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ECOSYSTEM ECOLOGY – ORIGINAL RESEARCH

Multiple metrics of diversity have different effects on temperate forest functioning over succession

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Abstract Biodiversity can be measured by taxonomic, phylogenetic, and functional diversity. How ecosystem functioning depends on these measures of diversity can vary from site to site and depends on successional stage. Here, we measured taxonomic, phylogenetic, and functional diversity, and examined their relationship with biomass in two successional stages of the broad-leaved Korean pine forest in northeastern China. Functional diversity was calculated from six plant traits, and aboveground biomass (AGB) and coarse woody productivity (CWP) were estimated using data from three forest censuses (10 years) in two large fully mapped forest plots (25 and 5 ha). 11 of the 12 regressions between biomass variables (AGB and CWP) and indices of diversity showed significant positive relationships, especially those with phylogenetic diversity. The mean tree diversity-biomass regressions increased from 0.11 in secondary forest to 0.31 in old-growth forest, implying a stronger biodiversity effect in more mature forest. Multi-model selection results showed that models including species richness, phylogenetic diversity, and single functional traits explained more variation in forest biomass than other candidate models. The models with a single functional trait, i.e., leaf area in secondary forest and wood density in mature forest, provided better explanations for forest biomass than models that combined all six functional traits. This finding may reflect different strategies in growth and resource acquisition in secondary and old-growth forests.

Keywords Functional diversity · Phylogenetic diversity · Natural forests · Biomass · Functional trait

Introduction

Biodiversity is a complex multifaceted concept that can be measured by taxonomic, phylogenetic, and functional diversity (Pavoine and Bonsall 2011). During the past decade, ample experimental studies, mostly in grasslands, have revealed the positive influence of biodiversity on ecosystem functioning, but the relative importance of different facets of diversity remains controversial (Cadotte et al. 2008; Paquette and Messier 2011; Cardinale et al. 2015; Cadotte 2015; Venail et al. 2015). Species richness, the simplest measure, is frequently used as the sole measure of diversity in the field of biodiversity and ecosystem functioning (BEF), which alone may be a poor predictor of ecosystem functioning in natural species-rich communities

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(Loreau 1998; Hooper et al. 2005; Paquette and Messier 2011; Ruiz-Jaen and Potvin 2011; Zhang et al. 2012). Many studies have suggested that including information on the evolutionary history and functional traits of species can provide mechanistic links between the composition of the ecological community and ecological functioning from both evolutionary and ecological perspectives (Petchey and Gaston 2002; Paquette and Messier 2011). For example, a meta-analysis of 29 BEF experiments showed that phylogenetic diversity (PD) within communities explained more variation in plant biomass accumulation than taxonomic diversity or functional group richness (Cadotte et al. 2008). This result suggests that longer evolutionary differentiation may generate greater trait variation related to ecological niches and provides evidence for the niche complementarity hypothesis (Cadotte et al. 2008; Flynn et al. 2011; Zuppinger-Dingley et al. 2014). However, recent re-examination of 16 grassland diversity studies showed that phylogenetic diversity was not a better predictor for community biomass than species richness (Cardinale et al. 2015; Venail et al. 2015). Further experiments and analyses, especially in natural ecosystems, are required to clarify whether phylogenetic diversity is more closely linked to ecosystem functioning than other diversity measures.

Several studies underscored the importance of combining different measures of diversity (taxonomic, PD, FD) in predicting BEF relationships (Flynn et al. 2011; Ruiz-Jaen and Potvin 2011; Liu et al. 2015; Lasky et al. 2014; Ruiz-Benito et al. 2014; Cavanaugh et al. 2014). Notably, Flynn et al. (2011) found that PD and FD calculated from leaf nitrogen, mean plant height, and N-fixation had similar abilities to predict biodiversity effects, suggesting that traits related to resource acquisition strategy can drive grassland ecosystem functioning. In another study, Ruiz-Jaen and Potvin (2011) showed that explaining maximum variation of carbon storage in a mixed-species plantation and a natural tropical forest in Panama required the combinations of species richness, FD, species dominance and functional dominance (e.g., community-weighted mean of maximum height) in a mixed-species plantation and a natural tropical forest in Panama. These results indicated that the relative importance of FD, PD, and taxonomic diversity varies from site to site and identifying which metric of diversity is most important in BEF relationships in different regions remains an important task.

Two mutually non-exclusive mechanisms have been proposed as explanations for the positive BEF relationships. Complementarity effects predict that diversity increases the production of biomass through niche complementarity (e.g., complementarity in resource use), which, reduces interspecific competition and increases the occurrence of facilitation (Forrester and Bauhus 2016). In contrast, the selection effect hypothesis highlights the role of dominant species or traits, and posits that the positive BEF relationships result from the enhanced probability for diverse communities to include high biomass species that will become dominant (Loreau 1998; Loreau and Hector 2001). Positive selection effects often occur when average species competitive ability is greater in higher diversity communities (Lasky et al. 2014). Recently, ecologists have emphasized that plant diversity effects on plant productivity get stronger over time (Reich et al. 2012). There is increasing evidence that complementarity effects among species increase over time, whereas selection effects decrease (Cardinale et al. 2007; Reich et al. 2012). Thus, short-term studies can be misleading because they incorrectly indicate the presence of functional redundancy and therefore undervalue biodiversity (Cardinale et al. 2007; Reich et al. 2012).

Forest successional communities are ideal systems for assessing BEF relationships due to natural temporal changes in species composition and ecosystem functioning (Letcher and Chazdon 2009). Both mathematical models and empirical studies suggest that species diversity can have different effects on biomass accumulation over succession (Cardinale et al. 2004; Weis et al. 2007; Lasky et al. 2014). For example, while some studies showed that the effect of biodiversity on ecosystem functioning became stronger over succession (Caldeira et al. 2001; Jonsson 2006), others reported the opposite pattern (Cardinale et al. 2006). Cardinale et al. (2004) used a Lotka–Volterra competition model and predicted that species richness should have no effect on community biomass during early stages of succession. However, in later successional stages, where intra- and interspecific competition operate, several mechanisms can increase community biomass in more diverse communities. Therefore, more empirical studies are required to examine whether and how BEF relationships change across successional stages (Vilà et al. 2003; Morin et al. 2011; Barrufol et al. 2013; Kunstler et al. 2016).

The objective of the present study is to investigate BEF relationships in two natural successional forests. Two large, fully mapped forest plots were established in two successional stages of the broad-leaved Korean pine forest in northeastern China, in which all stems ≥ 1 cm in trunk diameter have been tagged, identified, and measured. The aboveground biomass (AGB) and coarse woody productivity (CWP) were estimated using data from three censuses. Taxonomic diversity, functional diversity calculated from six functional traits (maximum height, wood density, leaf phosphorus content, leaf nitrogen content, leaf area, specific leaf area) and phylogenetic diversity were calculated as different measures of diversity. Specifically, we aimed to answer the following questions:

Table 1 Site, community structure, diversity and biomass characteristics for the two studied forest plots

Variables	Poplar-birch forest (PBF)	Old-growth forest plot (CBS)
Location	42°22′N and 128°00′E	42°23′N and 128°05′E
Established year	2005	2004
First census year	2010	2009
Plot elevation (m)	796.3 (788.5–800.4)	801.5 (791.8–809.5)
Plot size (m)	200 × 250	500 × 500
Canopy species year	~80	~280
Dominant species	*Betula platyphylla* *Populus davidiana*	*Pinus koraiensis* *Tilia amurensis Quercus mongolica*
Soil type	Albi-Boric Argosols	Albi-Boric Argosols
pH* (0–10 cm)	5.41	5.45
Stem density (ha^{-1})	4021.4	2365.5
Total species	50 (28 genera,16 families)	52 (32 genera, 18 families)
Species richness (10 × 10 m)	10.5 ± 2.3 (4–18)	6.2 ± 1.8 (0–13)
Functional diversity (FDis) (10 × 10 m)	1.74 ± 0.33 (0.54–2.69)	1.53 ± 0.32 (0–2.55)
Phylogenetic diversity Faith index (10 × 10 m)	1769.1 ± 300.1 (771.9–2594.9)	1089.2 ± 281.5 (0–1955.1)
AGB stock (Mg ha^{-1})	137.1 ± 56.7 (16.7–332.6)	279.4 ± 186.8 (30.0–970.2)
CWP (Mg $ha^{-1}year^{-1}$)	5.0 ± 3.0 (0.07–20.8)	3.3 ± 3.5 (0–38.9)

* Soil pH value in water (1:1 soil:solution ratio) was determined using a Beckman glass electrod

1. Are phylogenetic diversity and functional diversity better predictors for ecosystem functioning (AGB and productivity) than species richness?
2. Does the combination of multiple metrics of diversity (taxonomic, phylogenetic, and functional) provide the most parsimonious explanation of ecosystem functioning than each alone?
3. Are BEF relationships stronger in later stages of forest succession?

Materials and methods

Study site

The Changbai Mountain Natural Reserve in northeastern China is the largest protected temperate forest in the world (Yang and Li 1985; Hao et al. 2007). This area has a temperate continental climate with long, cold winters and warm summers. Rainfall averages 700 mm $year^{-1}$, most of which occurs from June to September (480–500 mm). Mean annual temperature is 2.8 °C, with a January mean of −13.7 °C, and a July mean of 19.6 °C (Yang and Li 1985). There has been little human disturbance in this area over the last 400 years because Changbai Mountain was protected as the legendary birthplace of the imperial family during the Qing Dynasty, and became a natural reserve at the beginning of 1960s. Broad-leaved Korean pine mixed forest is the most common vegetation type in this area. The poplar-birch forest following a fire or clear-cutting is an important stage in the secondary succession of broad-leaved Korean pine mixed forest (Xu 2001).

Data collection

Plot censuses and aboveground biomass dynamics

A 25-ha (500 m × 500 m) plot was established in the core zone of the broad-leaved Korean pine mixed forest (hereafter BKF plot) in 2004 (Hao et al. 2007; Zhao et al. 2014), and a 5-ha (250 m × 200 m) plot was established in the secondary poplar-birch forest (hereafter PBF plot) in 2005 (Hao et al. 2008). All free-standing woody stems ≥1 cm in trunk diameter were mapped, measured, and identified to species following a standard field protocol (Condit 1998). The diameter at breast height (DBH) of each stem in CBS and PBF plots was recensused every 5 years to accurately reflect the forest dynamic (Yuan et al. 2016). This work was conducted based on Forestry Standards "Observation Methodology for Long-term Forest Ecosystem Research" of the People's Republic of China (LY/T 1952-2011). Overall, 44 plant species were encountered in PBF and 52 species in BKF with 39 common species (Table S1 in Supporting Information). The detailed description of these two successional forest plots is displayed in Table 1.

The AGB of all individual trees in these two plots was estimated using published species-specific allometric regression equations, which were summed for all stems in each 10 × 10 m quadrat to estimate total AGB (Table S2 in

Supporting Information). The chosen quadrat size reflects the scales of individual tree competition. A high proportion of negative associations among species (competitive interaction) can be detected in a radius of <10 m (Wang et al. 2010). Moreover, the small quadrat size helps to control for the effect of habitat heterogeneity (Ruiz-Jaen and Potvin 2011).

Based on the AGB estimates during the three censuses, we calculated the coarse woody productivity (CWP) (Mg ha^{-1} year^{-1}) as follows:

$$\text{CWP} = (G + R)/10 \tag{1}$$

Here, CWP is the yearly growth of total aboveground biomass during 2004–2014 (for BKF) or 2005–2015 (for PBF); G is the annual growth in AGB of trees that were alive during two successive censuses (e.g., 5 years in this study); R is the annual increment of AGB attributable to recruitment into the minimum diameter class between the first and second censuses.

Multivariate biodiversity indices

Taxonomic diversity was calculated as species richness in each quadrat. Based on the recommendations of Pérez-Harguindeguy et al. (2013) and Paquette and Messier (2011), we collected six functional traits (wood density, maximum height, leaf phosphorus content, leaf nitrogen content, leaf area and specific leaf area) to represent major axes of plant functional strategy. Wood density (WD) is a good indicator of whether a species displays fast growth and early reproduction or slow growth and resistance to environmental hazards. Maximum height (H) can serve as a proxy for potential height, which is considered an important indicator of the light capture strategy. Leaf traits reflect the light capture ability and trade-offs between the construction cost and longevity (Wright et al. 2004; Chave et al. 2009). Wood density for each species was collected from more than 10 individuals randomly distributed within or around the plots using cores collected with an increment borer. To estimate the maximum tree height, we first selected the top ten individuals with largest DBH from the dataset, and then measured their tree heights using a laser rangefinder (Laser Technology, Inc). Leaf phosphorus content (LPC), leaf nitrogen content (LNC), leaf area (LA) and specific leaf area (SLA) were collected from more than 10 individuals using undamaged, sun-exposed leaves (Wang et al. 2013). LPC was determined by molybdate colorimetry, after digestion in H_2SO_4–$HClO_4$. LNC was estimated colorimetrically on KCl extracts, using the Kjeldahl method. Leaf area measured as leaf size was estimated using a portable scanning planimeter. We used mean trait values for a species in our analyses.

We computed functional diversity using the Functional dispersion index (FDis) proposed by Laliberté and Legendre (2010). FDis quantifies functional diversity as the mean distance in multidimensional trait space of individual species to the centroid of all species. This index has several desirable properties since it is independent of species richness, the distance of each species to the centroid can be weighted by species relative abundance, and it can be calculated for single or multiple traits (Laliberté and Legendre 2010). Before we calculated FD, we rescaled the trait data to a mean of 0 with a standard deviation of 1 (Cadotte et al. 2009). To gain insight into ecophysiological mechanisms driving BEF relationships, we further calculated functional diversity (FD) indices separately for each single trait (FD_H, FD_wd, FD_lpc, FD_lnc, FD_la and FD_sla) and for the combination of all six traits (FD_com) in each 10 × 10 m quadrat.

A phylogenetic supertree was constructed by inputting all the species found in plots into the plant phylogeny database Phylomatic, an online interface that supplies a phylogeny based on a user-defined set of plant species taxonomic names (http://www.phylodiversity.net) (Webb and Donoghue 2005). Phylomatic utilizes the Angiosperm Phylogeny Group III (APG III 2010) phylogeny as a backbone. This supertree was then assigned branch lengths estimated from multi-gene molecular and fossil data implemented in Phylomatic, which is the largest and most up-to-date time calibrated species-level phylogeny of seed plants (Zanne et al. 2014). We then calculated the Faith's phylogenetic diversity index that quantifies the shared branch lengths of the phylogeny among species in a sample with the root node included in all calculations (Faith 1992a). Faith's phylogenetic diversity index is perhaps the most widely used measure of PD (Paquette and Messier 2011; Lasky et al. 2014; Liu et al. 2015).

In PBF and BKF plots, negative CWP estimates for trees or stems that apparently shrunk were removed from the data set. In total, 2412 10 × 10 m quadrats in the BKF plot and 495 quadrats in the PBF plot were used in data analyses.

Data analyses

All biomass variables (AGB and CWP) were log-transformed prior to analysis. In order to search for the best single-variable models across the three categories of biodiversity (richness, PD, and FD_com), we used linear regressions to evaluate the relationship between a biomass variable and each diversity metric. In the diversity–biomass regressions, we treated biomass as the dependent variable assuming that the causal effects of diversity on AGB and CWP would be stronger than those in the reverse direction due to minimal environmental gradients at this spatial scale. First, we accounted for spatial autocorrelation among quadrats using generalized least-squares models, which is an appropriate method for testing whether quadrats are independent from each other in large forest plots (Chisholm et al. 2013). We fit linear models with and without spherical autocorrelation structure for each diversity–biomass combination to compare the separate models with Akaike Information Criterion (AIC) (Zuur et al. 2009). The goodness-of-fit of these models was assessed by the AIC value and adjusted r^2. Our results showed that models without spherical autocorrelation structures always had the lower AIC values (Table S3 in Supporting Information).

We constructed a series of univariate and multivariate linear models to find the most parsimonious models from three diversity categories: TD, PD, and FD. While there were seven different functional diversity metrics (FD_H, FD_{wd}, FD_{lpc}, FD_{lnc}, FD_{la},FD_{sla} and FD_{com}), we avoided including more than one of these metrics in any one model. Variables that we used in model construction are listed in Table S4 (Supporting Information). These models were compared and ranked following AIC adjusted for small sample sizes (AIC_c) in the “MuMIn” package R software (Barton 2014; *dredge* function of R 3.1.2; http://www.r-project.org). This method compares the explanatory ability of these models using AIC weight, which can assess the probability that a given model is the most appropriate description for the observed data (Burnham and Anderson 2002).

All analyses were performed in R software. PD and FD indices were computed using the packages “picante” (Kembel et al. 2010) and “FD” (Laliberté and Legendre 2010), respectively.

Results

Successional changes in diversity and aboveground biomass

Diversity indices and biomass (AGB and CWP) exhibited considerable spatial variation at both study sites (Table 1). In the early successional forest (PBF plot), species richness per quadrat (100 m^2) ranged from 4 to 18, with a mean of 10.5 species, and AGB ranged from 16.7 to 332.6 Mg ha^{-1}, with a mean of 137.1 Mg ha^{-1} (Table 1). The old-growth forest (BKF plot) had lower richness, with a mean of 6.2 species, ranging from 0 to 13. However, the mean AGB (279.4 Mg ha^{-1}) in the old-growth forest (BKF plot) was more than twice that in the early successional forest (PBF plot, 137.1 Mg ha^{-1}).

BEF relationships

Nearly all the regressions between biomass and indices of diversity showed significant positive BEF relationships (Figs. 1, 2). Species richness was not significantly related to biomass in the PBF plot but exhibited strong positive relationships with biomass in the BKF plot (Fig. 1). FD_{com}, as calculated from six functional traits, was positively related to biomass in both plots. The mean slope of these positive diversity-biomass regressions increased from 0.12 (average of 0.0002, 0.21, 0.02, 0.00023 and 0.39) in the PBF plot to 0.31 (average of 0.16, 0.0018, 0.68, 0.26, 0.0016 and 0.76) in the BKF plot, suggesting enhanced BEF relationships through succession (Figs. 1, 2).

In the multi-model comparative approach, we found that models including single functional traits consistently explained more variation in biomass than those with multivariate functional diversity (FD_{com}) (Tables 2, 3 and Table S4 in Supporting Information). In particular, leaf area was the best predictor of tree productivity in the PBF plot (Table 2), while species richness, PD, and other traits had little additional explanatory power for variance. The combination of species richness, PD, and leaf area represented the most parsimonious model in the PBF plot, accounting for about 9 % of the variance in AGB (Table 2). The model including species richness, PD, and wood density together was the most parsimonious predictor in the BKF plot (wAICc $>$ 0.97), explaining 19 % of the variance in AGB (Table 3).

Discussion

Over the past two decades, BEF studies have mainly been conducted in controlled, small-scale experiments (Tilman et al. 1997; Flynn et al. 2011; Liu et al. 2015; Zuppinger-Dingley et al. 2014). However, whether biodiversity influences ecosystem functioning in natural communities remains a long-standing controversy (Hooper et al. 2005; Ruiz-Jaen and Potvin 2011; Chisholm et al. 2013; Wu et al. 2014). Our findings suggest positive BEF relationships in both secondary and old-growth forest. The positive biodiversity effects on biomass are often attributed to increased complementarity between species in resource use that reduces competition and increases the occurrence of facilitation (Reich et al. 2012). Complementarity among species is expected to be higher in more stable ecosystems (Paquette and Messier 2011), and a meta-analysis of the results of 44 grassland experiments revealed that the impacts of plant diversity on biomass production increase with the duration of experiments as a result of species complementarity (Cardinale et al. 2007). Thus, our results are

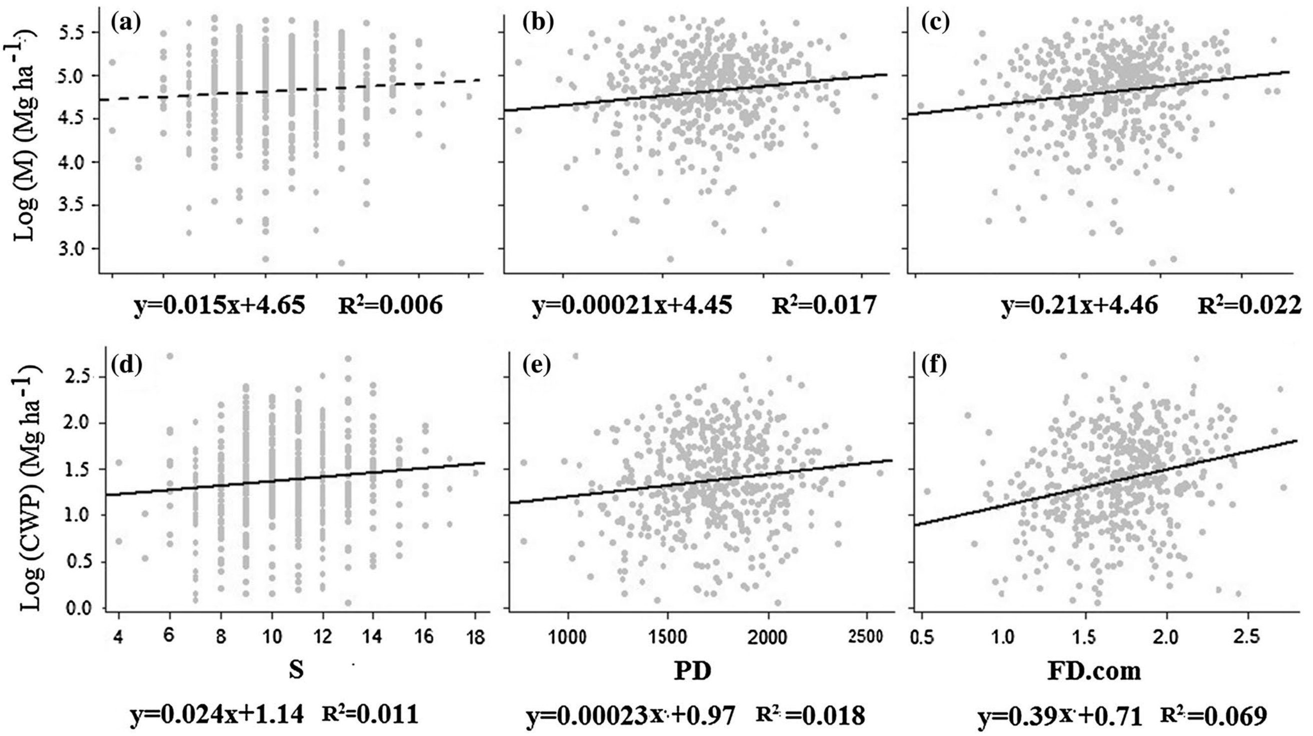

Fig. 1 Relationship between forest biomass and **a** species richness (S), **b** faith's phylogenetic diversity (PD) and **c** functional dispersion index as calculated from six traits (FD_{com}), and relationship between coarse woody productivity and **d** species richness (S) **e** faith's phylogenetic diversity (PD) and **f** functional dispersion index as calculated from six traits (FD_{com}) in the secondary poplar-birch forest plot. *Solid black lines* represent statistically significant positive slopes, and *dashed lines* represent insignificant slopes. Goodness-of-fit as determined by Akaike weights (wi) are reported in Table 2. On the *Y*-axes, *M* above ground biomass and *CWP* coarse woody productivity

consistent with these studies since we found stronger slope BEF relationship in the old-growth forest in comparison to the secondary forest (Caldeira et al. 2001; Cardinale et al. 2004; Venail et al. 2015). Morin et al. (2011) found that positive relationships between species richness and productivity in European forests were mainly caused by a strong complementarity among species due to light partitioning. In our study, a more diverse vertical structure (e.g., canopy, sub-canopy, and shrub layers) in the old-growth forest as compared to the secondary forest may have increased the light absorption or light-use efficiency, resulting in increased facilitation and reduced competition among species (Moore 1989; Yuan et al. 2012; Forrester and Bauhus 2016).

However, several previous studies of BEF relationships along successional gradients concluded that positive BEF relationships may be stronger early in succession (Balvanera et al. 2006; Ruiz-Jaen and Potvin 2011). For example, recent study demonstrated that BEF relationships often shift from positive (early in succession) to non-significant (in old-growth stands) in tropical forests, suggesting that mortality of early successional species during stand thinning may overwhelm growth effects (Lasky et al. 2014). One possible explanation for the difference in the direction of biodiversity effect on ecosystem function over succession is the definition of different stages of succession (Nguyen et al. 2012). The early and late successional stage of subtropical forests were often assigned to 10–23 years and >80 year-old (Barrufol et al. 2013; Lasky et al. 2014) respectively, while we selected the stand age of 80 and 280 years as the early and late successional stage of temperate forest in this study (Table 1). Thus, successional context is essential to understanding BEF relationships in a given system in future researches (Brose and Hillebrand 2016).

Our results show that the combination of multiple metrics of diversity yields better performance than single metrics in natural temperate forests, in line with previous findings (Flynn et al. 2011; Paquette and Messier 2011; Lasky et al. 2014; Liu et al. 2015). Furthermore, our results do not fully support the idea that PD is a "strong" predictor of ecosystem functioning, or a "better" predictor than species richness (Cadotte 2015). As shown in Figs. 1 and 2, species richness is a significant but weak predictor of ecosystem functioning in early successional forest but a good predictor in old-growth forest, probably due to saturation of the positive BEF effect when additional species become functionally redundant (Loreau 1998; Wu et al. 2014; Lasky

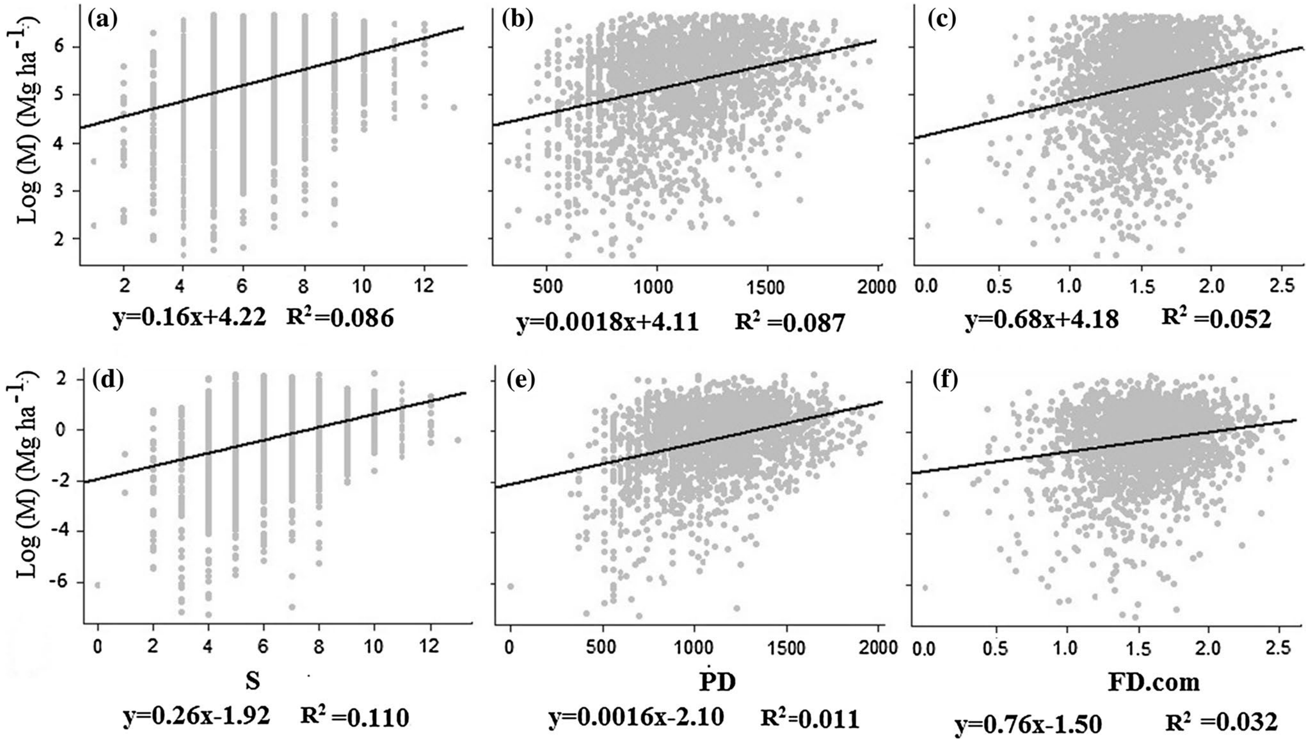

Fig. 2 Relationship between forest biomass and **a** species richness (S), **b** faith's phylogenetic diversity (PD) and **c** functional dispersion index as calculated from six traits (FD_{com}), and relationship between coarse woody productivity and **d** species richness (S) **e** faith's phylogenetic diversity (PD) and **f** functional dispersion index as calculated from six traits (FD_{com}) in the old-growth forest plot. *Solid black lines* represent statistically significant positive slopes, and *dashed lines* represent insignificant slopes. Goodness-of-fit as determined by Akaike weights (wi) are reported in Table 2. On the *Y*-axes, *M* above ground biomass and *CWP* coarse woody productivity

Table 2 Model comparison results of general linear models predicting the log response ratio of biomass stock in the Poplar-birch forest (PBF) plot

Dependent variable	Model	*df*	LL	AICc	Δ AICc	w_i	r^2
AGB	~S + PD + FD_{la}	5	−270	551	0	0.63	0.086
	~PD + FD_{la}	4	−272	552	1.6	0.29	0.079
	~FD_{la}	3	−275	556	5.4	0.04	0.068
	~S + FD_{la}	4	−274	557	5.8	0.04	0.071
	~S + PD + FD_{sla}	5	−278	566	15	<0.01	0.057
CWP	~FD_{la}	3	−470	947	0	0.37	0.090
	~PD + FD_{la}	4	−470	947	0.49	0.29	0.089
	~S + FD_{la}	4	−470	948	0.91	0.23	0.086
	~S + PD + FD_{la}	5	−470	949	2.52	0.10	0.089
	~FD_{com}	3	−470	965	18.2	<0.01	0.052

Variables are number of species (S), phylogenetic diversity (PD), and community-level means of single functional traits (FD_{sla}, specific leaf area; FD_{wd}, wood density, FD_{la}, leaf area). Shown are the estimated number of model parameters (*df*), maximum log-likelihood (LL), the information-theoretic Akaike's information criterion corrected for small samples (AICc), change in AICc relative to the top-ranked model (ΔAICc), and w_i is model probability

et al. 2014). The use of PD as a predictor of ecosystem functioning assumes that evolutionary diversification has generated trait diversity, which in turn may result in greater niche complementarity (Cadotte et al. 2008; Cadotte 2015). Venail et al. (2015) argued that functional complementarity between species did not always increase with increasing PD, because there may be functionally important trait differences among species that are not fully explained by phylogenetic relatedness (Kelly et al. 2014).

Our results support the idea that multivariate functional diversity may reduce the predictive power of traits on ecosystem functioning when traits are associated with

Table 3 Model comparison results of general linear models predicting the log response ratio of biomass stock in the old-growth forest (CBS) plot

Dependent variables	Model	*df*	LL	AICc	Δ AICc	w_i	r^2
AGB	$\sim S + PD + FD_{wd}$	5	−3012	6033	0	0.97	0.187
	$\sim S + FD_{wd}$	4	−3016	6040	6.9	0.03	0.170
	$\sim PD + FD_{wd}$	4	−3027	6062	28.6	<0.01	0.167
	$\sim S + FD_{com}$	4	−3084	6176	143.4	<0.01	0.160
	$\sim S + FD_{sla}$	4	−3084	6178	145.3	<0.01	0.118
CWP	$\sim S + PD + FD_{wd}$	5	−3899	7807	0	0.99	0.169
	$\sim PD + FD_{wd}$	4	−3906	7819	12	<0.01	0.165
	$\sim S + PD + FD_{sla}$	5	−3910	7829	22	<0.01	0.162
	$\sim S + FD_{sla}$	4	−3911	7830	23	<0.01	0.158
	$\sim S + PD + FD_{com}$	5	−3913	7833	26	<0.01	0.158

Variables are number of species (S), phylogenetic diversity (PD), and community-level means of single functional traits (FD_{sla}, specific leaf area; FD_{wd}, wood density, FD_{la}, leaf area). Shown are the estimated number of model parameters (*df*), maximum log-likelihood (LL), the information-theoretic Akaike's information criterion corrected for small samples (AICc), change in AICc relative to the top-ranked model (ΔAICc), and w_i is model probability

opposing niche axes (Cadotte et al. 2009; Laliberté and Legendre 2010; Flynn et al. 2011; Ruiz-Jaen and Potvin 2011; Liu et al. 2015; Kunstler et al. 2016). The underlying assumption of the functional trait approach is that FD represents how species are distributed in multidimensional niche space. As a consequence, FD measured from multiple traits should provide a better explanation for ecosystem functioning than does single trait diversity (Petchey and Gaston 2002). Our results show that multivariate functional diversity was always outranked by some single functional trait. This may suggest that the six functional traits used here are associated with different (or opposing) ecological processes related to resource acquisition or resource storage (Wright et al. 2004; Violle et al. 2007; Reich 2014), and the predictive power of their combination is decreased when compared to individual traits due to interactions among traits (Cadotte et al. 2009; Lasky et al. 2014). There is considerable evidence that growth strategy differences between species are the result of allocation of limited resources (Campanello et al. 2008; Meinzer et al. 2008b; Baraloto et al. 2010). For example, individuals with higher reproduction often have a shorter life span (Wright et al. 2004). Diversity measures may not capture these trait interactions. For example, multivariate functional diversity did not change in wet and dry chaparral sites as a result of trade-offs among traits in water use and transport (Cornwell et al. 2006). Recently, Liu et al. (2015) also reported that a combination of plant height and phylogenetic diversity provided the most informative model for recent field grass experiments, while other traits such as specific leaf area, and leaf nitrogen and phosphorus content had little additional explanatory power. Thus, studies focusing solely on multivariate functional diversity may mask the underlying ecological processes associated with opposing niche axes, and the role of individual traits in ecosystem functioning should also be considered in future work (Spasojevic and Suding 2012; Liu et al. 2015).

A comparison between secondary and old-growth forests further shows that complementarity among species in several traits may regulate competitive interactions and is fundamental for a mechanistic understanding of the role of plant diversity in AGB production (Ruiz-Jaen and Potvin 2011; Roscher et al. 2011b, 2012). The competitive ability of a tree is often characterized by a high productivity in early successional stages, while later in succession, competitive ability is characterized by the ability to persist under scarce resources (Goldberg 1990). In our analysis, complementarity among species in leaf area, which is related to photosynthetic ability, is the only parsimonious predictor of forest biomass accumulation in the secondary forest dominated by pioneer or fast-growing species (Table 2). These species usually invest in structures for rapid resource acquisition and grow rapidly, profiting greatly from favorable conditions, but then decline in a deteriorating environment (Reich 2014). In contrast, species with longer life spans and low growth rates, which are often characterized by a high wood density, might respond less rapidly to environmental changes, conferring greater survival through resistance to disease, drought, and physical damage (Chave et al. 2009; Májeková et al. 2014). Field surveys often show an increase in both stand biomass and diversity during early succession, followed by a decline in diversity and abundance due to competition or small-scale disturbance, which leads to dominance by local competitors in old-growth forests (Chazdon 2008; Paquette and Messier 2011). For example, Slik et al. (2008) confirmed that old-growth forests are generally characterized by a higher average wood density than disturbed forests.

Some studies have explored how environmental factors can influence both diversity and productivity simultaneously in natural ecosystems, such as topography, soil fertility, soil moisture, and soil depth (Hooper et al. 2005; Paquette and Messier 2011; Barrufol et al. 2013). In the two plots studied here, topography is smooth and soil conditions exhibit small variations within each plot. Thus, our results should not be influenced by environmental heterogeneities. Moreover, in the BKF plot we found that topography had little influence on species diversity variation (Yuan et al. 2011). In our study, the amount of variance explained by diversity was smaller than that found in a grassland study (e.g., Liu et al. 2015; 77 %) and is more comparable to the amount found by Vilà et al. (2003, 2007) in forests.

Conclusions

Based on 10 years of forest monitoring data, our findings provide several important insights for understanding BEF relationships in temperate forests. First, our analysis did not support the conclusion that phylogenetic diversity and functional diversity are better predictors of ecosystem functioning (AGB and CWP) than taxonomic diversity, as evidenced by more explanatory power of species richness than phylogenetic diversity or functional diversity in the old-growth forest. Second, species richness, phylogenetic diversity, and single functional traits are required simultaneously to best predict AGB and CWP. In particular, plant functional traits related to the leaf economic spectrum are important to understand the role of plant diversity in biomass production. Finally, regardless of diversity indices, stronger positive BEF relationships were found in the later stage of forest succession, implying the diversity effect on ecosystem functioning becomes stronger over time. Overall, our results demonstrate that the multiple metrics of diversity have different effects on temperate forest functioning over time; thus, we suggest that the specific role of each diversity metric, each functional traits on BEF should be carefully considered in future research.

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Author contribution statement ZQ and WX conceived and designed the experiments, ZQ, YJ, LF and WX performed the experiments, ZQ, SW and AG analyzed the data, ZQ, SW, AG and ML wrote the manuscript, other authors provided editorial advice.

References

Balvanera P, Pfisterer AB, Buchmann N et al (2006) Quantifying the evidence for biodiversity effects on ecosystem functioning and services. Ecol Lett 9:1146–1156. doi:10.1111/j.1461-0248.2006.00963.x

Baraloto C, Paine CET, Poorter L, Beauchene J, Bonal D, Domenach AM, Hérault B, Patiño S, Roggy JC, Chave J (2010) Decoupled leaf and stem economics in rain forest trees. Ecol Lett 13(11):1338–1347

Barrufol M, Schmid B, Bruelheide H et al (2013) Biodiversity promotes tree growth during succession in subtropical forest. PLoS One 8:e81246

Barton K (2014) Package 'MuMIn'. R package version 1:0–7

Brose U, Hillebrand H (2016) Biodiversity and ecosystem functioning in dynamic landscapes. Philos Trans R Soc B 371:20150267. doi:10.1098/rstb.2015.0267

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer-Verlag, New York

Cadotte MW (2015) Phylogenetic diversity and productivity: gauging interpretations from experiments that do not manipulate phylogenetic diversity. Funct Ecol 29(12):1603–1606

Cadotte MW, Cardinale BJ, Oakley TH (2008) Evolutionary history and the effect of biodiversity on plant productivity. Proc Natl Acad Sci USA 105:17012–17017. doi:10.1073/pnas.0805962105

Cadotte MW, Cavender-Bares J, Tilman D et al (2009) Using phylogenetic, functional and trait diversity to understand patterns of plant community productivity. PLoS One 4:e5695. doi:10.1371/journal.pone.0005695

Caldeira MC, Ryel RR, Lawton JH et al (2001) Mechanisms of positive biodiversity-production relationships: insights provided by ^{13}C analysis in experimental Mediterranean grassland plots. Ecol Lett 4:439–443. doi:10.1046/j.1461-0248.2001.00238.x

Campanello PI, Gatti MG, Goldstein G (2008) Coordination between water-transport efficiency and photosynthetic capacity in canopy tree species at different growth irradiances. Tree Physiol 8:85–94. doi:10.1093/treephys/28.1.85

Cardinale BJ, Ives AR, Inchausti P (2004) Effects of species diversity on the primary productivity of ecosystems: extending our spatial and temporal scales of inference. Oikos 104:4376–4450. doi:10.1111/j.0030-1299.2004.13254.x

Cardinale BJ, Srivastava DS, Duff JE et al (2006) Effects of biodiversity on the functioning of trophic groups and ecosystems. Nature 443:9896–9992. doi:10.1038/nature05202

Cardinale BJ, Wright JP, Cadotte MW et al (2007) Impact of plant diversity on biomass production increase through time because of species complementarity. Proc Natl Acad Sci 104:18123–18128. doi:10.1073/pnas.0709069104

Cardinale BJ, Venail P, Gross K et al (2015) Further re-analyses looking for effects of phylogenetic diversity on community biomass and stability. Funct Ecol 29:1607–1610. doi:10.1111/1365-2435.12540

Cavanaugh KC, Gosnell JS, Davis SL et al (2014) Carbon storage in tropical forest correlates with taxonomic diversity and functional dominance on a global scale. Glob Ecol Biogerogr 23:563–573. doi:10.1111/geb.12143

Chave J, Coomes D, Jansen S et al (2009) Towards a worldwide wood economics spectrum. Ecol Lett 12:351–366. doi:10.1111/j.1461-0248.2009.01285.x

Chazdon RL (2008) Chance and determinism in tropical forest succession. In: Carson WP, Schnitzer SA (eds) Tropical forest community ecology. Wiley, Chichester, pp 384–408

Chisholm RA, Muller-landau HC, Rahman KA et al (2013) Scale-dependent relationships between tree species richness and ecosystem function in forests. J Ecol 101:1214. doi:10.1111/1365-2745.12132

Condit R (1998) Tropical forest census plots. Springer, Berlin

Cornwell WK, Schwilk DW, Ackerly DD (2006) A trait-based test for habitat filtering: convex hull volume. Ecology 87(6):1465–1471

Faith DP (1992) Conservation evaluation and phylogenetic diversity. Biol Conserv 61:1–10. doi:10.1016/0006-3207(92)91201-3

Flynn DFB, Mirotchnick N, Jain M et al (2011) Functional and phylogenetic diversity as predictors of biodiversity-ecosystem function relationships. Ecology 92:1573–1581. doi:10.1890/10-1245.1

Forrester DI, Bauhus J (2016) A review of processes behind diversity—productivity relationships in forests. Curr For Rep 2(1):45–61. doi:10.1007/s40725-016-0031-2

Goldberg DE (1990) Components of resource competition in plant communities. In: Grace JB, Tilman D (eds) Perspectives on plant competition. Academic Press, San Diego, pp 27–49

Hao ZQ, Zhang J, Song B et al (2007) Vertical structure and spatial associations of dominant tree species in an old growth temperate forest. For Ecol Manag 25:1–11. doi:10.1016/j.foreco.2007.06.026

Hao ZQ, Zhang J, Li BH et al (2008) Natural secondary poplar-birch forests in Changbai mountain: species composition and communities structure. J Plant Ecol 32:251–261 **(in Chinese with English abstract)**

Hooper DU, Chapin FS, Ewel JJ et al (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecol Monogr 75:3–35. doi:10.1890/04-0922

Jonsson M (2006) Species richness effects on ecosystem functioning increase with time in an ephemeral resource system. Acta Oecol 29:72–77. doi:10.1016/j.actao.2005.08.002

Kelly ME, Loughrey D, Lawlor BA, Robertson LH, Walsh C, Brennan S (2014) The impact of cognitive training and mental stimulation on cognitive and everyday functioning of healthy older adults: a systematic review and meta-analysis. Ageing Res Rev 15:28–43

Kembel SW, Cowan PD, Helmus MR et al (2010) Picante: R tools for integrating phylogenies and ecology. Bioinformatics 26:1463–1464. doi:10.1093/bioinformatics/btq166

Kunstler G, Falster D, Coomes DA, Hui F, Kooyman RM, Laughlin DC, Poorter L, Vanderwel M, Vieilledent G, Wright SJ, Aiba M, Baraloto C, Caspersen J, Cornelissen JH, Gourlet-Fleury S, Hanewinkel M, Herault B, Kattge J, Kurokawa H, Onoda Y, Peñuelas J, Poorter H, Uriarte M, Richardson S, Ruiz-Benito P, Sun IF, Ståhl G, Swenson NG, Thompson J, Westerlund B, Wirth C, Zavala MA, Zeng H, Zimmerman JK, Zimmermann JK, Westoby M (2016) Plant functional traits have globally consistent effects on competition. Nature 529(7585):204–207

Laliberté E, Legendre P (2010) A distance-based framework for measuring functional diversity from multiple traits. Ecology 91:299–305. doi:10.1890/08-2244.1

Lasky JR, Uriarte M, Boukili V et al (2014) The relationship between tree biodiversity and biomass dynamics changes with tropical forest succession. Ecol Lett 17:1158–1167. doi:10.1111/ele.12322

Letcher SG, Chazdon RL (2009) Rapid recovery of biomass, species richness, and species composition in a forest chronosequence in northeastern Costa Rica. Biotropica 41:608–617. doi:10.1111/j.1744-7429.2009.00517.x

Liu JJ, Zhang XX, Song FF et al (2015) Explaining maximum variation in productivity requires phylogenetic diversity and single functional traits. Ecology 96(1):176–183. doi:10.1890/14-1034.1

Loreau M (1998) Biodiversity and ecosystem functioning: a mechanistic model. Proc Natl Acad Sci USA 95:5632–5636

Loreau M, Hector A (2001) Partitioning selection and complementarity in biodiversity experiments. Nature 412(6842):72–76

Májeková M, de Bello F, Doležal J et al (2014) Plant functional traits asdeterminants of population stability. Ecology 95:2369–2374. doi:10.1073/pnas.95.10.5632

Meinzer FC, Woodruff DR, Domec J-C et al (2008) Coordination of leaf and stem water transport properties in tropical forest trees. Oecologia 156:31–41. doi:10.1007/s00442-008-0974-5

Moore AD (1989) On the maximum growth equation used in forest gap simulation models. Ecol Model 45:63–67. doi:10.1016/0304-3800(89)90100-2

Morin X, Fahse L, Scherer-Lorenzen M, Bugmann H (2011) Tree species richness promotes productivity in temperate forests through strong complementarity between species. Ecol Lett 14:1211–1219. doi:10.1111/j.1461-0248.2011.01691.x

Nguyen H, Herbohn J, Firn J et al (2012) Biodiversity–productivity relationships in small-scale mixed-species plantations using native species in Leyte province, Philippines. For Ecol Manag 274:81–90. doi:10.1016/j.foreco.2012.02.022

Paquette A, Messier C (2011) The effect of biodiversity on tree productivity: from temperate to boreal forest. Glob Ecol Biogeogr 20:170–180. doi:10.1111/j.1466-8238.2010.00592.x

Pavoine S, Bonsall MB (2011) Measuring biodiversity to explain community assembly: a unified approach. Biol Rev 86:792–812. doi:10.1111/j.1469-185X.2010.00171.x

Pérez-Harguindeguy N, Díaz S, Garnier E et al (2013) New handbook for standardised measurement of plant functional traits worldwide. Aust J Bot 61:167–234. doi:10.1071/BT12225

Petchey OL, Gaston KJ (2002) Functional diversity (FD), species richness and community composition. Ecol Lett 5:402–411. doi:10.1046/j.1461-0248.2002.00339.x

Reich PB (2014) The worldwide "fast–slow" plant economics spectrum: a traits manifesto. J Ecol 102:275–301. doi:10.1111/1365-2745.12211

Reich PB, Tilman D, Isbell F et al (2012) Impacts of biodiversity loss escalate through time as redundancy fades. Science 336:589–592. doi:10.1126/science.1217909

Roscher C, Schmid B, Buchmann N et al (2011) Legume species differ in the responses of their functional traits to plant diversity. Oecologia 165:437–452. doi:10.1007/s00442-010-1735-9

Roscher C, Schumacher J, Gubsch M et al (2012) Using plant functional traits to explain diversity-productivity relationships. PLoS One 7:e36760. doi:10.1371/journal.pone.0036760

Ruiz-Benito P, Gómez-Aparicio L, Paquette A et al (2014) Diversity increases carbon storage and tree productivity in Spanish forests. Glob Ecol Biogeogr 23:311–322. doi:10.1111/geb.12126

Ruiz-Jaen MC, Potvin C (2011) Can we predict carbon stocks in tropical ecosystems from tree diversity? Comparing species and functional diversity in a plantation and a natural forest. New Phytol 189:978–987. doi:10.1111/j.1469-8137.2010.03501.x

Slik JWF, Bernard CS, Breman FC, van Beek M, Salim A, Sheil D (2008) Wood density as a conservation tool: quantification of disturbance and identification of conservation-priority areas in tropical forests. Conserv Biol 22(5):1299–1308

Spasojevic MJ, Suding KN (2012) Inferring community assembly mechanisms from functional diversity patterns: the importance of multiple assembly processes. J Ecol 100:652–661. doi:10.1111/j.1365-2745.2011.01945.x

Tilman D, Knops J, Wedin D, Reich P, Ritchie M, Siemann E (1997) The influence of functional diversity and composition on ecosystem processes. Science 277:1300–1302. doi:10.1126/science.277.5330.1300

Venail P, Gross K, Oakley TH et al (2015) Species richness, but not phylogenetic diversity, influences community biomass production and temporal stability in a re-examination of 16 grassland biodiversity studies. Funct Ecol 29(5):615–626. doi:10.1111/1365-2435.12432

Vilà M, Vayreda J, Gracia C et al (2003) Does tree diversity increase wood production in pine forests? Oecologia 135:299–303. doi:10.1007/s00442-003-1182-y

Vilà M, Vayreda J, Comas L et al (2007) Species richness and wood production: a positive association in Mediterranean forests. Ecol Lett 10:241–250. doi:10.1111/j.1461-0248.2007.01016.x

Violle C, Navas ML, Vile D et al (2007) Let the concept of trait be functional! Oikos 116:882–892. doi:10.1111/j.2007.0030-1299.15559.x

Wang XG, Wiegand T, Hao Z et al (2010) species association in an old-growth temperate forest in north-eastern China. J Eco 98:674–686. doi:10.1111/j.1365-2745.2010.01644.x

Wang XG, Swenson NG, Wiegand T et al (2013) Phylogenetic and functional diversity area relationships in two temperate forests. Ecography 36:1–11. doi:10.1111/j.1600-0587.2012.00011.x

Webb CO, Donoghue MJ (2005) Phylomatic: tree assembly for applied phylogenetics. Mol Ecol Notes 5:181–183. doi:10.1111/j.1471-8286.2004.00829.x

Weis JJ, Cardinale BJ, Forshay KJ et al (2007) Effect of species diversity on community biomass production change over the course of succession. Ecology 88:929–939. doi:10.1890/06-0943

Wright IJ, Reich PB, Westoby M et al (2004) The worldwide leaf economics spectrum. Nature 428:821–827. doi:10.1890/09-2335.1

Wu X, Wang XP, Tang ZY et al (2014) The relationship between species richness and biomass change form boreal to subtropical forest in China. Ecography 37:1–12. doi:10.1111/ecog.00940

Xu HC (2001) Natural forests of Pinus Koraiens is in China. China Forestry Publishing House, Beijing **(in Chinese)**

Yang H, Li D (1985) Distribution patterns of dominant tree species on northern slope of Changbai Mountain. Res For Ecosyst 5:1–14 **(in Chinese)**

Yuan ZQ, Gazol A, Wang X et al (2011) Scale specific determinants of tree diversity in an old growth temperate forest in China. Basic Appl Ecol 12:488–495. doi:10.1016/j.baae.2011.07.008

Yuan ZQ, Gazol A, Wang XG et al (2012) What happens below the canopy? Direct and indirect influences of the dominant species on forest vertical layers. Oikos 121:1145–1153. doi:10.1111/j.1600-0706.2011.19757.x

Yuan ZQ, Gazol A, Wang XG et al (2016) Pattern and dynamics of biomass stock in old growth forests: the role of habitat and tree size. Acta Oecol 75:15–23. doi:10.1016/j.actao.2016.06.007

Zanne AE, Tank DC, Cornwell WK et al (2014) Three keys to the radiation of angiosperms into freezing environments. Nature 506:89–92. doi:10.1111/j.1600-0706.2011.19757.x

Zhang Y, Chen HYH, Reich PB (2012) Forest productivity increases with evenness, species richness and trait variation: a global meta-analysis. J Ecol 100:742–749. doi:10.1111/1365-2745.12425

Zhao FQ, He HS, Dai L et al (2014) Effects of humans disturbances on Korean pine coverage andage structure at a landscape scale n northeast China. Ecol Eng 71:375–379. doi:10.1016/j.ecoleng.2014.07.072

Zuppinger-Dingley D, Schmid B, Petermann JS et al (2014) Selection for niche differentiation in plant communities in increased biodiversity effects. Nature 515:108–111. doi:10.1038/nature12872

Zuur AF, Ieno EN, Valker NJ et al (2009) Mixed effects models and extensions in ecology with R. Springer, New York