

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

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33 Abstract: Biodiversity can be measured by taxonomic, phylogenetic, and functional  
34 diversity. How ecosystem functioning depends on these measures of diversity can  
35 vary from site to site and depends on successional stage. Here, we measured  
36 taxonomic, phylogenetic, and functional diversity, and examined their relationship  
37 with biomass in two successional stages of the broad-leaved Korean pine forest in  
38 northeastern China. Functional diversity was calculated from six plant traits, and  
39 aboveground biomass (AGB) and coarse woody productivity (CWP) were estimated  
40 using data from three forest censuses (10 years) in two large fully mapped forest plots  
41 (25 ha and 5 ha). 11 of the 12 regressions between biomass variables (AGB and CWP)  
42 and indices of diversity showed significant positive relationships, especially those  
43 with phylogenetic diversity. The mean tree diversity-biomass regressions increased  
44 from 0.11 in secondary forest to 0.31 in old growth forest, implying a stronger  
45 biodiversity effect in more mature forest. Multi-model selection results showed that  
46 models including species richness, phylogenetic diversity, and single functional traits  
47 explained more variation in forest biomass than other candidate models. The models  
48 with a single functional trait, i.e. leaf area in secondary forest and wood density in  
49 mature forest, provided better explanations for forest biomass than models that  
50 combined all six functional traits. This finding may reflect different strategies in  
51 growth and resource acquisition in secondary and old growth forests.

52 *Keywords:* functional diversity, phylogenetic diversity; natural forests; biomass;  
53 competitive ability.

54

## 55 **Introduction**

56 Biodiversity is a complex multifaceted concept that can be measured by  
57 taxonomic, phylogenetic, and functional diversity (Pavoine and Bonsall 2011). During  
58 the past decade, ample experimental studies, mostly in grasslands, have revealed the  
59 positive influence of biodiversity on ecosystem functioning, but the relative  
60 importance of different facets of diversity remains controversial (Flynn et al. 2008;  
61 Cadott et al. 2008; Paquette and Messier 2011; Cardinale et al. 2015; Coadotte et al.  
62 2015; Venail et al. 2015). Species richness, the simplest measure, is frequently used as  
63 the sole measure of diversity in the field of biodiversity and ecosystem functioning  
64 (BEF), which alone may be a poor predictor of ecosystem functioning in natural  
65 species-rich communities (Loreau 1998; Hooper et al. 2005; Paquette and Messier  
66 2011; Ruiz-Jaen and Potvin 2011). Many studies have suggested that including  
67 information on the evolutionary history and functional traits of species can provide  
68 mechanistic links between the composition of the ecological community and  
69 ecological functioning from both evolutionary and ecological perspectives (Petchey  
70 and Gaston 2002; Paquette and Messier 2011). For example, a meta-analysis of 29  
71 BEF experiments showed that phylogenetic diversity (PD) within communities  
72 explained more variation in plant biomass accumulation than taxonomic diversity or  
73 functional group richness (Cadotte et al. 2008). This result suggests that longer  
74 evolutionary differentiation may generate greater trait variation related to ecological  
75 niches and provides evidence for the niche complementarity hypothesis (Cadotte et al.  
76 2008; Flynn et al 2011; Zuppinger-Dingley et al. 2014). However, recent re-

77 examination of 16 grassland diversity studies showed that phylogenetic diversity was  
78 not a better predictor for community biomass than species richness (Cardinale et al.  
79 2015; Venail et al. 2015). Further experiments and analyses, especially in natural  
80 ecosystems, are required to clarify whether phylogenetic diversity is more closely  
81 linked to ecosystem functioning than other diversity measures.

82 Several studies underscored the importance of combining different measures of  
83 diversity (taxonomic, PD, FD) in predicting BEF relationships (Flynn et al. 2011;  
84 Ruiz-Jazen and Potvin et al. 2011; Liu et al. 2015; Lasky et al. 2014; Ruiz-Benito et al.  
85 2014; Cavanaugh et al. 2014). Notably, Flynn et al. (2011) found that PD and FD  
86 calculated from leaf nitrogen, mean plant height, and N-fixation had similar abilities  
87 to predict biodiversity effects, suggesting that traits related to resource acquisition  
88 strategy can drive grassland ecosystem functioning. In another study, Ruiz-Jazen and  
89 Potvin (2011) showed that explaining maximum variation of carbon storage in a  
90 mixed-species plantation and a natural tropical forest in Panama required the  
91 combinations of species richness, FD, species dominance and functional dominance  
92 (e.g. community-weighted mean of maximum height) to best predict the carbon  
93 storage in a mixed-species plantation and a natural tropical forest in Panama. These  
94 results indicated that the relative importance of FD, PD, and taxonomic diversity  
95 varies from site to site and identifying which metric of diversity is most important in  
96 BEF relationships in different regions remains an important task.

97 Two mutually non-exclusive mechanisms have been proposed as explanations  
98 for the positive BEF relationships. Complementarity effects predict that diversity

99 increases the production of biomass through niche complementarity (*e.g.*  
100 complementarity in resource use), which, reduces interspecific competition and  
101 increases the occurrence of facilitation (Forrester and Bauhus 2016). In contrast, the  
102 selection effect hypothesis highlights the role of dominant species or traits, and posits  
103 that the positive BEF relationships result from the enhanced probability for diverse  
104 communities to include high biomass species that will become dominant (Loreau  
105 1998; Loreau and Hector 2001). Positive selection effects often occur when average  
106 species competitive ability is greater in higher diversity communities (Lasky et al.  
107 2014). Recently, ecologists have emphasized that plant diversity effects on plant  
108 productivity get stronger over time (Reich et al. 2012). There is increasing evidence  
109 that complementarity effects among species increase over time, whereas selection  
110 effects decrease (Cardinale et al. 2007; Reich et al. 2012). Furthermore, short-term  
111 studies can be misleading because they incorrectly indicate the presence of functional  
112 redundancy and therefore undervalue biodiversity (Cardinale et al. 2007; Reich et al.  
113 2012).

114 Forest successional communities are ideal systems for assessing BEF  
115 relationships due to natural temporal changes in species composition and ecosystem  
116 functioning (Letcher and Chazdon 2009). Both mathematical models and empirical  
117 studies suggest that species diversity can have different effects on biomass  
118 accumulation over succession (Cardinale et al. 2004; Weis el al. 2007; Lasky et al.  
119 2014). For example, while some studies showed that the effect of biodiversity on  
120 ecosystem functioning became stronger over succession (Caldeira et al. 2001; Jonsson

121 2006), others reported the opposite pattern (Cardinale et al. 2006). Cardinale et al.  
122 (2004) used a Lotka-Volterra competition model and predicted that species richness  
123 should have no effect on community biomass during early stages of succession.  
124 However, in later successional stages, where intra- and interspecific competition  
125 operate, several mechanisms can increase community biomass in more diverse  
126 communities. Therefore, more empirical studies are required to examine whether and  
127 how BEF relationships change across successional stages (Vilà et al. 2003; Morin et al.  
128 2011; Barrufol et al. 2013; Kunstler et al. 2016).

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

139 1. Are phylogenetic diversity and functional diversity better predictors for  
140 ecosystem functioning (AGB and productivity) than species richness?

141 2. Does the combination of multiple metrics of diversity (taxonomic,  
142 phylogenetic, and functional) provide the most parsimonious explanation of

143 ecosystem functioning than each alone?

144 3. Are BEF relationships stronger in later stages of forest succession?

## 145 **Materials and methods**

### 146 **Study site**

147 The Changbai Mountain Natural Reserve in northeastern China is the largest  
148 protected temperate forest in the world (Yang and Li 1985; Hao et al. 2007). This area  
149 has a temperate continental climate with long, cold winters and warm summers.  
150 Rainfall averages 700 mm yr<sup>-1</sup>, most of which occurs from June to September (480–  
151 500 mm). Mean annual temperature is 2.8°C, with a January mean of –13.7°C, and a  
152 July mean of 19.6°C (Yang and Li 1985). There has been little human disturbance in  
153 this area over the last 400 years because Changbai Mountain was protected as the  
154 legendary birthplace of the imperial family during the Qing Dynasty, and became a  
155 natural reserve at the beginning of 1960s. Broad-leaved Korean pine mixed forest is  
156 the most common vegetation type in this area. The poplar-birch forest following a fire  
157 or clear-cutting is an important stage in the secondary succession of broad-leaved  
158 Korean pine mixed forest (Xu 2001).

### 159 **Data collection**

#### 160 **Plot censuses and aboveground biomass dynamics**

161 A 25-ha (500m×500 m) plot was established in the core zone of the broad-leaved  
162 Korean pine mixed forest (hereafter CBS plot) in 2004 (Hao et al. 2007), and a 5-ha  
163 (250m×200 m) plot was established in the secondary poplar-birch forest (hereafter  
164 PBF plot) in 2005 (Hao et al. 2008). All free-standing woody stems  $\geq 1$  cm in trunk

165 diameter were mapped, measured, and identified to species following a standard field  
166 protocol (Condit 1998). The diameter at breast height (DBH) of all the stems in CBS  
167 and PBF plots were recensused every five years to accurately reflect the forest  
168 dynamic. This work was conducted based on Forestry Standards “Observation  
169 Methodology for Long-term Forest Ecosystem Research” of the People’s Republic of  
170 China (LY/T 1952-2011). Overall, 44 plant species were encountered in PBF and 52  
171 species in CBS with 39 common species (Table S1 in Supporting Information). The  
172 detailed description of these two successional forest plots is displayed in Table 1.

173 The AGB of all individual trees in these two plots was estimated using published  
174 species-specific allometric regression equations, which were summed for all stems in  
175 each 10×10 m quadrat to estimate total AGB (Table S2 in Supporting Information).  
176 The chosen quadrat size reflects the scales of individual tree competition. A high  
177 proportion of negative associations among species (competitive interaction) can be  
178 detected in a radius of <10 m (Wang et al. 2010). Moreover, the small quadrat size  
179 helps to control for the effect of habitat heterogeneity (Ruiz-Jaen and Potvin 2011).

180 Based on the AGB estimates during the three censuses, we calculated the coarse  
181 woody productivity (CWP) ( $\text{Mg ha}^{-1} \text{y}^{-1}$ ) as follows:

$$182 \quad \text{CWP} = (G+R)/10 \quad (1)$$

183 Here, CWP is the yearly growth of total aboveground biomass during 2004-2014 (for  
184 CBS) or 2005-2015 (for PBF);  $G$  is the annual growth in AGB of trees that were alive  
185 during two successive censuses (e.g. five years in this study);  $R$  is the annual  
186 increment of AGB attributable to recruitment into the minimum diameter class



187 between the first and second censuses.

## 188 **Multivariate biodiversity indices**

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

209 values for a species in our analyses.

210 We computed functional diversity using the Functional dispersion index (FDis)  
211 proposed by Laliberté and Legendre (2010). FDis quantifies functional diversity as  
212 the mean distance in multidimensional trait space of individual species to the centroid  
213 of all species. This index has several desirable properties since it is independent of  
214 species richness, the distance of each species to the centroid can be weighted by  
215 species relative abundance, and it can be calculated for single or multiple traits  
216 (Laliberté and Legendre 2010). Before we calculated FD, we rescaled the trait data to  
217 a mean of 0 with a standard deviation of 1 (Cadotte et al. 2009). In order to gain  
218 insight into ecophysiological mechanisms driving BEF relationships, we further  
219 calculated functional diversity (FD) indices separately for each single trait (FD<sub>H</sub>,  
220 FD<sub>wd</sub>, FD<sub>lpc</sub>, FD<sub>lnc</sub>, FD<sub>la</sub> and FD<sub>sla</sub>) and for the combination of all six traits (FD<sub>com</sub>) in  
221 each 10×10 m quadrat.

222 A phylogenetic supertree was constructed by inputting all the species found in  
223 plots into the plant phylogeny database Phylomatic, an online interface that supplies a  
224 phylogeny based on a user-defined set of plant species taxonomic names  
225 (<http://www.phylodiversity.net>) (Webb and Donoghue 2005). Phylomatic utilizes the  
226 Angiosperm Phylogeny Group III (APG III 2010) phylogeny as a backbone. This  
227 supertree was then assigned branch lengths estimated from multi-gene molecular and  
228 fossil data implemented in Phylomatic, which is the largest and most up-to-date time  
229 calibrated species-level phylogeny of seed plants (Zanne et al. 2014). We then  
230 calculated the Faith's phylogenetic diversity index that quantifies the shared branch

231 lengths of the phylogeny among species in a sample with the root node included in all  
232 calculations (Faith 1992a). Faith's phylogenetic diversity index is perhaps the most  
233 widely used measure of PD (Paquette and Messier 2011; Lasky et al. 2014; Liu et al.  
234 2015).

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

## 238 **Data analyses**

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

253 without spherical autocorrelation structures always had the lower AIC values (Table  
254 S3 in Supporting Information).

255 We constructed a series of univariate and multivariate linear models to find the  
256 most parsimonious models from three diversity categories: TD, PD, and FD. While  
257 there were seven different functional diversity metrics ( $FD_H$ ,  $FD_{wd}$ ,  $FD_{lpc}$ ,  $FD_{inc}$ ,  
258  $FD_{la}$ ,  $FD_{sla}$  and  $FD_{com}$ ), we avoided including more than one of these metrics in any  
259 one model. Variables that we used in model construction are listed in Table S4  
260 (Supporting Information). These models were compared and ranked following AIC  
261 adjusted for small sample sizes ( $AIC_c$ ) in the “MuMIn” package R software (Barton  
262 2014; *dredge* function of R 3.1.2; <http://www.r-project.org>). This method compares  
263 the explanatory ability of these models using AIC weight, which can assess the  
264 probability that a given model is the most appropriate description for the observed  
265 data (Burnham and Anderson 2002).

266 All analyses were performed in R software. PD and FD indices were computed  
267 using the packages “picante” (Kembel et al. 2010) and “FD” (Laliberté and Legendre  
268 2010), respectively.

269

## 270 **Results**

### 271 **Successional changes in diversity and aboveground biomass**

272 Diversity indices and biomass (AGB and CWP) exhibited considerable spatial  
273 variation at both study sites (Table 1). In the early successional forest (PBF plot),  
274 species richness per quadrat ( $100\text{ m}^2$ ) ranged from 4 to 18, with a mean of 10.5

275 species, and AGB ranged from 16.7 to 332.6 Mg ha<sup>-1</sup>, with a mean of 137.1 Mg ha<sup>-1</sup>  
276 (Table 1). The old-growth forest (CBS plot) had lower richness, with a mean of 6.2  
277 species, ranging from 0 to 13. However, the mean AGB (279.4 Mg ha<sup>-1</sup>) in the old-  
278 growth forest (CBS plot) was more than twice that in the early successional forest  
279 (PBF plot, 137.1 Mg ha<sup>-1</sup>).

## 280 **BEF relationships**

281 Nearly all the regressions between biomass and indices of diversity showed  
282 significant positive BEF relationships (Fig.1 and Fig. 2). Species richness was not  
283 significantly related to biomass in the PBF plot but exhibited strong positive  
284 relationships with biomass in the CBS plot (Fig.1).  $FD_{com}$ , as calculated from six  
285 functional traits, was positively related to biomass in both plots. The mean slope of  
286 these positive diversity-biomass regressions increased from 0.12 (average of 0.0002,  
287 0.21, 0.02, 0.00023 and 0.39) in the PBF plot to 0.31 (average of 0.16, 0.0018, 0.68,  
288 0.26, 0.0016 and 0.76) in the CBS plot, suggesting enhanced BEF relationships  
289 through succession (Fig. 1 & Fig. 2).

290 In the multi-model comparative approach, we found that models including  
291 single functional traits consistently explained more variation in biomass than those  
292 with multivariate functional diversity ( $FD_{com}$ ) (Table 2, Table 3, and Table S4 in  
293 Supporting Information). In particular, leaf area was the best predictor of tree  
294 productivity in the PBF plot (Table 2), while species richness, PD, and other traits had  
295 little additional explanatory power for variance. The combination of species richness,  
296 PD, and leaf area represented the most parsimonious model in the PBF plot,

297 accounting for about 9 % of the variance in AGB (Table 2). The model including  
298 species richness, PD, and wood density together was the most parsimonious predictor  
299 in the CBS plot ( $wAICc > 0.97$ ), explaining 19% of the variance in AGB (Table 3).

300

## 301 **Discussion**

302 Over the past two decades, BEF studies have mainly been conducted in  
303 controlled, small-scale experiments (Tilman et al. 1997; Flynn et al. 2011; Liu et al.  
304 2015; Zuppinger-Dingley et al. 2014). However, whether biodiversity influences  
305 ecosystem functioning in natural communities remains a long-standing controversy  
306 (Hooper et al. 2005; Ruiz-Jaen and Potvin 2011; Chisholm et al. 2013; Wu et al.  
307 2014). Our findings suggest positive BEF relationships in both secondary and old-  
308 growth forest. The positive biodiversity effects on biomass are often attributed to  
309 increased complementarity between species in resource use that reduces competition  
310 and increases the occurrence of facilitation (Reich et al. 2012). Complementarity  
311 among species is expected to be higher in more stable ecosystems (Paquette and  
312 Messier 2011), and a meta-analysis of the results of 44 grassland experiments  
313 revealed that the impacts of plant diversity on biomass production increase with the  
314 duration of experiments as a result of species complementarity (Cardinale et al. 2007).  
315 Thus, our results are consistent with these studies and results from short-term  
316 experiments in herbaceous communities as well as simulation studies (Caldeira et al.  
317 2001; Cardinale et al. 2004; Venail et al. 2015), since we found a more positive slope  
318 BEF relationship in the old-growth forest in comparison to the secondary forest.

319 Morin et al. (2011) found that positive relationships between species richness and  
320 productivity in European forests were mainly caused by a strong complementarity  
321 among species due to light partitioning. In our study, a more diverse vertical structure  
322 (e.g. canopy, sub-canopy, and shrub layers) in the old growth forest as compared to  
323 the secondary forest may have increased the light absorption or light-use efficiency,  
324 resulting in increased facilitation and reduced competition among species (Moore  
325 1989; Yuan et al. 2012; Forrester and Bauhus et al. 2016). However, several previous  
326 studies of BEF relationships along successional gradients concluded that positive BEF  
327 relationships may be stronger early in succession (Balvanera et al. 2006; Ruiz-Jaen  
328 and Potvin 2011). For example, Lasky et al. (2014) demonstrated that BEF  
329 relationships often shift from positive (early in succession) to non-significant (in old-  
330 growth stands) in tropical forests, suggesting that mortality of early successional  
331 species during stand thinning may overwhelm growth effects. Thus, successional  
332 context is essential to understanding BEF in a given system (Brose and Hillebrand  
333 2016).

334         Our results show that the combination of multiple metrics of diversity yields  
335 better performance than single metrics in natural temperate forests, in line with  
336 previous findings (Flynn et al. 2011; Paquette and Messier 2011; Lasky et al. 2014;  
337 Liu et al. 2015). Furthermore, our results do not fully support the idea that PD is a  
338 “strong” predictor of ecosystem functioning, or a “better” predictor than species  
339 richness (Cadotte et al. 2015). As shown in Fig. 1 and Fig. 2, species richness is a  
340 significant but weak predictor of ecosystem functioning in natural species-rich

341 communities but a good predictor in old growth forest, probably due to saturation of  
342 the positive BEF effect when additional species become functionally redundant  
343 (Loreau 1998; Wu et al. 2014; Lasky et al. 2014). The use of PD as a predictor of  
344 ecosystem functioning assumes that evolutionary diversification has generated trait  
345 diversity, which in turn may result in greater niche complementarity (Caddte et al.  
346 2008; Caddte et al. 2015). Venail et al. (2015) argued that functional complementarity  
347 between species did not always increase with increasing PD, because there may be  
348 functionally important trait differences among species that are not fully explained by  
349 phylogenetic relatedness (Kelly et al. 2014).

350         Our results support the idea that multivariate functional diversity may reduce the  
351 predictive power of traits on ecosystem functioning when traits are associated with  
352 opposing niche axes (Cadotte et al. 2009; Laliberté and Legendre 2010; Flynn et al.  
353 2011; Ruiz-Jaen and Potvin 2011; Liu et al. 2015; Kunstler et al. 2016). The  
354 underlying assumption of the functional trait approach is that FD represents how  
355 species are distributed in multidimensional niche space. As a consequence, FD  
356 measured from multiple traits should provide a better explanation for ecosystem  
357 functioning than does single trait diversity (Petchey and Gaston 2002). In a global  
358 study, Kunstler et al. (2016) showed little effect of complementarity in leaf area and  
359 wood density among tree species on competition and a stronger link between wood  
360 density and maximum height, pointing to differences among these phenotypic traits  
361 and what they represent ecologically. Our results show that multivariate functional  
362 diversity was always outranked by some single functional trait. This may suggest that



363 the six functional traits used here are associated with different (or opposing)  
364 ecological processes related to resource acquisition or resource storage (Wright et al.  
365 2004; Violle et al. 2007; Reich et al. 2014), and the predictive power of their  
366 combination is decreased when compared to individual traits due to interactions  
367 among traits (Cadotte et al. 2009; Lasky et al. 2014). There is considerable evidence  
368 that growth strategy differences between species are the result of allocation of limited  
369 resources (Campanello et al. 2008; Meinzer et al. 2008b; Baraloto et al. 2010). For  
370 example, individuals with higher reproduction may or may not have a longer life span  
371 (Wright et al. 2004). Diversity measures may not capture these trait interactions. For  
372 example, multivariate functional diversity did not change in wet and dry chaparral  
373 sites as a result of trade-offs among traits in water use and transport (Cornwell et al.  
374 2006). Recently, Liu et al. (2015) also reported that a combination of plant height and  
375 phylogenetic diversity provided the most informative model for recent field grass  
376 experiments, while other traits such as specific leaf area, and leaf nitrogen and  
377 phosphorus content had little additional explanatory power. Thus, studies focusing  
378 solely on multivariate functional diversity may mask the underlying ecological  
379 processes associated with opposing niche axes, and the role of individual traits in  
380 ecosystem functioning should also be considered in future work (Spasojevic and  
381 Suding 2012; Liu et al. 2015).

382         A comparison between secondary and old-growth forests further shows that  
383 complementarity among species in several traits may regulate competitive interactions  
384 and is fundamental for a mechanistic understanding of the role of plant diversity in

385 AGB production (Ruiz-Jaen and Potvin 2011; Roscher et al. 2011b; Roscher et al.  
386 2012). The competitive ability of a tree is often characterized by a high productivity  
387 in early successional stages, while later in succession, competitive ability is character-  
388 ized by the ability to persist under scarce resources (Goldberg 1990). In our analysis,  
389 complementarity among species in leaf area, which is related to photosynthetic abil-  
390 ity, is the only parsimonious predictor of forest biomass accumulation in the second-  
391 ary forest dominated by pioneer or fast-growing species (Table 2). These species usu-  
392 ally invest in structures for rapid resource acquisition and grow rapidly, profiting  
393 greatly from favorable conditions, but then decline in a deteriorating environment  
394 (Reich 2014). In contrast, species with longer life spans and low growth rates, which  
395 are often characterized by a high wood density, might respond less rapidly to envi-  
396 ronmental changes, conferring greater survival through resistance to disease, drought,  
397 and physical damage (Chave et al. 2009; Májerková et al. 2014). Field surveys often  
398 show an increase in both stand biomass and diversity during early succession, fol-  
399 lowed by a decline in diversity and abundance due to competition or small-scale dis-  
400 turbance, which leads to dominance by local competitors in old-growth forests  
401 (Chazdon 2008; Paquette and Messier 2011). For example, Silk et al. (2008) con-  
402 firmed that old-growth forests are generally characterized by a higher average wood  
403 density than disturbed forests.

404       Some studies have explored how environmental factors can influence both  
405 diversity and productivity simultaneously in natural ecosystems, such as topography,  
406 soil fertility, soil moisture, and soil depth (Hooper et al. 2005; Paquette and Messier

407 2011; Barrufol et al. 2013). In the two plots studied here, topography is smooth and  
408 soil conditions exhibit small variations within each plot. Thus, our results should not  
409 be influenced by environmental heterogeneities. Moreover, in the CBS plot we found  
410 that topography had little influence on species diversity variation (Yuan et al. 2011).  
411 In our study, the amount of variance explained by diversity was smaller than that  
412 found in a grassland study (e.g. Liu et al. 2015; 77%) and is more comparable to the  
413 amount found by Vila et al. (2003 & 2007) in forests.

414

## 415 **Conclusions**

416 Based on ten years of forest monitoring data, our findings provide several  
417 important insights for understanding BEF relationships in temperate forests. First, our  
418 analysis did not support the conclusion that phylogenetic diversity and functional  
419 diversity are better predictors of ecosystem functioning (AGB and CWP) than  
420 taxonomic diversity, as evidenced by more explanatory power of species richness than  
421 phylogenetic diversity or functional diversity in the old growth forest. Second, species  
422 richness, phylogenetic diversity, and single functional traits are required  
423 simultaneously to best predict AGB and CWP. In particular, plant functional traits  
424 related to the leaf economic spectrum are important to understand the role of plant  
425 diversity in biomass production. Finally, regardless of diversity indices, stronger  
426 positive BEF relationships were found in the later stage of forest succession, implying  
427 the diversity effect on ecosystem functioning becomes stronger over time. Overall,  
428 our results demonstrate that the multiple metrics of diversity have different effects on

429 temperate forest functioning over time, thus the specific role of each diversity metric  
430 is essential for understanding BEF in any given ecosystem.

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### 623 **Figure legend**

624 Fig.1 Relationship between diversity and forest biomass variables in the secondary  
625 poplar-birch forest (PBF) plot. Solid black lines represent statistically significant  
626 positive slopes, and red dashed lines represent insignificant slopes. Goodness-of-fit is  
627 shown by Akaike weights ( $w_i$ ) and  $R^2$ .

628 Fig.2 Relationship between diversity and forest biomass variables in the old growth

629 forest (CBS) plot. Solid black lines represent statistically significant positive slopes.

630 Goodness-of-fit is shown by Akaike weights ( $w_i$ ) and  $R^2$ .

631