the relationship between biodiversity and aboveground biomass might be weakened in understorey strata by the mixture effects of development or life stage and high degree of biotic interaction and resource heterogeneity. In addition, tree species in overstorey strata with high aboveground biomass and great tree size may consume a large part of resource, thus probably reducing resources availability to understorey species (Gilliam 2007, Mason *et al.* 2011). As such, the dominant role of overstorey strata on the available resources likely weakens the biodiversity – aboveground biomass relationships in understorey strata (Hooper *et al.* 2005, Zhang *et al.* 2016a). The strong response of overstorey species diversity and weak response of understorey species diversity to soil nutrients collectively suggest a dominant filtering role of the overstorey trees in shaping understorey structure and function (Zhang *et al.* 2016a).

The major resources needed for plant growth and survival are light, water and nutrients. It is well-known that light is limiting in the understorey strata of (sub-) tropical forests (Brenes-Arguedas *et al.* 2011, Canham *et al.* 1990, Wright 2002). Whether water and nutrients are more plentiful for the overstorey because they have large root systems that efficiently absorb these resources, or for the understory that is characterized by a less extreme environment is less well-known. Some studies point at the vulnerability of big trees for drought (Lindenmayer & Laurance 2017) while understorey trees are protected against extreme drought (Qiu *et al.* 2012). This difference in knowledge on the effects of light *versus* those of nutrients and water also points to the relative ease of studying aboveground plant strategies and environmental conditions compared to the difficulty of studying belowground strategies and environmental conditions. We thus cannot exclude the effects of water and nutrients on our findings (chapter 5) but suggest the differential effect of functional trait diversity of understorey and overstorey strata on aboveground biomass is likely driven by light, in line with previous research (Ali & Yan 2017b, Bartels & Chen 2010, Rüger *et al.* 2012). Further research testing the influence of functional traits related to the uptake of water and soil nutrients across different forest strata will have to elucidate their effects on aboveground biomass and other functions in natural forests (but see Ali & Yan 2017c, Ali & Yan 2017b).

Overstorey strata impose competitive constraints on understorey because of their large stem volumes (Zhang *et al.* 2016a), and hence altering resource availability such as light, water and space (Gilliam 2007, Gilliam *et al.* 1995, Mason *et al.* 2011). In chapter 5, this was strongly evident by the negative direct effect of overstorey functional evenness on understorey functional evenness, and as a consequence negative indirect effect on aboveground biomass via understorey functional evenness. Interestingly, we show that understorey functional evenness had non-significant positive effect on aboveground biomass, which might be resulted due to the dominant role of overstorey strata on available resources (Ali & Yan 2017b, Zhang *et al.* 2016a). Resource filtering, caused by the overstorey strata (Anderson *et al.* 1969, Bartels & Chen 2013), likely reduced the strength of the effect of understorey diversity on increased resource utilization in the resource-limited understorey environment (Hooper *et al.* 2005). This result supports the general notion that niche overlap reveals the effects of competition and contrasting assembly processes (Mason *et al.* 2011), which is true for woody species groups with overlapping niches such as overstorey strata (Zhang *et al.* 2016a).

Soil fertility hypothesis predicts that aboveground biomass or productivity increases with increase in soil nutrients availability, and plants can grow faster when resource availability is high (Quesada *et al.* 2012, Wright *et al.* 2011). However, high nutrients availability may also lead to increased competition, and hence high mortality and biomass turnover rates of plant species (Prado-Junior *et al.* 2016). Consequently, high aboveground biomass or productivity in (sub-) tropical forests associates often with nutrient-poor soils (Chiang *et al.* 2016, Poorter *et al.* 2015, Prado-Junior *et al.* 2016). Overstorey strata with great tree size consume a plenty of resources such as light and water, thus remaining few resources to the trees in understorey strata (Bartels & Chen 2010, 2013). The dominant filtering role of overstorey strata on the available resources may therefore impose negative influence on the aboveground biomass in understorey strata probably due to the limited resources availability (Bartels & Chen 2013, Hooper *et al.* 2005, Zhang *et al.* 2016a). In chapter 6, we show the positive effect of soil nutrients on CWM of overstorey tree height and the negative effect of soil nutrients on CWM of understorey stem wood density. Water and nutrients are more plentiful for trees in overstorey strata because they have large root systems that efficiently absorb these resources. Hence, the positive response of overstorey functional identity of tree height to soil nutrients has probably indirectly reduced resources in understorey strata. However, the big trees effect does not work directly on functional identity and aboveground biomass of understorey strata in this study. This might happen due to the resource heterogeneity in understorey strata caused by overstorey stand structure, which in turn affects species diversity and thus functional identity of understorey (Bartels & Chen 2013, Zhang *et al.* 2016a).

In chapter 7, we also show that, on the one hand, soil nutrients positively affect functional identity of tree height in overstorey strata but negatively affect the overstorey aboveground biomass, indicating a fast-growing strategy for overstorey trees. On the other hand, strong negative direct effects of soil nutrients and physicochemical on understorey functional identity and aboveground biomass indicate a slow-growing conservative strategy for nutrient-tolerant trees in understorey strata. It is plausible that trees with conservative trait values (e.g. high wood density) dominate on nutrient-poor soils because dense-wooded trees enhance nutrient residence time in the trees (e.g. Prado-Junior *et al.* 2016). In our studied forest, the same conservative trait values are important to deal with nutrient-limited environment (i.e. understorey strata), and hence enhances aboveground biomass through conservative strategy. In addition, direct effect of overstorey functional identity of tree height had no significant effects on the understorey’s functional identity and aboveground biomass. In combination, research in this thesis suggests that in understorey strata of the forest, soil nutrients (i.e. the big trees effect on the available resources) may be a stronger driver of aboveground biomass than light availability in a subtropical forest.

9.5. Outlook: the way forward in subtropical forest ecology

In this thesis, the mechanisms predicted by the niche complementarity effect, mass ratio effect, big trees effect and soil nutrients effect are generally applicable for the multivariate relationships between biodiversity and ecosystem functions at overstorey and understorey strata, and whole-community level in a subtropical forest in Eastern China. Yet, the complex nature of subtropical forests makes it difficult to understand how relationships of stand structure and biodiversity with aboveground biomass or productivity change with abiotic site conditions, with spatial and temporal scales. To improve such understanding, further research will need to focus on 1) long-term forest inventory; 2) the use of mechanistic approaches; 3) the combination of different research approaches such as empirical, remote sensing, and modelling studies; and 4) sustainable forest management and ecosystem services.

Long-term forest inventory and monitoring (i.e. decades to centuries) is obligatory to investigate the patterns and magnitude of the underlying mechanisms for biodiversity – ecosystem functions, as this is the timescale that relates to the life cycle of most tree species and during which environmental change, adaptation, and natural large-scale disturbances may take place (Zuidema *et al.* 2013). Diverse forest ecosystems that consist of long-lived plants, such as subtropical evergreen broadleaf forests, are more complex because many factors are at play that cannot be easily controlled for, and because most studies are of short duration whereas the time difference between change and influence is long. Although recent studies at the community level are able to describe patterns for biodiversity – ecosystem functions relationships, unable to identify the underlying mechanisms for net biomass change over time in subtropical forests (Ali *et al.* 2017, Ali *et al.* 2016b, Lin *et al.* 2016). It is important to understand the underlying processes for net biomass change in order to provide suggestions for decision makers and stakeholders on how to maintain productive stand structure and conserve biodiversity of subtropical forests that provide multiple important functions such as carbon sequestration, nutrient retention, and water cycling (but see Yu *et al.* 2014). Long-term forest inventory and monitoring would allow the assessment of the response of the forests to future environmental changes, which may be more extreme than the changes that have occurred during recent decades. Besides long-term monitoring in the future, long-term time series of past vegetation development (i.e. obtained from pollen records) may also provide important understandings on changes in community assembly and underlying drivers of biodiversity – ecosystem functions (Gosling *et al.* 2009, Mayle *et al.* 2000).

The use of mechanistic methodological approaches will be crucial in developing an understanding of mechanisms underlying ecosystem processes and functions. These approaches range from analytical approaches that allow the testing for casual path relationships, such as structural equation modelling (Grace *et al.* 2016, Malaeb *et al.* 2000), to mechanistic models based on simulations (Bunker *et al.* 2005) or process-based dynamic global vegetation models (DGVMs). Data analytical approaches such as structural equation modelling can critically teasing apart various abiotic and biotic effects (Ali *et al.* 2016b, Poorter *et al.* 2015), but can never fully account for variables inherent to empirical field data that confound the observed relationships. Ecosystem models such as DGVMs are powerful tools for creating experiment settings and testing hypotheses, assumptions and scenarios, but the results depend on model assumptions that are difficult to verify, especially if there is no long-term monitoring. Recently, several ecosystem models have become more realistic by taking into account for higher levels of functional trait diversity, for example LPJmL-FIT (Lund-Potsdam-Jena managed Land - Flexible Individual Traits) and trait-based model (TFS) (Fyllas *et al.* 2014, Sakschewski *et al.* 2015). The processes or relationships in these models are based on a small amount of interference between abiotic conditions, traits and performance that are still poorly understood. Many of these relationships have been well documented under optimal conditions at the species level (Poorter *et al.* 2008, Wright *et al.* 2004). For example, specific leaf area generally increases growth rate at the species level (Poorter & Bongers 2006), but CWM of specific leaf area and wood density enhance species aboveground biomass productivity in dry tropical forests (Prado-Junior *et al.* 2016) whereas these conservative trait values are found to decrease aboveground biomass productivity in moist and wet tropical forests (Finegan *et al.* 2015, Malhi *et al.* 2004). This thesis suggests that separating the overstorey and understorey strata of complex (sub-) tropical forest can improve the ecological modelling of biodiversity and aboveground biomass, but many uncertainties remain such as aboveground biomass dynamic processes (growth, recruitment, and mortality) for net biomass change over temporal and spatial scales. A more systematic testing of such relationships is thus urgently needed in complex subtropical forests across forest strata and at whole-community level, in order to understand the underlying mechanisms for biodiversity, stand structure and aboveground biomass dynamic processes in the field, and to improve ecological model predictions at large spatial and temporal scales.

Alternative and reliable mechanistic approach that does not depend on the assumptions of stimulation models is the use of **manipulation field experiments**. In temperate grasslands, fully manipulated (e.g. van Ruijven & Berendse 2005) or semi-manipulated (Hautier *et al.* 2014) field experiments have provided strong evidence for the importance of species and functional trait diversity and functional composition on the strength and stability of community processes. Several biodiversity experiments have also been carried out in plantation forests (Bruelheide *et al.* 2014, Ruiz-Jaen & Potvin 2011), but these do not represent structurally more complex and species-rich natural (sub-) forests. Species-removal experiments could provide a way to test for biodiversity effects in natural forests. Although these experiments may be difficult to implement because of costly and time-consuming, they could be a powerful way of demonstrating the relationships between biodiversity and ecosystem functions.

Empirical studies include direct measurements of field data but are limited in their spatial and temporal scales, e.g., in this thesis (one-time sampling of a 5-ha forest). The **remote sensing method** can be easily extended to large spatial areas but can oversight the detail information. Modelling methods are powerful tools that transcend measurement data and explore time scales, hypotheses, assumptions, and scenarios that cannot be evaluated through empirical or remote sensing data, but they depend on assumptions that are critical to data generation. These methods have their own significances, but they can also overcome the limitations of each other, for instance, a combined approach may provide much better information than that of isolation approach. Moreover, the remote sensing data needs to be associated with the empirical data to prove that the images provide realistic information (Jetz *et al.* 2016). Empirical data should be used as input and validation for vegetation models (such as DGVMs or other Earth System Models) in order to increase the realism of their concepts, assumptions, and results (Sakschewski *et al.* 2015). **Remote sensing data related to field data validation or empirical measurements** can also be used to develop land use change scenarios, for example with the CLUE model (Conversion of Land Use and its Effects) (Verburg *et al.* 2006). Then, these stimulation models and remote sensing outputs that are validated by field data will provide very valuable information to decision makers.

Sustainable forest management and ecosystem services: Forest ecosystems provide four main types of services: provisioning (e.g. timber and non-timber forest products), regulating (e.g. atmospheric regulation, water quality regulation and pollination), cultural (e.g. recreation) and supporting (e.g. nutrient cycling) (Millennium Ecosystem Assessment 2005). Growingly scientific evidences suggest that biodiversity cannot simply respond to environmental changes, but also to ecosystem functions (such as aboveground biomass and productivity) and services (e.g. atmospheric regulation in the term of carbon sequestration) that are crucial for supporting human well-being (Cardinale *et al.* 2012). The relationships between biodiversity and ecosystem functions are still debating, and current knowledge has played a vital role in policy-based information on a wide range of legislative (Mori *et al.* 2017). A number of successful biodiversity conservation frameworks have been developed in the forestry sector, which are related to the rapid expansion of applied forest ecology and sustainable forest management (Mori *et al.* 2017, Tittensor *et al.* 2014). No comparable, global synthesis has yet been provided for forestry, possibly reflecting the difficulty in assessing trade-offs among different biodiversity indicators and multiple ecosystem services (see Mori *et al.* 2017, and references therein). So far, the functional consequences of biodiversity conservation for ecosystem services have not been well integrated into these models (Isbell *et al.* 2015). In this regard, ecosystem models of biodiversity conservation, such as the InVEST (Integrated Valuation of Environmental Services and Tradeoff) model, (Kareiva *et al.* 2011), may also be considered with great potential to inform sustainable forest management (Mori *et al.* 2017). The scenarios and policy choices obtained from these models would be fundamentally helpful for policy-making. However, a recent study suggest that biodiversity has an independent, positive effect on aboveground biomass and ecosystem functioning in species-rich tropical forests, and hence biodiversity conservation should therefore be a key component of the REDD+ strategy (Poorter *et al.* 2015). Consequently, this thesis also shows that biodiversity and stand structure have positive effects on aboveground biomass across forest strata in the studied subtropical forest, and hence provide better ecosystem services in the shape of carbon sequestration for atmospheric regulation. The question is how to manage an ecosystem in a sustainable way to get ecosystem services (e.g., atmospheric regulation) from generation to generation. Biodiversity affects atmospheric regulations and ecosystem management through the impact of aboveground biomass or carbon storage. Lastly, it is recommended that future studies should include all basic components, not just species diversity or richness, of an ecosystem to fully understand the biodiversity – aboveground biomass or carbon storage relationships for the purpose of managing an ecosystem in a sustainable way (Ali & Yan 2017a, Mori *et al.* 2017).

9.6. Conclusions

Research in this thesis provides strong evidences for the forest strata-dependent multivariate relationships between biodiversity and aboveground biomass in a subtropical forest, while accounting for the effects of environmental factors. Particularly, this thesis suggests the general notion that no sole and ubiquitous relationship between biodiversity and aboveground biomass exists, but rather that the magnitude and direction and the underlying mechanisms of this relationship is forest strata-specific where available resources shift greatly.

In overstorey strata, the positive relationship of aboveground biomass with species diversity and individual tree size variation indicating the niche complementarity effect. In understorey strata, the mixture effects of tree development, high degree of biotic interaction, and increased resource heterogeneity might complicate the relationship between biodiversity and aboveground biomass. However, high aboveground biomass was potentially driven by functional identity of tree height through making use of plentiful soil nutrients at overstorey strata, whereas by conservative strategy at understorey strata through enduring nutrient-poor soils. Therefore, different forest strata affect whole-community aboveground biomass differently, i.e., high functional trait diversity of understorey enhances aboveground biomass through the niche complementarity effect while low functional trait diversity of overstorey enhances aboveground biomass through functionally-similar big trees effect. The strong negative relationship between overstorey functional trait diversity and whole-community aboveground biomass suggests that functional dominance and/or niche overlap rather than niche complementarity may better explain aboveground biomass. The weak positive effect of understorey functional trait diversity on whole-community aboveground biomass suggests the complementarity mechanism among slow-growing conservative species rather than acquisitive species of understorey in the studied forest, and hence supporting the niche complementarity effect. Separating functional trait diversity of overstorey and understorey strata improves predictions of whole-community aboveground biomass. As such, intraspecific versus interspecific functional trait diversity plays a central role for linking the direct and indirect responses of aboveground biomass to species richness, but these relationships depend on the forest strata of a community. Furthermore, 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. High overstorey aboveground biomass is related with groups of phylogenetically close species having low functional trait diversity due to the evolutionary relatedness. High evolutionary relatedness of overstorey species has modulated the relationship of functional trait diversity and aboveground biomass at understorey strata. The mechanism at the whole-community level is resulted from the mixed effects of overstorey evolutionary relatedness and understorey functional trait diversity.

Finally, this thesis concluded that functional identity of overstorey tree height with low functional trait diversity at overstorey, whereas niche complementarity with conservative strategy on nutrient-poor soils are of great importance for driving aboveground biomass. At whole-community level, aboveground biomass is most strongly determined by soil nutrients, individual tree size variation and functional dominance of big trees. Insightfully, ecological models for predicting aboveground biomass would be improved by including separate effects of overstorey and understorey diversity. Combining data across forest strata may swamp the relationships between biodiversity and aboveground biomass, and that to better understand the underlying mechanisms it is worth to analyse the understorey and overstorey strata separately. Hence, research in this thesis suggests that conserving biodiversity and maintaining stand structure at both overstorey and understorey strata are sustainable ecological strategies because high biodiversity with productive stand structure is crucial for forest functioning.

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Snapshots

Subtropical evergreen broad leaf forests of Ningbo region in Eastern China

Author and other research fellows during wood and leaf samples collection

Author during soil samples collection in the field

&

Lab experiments at East China Normal University

Author during wood density measurement

EAST CHINA NORMAL UNIVERSITY

国家自然科学基金委员会
1986
NATIONAL NATURAL SCIENCE FOUNDATION OF CHINA

国家留学基金管理委员会
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Arshad Ali

Personal curriculum vitae

Short biography

Arshad Ali was born on the 30th of March 1988 in Khyber Pakhtunkhwa, Pakistan. Born in Shangla, Swat in the Province of Khyber Pakhtunkhwa, he received his primary, middle and high schooling in English language in the International Public High School, Shahpur, during 1993-2004. He did his intermediate schooling from Government Postgraduate Jehanzeb College, Swat, during 2004-2006.

Arshad Ali did his BS Forestry (4-year) degree from Shaheed Benazir Bhutto University, Dir (U) Khyber Pakhtunkwa, Pakistan. He was awarded the Gold Medal in BS Forestry during session 2006-2010. His BS thesis was entitled "*Role of farm forestry in poverty alleviation and natural resources conservation in Swat valley, Pakistan*". After that, he started to work in Non-Government Organizations (NGOs) where he was Social Organizer in Interfaith League Against Poverty (I-LAP) during 2010-2011, and then he joined Resource Organization for Advancement and Development (ROAD) as a Project Manager during 2011-2012.

In July 2012, he received Chinese Government Scholarship from China Scholarship Council for conducting Master's (MS) degree in Ecology at East China Normal University, Shanghai, China. On the 13th of July 2012 he came to China and started MS degree at East China Normal University in September 2012. During his MS, he was privileged to work with a variety of people and in a variety of places, and did fieldwork in different subtropical forests of Ningbo region in Eastern China. Those opportunities and almost two years of work (July 2012-July 2014) resulted in the MS thesis "*The relationships between biodiversity and ecosystem carbon stocks in subtropical forests in Ningbo region, eastern China*".

In July 2014 Arshad Ali finished his MS Ecology, and in September 2014 he started PhD at East China Normal University in the same lab (Functional Ecology Lab) under the supervision of Professor Dr. En-Rong Yan, through the support of Shanghai Government Scholarship (A-class). He continued his research on *biodiversity and ecosystem functions of subtropical forests*, and at the same time also involved in different research projects granted to his PhD supervisor. These opportunities and almost three and half years of work (July 2014-November 2017) resulted in the PhD thesis "*The forest strata-dependent relationships among* *environment, biodiversity and aboveground biomass in a subtropical forest in Tiantong, Zhejiang Province*” that you are now holding in your hands. During 2012-2017, he was given several Research and Academic Awards by the School of Ecological and Environmental Sciences, China Scholarship Council, and International Students Office of East China Normal University.

Now, having finished his PhD thesis, Arshad Ali is ready to move on ecological science. By doing so he aims and hopes to contribute to the understanding of *biodiversity and ecosystem functions* of forests, agroforests, rangelands, etc., which is crucially important to assure the existence and persistence of these ecosystems and thereby the quality of life of many organisms – including humans.

Research interest

Arshad Ali is mainly interested in *biodiversity and ecosystem functions* particularly aboveground biomass, carbon storage and productivity. He is also interested in the studies regarding plant functional traits and community assembly. Specifically, he is highly interested in:

1. Development of allometric equations for estimation of aboveground biomass in forests
2. Functional trait diversity, composition, species-stand structure, and aboveground biomass
3. Plant functional traits and community assembly
4. Biodiversity research in Agroforestry Systems
5. Impact of climate change scenarios on biodiversity and ecosystem functions

Publications

Published articles in SCI / SCIE / international peer-reviewed journals

22) **Ali, A.** & Yan, E.R. (2018) The mediation roles of intraspecific and interspecific functional trait diversity for linking the response of aboveground biomass to species richness across forest strata in a subtropical forest. *Ecological Indicators* 85, 493-501. DOI: 10.1016/j.ecolind.2017.10.057

21) **Ali, A.** & Yan, E.R. (2017) Functional identity of overstorey tree height and understorey conservative traits drive aboveground biomass in a subtropical forest. *Ecological Indicators* 83, 158-168. DOI: 10.1016/j.ecolind.2017.07.054

20) **Ali, A.** & Yan, E.R. (2017) The forest strata-dependent relationship between biodiversity and aboveground biomass within a subtropical forest. *Forest Ecology and Management* 401, 125-134. DOI: 10.1016/j.foreco.2017.06.056

19) **Ali, A.** & Mattsson, E. (2017) Disentangling the effects of species diversity, and intraspecific and interspecific tree size variation on aboveground biomass in dry zone homegarden agroforestry systems. *Science of the Total Environment* 598, 38–48. DOI: 10.1016/j.scitotenv.2017.04.131.

18) Yang, X.D., Lv, G.H., **Ali, A.,** Ran, Q.Y., Gong, X.W., Wang, F., Liu, Z.D., Qin, L. & Liu, W.G. (2017) Variations in functional traits and population dynamics of an ephemeral plant *Lappula semiglabra* with dew amount gradients in Ebinur Desert in NW, China. *Ecohydrology*. DOI:10.1002/eco.1858.

17) **Ali, A.** & Mattsson, E. (2017) Individual tree size inequality enhances aboveground biomass in homegarden agroforestry systems in the dry zone of Sri Lanka. *Science of the Total Environment* 575, 6–11. DOI: 10.1016/j.scitotenv.2016.10.022.

16) **Ali, A.,** Yan, E.R., Scott, X.C., Cheng, J.Y. & Liu, X.Y. (2017) Community-weighted mean of leaf traits and divergence of wood traits predict aboveground biomass in secondary subtropical forests. *Science of the Total Environment* 574, 654–662. DOI: 10.1016/j.scitotenv.2016.09.022.

15) **Ali, A.** & Yan, E.R. (2017) Relationships between biodiversity and carbon stocks in forest ecosystems: a systematic literature review. *Tropical Ecology* 58(1), 1–14.

14) **Ali, A.,** Molau, U., Yang, B., Jägerbrand, A.K. & Alatalo, J.M. (2016) Diversity-productivity dependent resistance of an alpine plant community to different climate change scenarios. *Ecological Research* 31(6), 935–945. DOI: 10.1007/s11284-016-1403-6.

13) Zhao, Y.T., **Ali, A.** & Yan, E.R. (2017) The plant economics spectrum is structured by leaf habits and growth forms across subtropical species *Tree Physiology* 37 (2), 173–185. DOI: 10.1093/treephys/tpw098

12) **Ali, A.,** Yan, E.R., Chen, H.Y.H., Chang, S.X., Zhao, Y.T., Yang, X.D. & Xu, M.S. (2016) Stand structural diversity rather than species diversity enhances aboveground carbon storage in secondary subtropical forests in Eastern China. *Biogeosciences* 13(16), 4627–4635. DOI: 10.5194/bg-13-4627-2016, *Biogeosciences Discussion*., DOI: 10.5194/bg-2016-6.

11) **Ali, A.,** Yan, E.R., Chen, H.Y.H., Chang, S.X., Zhao, Y.T., Yang, X.D. & Xu, M.S. (2016) Data from: Stand structural diversity rather than species diversity enhances

aboveground carbon storage in secondary subtropical forests in Eastern China. *Dryad Digital Repository*. DOI:10.5061/dryad.8bp7m

10) **Ali, A.,** Xu, M.S., Zhao, Y.T., Zhang, Q.Q., Zhou, L.L., Yang, X.D. & Yan, E.R. (2015) Allometric biomass equations for shrub and small tree species in subtropical China. *Silva Fennica* 49 (4), 1–10. DOI:10.14214/sf.1275.

9) **Ali, A.** (2015) A review of strong evidence for the effect of functional dominance on carbon stocks in natural forest ecosystems. *Research Journal of Forestry* 9(3), 65–70. DOI:10.3923/rjf.2015.65.70

8) Yang, X.D., Zhang, X.N., Lv, G.H. & **Ali, A.** (2014) Linking *Populus euphratica* hydraulic redistribution to diversity assembly in the arid desert zone of Xinjiang, China. *PLoS ONE* 9(10), e109071. DOI:10.1371/journal.pone.0109071.

7) **Ali, A.,** Ma, W.J., Yang, X.D., Sun, B.W., Shi, Q.R. & Xu, M.S. (2014) Biomass and carbon stocks in *Schima superba* dominated subtropical forests of eastern China. *Journal of Forest Science* 60(5), 198–207.

Published articles in Chinese Science Citation Database (CSCD)

6) Song, Y.J., Tian, W.B., Liu, X.Y., Ying, F., Cheng, J.Y., Zhu, D.N., **A. Ali.** & Yan, E.R. (2016) Associations between litterfall dynamics and micro-climate in forests of Putuoshan Island, Zhejiang, China. *Chinese Journal of Plant Ecology* 40 (11), 1154–1163. DOI: 10.17521/cjpe.2016.0157.

5) Xu. M.S., Zhao, Y.T., Yang, X.D., Shi, Q.R., Zhou, L.L., Zhang, Q.Q., **Ali. A.** & Yan. E.R. (2016) Geostatistical analysis of spatial variations in leaf traits of woody plants in Tiantong, Zhejiang Province. *Chinese Journal of Plant Ecology* 40 (1), 48–59. DOI:10.17521/cjpe.2015.0246.

4) Zhao Y.T., Xu, M.S., Zhang, Z.H., Zhou, L.L., Zhang, Q.Q., **Ali, A.,** Song, Y.J. & Yan, E.R. (2016) Characteristics of hydraulic architecture in woody plants across successional stages in evergreen broad-leaved forests in Tiantong, Zhejiang Province. *Chinese Journal of Plant Ecology* 40(2), 116–126. DOI: 10.17521/cjpe.2015.0258.

3) Ma, W.J., Zhao, Y.T., Zhang, Q.Q., **Ali, A.,** Shi, Q.R. & Yan, E.R. (2014) C:N:P stoichiometry in forest floor litter of evergreen broad-leaved forests at different successional stages in Tiantong, Zhejiang, eastern China. Chinese *Journal of Plant Ecology* 38(8), 833-842. DOI: 10.3724/SP.J.1258.2014.00078

2) Sun, B.W., Yang, X.D., Zhang, Z.H., Ma, W.J., **Ali, A.,** Huang, H.X. & Yan, E.R. (2013) Relationships between soil carbon pool and vegetation carbon return through

succession of evergreen broad-leaved forests in Tiantong region, Zhejiang Province, Eastern China. *Chinese Journal of Plant Ecology* 37(9), 803-810. DOI: 10.3724/SP.J.1258.2013.00084.

1) Yang, X.D., Yan, E.R., Zhang, Z.H., Sun, B.W., Huang, H.X., **Ali, A.,** Ma, W.J. & Shi, Q.R. (2013) Tree architecture of overlapping species among successional stages in evergreen broad-leaved forests in Tiantong region, Zhejiang Province, China. *Chinese Journal of Plant Ecology* 37(7), 611-619. DOI: 10.3724/SP.J.1258.2013.00063

Under process articles for publications in SCI/SCIE journals

3) **Ali, A.,** Lohbeck, M. & Yan, E.R. (2017) Forest strata-dependent effects of functional trait diversity on aboveground biomass in a subtropical forest.

2) **Ali, A.** & Yan, E.R. (2017) Consequences of phylogenetic conservativeness and functional trait similarity on aboveground biomass vary with subtropical forest strata.

1) **Ali, A.** & Yan, E.R. (2017) Disentangling the effects of taxonomic, functional, evolutionary and stand structural attributes on aboveground biomass: differential effects across subtropical forest strata.

Seminar's posters and presentations

5) **Ali. A.** (2017) Represented East China Normal University as the main organizer or student in charge in *The 15th Challenge Cup Carnival on Technological Innovation of Overseas Students in China*. Presented 10 posters on "*Biodiversity and the functioning of forests in Eastern China*" on 26th April 2017 held in Shanghai University, Baoshan Campus Shanghai.

4) **Ali, A.** (2016) Stand structural diversity rather than species diversity enhances aboveground carbon storage in secondary subtropical forests in Eastern China. *2016 2nd graduate students' forum (Guang Hua forum)* held at School of Ecological and Environmental Sciences, East China Normal University. Available at http://www.sees.ecnu.edu.cn/index.php?classid=7345&newsid=10911&t=show (First presentation on 18th December, 2016)

3) **Ali, A.,** Yan, E.R., Xu, M.S., Zhao, Y.T. & Zhou, L.L. (2015) Functional dominance and divergence predict carbon stocks in subtropical forests: Testing the mass ratio and niche complementarity hypotheses. *64th International symposium on ecology held at East China Normal University, Shanghai* (Research Poster on 26th Sep, 2015). Available at http://www.sees.ecnu.edu.cn/index.php?classid=7345&newsid=10609&t=show

2) **Ali, A.** (2014) Deforestation: a key ecological issue. *The Express Tribune*, opinion letter no. 697344. Available at http://tribune.com.pk/story/697344/deforestation-a-key-ecological-issue/

1) **Ali, A.,** Yan, E.R. & Yang. X.D. (2013) Effects of stand structural diversity on carbon stocks in the subtropical forests of eastern China. *2013 national conference of Ecological Society of China* (held at Nanchang China). Available at http://www.planta.cn/forum/files_planta/oeparagraphae__104.pdf (Page 26, Poster no. P38)

Awards, honors and scholarships

Time	Type	Title	Awarding organization
Sep 2017	Scholarship and award	Wisdom scholar award for academic performance	School of Ecological and Environmental Sciences, East China Normal University
April 2017	Scholarship and award	Wisdom scholar award for academic performance	School of Ecological and Environmental Sciences, East China Normal University
Mar 2017	Honor award	Excellent young researcher	East China Normal University; National Excellent Society; and the Shanghai Star Community Local Construction Society
Nov 2016	Scholarship and award	Outstanding foreign student scholarship for excellent performance, only 2 positions	China Scholarship Council, East China Normal University
Dec 2015	Scholarship and award	Outstanding foreigner scholarship and academic performance award	International students office, East China Normal University
Sep 2015	Scholarship and award	Wisdom scholar award for academic performance	School of Ecological and Environmental Sciences, East China Normal University
Feb 2015	Scholarship and job (Declined)	Overseas PhD scholarship with offer of lecturer (BS 18, regular) in environmental sciences	Abdul Wali Khan University Mardan & Pakistan Higher Education Commission, Pakistan

Sep 2014	Scholarship	Shanghai Government Scholarship (Class-A, full funded) for PhD degree at ECNU	Shanghai Education Commission, Shanghai
July 2014	Certificate	Certificate of Excellence for completing 3-years master's degree in 2-years	International students office, East China Normal university
Dec 2013	Certificate	Excellent Master's Student	School of Ecological and Environmental Sciences, East China Normal University
Dec 2013	Scholarship and award	Outstanding foreigner scholarship and academic performance award	International students office, East China Normal University
Sep 2012	Scholarship	China Government Scholarship, full funded, for Master's degree at ECNU	China Scholarship Council (CSC)
Feb 2012	Award	Gold Medal for getting top position among all students at BS Forestry degree	Shaheed Benazir Bhutto University, Pakistan
May 2008	Scholarship	Encouraging talented BS students	Frontier Education Foundation, Pakistan

Scientific society's memberships

1) Italian Society of Silviculture and Forest Ecology, since 2014
2) Ecological Society of China, since 2013
3) The International Association for Ecology, since 2013
4) Snow Leopard Network, since 2011

Journal (SCI/SCIE) reviewer

Journal of Ecology (1); Global Change Biology (1); Frontiers in Plant Science (1); Ecological Indicators (8); Forestry: An International Journal of Forest Research (1); Journal of Forestry Research (9); Pakistan Journal of Botany (1); Web Ecology (1); Energy, Ecology and Environment (1); Ecological Processes (1).

Contact information

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