Forest Ecology and Management 424 (2018) 439–447

Contents lists available at ScienceDirect

Forest Ecology and Management

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

Forest strata-dependent functional evenness explains whole-community aboveground biomass through opposing mechanisms

Arshad Ali[a,b], Madelon Lohbeck[c,d], En-Rong Yan[a,e,*]

[a] Forest Ecosystem Research and Observation Station in Putuo Island, Tiantong National Forest Ecosystem Observation and Research Station, and Shanghai Key Lab for Urban Ecological Processes and Eco-Restoration, School of Ecological and Environmental Sciences, East China Normal University, Shanghai 200241, China
[b] Spatial Ecology Lab, School of Life Sciences, South China Normal University, Guangzhou 510631, Guangdong, China
[c] Forest Ecology and Forest Management Group, Wageningen University, PO Box 47, 6700, AA Wageningen, The Netherlands
[d] World Agroforestry Centre, ICRAF, United Nations Avenue, Gigiri, Nairobi, Kenya
[e] Institute of Eco-Chongming (IEC), 3663 N. Zhongshan Rd., Shanghai 200062, China

ARTICLE INFO

Keywords:
Big trees effect
Ecosystem function
Evergreen broadleaf forest
Functional diversity
Niche complementarity
Niche overlap
Overstorey and understorey
Soil nutrients

ABSTRACT

A positive biodiversity – aboveground biomass relationship is often attributed to the niche complementarity hypothesis. This hypothesis has received much less support when based on functional trait diversity and when tested in complex natural forests. Here, we hypothesized that niche complementarity (high trait diversity) in the understorey and niche overlap (low trait diversity) in the overstorey would drive whole-community aboveground biomass. To test this hypothesis, we used multiple linear regression models to evaluate how functional trait diversity (functional richness, evenness, divergence and dispersion) of overstorey, understorey, and whole-community determine aboveground biomass across 125 plots in a 5-ha subtropical forest of Eastern China. A structural equation model was used to evaluate whether the functional trait diversity of overstorey affects the relationships between understorey functional trait diversity and whole-community aboveground biomass while considering for the effect of environmental factors. We additionally considered the effects of mass ratio (i.e. community-weighted mean of trait values) and stand structural complexity. The strong negative effect of overstorey functional evenness on aboveground biomass provides support to the functional dominance and/or niche overlap rather than niche complementarity effect. The negative effect of overstorey functional evenness on aboveground biomass was also partially mediated by its direct negative effect on understorey functional evenness. The weak positive effect of understorey functional evenness on aboveground biomass provides support to the niche complementarity effect. We conclude that functional evenness of overstorey and understorey strata affect whole-community aboveground biomass differently through opposing mechanisms, regardless of the effects of mass ratio and stand structural complexity.

1. Introduction

Understanding the ecological mechanisms for the relationships between biodiversity and ecosystem function has been a central debate in ecology for more than four decades (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 large numbers of species (i.e. species diversity) (Tilman, 1999) or varieties of functional traits (i.e. functional trait diversity) (Díaz et al., 2007) can efficiently utilize the available resources, and thereby increasing the realized degree of niche differentiation for determining high ecosystem functions in forests (Zhang et al., 2012). Most of the recent studies found no or a little support for the niche complementarity hypothesis, based on functional trait diversity in forest ecosystems (Conti and Díaz, 2013; Finegan et al., 2015; Chiang et al., 2016; Fotis et al., 2017; van der Sande 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 stratum 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) (Wright, 2002; Rüger et al., 2012).

Understorey stratum contributes much to the majority of biodiversity and has a high turnover rate in comparison with overstorey

* Corresponding author at: Forest Ecosystem Research and Observation Station in Putuo Island, Tiantong National Forest Ecosystem Observation and Research Station, and Shanghai Key Lab for Urban Ecological Processes and Eco-Restoration, School of Ecological and Environmental Sciences, East China Normal University, Shanghai 200241, China.
E-mail addresses: arshadforester@m.scnu.edu.cn (A. Ali), madelon.lohbeck@wur.nl (M. Lohbeck), eryan@des.ecnu.edu.cn (E.-R. Yan).

https://doi.org/10.1016/j.foreco.2018.05.015
Received 22 March 2018; Received in revised form 3 May 2018; Accepted 8 May 2018

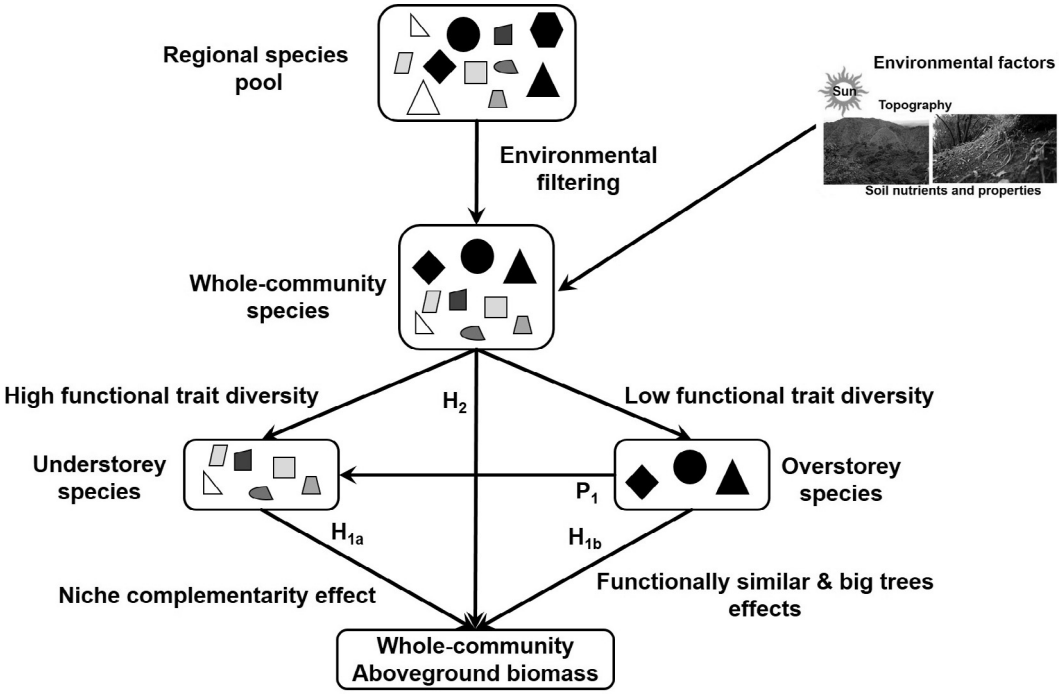

Fig. 1. A conceptual framework showing how changes in aboveground biomass are determined by underlying mechanisms (niche complementarity and/ or niche overlap and big trees effects). Species pool having different symbols and colors represents different species and traits dissimilarity, respectively, while the size of the symbols represents the overstorey (big size) and understorey (small size) species. H_{1a}, H_{1b}, H_2 and P_1 indicate the proposed hypotheses, prediction or questions (see introduction section).

stratum (Nilsson and Wardle, 2005; Gilliam, 2007; Barbier et al., 2008). Overstorey stratum stores a large amount of aboveground biomass due to their large wood volumes and uneven contribution of large trees to the whole-community level aboveground biomass (Slik et al., 2013). Environmental conditions affecting plant performance can strongly differ across forest strata in natural forests, and therefore important resources like the light are often limiting in the understorey while abundant in overstorey stratum of forests (e.g., Wright, 2002; Brenes-Arguedas et al., 2011). Based on the functional trait diversity, the niche complementarity effect may be less crucial in the overstorey stratum probably due to the dominance of few large trees, and hence it is expected that low functional trait diversity or high functional dominance or niche overlap would drive aboveground biomass (Prado-Junior et al., 2016; Fotis et al., 2017). In understorey stratum, it is expected that high functional trait diversity would enhance aboveground biomass because strong interactions among coexisting species could lead niche differentiation, facilitation and competition in a more stressful and resource-limited environment (Paquette and Messier, 2011).

Despite many efforts in understanding the niche complementarity effect on ecosystem function, uncertainties still remain (Hooper et al., 2005; Díaz et al., 2007). For instance, the mass ratio and stand structural complexity also strongly influence ecosystem function (Chiang et al., 2016; Prado-Junior et al., 2016). The mass ratio hypothesis suggests that aboveground biomass or productivity is strongly driven by the functional identity or composition of the most dominant species or traits (Grime, 1998), which can be quantified in term of community-weighted mean (CWM) of a trait values (Garnier et al., 2004; Díaz et al., 2007; Finegan et al., 2015). By evaluating the mass ratio effect, we have previously reported that high aboveground biomass was markedly determined by the functional identity of overstorey tree height on nutrient-rich soils, whereas by understorey conservative traits on nutrient-poor soils (Ali and Yan, 2017b). Besides the mass ratio effect, stand structural complexity, quantified in terms of individual tree size inequality and species diversity, is also important for determining ecosystem function because it reflects the capability of resource acquisition and utilization among component species and interacting individuals in natural forests (Fotis et al., 2017). Consequently, aboveground biomass increases with stand structural complexity in overstorey stratum but not in understorey stratum in a subtropical forest (Ali and Yan, 2017a). In sum, the niche complementarity and mass ratio effects, based on functional traits, on aboveground biomass or productivity are not necessarily mutually exclusive in natural forests (Conti and Díaz, 2013; Chiang et al., 2016; Prado-Junior et al., 2016). In this context, considering the confounding effects of mass ratio and stand structural complexity on ecosystem function may clarify the role of niche complementarity played for driving the relationships between functional trait diversity and aboveground biomass across forest strata. In addition, studies in (sub-) tropical forests also show that environmental factors such as topography and soil nutrients may modulate the multivariate relationships between functional trait diversity and ecosystem functions (Chiang et al., 2016; Prado-Junior et al., 2016; Ali and Yan, 2017b).

In this study, we were particularly interested to explore whether the functional (multivariate) trait diversity of overstorey and understorey strata have differential effects on the whole-community aboveground biomass while accounting for the effects of local environmental conditions. Using forest inventory, functional traits and environmental factors datasets across 125 plots in a 5-ha natural subtropical forest in Eastern China, we addressed the following three main questions with associated hypotheses or predictions. (1) How does functional trait diversity of overstorey and understorey strata, alone or jointly, affect whole-community (overstorey plus understorey strata) aboveground biomass (hereafter simply referred to 'aboveground biomass')? We hypothesize that high functional trait diversity of understorey stratum due to the niche complementarity (H_{1a}), while low functional trait diversity of overstorey stratum due to the presence of few large trees or niche overlap (H_{1b}) drives high aboveground biomass in a community (Fig. 1). In comparison, we hypothesize (H_2) that low functional trait diversity of whole-community drives high aboveground biomass in a community due to the dominant role of functionally-similar large trees