



# Abiotic and biotic determinants of coarse woody productivity in temperate mixed forests

Zuoqiang Yuan <sup>a,1</sup>, Arshad Ali <sup>b</sup>, Shaopeng Wang <sup>c</sup>, Antonio Gazol <sup>d</sup>, Robert Freckleton <sup>e</sup>, Xugao Wang <sup>a</sup>, Fei Lin <sup>a</sup>, Ji Ye <sup>a</sup>, Li Zhou <sup>a</sup>, Zhanqing Hao <sup>a,\*</sup>, Michel Loreau <sup>f</sup>

<sup>a</sup> CAS Key Laboratory of Forest Ecology and Management, Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang 110164, PR China

<sup>b</sup> Spatial Ecology Lab, School of Life Science, South China Normal University, Guangzhou 510631, Guangdong, China

<sup>c</sup> Department of Ecology, College of Urban and Environmental Science, and Key Laboratory for Earth Surface Processes of the Ministry of Education, Peking University, 100871 Beijing, China

<sup>d</sup> Instituto Pirenaico de Ecología, IPE-CSIC, Avenida Montañana 1005, 50010 Zaragoza, Spain

<sup>e</sup> Department of Animal and Plant Sciences, University of Sheffield, Alfred Denny Building, Sheffield S10 2TN, United Kingdom

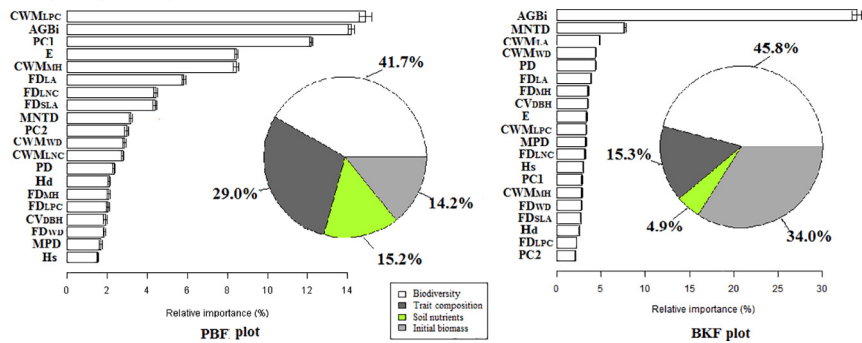
<sup>f</sup> Centre for Biodiversity Theory and Modelling, Theoretical and Experimental Ecology Station, CNRS and Paul Sabatier University, 09200 Moulis, France

## HIGHLIGHTS

- Vegetation quantity outperforms vegetation quality among biotic factors for driving productivity.
- Productivity markedly increased with functional composition in secondary forest.
- In old growth forest, productivity greatly increased with initial stand biomass.
- Soil nutrients enhanced productivity in secondary forest but not in old growth forest.
- The effects of vegetation quantity and quality on productivity increased over succession.

## GRAPHICAL ABSTRACT

Relative importance of different predictors on coarse woody productivity (CWP) in secondary (PBF plot) and old growth forest (BKF plot) using the boosted regression tree analysis. Pie charts show the summed relative influences of biodiversity indices, trait composition, soil nutrients, stand structure, initial stand biomass and first two principal component axes (PC) of soil nutrients variables.



## ARTICLE INFO

### Article history:

Received 12 December 2017

Received in revised form 8 February 2018

Accepted 11 February 2018

Available online xxxx

Editor: Elena Paolletti

### Keywords:

Functional traits

Mass ratio

Niche complementarity

Soil nutrients

## ABSTRACT

Forests play an important role in regulating the global carbon cycle. Yet, how abiotic (i.e. soil nutrients) and biotic (i.e. tree diversity, stand structure and initial biomass) factors simultaneously contribute to aboveground biomass (coarse woody) productivity, and how the relative importance of these factors changes over succession remain poorly studied. Coarse woody productivity (CWP) was estimated as the annual aboveground biomass gain of stems using 10-year census data in old growth and secondary forests (25-ha and 4.8-ha, respectively) in north-east China. Boosted regression tree (BRT) model was used to evaluate the relative contribution of multiple metrics of tree diversity (taxonomic, functional and phylogenetic diversity and trait composition as well as stand structure attributes), stand initial biomass and soil nutrients on productivity in the studied forests. Our results showed that community-weighted mean of leaf phosphorus content, initial stand biomass and soil nutrients were the three most important individual predictors for CWP in secondary forest. Instead, initial stand biomass, rather than diversity and functional trait composition (vegetation quality) was the most parsimonious predictor of CWP in old growth forest. By comparing the results from secondary and old growth forest, the summed relative

\* Corresponding author.

E-mail address: [hzzq@iae.ac.cn](mailto:hzzq@iae.ac.cn) (Z. Hao).

<sup>1</sup> ZY & ZH conceived the ideas and approach. YZ & ZH designed the experiments. ZY, FL, XW, JY, LZ & ZH collected the data. ZY analyzed the data and led the writing of the manuscript, and other authors contributed critically to the draft and gave final approval for publication.

Succession  
Vegetation quantity

contribution of trait composition and soil nutrients on productivity decreased as those of diversity indices and initial biomass increased, suggesting the stronger effect of diversity and vegetation quantity over time. Vegetation quantity, rather than diversity and soil nutrients, is the main driver of forest productivity in temperate mixed forest. Our results imply that diversity effect for productivity in natural forests may not be so important as often suggested, at least not during the later stage of forest succession. This finding suggests that as a change of the importance of different drivers of productivity, the environmentally driven filtering decreases and competitively driven niche differentiation increases with forest succession.

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## 1. Introduction

Forests play a critical role in regulating the global carbon cycle and contain approximately two thirds of terrestrial diversity (Luyssaert et al., 2008; Chapin et al., 2013). Improved understanding of the patterns and drivers of aboveground biomass productivity in natural forests is important for setting climate change mitigation strategies and predicting the consequences of biodiversity loss caused by anthropogenic activities (Violle et al., 2014). Previous studies have revealed that higher diversity can enhance the productivity of ecological systems (Loreau et al., 2001; Tilman et al., 2014), including forests (Scherer-Lorenzen, 2014). Yet, few studies have simultaneously assessed the relative influence of abiotic (i.e. soil nutrients) and biotic (i.e. diversity including stand structure and initial biomass) factors on ecosystem function such as aboveground biomass productivity in natural forests (Fotis et al., 2018; Sande et al., 2017).

There is an interesting and lasting debate on which metrics of diversity (i.e. biotic factors) is actually relevant to aboveground biomass productivity and how it should be quantified (Díaz et al., 2007; Paquette and Messier, 2011; Ouyang et al., 2016). Species richness, the simplest measure of taxonomic diversity, has commonly been used as a biotic predictor for aboveground biomass productivity, which however explains only a small fraction of variation (Zhang et al., 2012; Ruiz-Benito et al., 2014). Recent trait-based approaches suggested that functional trait diversity represents a more mechanistic approach for explaining variation in ecosystem function compared to species richness (Petchey and Gaston, 2006; Gazol and Camarero, 2016). By measuring distances between species in the trait spaces, communities with higher functional trait diversity suggest greater niche differentiation (Laliberté and Legendre, 2010). In addition, the evolutionary history of species within a community can be a good proxy for functional trait diversity under the assumption that longer evolutionary distances are due to functionally dissimilar species, and vice versa (Cadotte et al., 2008; Paquette and Messier, 2011). However, recent studies showed that phylogenetic diversity is not always a better predictor for aboveground biomass productivity than species richness or functional trait diversity (Venail et al., 2015; Toigo et al., 2017).

Two main mechanisms are proposed to explain how plant functional traits can affect ecosystem functions: the niche complementarity hypothesis (Tilman et al., 1997) and the mass ratio hypothesis (Grime, 1998). The niche complementarity hypothesis suggests that higher number of species and variety of functional traits enhance resource-use efficiency and thereby promote ecosystem functions (Tilman et al., 1997; Loreau and Hector, 2001; Díaz et al., 2007). The mass ratio hypothesis postulates that ecosystem function is mainly determined by the traits of the dominant species (Grime, 1998), which can be quantified by functional trait composition measured through community-weighted mean (CWM) of a trait values (Tobner et al., 2016; Ali et al., 2017). Trait values that intensify resource conservation (i.e. high CWM of wood density) are expected to be associated with low aboveground biomass productivity, whereas trait values that intensify resource acquisition (i.e. high CWM of leaf nutrients) are expected to be related with high aboveground biomass productivity (Garnier et al., 2004; Poorter et al., 2008; Reich, 2014).

To date, most of the previous studies have supported the mass ratio hypothesis rather than the niche complementarity hypothesis when evaluating the influences of functional trait diversity and composition on aboveground biomass productivity in forests (Conti et al., 2013; Finegan et al., 2015; Prado-Junior et al., 2016; Fotis et al., 2018). Besides taxonomic, functional trait and phylogenetic diversity indices, several other abiotic and biotic factors have also been recognized to influence aboveground productivity in forests, e.g., initial biomass, tree size diversity and inequality, soil nutrients, and stand age (Lohbeck et al., 2015; Ali et al., 2016; Yuan et al., 2016b; Ali et al., 2017). For instance, a recent study has reported that soil factors drive aboveground biomass productivity whereas the niche complementarity and mass ratio mechanisms have negligible importance in natural forests (Sande et al., 2017). The soil fertility hypothesis predicts that plant can grow faster under high availability of soil nutrients resulting in high aboveground biomass productivity (Quesada et al., 2012), but it may also promote competition, leading to higher mortality and turnover rates (Malhi et al., 2006).

Besides the roles of soil fertility and diversity, initial aboveground biomass of a stand has been found to be the key driver of productivity in forests. This suggests that vegetation quantity (i.e. initial biomass) rather than quality (i.e. diversity) plays an important role in driving ecosystem functions (Lohbeck et al., 2015). In addition, stand structure attributes (i.e. tree size diversity and individual tree size inequality) enhance aboveground biomass due to the niche complementarity effect (Zhang and Chen, 2015; Ali et al., 2016), which progressively leads to great site resource utilization by allowing trees to utilize resources more efficiently such as light and soil nutrients (Hardiman et al., 2013). As the metabolic scaling theory prediction, the biomass accumulation rate of plant should increase with tree size (Enquist et al., 1999), and this assumption has been confirmed by ample empirical studies in forests (Sillett et al., 2010; Stephenson et al., 2014; Sheil et al., 2017). Therefore, stand age is positively related to stand structural diversity, which in turn enhances aboveground carbon storage, biomass or productivity in forests (Zhang and Chen, 2015; Ali et al., 2016).

In addition, it has been hypothesized that the strength of the relationship between diversity and productivity will change over time (Cardinale et al., 2007; Reich et al., 2012; Tobner et al., 2016). Forests across successions are optimal platforms for evaluating the drivers of productivity, probably due to the temporal changes in abiotic factors, trait composition and ecosystem function (Caspersen and Pacala, 2001; Lasky et al., 2014). For instance, some of the previous studies have suggested that forests at early stage are mainly driven by CWM of a trait values (Kröber et al., 2015; Tobner et al., 2016), whereas others reported that abiotic factors (Li et al., 2014) and/or vegetation quantity are the main drivers (Lohbeck et al., 2015). As the forests developing, forest communities will experience gradually shifting in species and trait composition probably caused by changes in biotic interaction and abiotic factors such as soil fertility and light, resulting in the shifts in the relative importance of different drivers over succession (Lohbeck et al., 2014; Sande et al., 2016). For example, the importance of environmental filtering will fade away rapidly (Lohbeck et al., 2014), and the importance of diversity may become stronger as a result of selection for niche differentiations between species in later successional stages (Ratcliffe et al., 2016; Yuan et al., 2016b). Since the dynamic

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