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Research paper

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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A B S T R A C T

Intraspecific functional trait diversity (FTD) has improved our understandings about the key mechanisms of species coexistence in plant communities. Yet, little is known about whether and how intraspecific and interspecific FTD mediate the response of aboveground biomass to species richness across forest strata (i.e. overstorey and understorey) and at whole-community in forests. To address this question, we tested the direct and indirect responses of aboveground biomass to species richness via intraspecific and interspecific FTD based on specific leaf area (FTD_{SLA}) and leaf dry matter content (FTD_{LDMC}) using structural equation modeling, in addition to the effects of soil nutrients, across 125 plots in a 5-ha subtropical forest in Eastern China. Results showed that intraspecific FTD mediates the response of aboveground biomass to species richness at overstorey and understorey strata, and whole-community level, while interspecific FTD did so at understorey strata only. At overstorey strata, 14% of the variation in aboveground biomass was accounted by the strong direct positive effect of species richness only. At understorey strata, soil nutrients had a strong negative direct effect followed by positive effects of species richness and FTD_{LDMC} on aboveground biomass with 44–45% of the variation in both intraspecific and interspecific FTD models. At whole community level, 14% of the variation in aboveground biomass was explained by the strong positive direct effect of species richness followed by negative direct effect of intraspecific FTD_{SLA}. Intraspecific and interspecific FTD_{LDMC} had positively mediated the response of aboveground biomass to species richness at understorey strata through niche differentiation. 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 with a specific functional strategy may largely determine community trait space. Intraspecific FTD_{SLA} had negative relationship with aboveground biomass at the whole-community, probably due to the presence of a few large trees occupying larger niche space in a community. We conclude that intraspecific versus interspecific FTD 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.

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., 2016). 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

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true in forest ecosystems (Szwagrzyk and 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 and 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 and 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 and 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. 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 and Yan, 2017a). 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 and Yan, 2017b). 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.

The niche complementarity hypothesis predicts that communities with a variety of species (Tilman, 1999) or functional traits (Díaz et al., 2011) are therefore able to use available resources more efficiently, thus enhancing the magnitude of ecosystem functions in natural forests (Zhang et al., 2012a). 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 and Yan, 2017a).

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 and 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

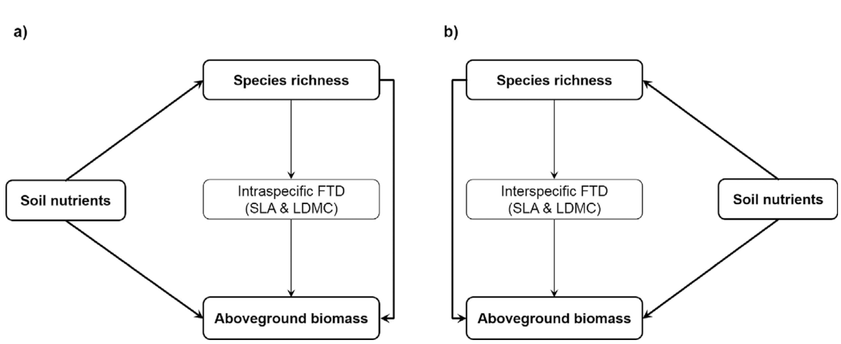

Fig. 1. Conceptual model showing how functional trait diversity mediates the response of aboveground biomass to species richness, in addition to the effects of soil nutrients. Conceptual model was constructed based on two theoretical frameworks, including (a) intraspecific functional trait diversity 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.