



Community-weighted mean of leaf traits and divergence of wood traits predict aboveground biomass in secondary subtropical forests☆☆☆



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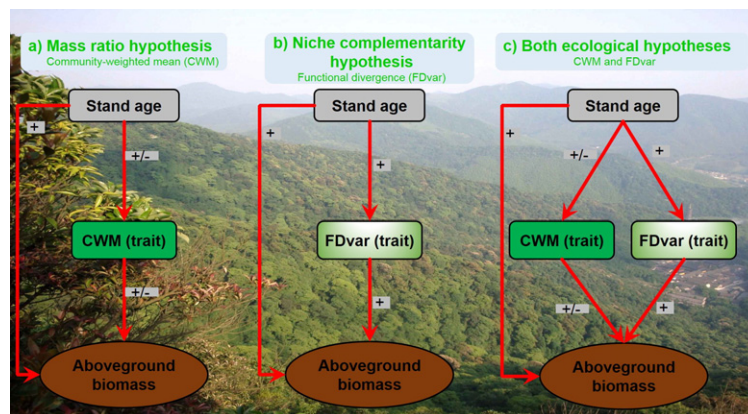
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HIGHLIGHTS

- Aboveground biomass is associated with functional divergence of wood traits.
- Aboveground biomass is associated with community-weighted mean of leaf traits.
- Leaf and wood economics are decoupled for influencing ecosystem functioning.
- Community-weighted mean of leaf and divergence of wood traits alone and jointly affect aboveground biomass.
- Both the mass ratio and niche complementarity hypotheses regulate aboveground biomass.

GRAPHICAL ABSTRACT



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ABSTRACT

Subtropical forests are globally important in providing ecological goods and services, but it is not clear whether functional diversity and composition can predict aboveground biomass in such forests. We hypothesized that high aboveground biomass is associated with high functional divergence (FDvar, i.e., niche complementarity) and community-weighted mean (CWM, i.e., mass ratio; communities dominated by a single plant strategy) of trait values. Structural equation modeling was employed to determine the direct and indirect effects of stand age and the residual effects of CWM and FDvar on aboveground biomass across 31 plots in secondary forests in subtropical China. The CWM model accounted for 78, 20, 6 and 2% of the variation in aboveground biomass, nitrogen concentration in young leaf, plant height and specific leaf area of young leaf, respectively. The FDvar model explained 74, 13, 7 and 0% of the variation in aboveground biomass, plant height, twig wood density and nitrogen concentration in young leaf, respectively. The variation in aboveground biomass, CWM of leaf nitrogen concentration and specific leaf area, and FDvar of plant height, twig wood density and nitrogen concentration in young leaf explained by the joint model was 86, 20, 13, 7, 2 and 0%, respectively. Stand age had a strong positive direct effect but low indirect positive effects on aboveground biomass. Aboveground biomass was negatively

☆ Nomenclature: Flora of China, database as of September 2004. <http://frps.eflora.cn/name1/a>

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related to CWM of nitrogen concentration in young leaf, but positively related to CWM of specific leaf area of young leaf and plant height, and FDvar of plant height, twig wood density and nitrogen concentration in young leaf. Leaf and wood economics spectra are decoupled in regulating the functionality of forests, communities with diverse species but high nitrogen conservative and light acquisitive strategies result in high aboveground biomass, and hence, supporting both the mass ratio and niche complementarity hypotheses in secondary subtropical forests.

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1. Introduction

Understanding the relationship between the plant functional trait diversity and aboveground biomass is important for managing carbon storage in aboveground biomass and mitigating the increasing atmospheric CO₂ concentration (Díaz et al., 2011). When compared to species and/or structural diversity – aboveground biomass relationships (Ali et al., 2016; Dănescu et al., 2016), our understanding of how functional trait diversity and composition influence aboveground biomass in forest ecosystems remains poor. Plant functional traits affect plant fitness and performance directly or indirectly (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. Functional divergence (FDvar, referring to niche complementarity) and community-weighted mean (CWM, or mass ratio, referring to the degree of a communities dominated by a single plant strategy) are two independent measures of biodiversity (Díaz et al., 2007). It is becoming increasingly evident that functional trait composition (i.e., CWM) rather than functional trait diversity (i.e., FDvar) strongly affects aboveground biomass in tropical forests (Becknell and Powers, 2014; Conti and Díaz, 2013; Finegan et al., 2015). However, relationships between functional traits and aboveground biomass may be fundamentally different among forest types because resource limitations to plant growth are specific in different types of forests (Lohbeck et al., 2013). In addition, aboveground biomass, and CWM and FDvar of plant trait values are at the same time influenced by stand age (Becknell and Powers, 2014). Stand age, hence, may directly and indirectly affect aboveground biomass via CWM and FDvar of trait values (Fig. 1). To date, our understanding of how FDvar and CWM of trait values predict aboveground biomass in forest communities remains unclear when stand age is considered.

The mass ratio hypothesis postulates that ecosystem processes are driven by the (traits of the) most abundant species in plant communities (Grime, 1998). According to this hypothesis, communities dominated by plants with a single resource use strategy have high aboveground biomass. If the mass ratio mechanism plays a role, aboveground biomass should be closely associated to CWM of trait values (Fig. 1a), a community metric that weighs species trait values by the relative abundance of the species in a community (Conti and Díaz, 2013; Díaz et al., 2007; Garnier et al., 2004). However, the relationship between CWM of trait values and aboveground biomass may be fundamentally dependent on stand age (Fig. 1). The niche complementarity hypothesis states that functional traits can mediate niche partitioning and lead to different resource utilization by plants across space (Petchey and Gaston, 2006); for example, through the formation of stratified mixtures of sun- and shade-adapted species in a community. Therefore, it is expected that a forest community with high aboveground biomass has a diverse group of species with a high variety of functional strategies (Zhang and Chen, 2015; Zhang et al., 2012; Fig. 1b).

In natural forests, the importance of functional trait diversity and composition to aboveground biomass has recently been recognized and debated (Becknell and Powers, 2014; Conti and Díaz, 2013; Finegan et al., 2015). The opposite relationships between aboveground biomass and CWM and/or FDvar of trait values 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

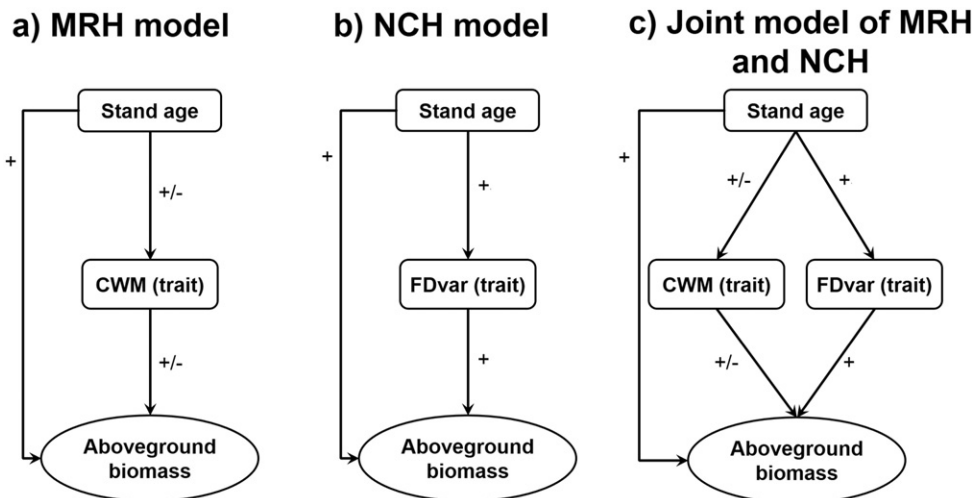


Fig. 1. Conceptual models for the prediction of aboveground biomass in secondary subtropical forests of eastern China, showing hypothesized relationships of how stand age affects functional divergence (FDvar) and community-weighted mean (CWM) of functional traits, and how stand age, FDvar and CWM concomitantly affect aboveground biomass. Three conceptual models were proposed based on individual and joint effects of FDvar and CWM of trait values, after accounting for the effects of stand age; a) MRH (mass ratio hypothesis) model; b) NCH (niche complementarity hypothesis) model; and c) joint model of MRH and NCH. The positive (+) and negative (–) signs indicate the direct effect of exogenous (independent) on endogenous (dependent) variables.

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