Ecological Indicators 83 (2017) 158–168

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind

Original Articles

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

Arshad Ali[a,b,c], En-Rong Yan[a,b,c,*]

[a] Forest Ecosystem Research and Observation Station in Putuo Island, School of Ecological and Environmental Sciences, East China Normal University, Shanghai 200241, China

[b] Tiantong National Forest Ecosystem Observation and Research Station, School of Ecological and Environmental Sciences, East China Normal University, Shanghai 200241, China

[c] Shanghai Key Lab for Urban Ecological Processes and Eco-Restoration, School of Ecological and Environmental Sciences, East China Normal University, Shanghai 200241, China

ARTICLE INFO

Keywords:
Evergreen broadleaf forest
Functional traits
Mass ratio
Plant strategies
Soil nutrients
Forest strata

ABSTRACT

The niche complementarity hypothesis has received empirical support but species differ in functional strategies for their contribution to ecosystem function, as predicted by the mass ratio hypothesis. Our understanding of how functional identity of conservative and acquisitive strategies of trees predicts aboveground biomass across forest strata (i.e. overstorey and understorey) remains unclear. Aboveground biomass, community-weighted mean (CWM − functional identity) of trait values (6 leaf and 2 stem traits), and soil physicochemical properties were estimated for 125 plots in a 5-ha subtropical forest in Eastern China. We used multiple linear regressions models to relate aboveground biomass to CWM indices at overstorey and understorey strata separately, and whole-community level. We finally employed the structural equation model to test for the effects of overstorey on understorey strata, in addition to the effects of soil physicochemical properties. Forest strata optimal models showed that overstorey strata had high aboveground biomass when they are dominated by functional identity of tree height, whereas high aboveground biomass in understorey strata was driven by functional identity of dense-wooded conservative strategy. Whole-community optimal model showed that communities dominated by functional identity of leaf dry matter content and mean leaf area had high aboveground biomass. Aboveground biomass was negatively related to soil nutrients across forest strata and whole-community level. The structural equation model showed that CWM of overstorey tree height did not affect understorey functional identity and aboveground biomass, when soil physicochemical properties were accounted. Soil nutrients had positive effect on functional identity of overstorey tree height whereas negative effect on functional identity of understorey dense-wooded strategy. This study highlights the fundamental roles of forest strata where overstorey and understorey strata contribute to their corresponding aboveground biomass with contrasting functional strategies across a range of soil nutrients. 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. To better understand the roles of functional identity of conservative and acquisitive strategies in driving ecosystem functions, it is worth to analyse forest strata separately.

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 and D & az, 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., 2016), but species differ in functional strategies

* Corresponding author at: Forest Ecosystem Research and Observation Station in Putuo Island, School of Ecological and Environmental Sciences, East China Normal University, Shanghai, 200241, China.
E-mail address: eryan@des.ecnu.edu.cn (E.-R. Yan).

http://dx.doi.org/10.1016/j.ecolind.2017.07.054
Received 26 May 2017; Received in revised form 26 July 2017; Accepted 27 July 2017

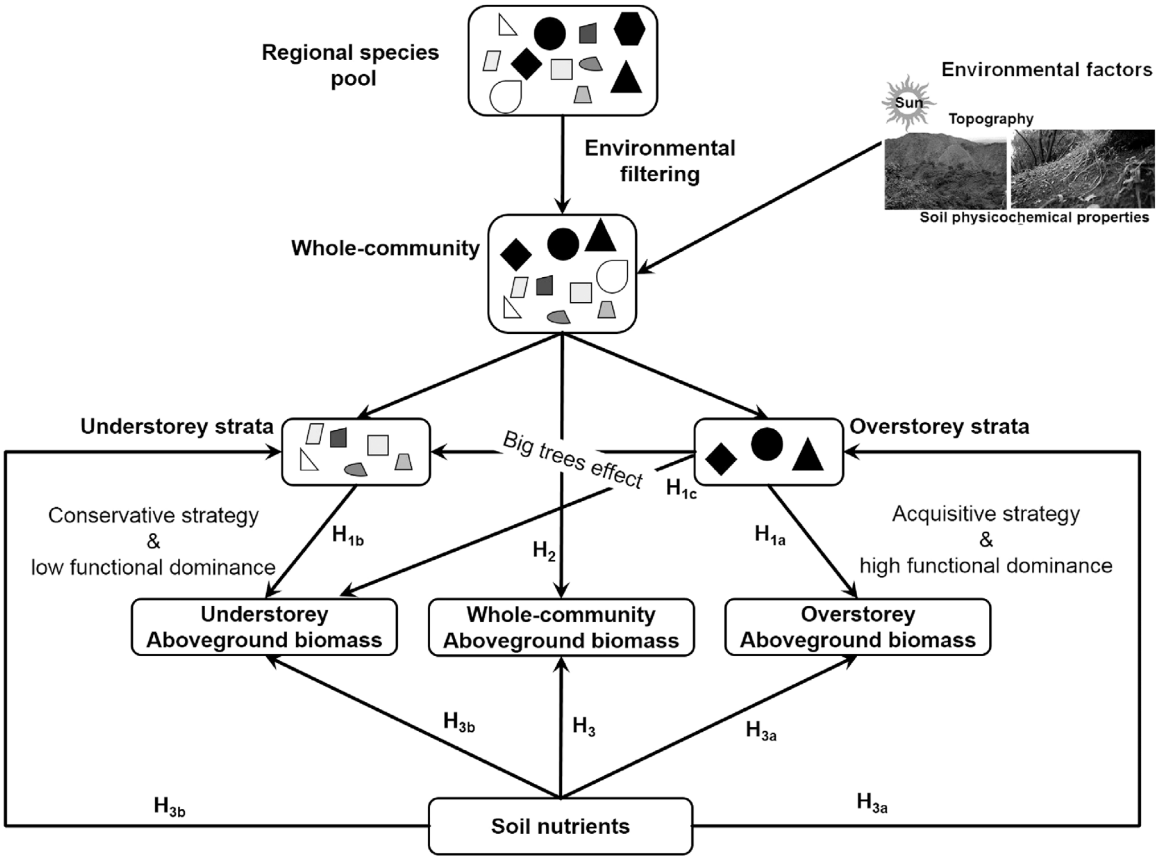

Fig. 1. Conceptual framework showing how changes in aboveground biomass are determined by the mass ratio mechanism. The acquisitive traits were CWM of specific leaf area, mean leaf area, leaf nitrogen and phosphorus concentrations, and ratio of leaf nitrogen to phosphorus concentrations. The conservative 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, predictions or questions (see introduction section).

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 and D & az, 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 and 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 and Chen, 2010; Zhang et al., 2016). 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., 2016).

In this study, we tested how aboveground biomass was driven by