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

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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.

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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 northeast 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

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1 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.

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1. Introduction

Forests play a critical role in regulating the global carbon cycle and contain approximately two thirds of terrestrial biodiversity (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 (Violette 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 (e.g., 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 (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 (Laliberté and Legendre, 2010), 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).

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; Li 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 fades away rapidly (Lohbeck et al., 2014), and the importance of diversity may became stronger as a result of selection for niche differentiations between species in later successional stages (Raichiffe et al., 2016; Yuan et al., 2016b).
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