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

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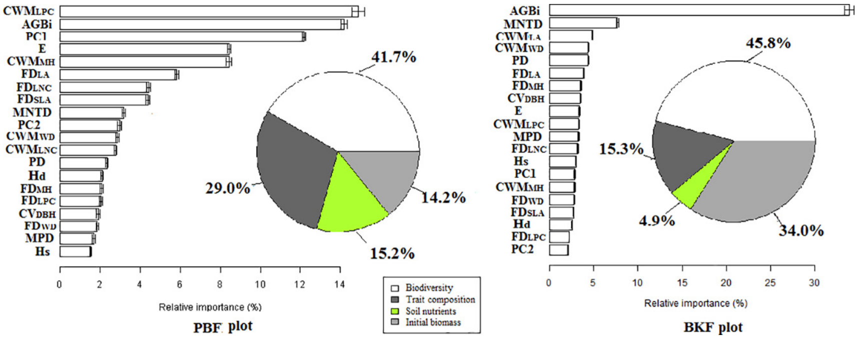
HIGHLIGHTS

- 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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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 divers of productivity, the environmentally driven filtering decreases and competitively driven niche differentiation increases with forest succession.

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; Toïgo 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 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 (Ratcliffe et al., 2016; Yuan et al., 2016b). Since the dynamic successional context is helpful for evaluating the diversity-productivity relationships in a given ecosystem (Lasky et al., 2014), more empirical studies are needed to better understand the relative importance of abiotic and biotic factors on productivity across successional natural forests (Chapin et al., 2013; Lasky et al., 2014; Ali et al., 2017).

We have previously reported that the taxonomic, phylogenetic, and functional diversity have differential effects on aboveground biomass and coarse woody productivity in temperate forests over succession (Yuan et al., 2016b). In order to contribute further to the knowledge of diversity – ecosystem function in temperate forests, we investigated the relative importance of biotic (i.e. multiple metrics of biodiversity, stand structural attributes and initial biomass) and abiotic (i.e. soil nutrients) factors on aboveground biomass (coarse woody) productivity. Specifically, we asked the following three major questions. 1) Which one is the best single predictor among abiotic and biotic factors for driving aboveground biomass productivity? 2) What are the relative contribution of each group of biotic factors such as multiple metrics of biodiversity (taxonomic, functional, phylogenetic and stand structure attributes), functional trait composition (i.e. CWM of a trait values), initial stand biomass, and abiotic factors such as soil nutrients to explain patterns in aboveground biomass productivity? 3) Whether the relative importance of different abiotic and biotic factors on aboveground biomass productivity change in secondary and old growth forests?

2. Materials and methods

2.1. Study site

This study was conducted at Changbai Mountain Natural Reserve (42°23′N, 128°05′E) in the Jilin Province of northeastern China, which is located at the border between China and North Korea. The Changbai Mountain is the biggest protected temperate forest around the world (Yang and Li, 1985; Hao et al., 2007). The climate of this region is characterized by a temperate continental pattern with warm summers and long, cold winters and. Mean annual temperature is 2.8 °C; mean monthly temperature of the warmest months (July) is 19.6 °C and coldest month (January) is −13.7 °C (Yang and Li, 1985; Hao et al., 2007). The average annual precipitation is 700 mm, most of which falls during June and September; Annual evaporation is 1250.9 mm and annual relative humidity is 72%.

The broad-leaved Korean pine (*Pinus koraiensis*) mixed forest is the dominant vegetation type in this studied area, which is famous for unique stand composition and rich species diversity in temperate forests (Stone, 2006). The dominant species includes *Pinus koraiensis*, *Tilia amurensis* and *Quercus mongolica*. The soils are classified as dark-brown soil according to the FAO soil classification system (Yang and Li, 1985). Parts border of this area had been suffered from human and natural disturbances such as logging, windthrow and variable intensities of human disturbances in the history. The secondary poplar-birch forest in this area resulting from disturbance such as a fire or clear-cutting, and had been protected from anthropogenic disturbance since the establishment of Changbai Mountain Natural Reserve at the beginning of 1960s. *Betula platyphylla* and *Populus davidiana* are the dominate species in poplar-birch forest. The average stand year of broad-leaved Korean pine mixed forest and poplar-birch forest are about 280 and 80 years, respectively (Yang and Li, 1985).

2.2. Data collection and analyses

2.2.1. Estimation of coarse woody productivity

Poplar-birch forest (PBF) and broad-leaved Korean pine mixed forest (BKF) represent secondary and old growth forests, respectively. A total of 120 and 625 contiguous permanent sample plots (20 × 20 m) were established during 2004–2005 in the secondary and old growth forest respectively, which result in 4.8 and 25 ha, respectively. The first forest inventory (i.e. T_0) of old growth and secondary forests was conducted in 2004 and 2005, respectively. During first inventory, all individuals with stem diameter at breast height (DBH) ≥ 1 cm were measured, mapped and identified to species level, by following a standard field protocol (Hao et al., 2007). The first inventory showed that there were 20,101 individuals in secondary forest, belonging to 44 species, 28 genera and 16 families, whereas 59,138 individuals in old growth forest, belonging to 52 species, 32 genera and 18 families. Comparison of variables between secondary and old growth forests is provided in Table 1. Overall, there were 39 common species between secondary and old growth forests (Table S1 in Appendix). Second (T_1, 2009 and 2010) and third (T_2, 2014 and 2015) forest inventories were correspondingly conducted after five years of the first and second forest inventory (T_0) in old growth and secondary forests. During the second and third forest inventories, all individuals were re-measured and the status of the trees (growth, mortality and recruitment) were recorded for the accurate estimation of coarse woody productivity (Yuan et al., 2016a). This work is guided on the "Observation Methodology for Long term Forest Ecosystem Research" of National Standards of the People's Republic of China (GB/T 33027-2016).

Aboveground biomass for each individual tree was calculated using published allometric regression equations based on tree DBH (cm) only, which were mainly developed based on the sites around the core of Changbai Mountain Natural Reserve (Chen and Zhu, 1989; Wang, 2006; Li et al., 2010). Initial stand biomass (AGB_i) within each 20 m × 20 m subplot was calculated from the first inventory. Based on the estimation of aboveground biomass stock during the two inventories (i.e., T_0 and T_2), we computed the coarse woody productivity (CWP; Mg ha^{-1} yr^{-1}) as follows (Eq. (1)):

$$\mathrm{CWP} = \frac{(\mathrm{G} + \mathrm{R})}{10} \tag{1}$$

where CWP represents the annual aboveground biomass increment between 2004 and 2014 (for old growth forests), and 2005 and 2015 (for secondary forest); G represents yearly growth in aboveground of survivors between two successive inventories (i.e. 10 years in current study); and R represents yearly recruitment of the individuals that were present in the minimal diameter (1 cm) class between the first and second inventories.

2.2.2. Quantification of biotic factors: multiple metrics of biodiversity and stand structural attributes

We calculated three metrics of biodiversity (such as taxonomic, phylogenetic and functional trait diversity), functional trait composition, and two attributes of stand structure including tree DBH diversity (H_d) and tree size inequality (CV_{DBH}) within each 20 m × 20 m subplot of BKF and PBF plots. Taxonomic diversity indices were quantified based on Shannon's species diversity (Hs), tree species richness (S) and Pielou's species evenness (E), using the *vegan* package (Oksanen et al., 2013) in R 3.2.2 (Team, R. D. C. 2015).

Phylogenetic diversity indices were computed using the informatics tool Phylomatic (http://www.phylodiversity.net), which can provide updated time-calibrated branch length of seed plants using multi-gene molecular and fossil data (Zanne et al., 2014). From these phylogenies, we then obtained several measures of phylogenetic diversity including Faith's phylogenetic diversity (PD_F), the sum lengths of all phylogenetic branches in a local community (Faith, 1992), the mean pairwise phylogenetic distance (MPD) and mean nearest taxon distance (MNTD) between a given group of species (Webb et al., 2008). Phylogenetic diversity indices were computed using the *picante* package in R 3.2.2 (Kembel et al., 2010).

Functional trait diversity indices were computed based on six functional traits which were closely related to plant life-history strategies and aboveground biomass or productivity (Petchey and Gaston, 2006; Conti et al., 2013), i.e., maximum tree height (MH), wood density (WD), leaf phosphorus content (LPC), leaf nitrogen content (LNC),

Table 1

Descriptive statistics of coarse woody productivity, biotic and abiotic factors in secondary (PBF plot) and old growth forest (BKF plot).

	Variables	Unit	Secondary No. samples: 120		Old growth No. samples: 625	
			Mean	Range	Mean	Range
	Coarse woody productivity (CWP)	Mg ha^{-1} y^{-1}	4.40b*	2.40–7.56	2.71a	0.15–13.6
Biotic factors						
Vegetation quantity	Initial AGB (AGBi)	Mg ha^{-1}	153.4a	76–225.8	269.9b	37.6–617.5
	Species richness (S)	No. of species	18.0b	11–24	11.5a	5–19
Niche complementarity hypothesis (Biodiversity indices)	Shannon-Weaver index (Hs)	Unitless	2.41b	1.93–2.76	1.99a	1.24–2.54
	Pielou's evenness (E)	Unitless	0.84a	0.68–0.94	0.82a	0.60–0.97
	Faith's phylogenetic diversity (PD_F)	Unitless	1659.7b	1072.3–2074.4	1435.3a	793.5–1967.1
	Mean pairwise phylogenetic distance (MPD)	Unitless	316.1 a	220.3–401.3	294.2 b	178.6–393.7
	Mean nearest taxon phylogenetic distance (MNTD)	Unitless	198.9 a	149.9–254.5	174.5 b	91.2–253.1
	Functional dispersion diversity based on six traits combined (FDcom)	Unitless	1.63b	1.10–2.13	1.26a	0.08–0.21
	Functional dispersion diversity based on maximum height (FD_{MH})	Unitless	0.59a	0.38–0.87	0.84b	0.40–1.15
	Functional dispersion diversity based on wood density (FD_{WD})	Unitless	0.46a	0.24–0.63	0.65b	0.27–1.02
	Functional dispersion diversity based on leaf nitrogen content (FD_{LNC})	Unitless	0.66b	0.29–1.09	0.39a	0.15–0.75
	Functional dispersion diversity based on leaf phosphorus content (FD_{LPC})	Unitless	0.39a	0.26–0.62	0.42b	0.14–1.07
	Functional dispersion diversity based on specific leaf area (FD_{SLA})	Unitless	0.52a	0.31–0.86	0.52a	0.13–0.99
	Functional dispersion diversity based on leaf area (FD_{LA})	Unitless	0.71b	0.32–1.10	0.53a	0.17–0.88
	Stand structure diversity (H_d)	Unitless	1.03#b	0.52–1.36	0.86#a	0.29–1.54
	Coefficient variation of diameter breast height (CV_{DBH})	Unitless	1.04a	0.74–1.45	1.71b	1.04–2.48
Mass ratio hypothesis (Trait composition)	CWM of tree maximum height (CWM_{MH})	m	20.4a	12.7–25.3	26.7b	18.9–30.8
	CWM of wood density (CWM_{WD})	(g cm^{-3})	0.52b	0.49–0.55	0.49a	0.41–0.61
	CWM of leaf phosphorus content (CWM_{LPC})	(%)	1.79a	1.65–1.91	1.73a	1.48–1.93
	CWM of leaf nitrogen content (CWM_{LNC})	(%)	2.26b	2.07–2.46	2.00a	1.63–2.33
	CWM of specific leaf area (CWM_{SLA})	(cm^2 g^{-1})	247.2b	195.5–326.5	195.2a	131.8–247.5
	CWM of leaf area (CWM_{LA})	(cm^2)	42.9b	23.8–65.2	31.0a	14.5–49.7
Abiotic factors						
Soil physicochemical properties	Water content	%	48.6b	34.8–63.3	40.0a	13.1–60.4
	pH value	Unitless	5.40a	4.88–5.79	5.45a	4.48–6.89
	Organic matter	g kg^{-1}	200.6b	110.8–372.3	162.9a	62.6–431.7
	Available nitrogen	mg kg^{-1}	–	–	502.4	282.2–753.9
	Available phosphorus	mg kg^{-1}	–	–	8.5	3.2–24.4
	Available potassium	mg kg^{-1}	–	–	258.6	102.6–407.3
	Total nitrogen	g kg^{-1}	7.1b	2.4–12.4	6.4a	2.5–12.4
	Total phosphorus	g kg^{-1}	1.1a	0.5–2.2	1.3b	0.6–2.5
	Total potassium	g kg^{-1}	13.8a	10.1–16.6	16.5b	6.8–21.2

* Different letters indicate significant differences (Kruskal-Wallis test, $P < 0.05$) between two forests; # Hd was obtained based on 6 cm DBH class; – indicates missing data for corresponding variables.

specific leaf area (SLA) and leaf area (LA). The detailed measurement method for these mentioned traits is descripted by Yuan et al. (2016b). We used functional dispersion (FDis) index, which quantifies multivariate dispersion in species' functional traits by integrating information on species' relative abundances (Laliberté and Legendre, 2010). Here, we computed FDis based on the multivariate-trait space (FD_{com}) and single-trait (FD_{MH}, FD_{WD}, FD_{LPC}, FD_{LNC}, FD_{LA} and FD_{SLA}).

Functional trait composition or identity measured as the community-weighted mean (CWM) of a single trait values was computed as the mean trait value within each subplot (CWM_{MH}, CWM_{WD}, CWM_{LPC}, CWM_{LNC}, CWM_{LA} and CWM_{SLA}), weighted by the species' relative basal area (Garnier et al., 2004). The species' relative basal area was used to weight the traits of species at each subplot because basal area is regarded as a best indicator for plant performance than species' relative abundance (Prado-Junior et al., 2016). Trait values were standardized before the computation of functional trait diversity and CWM indices. All indices were obtained using the *FD* package in R 3.2.2 (Laliberté and Legendre, 2010).

For the quantification of stand structural attributes, we used Shannon-Wiener diversity index based on DBH classes and coefficient of variation of DBH (CV_{DBH}). Shannon-Wiener DBH diversity was calculated based on the proportions of tree DBH classes for a given DBH discrete class within in each 20 m × 20 m subplot. Specifically, tree DBH diversity (Eq. (2)) was calculated by evaluating four different DBH discrete classes (i.e. 2, 4, 6 and 8 cm) by following Ali et al. (2016). Here, we evaluated the bivariate relationship between aboveground biomass productivity and each of tree DBH diversity based on different discrete classes, and selected the discrete class based on lowest AIC (Table S2).

$$Hd = -\sum_{i=1}^{d} p_i \times \ln(p_i) \tag{2}$$

where p_i is the proportion of individuals of *i*th DBH classes while *d* is the number of DBH classes of a given discrete class within each subplot.

The coefficient of variation was used to quantify DBH variation within each subplot as a proxy of individual tree size inequality since the overall DBH variation can represent the extent of the realized niche differentiation through positive interaction (Chu et al., 2009; Zhang and Chen, 2015).

2.2.3. Measurement of abiotic factors: soil physicochemical properties

In order to cover the entire plots and capture fine scale variations in soil nutrients, 967 points in BKF plot and 210 points in PBF plot were sampled respectively using the standard sampling protocol of the 50-ha BCI plot (Barro Colorado Island) soil survey method (John et al., 2007). The detailed description of the soil sampling points is described in a previous study (Yuan et al., 2011). Soil nutrients including soil moisture, pH value, soil carbon content, available nitrogen, available phosphorus, available potassium, total nitrogen, total phosphorus and total potassium were measured. The volumetric soil moisture content (%) of each sample location at a depth of 20 cm was derived using a time domain reflectometer probe in October (Field Scout TDR200, Spectrum Technologies, Inc. Aurora, IL). After the soil samples were air-dried, samples were passed through a 2-mm mesh to remove stones and roots. We measured eight soil nutrients variables by following Lu (1999). Soil pH was determined by means of a Beckman pH meter in 1:1 soil-water. Soil organic carbon was measured by the acidified dichromate ($K_2Cr_2O_7$–H_2SO_4) oxidation method. Total N was analyzed according to the Kjeldahl method. Available N was detected using hydrochloric acid titration method. Total P was measured by molybdate colorimetry, after digestion in H_2SO_4–$HClO_4$. Available P was extracted using the method of Mehlich 1. Total K and available K was analyzed using atomic absorption spectrometry (AAS).

Semivariograms was generated for each of soil variables to evaluate the degree of spatial autocorrelation among sample locations, and suitable spherical models functions were fitted to the semivariograms using geostatistical approach. Then, predicted values of each soil variables for every 20 × 20 m subplot were kriged from the sampled soil points using ordinary (block) kriging. In order to reduce the number of local soil properties and to avoid the strong correlations among them (see Tables S3 & S4 for correlations), we ran a principal component analyses (PCA) using the kriged soil physicochemical data within each 20 m × 20 m subplot. The principal component analysis (PCA) of secondary forest revealed that first axis of PCA (PC1) explained 42.7% of the total variation in the dataset by demonstrating soil fertility gradient from fertile to infertile soils, while second axis of PCA (PC2) explained 20.1% of the variation by showing a trend from low to high total potassium (Table S5). In the old growth forest, PC1 captured two third (67.5%) of the total variation in the dataset by describing a gradient from high organic matter to low, and with less available water capacity. The second axis (PC2) explained 16.5% of the variation by describing a gradient from poor available nutrients to rich available nutrients (i.e. higher available P and K) along with more-acidic sites. In all statistical analyses, we used both axes of PCA for representing soil physicochemical properties.

2.3. Statistical analyses

The difference in productivity, initial stand biomass, diversity including stand structure indices, trait composition, and soil nutrients variables between secondary and old growth forests was tested using one-way analysis of variance (ANOVA) at a significance level of 0.05. Since some variables did meet the assumptions of ANOVA (i.e. homoscedasticity) (Table S6), we applied Kruskal-Wallis test to compare the difference in those variables.

Boosted regression tree (BRT) analysis (Elith et al., 2008) was often used to evaluate the relative importance of abiotic and biotic factors for driving coarse woody productivity of secondary and old growth temperate forests. The biotic factors were multiple metrics of biodiversity (Hs, E, PD_F, FDcom, FD_{MH}, $FD_{WD,}$ FD_{LPC}, FD_{LNC}, FD_{LA} and FD_{SLA}), stand structural attributes (H_d and CV_{DBH}), functional trait composition (CWM_{MH}, $CWM_{WD,}$ CWM_{LPC}, CWM_{LNC}, CWM_{LA} and CWM_{SLA}), and initial aboveground biomass of a stand (AGB_i), and abiotic factors were the first and second axes of the PCA of kriged soil physicochemical data (PC1 and PC2). Here, we opted to use BRT model because it can handle nonlinear relationships, and accommodate autocorrelation and multicollinearity among predictor variables (Elith et al., 2008; Zhang et al., 2012).

Prior to BRT analysis, we removed those predictors (species richness, FD_{com}, CWM_{SLA} and CWM_{LA} in secondary forest, whereas species richness, FD_{com}, CWM_{SLA} and CWM_{LNC} in old growth forest) having strong correlations with other variables (Spearman's $r > 0.80$, $P < 0.001$; Tables S7 and S8). According to the recommended optimal settings for empirical ecological studies (Zhang et al., 2012; Lin et al., 2016), we fitted BRT models using the combinations of the following parameters: learning rates of 0.001, bag fractions of 0.60, and 10-fold cross-validations. To explore potential higher order of interactions and determine suitable tree complexity, we compared alternative models with tree complexity of 1, 2, 3, 4, 5, 6 and 7. We selected the model with a lower tree complexity as the optimal BRT model, if the models with a higher tree complexity did not reduce prediction error considerably (i.e. <5%; Table S8), by following Lin et al. (2016). Since cross-validation results can vary with the bag fraction parameter selection, and hence depend on the randomly selected points for the folds. Therefore, we repeated all of the procedure for each model 99 times to obtain overall mean of the optimal number of trees, the prediction error, R^2 and relative importance of the different predictors (Table S9). Furthermore, we checked for spatial autocorrelation in the residuals of BRT models of coarse woody productivity using Moran's I statistic, and found no strong evidence (Table S10).

Visualization of the fitted functions of BRT models was assessed using partial dependence plots, which demonstrate how the dependent variable is influenced by focal predictor by removing the average influence of all other predictors (i.e. marginal effect of a predictor). The relative importance of predictors was represented as proportions in totaling of 100%, where a higher proportion reflects a greater contribution to the dependent variable (Elith et al., 2008). All the above detailed analyses were conducted based on 625 and 120 subplots (each size of 20 m × 20 m) in old growth forest and secondary forest respectively.

To assess the effect of sample size on the relative contribution of different variables on dependent variable, we additionally run the BRT model on the subset of 120 subplots (equivalent to the sample size of secondary forest) from the total dataset (625 plots) of old growth forest. Since a one-time selection of subplots from the total dataset ignores the impact of sampling fluctuations on prediction performances, we reported the averaged BRT result based on the 49 bootstraps resampling subset datasets. Our results indicated that the small sample size (120 subplots) did not change our conclusion obtained from original dataset (Table S11). The BRT analyses were carried out in *gbm* package, in R 3.2.2, using a normal distribution of dependent variable.

3. Results

3.1. Comparison of response and predictor variables between secondary and old growth forests

The mean CWP of secondary forest was 4.40 Mg ha^{-1} yr^{-1} which was significantly lower than that in old growth forest (2.71 Mg ha^{-1} yr^{-1}; Table 1). Old growth forest had lower values for diversity indices (i.e. S, H_s, PD_F, FD_{LNC} and FD_{LA}) and community-weighted mean of a trait values (i.e. CWM_{WD}, CWM_{LPC}, CWM_{LNC}, CWM_{LA} and CWM_{SLA}), but it had higher functional diversity calculated based on maximum height and wood density, community-weighted mean of maximum height and CV_{DBH} than that of secondary forest. All other predictor variables (E, FD_{LPC} and FD_{SLA}) for CWP had no significant differences between secondary and old growth forests (Table 1).

3.2. The relative contribution of abiotic and biotic factors on productivity in secondary and old growth forests

Overall, the best BRT model explained 60% and 38% of variation in CWP of secondary and old growth, respectively (Table S8). The relative contributions of explanatory variables differ between two different forests (Fig. 1). In the secondary forest, CWM_{LPC} (14.9%), AGBi (14.2%), soil PC1 (12.2%), evenness (8.4%), CWM_{MH} (5.8%) and FD_{LA} (8.4%) were the six most important individual predictors for CWP (Fig. 1), each of them accounted for at least 5% of the explained variation. In the old growth forest, AGBi was the most parsimonious predictor which explained 34.0% of the variation in CWP, followed by MNTD (7.7%), CWM_{LA} (4.8%), CWM_{WD} (4.4%) and PD (4.3%) (Fig. 1).

Compared to the secondary forest, the averaged relative contribution of diversity and initial stand aboveground biomass (AGBi) was higher in old growth forest, whereas functional trait composition and soil nutrients had lower contribution to CWP (Fig. 1). The relative contribution of multiple metrics of biodiversity, functional trait composition (CWM of a trait values), soil nutrients, and AGBi on CWP in the secondary forest was 41.7%, 29.0%, 15.2% and 14.2%, respectively, while these variables contributed for 45.8%, 15.3%, 4.9% and 34.0% of the explained variation in the old growth forest, respectively (Fig. 1).

3.3. Marginal effects of abiotic and biotic factors on productivity in secondary and old growth forests

In the secondary forest, CWP markedly increased with CWM_{LPC} between 1.73 and 1.85 g cm^{-3} and increased with AGB_i between 100 and 180 Mg ha^{-1}, while CWP decreased with soil PC1 and CWM_{MH} (between 17.8 and 23 m). CWP dramatically increased with species evenness between 0.81 and 0.87, while decreased with CWM_{MH} from 18 to 23 m. CWP had a moderate positive relationship with each of the FD_{LA}, FD_{SLA} and CWM_{LNC}, while weak negative relationship with FD_{LNC} (Fig. 2).

In the old growth forest, CWP greatly increased with AGB_i from 100 to 450 Mg ha^{-1}, then plateaued with $AGB_i > 450$ Mg ha^{-1} but no effect when $AGB_i < 100$ Mg ha^{-1}. CWP had moderate positive relationship with each of the MNTD, CWM_{LA}, CWM_{WD} and PD, while weak negative relationship with each of the species evenness, FD_{LA}, FD_{MH} and CV_{DBH} (Fig. 3).

4. Discussion

We assessed the relative contributions of taxonomic, functional, phylogenetic and stand structural attributes, initial biomass, and soil nutrients on aboveground biomass productivity in two temperate mixed forests that vary in stand development. We found that CWM of leaf phosphorus content, initial stand biomass, soil organic matter and species evenness were important for explaining the patterns of productivity in secondary forest. Instead, productivity in old growth forest was mainly driven by initial stand biomass. These results concur with previous findings indicating that vegetation quantity (i.e. stand biomass) rather than vegetation quality (i.e. functional diversity and community-weighted mean of a trait values) is a major factor determining productivity in old growth forests (Lohbeck et al., 2015).

4.1. Vegetation quantity outperforms vegetation quality for driving productivity

The positive relationship between initial stand biomass and forest productivity was consistent with previous studies showing that the effect of basal area on productivity was greater than that of other predictors (Paquette and Messier, 2011; Vilà et al., 2013; Lohbeck et al., 2015). It is theoretically plausible that as trees grow and accumulate more biomass in secondary forest, the mean size of the individuals in a community also increases. This result might be attributable to the increasing rate of aboveground biomass in a positive relation to the individual tree size in a community (Stephenson et al., 2014; Ali and Yan, 2017a). In addition, our analysis showed that the sharp positive relationship between initial stand biomass and productivity becomes plateaued (Fig. 3) when subplot containing highest biomass resulting from a negative density-dependent effect of aboveground biomass (Finegan et al., 2015). This result is in accord with a recent study which reported that over 70% of coarse woody productivity was attributed to the increases in biomass of medium size trees (i.e. 30–70 cm DBH) in old growth forest (Yuan et al., 2016a). Other studies suggested that dense forests exhibited a higher turnover rate and lower biomass recruitment probably due to the light limitation and hence stronger resource competition in a closed-canopy forests (Prado-Junior et al., 2016), resulting in negligible or negative relationships between aboveground biomass productivity and initial standing biomass (Peña-Claros et al., 2008).

Although initial biomass outperforms diversity as a predictor of productivity when considered in isolation, it is worth to note that vegetation quantity (i.e. initial biomass), in turn, can be affected by quality (i.e. diversity and functional trait composition), as reported by many previous studies (Conti et al., 2013; Lin et al., 2016). Biomass and productivity are the two different types of ecosystem functions (stock and rate, respectively), they may respond differently to abiotic and biotic factors (Schmid et al., 2009). Consequently, forest biomass and productivity are often decoupled, i.e. slowing growing forests (i.e. old growth forest in this study) commonly have higher biomass storage capacity than fast growing forests (i.e. secondary forest) (Caspersen and Pacala, 2001).

4.2. Soil nutrients enhanced productivity in secondary forest but not in old growth forest

Our finding that higher aboveground biomass productivity was found on nutrient-rich soils in secondary forests is in accord with the general notion that soil nutrient availability is the key limiting driver for recruitment and growth of small trees (Chase and Leibold, 2003).

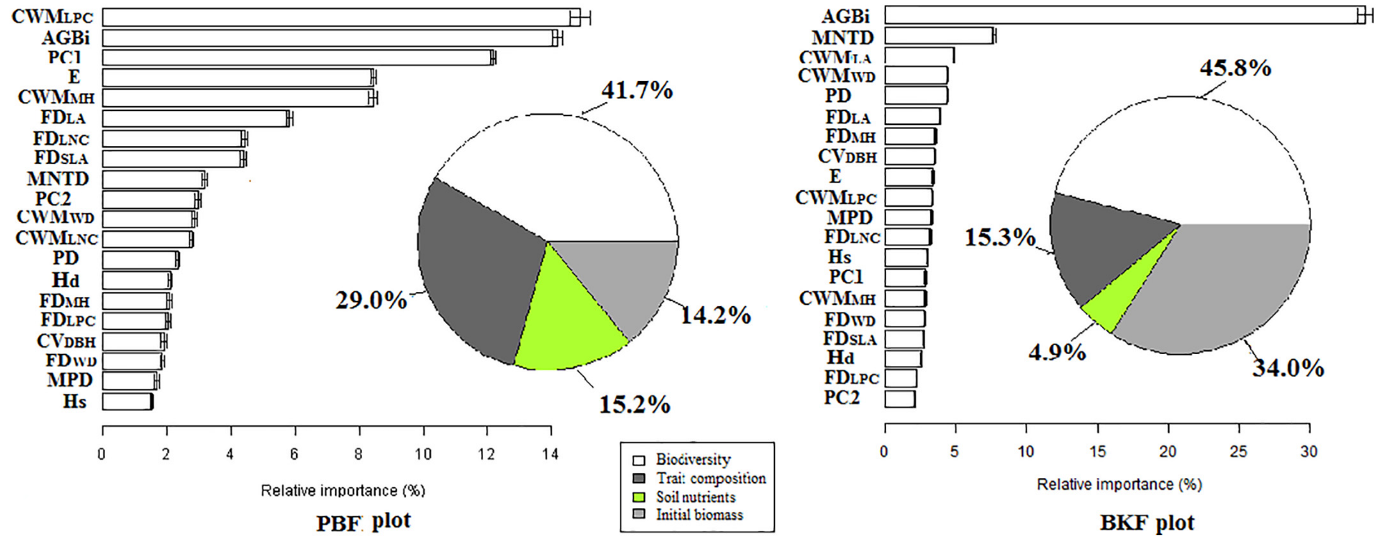

Fig. 1. Relative contribution of different predictors on coarse woody productivity (CWP) in secondary (PBF plot) and old growth forest (BKF plot) using the boosted regression tree analysis. Error bars show 95% confidence intervals obtained from 1000 bootstrap samples of the original dataset ($n = 99$). Pie charts show the summed relative influences of biodiversity indices, trait composition, soil nutrients, stand structure, initial biomass stock, and first two principal component axes (PC) of soil physicochemical (nutrients) variables. Abbreviation and unit for each given variable is explained in Table 1.

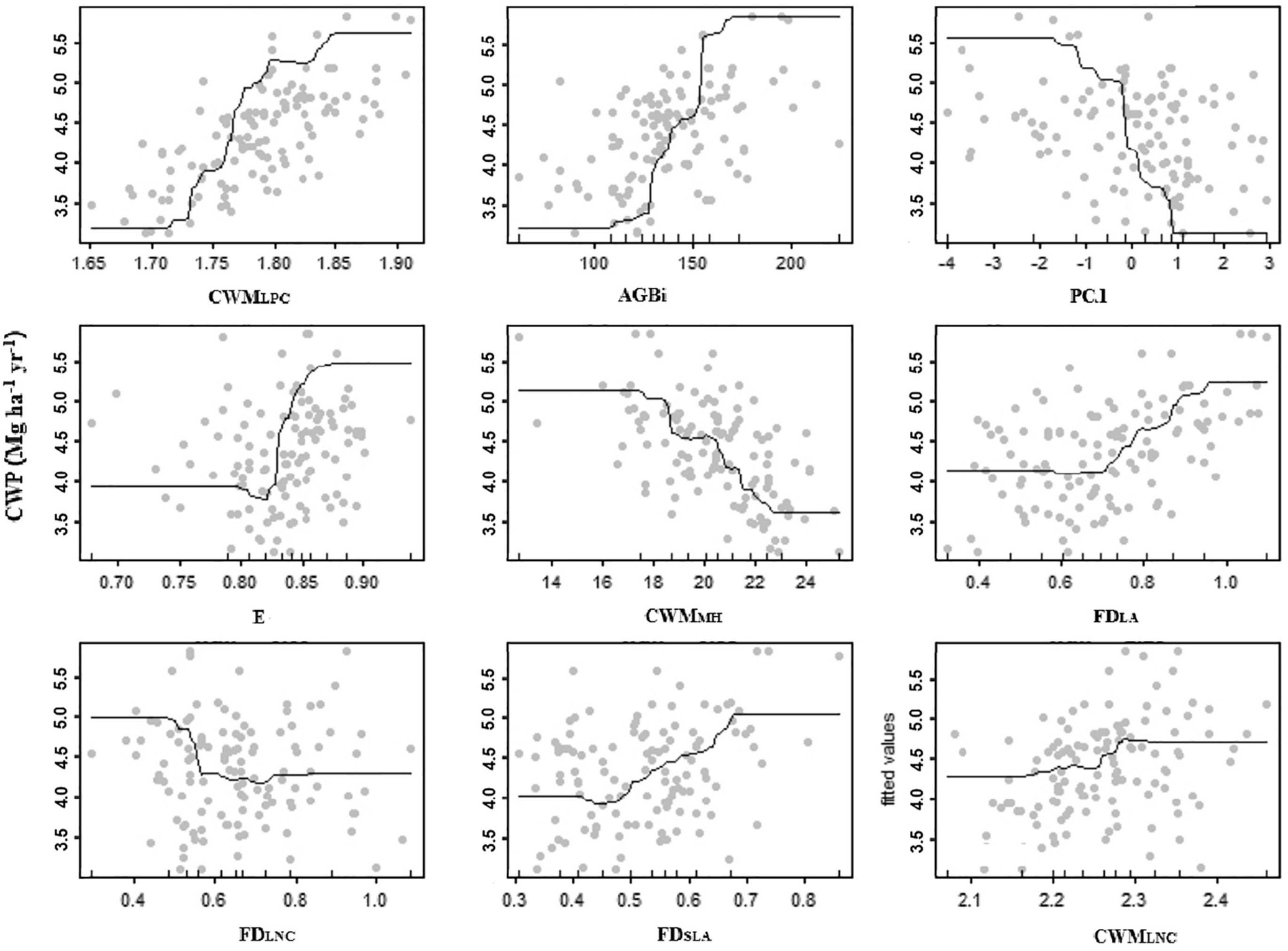

Fig. 2. Partial dependence plots showing the marginal relationship between coarse woody productivity and each predictor while accounting for the average effects of the other predictors in boosted regression tree analysis in secondary forest (PBF plot). Background points show the observed values for the subplots. Only the marked relationships are showed here (Fig. S1 for more details). Variable abbreviations are given in Table 1.

Previous studies have demonstrated that the impact of nutrient addition is positive in temperate forests (de Vries et al., 2009), and limited additions of key soil elements could lead to doubled stem growth rates for small individuals, though no significant effect on large individuals (Alvarez-Clare et al., 2013). In contrast, soil nutrients had a negligible effect on productivity in old growth forests where large trees are common in the stands, supporting the idea that other abiotic factors such as light availability or water may be the limiting factors for the growth of larger trees (Jucker et al., 2014). For example, competition for light in forest ecosystems is often regarded as the limiting process, and is often characterized by strong asymmetry since bigger individuals monopolize much light than proportionally to their size (i.e. volume, or mass) by comparing with small individuals (Pretzsch, 2014; Ali and Yan, 2017b). In addition, large trees are acquisitive in nature and also have a higher evaporative requirement and might be depended on deep groundwater especially in the dry season (Nepstad et al., 1994). In addition, it is also reasonable that the growth of large trees in canopy was most strongly influenced by their sapwood area relating with water transporting, suggesting that big trees can be strongly limited by water availability (van der Sande et al., 2015).

4.3. What mechanism – mass ratio or niche complementarity hypothesis – best explains productivity?

Understanding how ecosystem function relates to biodiversity in natural ecosystems is critical for predicting the consequences of biodiversity loss and for designing conservation strategies. Our analysis revealed that mass-ratio related variable, CWM of leaf phosphorus content, was the best predictor for productivity as compared with taxonomic, phylogenetic, functional trait diversity and stand structure attributes in secondary forest. This result agrees with the idea that mass ratio effect plays a critical role in ecosystem functions in young or secondary forests (Conti et al., 2013; Lin et al., 2016; Tobner et al., 2016). The positive CWM and productivity relationship suggested that secondary forest dominated by fast-growing acquisitive species (low maximum height and high leaf phosphorous) with high photosynthetic rates and hydraulic conductivity would have high biomass growth rates. It has been suggested that a few key traits that reflect the leaf economics spectrum (Reich, 2014), such as leaf nutrients content or specific leaf area, can successfully predict young forest growth (Kröber et al., 2015). One possible explanation for stronger mass ratio effect in secondary forest is that, species experience strong habitat filtering, and the selection for specific functional traits is important (Sande et al., 2016).

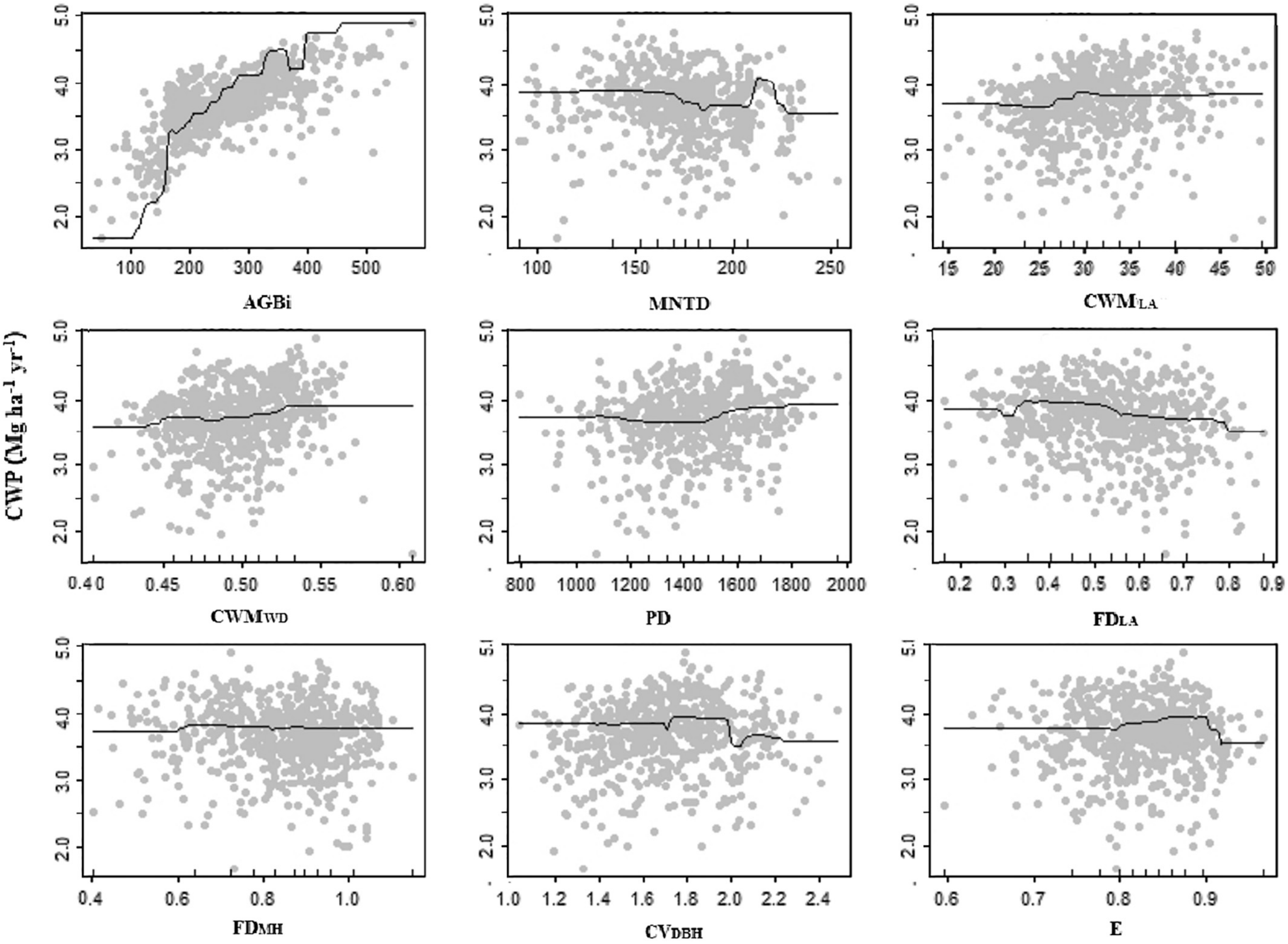

Fig. 3. Partial dependence plots showing the marginal relationship between coarse woody productivity and each predictor while accounting for the average effects of the other predictors in boosted regression tree analysis in old growth forest (BKF plot). Background points show the observed values for the subplots. Only the marked relationships are showed here (Fig. S2 for more details). Variable abbreviations are given in Table 1.

These species, mainly pioneer species, often invest resources for rapid resource acquisition and grow quickly, especially in favorable environment, but then decreased in a deteriorating conditions less investment in physical defense as forest develops (Reich, 2014).

Because trait-based approaches can be biased by the researchers' knowledge on which traits regulate forest ecosystem functioning and the number of traits that can be measured (Shipley et al., 2016), the application of phylogenies can provide a suitable proxy for functional diversity if phylogenetic diversity positively correlates with the diversity of functionally important traits in plant communities (Srivastava et al., 2012). Our analysis showed that MNTD, which reflects the redundancy of closely related species at the branch tips (Kembel et al., 2010), was the best predictor of the effect of diversity on productivity in old growth forests, supporting the idea that evolutionarily diverse communities will result in higher productivity (Cadotte et al., 2008). For example, comparisons of taxonomic and phylogenetic diversity across 79,324 forest plots in the United States indicated that phylogenetic diversity is a more suitable measure of diversity in terms of predicting biomass accumulation (Potter and Woodall, 2014). Paquette et al. (2015) argued that the use of phylogenies can better predict ecosystem functioning in temperate and boreal forests in Canada, where key functional traits are unavailable. Here, we showed that species richness declined in old growth forest compared with secondary forest, whereas some functional diversity and stand structure diversity indices increased indicating that diversity is maintained and productivity is enhanced despite redundant species losses with forest succession.

4.4. Other multiple factors driving productivity in forests

Although many different predictors were considered in our full model, a substantial amount of variation remained unexplained especially in old growth forests, which is typical of tree growth studies (Poorter et al., 2008; Rüger et al., 2012; Kröber et al., 2015). Possible reasons for unexplained variations in productivity might include negative biotic interactions such as herbivores or pathogens, both of which reduce the biomass production measured as differences between standing biomass across time. As such, field studies may generate different conclusions from those of greenhouse trials, which evaluate potential growth rates under the exclusion of trophic interactions and demonstrate stronger effects of functional leaf traits (Böhnke and Bruelheide, 2013). Also, trees biomass allocation to stems, leaves and roots may vary with size and environment (Poorter et al., 2012), and tree allocate resources to the expansion of their root or leaf system may without exhibiting apparent diameter growth (Doughty et al., 2014). Future studies are required across spatial scales in natural and more complex systems, to disentangle the mechanisms of various contexts under various conditions and across a spectrum of species diversity.

5. Conclusion

This study presents, to the best of our knowledge, the first empirical evaluation for the relative contribution of multiple metrics of biodiversity including stand structure, functional trait composition, initial stand biomass (vegetation quantity) and soil nutrients on coarse woody productivity in temperate mixed forests. Our analysis showed that the CWM of leaf phosphorus content was the most important single predictor of productivity in secondary forest, suggesting acquisitive species rather than conservative species were related to higher productivity. In addition, initial stand biomass, soil fertility and species evenness also contributed to the explained variation on productivity in secondary forest. In old growth forests, productivity was mainly driven by initial stand biomass, implying that vegetation quantity is a better predictor for aboveground biomass productivity compared to vegetation quality (i.e. diversity) despite quantity and quality are not fully independent. This result is in accordance with the idea that subtle effects of community functional properties on productivity might be over-ridded by steep biomass buildup over succession. Since coarse woody productivity was simultaneously driven by different components (quantitative and qualitative) of the forest community, future researches on biodiversity and ecosystem function should unravel the influences of vegetation quality (i.e. functional diversity and community-weighted mean of a trait values) from those of vegetation quantity (i.e. initial standing biomass) and/or abiotic factors (i.e. soil nutrients) on ecosystem processes, functions and services.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2018.02.125.

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