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

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ABSTRACT

The relationships between biodiversity and aboveground biomass in forest ecosystems have been intensively studied in recent decades. Still, the mechanisms that underlie it remain highly debated. We hypothesized 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. The integrative relationships of species diversity and tree size variation (variation in diameter at breast height-DBH) with aboveground biomass were analysed at overstorey and understorey strata across 125 plots in a 5-ha subtropical forest in Eastern China. For comparison, we tested these relationships at individual strata (isolation modelling), and whole-community level, by using linear structural equation model while accounting for the effects of soil nutrients. The integrative modelling 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. Overstorey DBH variation and species diversity had the positive direct effects on overstorey aboveground biomass. Overstorey species diversity significantly promoted the understorey species diversity, but DBH variation and aboveground biomass of overstorey strata had negligible effects on the diversity and aboveground biomass of understorey strata. Soil nutrients had positive direct effect on overstorey DBH variation, but negative direct effects on overstorey and understorey aboveground biomass and overstorey species diversity. These results provide strong evidence for the niche complementarity effect for driving positive relationships of species diversity and individual tree size variation with aboveground biomass at overstorey strata. The strong and consistent negative effects of soil nutrients on overstorey aboveground biomass and 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. In conclusion, this study suggests 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. We argue that ecological models for predicting aboveground biomass would be improved by including separate effects of overstorey and understorey diversity.

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 (Wang et al., 2014; Poorter et al., 2015; Zhang and Chen, 2015; Ali and Mattsson, 2017). 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

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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 (Cavanaugh et al., 2014; Poorter et al., 2015; Zhang and Chen, 2015; Ali and Mattsson, 2017). 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. 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 and 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 and 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 (Poorter et al., 2015; Zhang and Chen, 2015; Ali et al., 2016; Ali and Mattsson, 2017). 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 and Chen, 2015). Theoretically, individual tree size variation enhance aboveground biomass through complementary light-use (Yachi and Loreau, 2007; Zhang and Chen, 2015; Ali and Mattsson, 2017).

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 (Nilsson and Wardle, 2005; Gilliam, 2007; Barbier et al., 2008). Moreover, local environmental conditions strongly affecting plant performance (Barbier et al., 2008; Bartels and 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 (Wright, 2002; Brenes-Arguedas et al., 2011). 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 (Slik et al., 2013; Poorter et al., 2015; Zhang et al., 2016). Additionally, species diversity of overstorey strata may promote species diversity in understorey strata as a result of reduced interspecific competition (Bartels and Chen, 2013; Zhang et al., 2016). Therefore, to understand the mechanism(s) by which aboveground biomass is

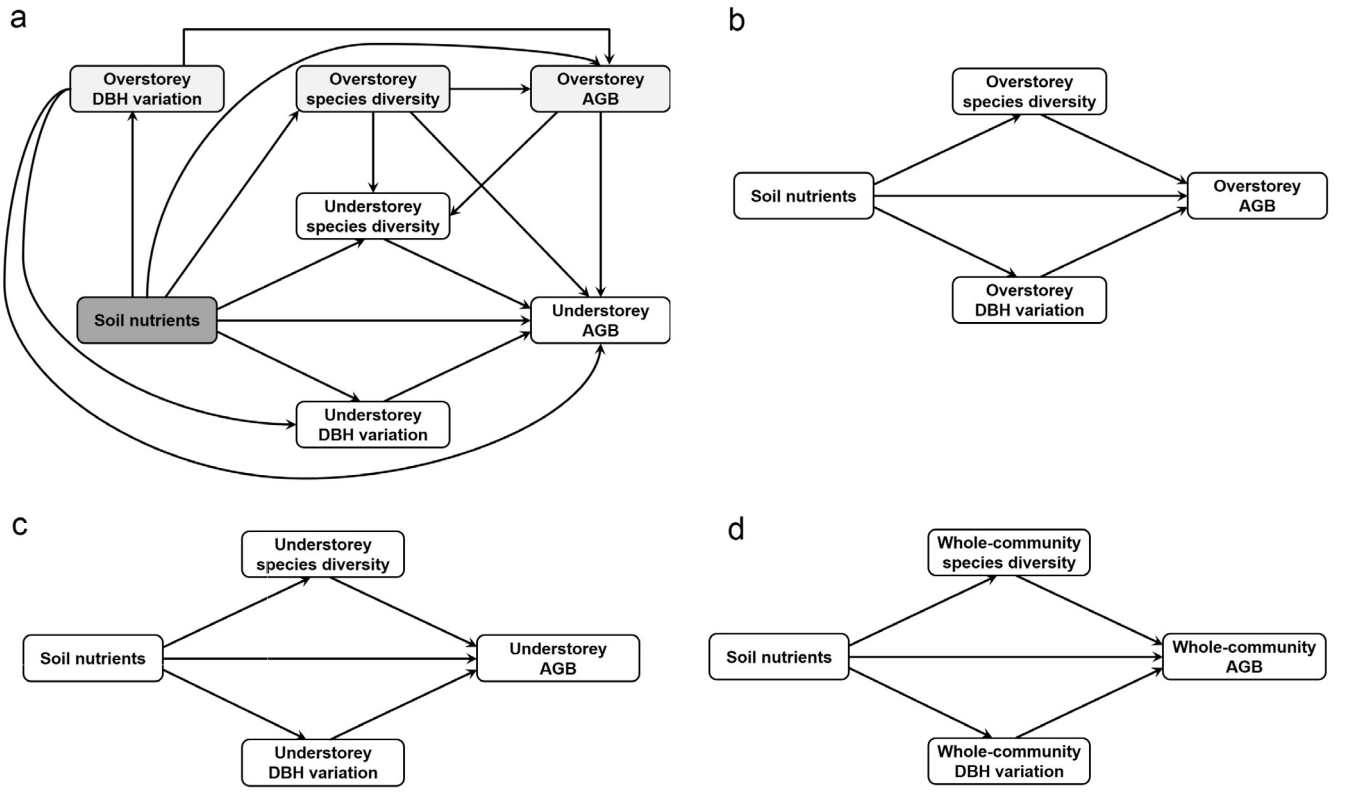

Fig. 1. Conceptual models for the relationships of aboveground biomass with species diversity and individual tree size variation (DBH variation) across forest strata in a subtropical evergreen broadleaf forest. (a) integrative modelling showing hypothesized relationships of how species diversity and 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.