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Species richness, but not phylogenetic diversity, influences community biomass production and temporal stability in a re-examination of 16 grassland biodiversity studies

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41

## 42 **Summary**

43 1. Hundreds of experiments have now manipulated species richness of various groups of  
44 organisms and examined how this aspect of biological diversity influences ecosystem  
45 functioning. Ecologists have recently expanded this field to look at whether  
46 phylogenetic diversity among species, often quantified as the sum of branch lengths on  
47 a molecular phylogeny leading to all species in a community, also predicts ecological  
48 function. Some have hypothesized that phylogenetic divergence should be a superior  
49 predictor of ecological function than species richness because evolutionary relatedness

50 represents the degree of ecological and functional differentiation among species. But  
51 studies to date have provided mixed support for this hypothesis.

52 2. Here, we re-analyze data from 16 experiments that have manipulated plant species  
53 richness in grassland ecosystems and examined the impact on aboveground biomass  
54 production over multiple time points. Using a new molecular phylogeny of the plant  
55 species used in these experiments, we quantified how the phylogenetic diversity of  
56 plants impacts average community biomass production as well as the stability of  
57 community biomass production through time.

58 3. Using four complementary analyses we show that, after statistically controlling for  
59 variation in species richness, phylogenetic diversity (the sum of branches in a molecular  
60 phylogenetic tree connecting all species in a community) is neither related to mean  
61 community biomass nor to the temporal stability of biomass. These results run counter  
62 to past claims. However, after controlling for species richness, phylogenetic diversity  
63 was positively related to variation in community biomass over time due to an increase  
64 in the variances of individual species, but this relationship was not strong enough to  
65 influence community stability.

66 4. In contrast to the non-significant relationships between phylogenetic diversity, biomass,  
67 and stability, our analyses show that species richness *per se* tends to increase the mean  
68 biomass production of plant communities, after controlling for phylogenetic diversity.  
69 The relationship between species richness and temporal variation in community  
70 biomass was either positive, non-significant or negative depending on which analysis  
71 was used. However, the increases in community biomass with species richness,  
72 independently of phylogenetic diversity, always led to increased stability. These results

73 suggest that phylogenetic diversity is no better as a predictor of ecosystem functioning  
74 than species richness.

75 **5. *Synthesis.*** Our study on grasslands offers a cautionary tale when trying to relate  
76 phylogenetic diversity to ecosystem functioning suggesting that there may be  
77 ecologically important trait and functional variation among species that is not explained  
78 by phylogenetic relatedness. Our results fail to support the hypothesis that the  
79 conservation of evolutionarily distinct species would be more effective than the  
80 conservation of species richness as a way to maintain productive and stable  
81 communities under changing environmental conditions.

82

83 **Key-words:** biodiversity, community biomass, data-synthesis, ecosystem functioning,  
84 grasslands, phylogenetic diversity, relatedness, stability.

85

## 86 **Introduction**

87 Over the past few decades, ecologists have completed hundreds of experiments exploring  
88 how the variety of life forms influences the fluxes of carbon and cycling of elements that  
89 control how ecosystems ‘function’ (Schulze & Mooney 1993, Tilman & Downing 1994).  
90 To date, the field of biodiversity and ecosystem functioning (BEF for short) has been  
91 dominated by studies that used species richness as their sole measure of biodiversity  
92 (Loreau *et al.* 2001, Hooper *et al.* 2005, Cardinale *et al.* 2011). However, ecologists have  
93 recently begun to explore how other aspects of diversity like genetic and trait variation can  
94 influence the functioning of ecosystems, and begun to ask whether certain measures of  
95 diversity are better predictors of ecosystem functioning than others (Diaz & Cabido 2001,  
96 Petchey & Gaston 2006, Cadotte *et al.* 2008, Cadotte *et al.* 2012). One form of diversity

97 that has received a growing amount of attention is phylogenetic diversity. Phylogenetic  
98 diversity is a measure of how much evolutionary divergence has occurred among the  
99 species in a community, often measured as the cumulative branch length differences that  
100 separate species on their molecular phylogeny. There are several reasons why ecologists  
101 have become interested in using phylogenetic diversity to predict ecosystem-level  
102 processes. First, this interest is part of a general trend to understand contemporary  
103 ecological patterns by looking at the evolutionary history of organisms in a community  
104 (Webb *et al.* 2002, Johnson & Stinchcombe 2007). As in the field of ‘community  
105 phylogenetics’, researchers in the field of biodiversity and ecosystem functioning have  
106 begun to think about how ecological and evolutionary processes might interact to control  
107 the functioning of ecosystems. Second and more importantly, ecologists have been enticed  
108 by the simplicity of using phylogenetics to predict ecological function. While it is difficult  
109 and time consuming to run manipulative experiments of species richness, and equally  
110 difficult to identify and measure the myriad of species traits that control the functioning of  
111 ecosystems, getting genetic information needed to characterize species relationships and  
112 thus to measure phylogenetic diversity, has become an increasingly straightforward task.

113         The ability to use phylogenetic diversity to predict ecological function is predicated  
114 on a sequence of assumptions that have rarely been tested directly, especially in an  
115 integrated fashion. The first assumption is that the biological traits that control ecological  
116 functions show a phylogenetic signal, meaning they tend to be more similar among closely  
117 related species than between distantly related species (Prinzing *et al.* 2001, Losos 2008,  
118 Wiens *et al.* 2010, Cavender-Bares & Reich 2012). The second assumption is that, when  
119 traits do show a phylogenetic signal, the trait variation leads to functional differentiation  
120 among species. The third and final assumption is that such functional differentiation

121 enhances the productivity or stability of an entire community. Productivity might be  
122 enhanced if, for example, expression of a greater variety of traits allows species to better  
123 exploit all of the available resources (Tilman *et al.* 1997, Loreau 2004, Reich *et al.* 2012,  
124 Srivastava *et al.* 2012). To date, the influence of phylogenetic diversity on ecosystem  
125 functioning has been explored in just twelve studies that we know of, and these span a  
126 relatively small number of systems (see **Table 1**). Eight of these have found a positive  
127 relationship between phylogenetic diversity and various aspects of ecosystem functioning,  
128 one found a negative relationship, and three showed either mixed results or more complex  
129 non-linear relationships. In the instances where phylogenetic diversity was positively  
130 related to ecosystem functioning, it tended to explain only a small fraction more of the  
131 variation than species richness (Cadotte *et al.* 2008, Cadotte *et al.* 2009, Cadotte 2013, but  
132 see Paquette & Messier 2011, Cadotte *et al.* 2012). Nonetheless, authors of these studies  
133 tend to strongly advocate for the importance of PD for ecosystem functioning.

134         Many studies have also shown that diverse communities have more temporally  
135 stable biomass production than less diverse communities. In most cases the temporal  
136 stability of community biomass production is commonly measured as the inverse of its  
137 coefficient of variation over time (Tilman 1999, Jiang & Pu 2009, Hector *et al.* 2010,  
138 Campbell *et al.* 2011), which is the biomass of the community averaged over time divided  
139 by its standard deviation through time. The standard deviation of community biomass can  
140 be influenced by changes in variances of individual species' biomasses as well as by  
141 changes in the synchrony of species' biomass fluctuations over time. Thus, diversity can  
142 influence temporal community biomass stability through the average biomass production of  
143 the community or through individual species' biomasses (e.g., their synchrony). Higher  
144 community biomass, lower sum of species variances and more asynchronized fluctuations

145 of species' biomasses would increase community stability. Assuming communities with  
146 higher phylogenetic diversity result in the expression of a greater variety of traits allowing  
147 species to better exploit resources, it can be predicted that the average community biomass  
148 will increase with phylogenetic diversity. Similarly, a greater variety of traits (assumed to  
149 be represented by a higher phylogenetic diversity) should allow communities to show a  
150 greater array of compensatory dynamics (Tilman 1999, Hector *et al.* 2010, Violle *et al.*  
151 2011, Cadotte *et al.* 2012, Verdu *et al.* 2012), reducing the standard deviation of  
152 community biomass over time. Overall, the temporal stability of community biomass,  
153 measured as the average community biomass divided by its standard deviation is expected  
154 to increase as phylogenetic diversity increases. To date, only three studies have explored  
155 the influence of phylogenetic diversity on the temporal stability of ecosystem function  
156 (**Table 1**). One found a positive effect of phylogenetic diversity on the stability of plant  
157 biomass in grasslands (Cadotte *et al.* 2012), one found a negative effect on the stability of  
158 algal biomass in microcosms (Venail *et al.* 2013), and one found a non-linear (U-shaped)  
159 relationship between phylogenetic diversity and the stability of protists' biomass in  
160 microcosms (Pu *et al.* 2014). The relatively small number of studies and their equivocal  
161 results suggest more comprehensive studies are needed.

162 Here, we reanalyze data from 16 biodiversity experiments using grassland plants to  
163 better assess how phylogenetic diversity influences the production of biomass and its  
164 stability over time. Twelve of the studies used here are a subset of the 29 studies used by  
165 Cadotte *et al.* (2008) to examine how phylogenetic diversity impacts biomass production,  
166 and all 16 studies are the same studies whose time-series were used by Cardinale *et al.*  
167 (2011) and Gross *et al.* (2014) to examine how species richness influences the stability of  
168 biomass production through time. The primary advance of our study is that we use four

169 different complementary analytical methods to separate the effects of phylogenetic  
170 diversity and species richness on community productivity and stability. These two forms of  
171 diversity are inherently correlated since a greater number of species almost always  
172 correlates with greater summed genetic divergence on a phylogeny. However, this  
173 correlation has not been adequately dealt with in prior studies and, as we will show, our  
174 analyses lead to several modified conclusions about the role of species vs. phylogenetic  
175 diversity in ecosystem functioning.

176

## 177 **Methods**

### 178 *Data*

179 Our study represents a new data synthesis of 16 previously published studies that have  
180 examined the relationship between plant biodiversity and the production and stability of  
181 population and community-level biomass in grasslands. Data from these studies were  
182 previously compiled for use in other data syntheses (Cadotte *et al.* 2008, Cardinale *et al.*  
183 2011, Gross *et al.* 2014) where studies were chosen based on the following criteria: 1)  
184 experiments had to be performed in grasslands, which is the system most frequently studied  
185 in BEF research and for which the most data are available; 2) studies had to include  
186 estimates of net annual aboveground plant biomass production or aerial coverage; 3) studies  
187 had to include at least three sampling occasions performed over time, thus allowing  
188 estimation of temporal stability; and 4) studies had to include species-level data for each  
189 experimental plot, thus allowing measurement of responses to environmental fluctuations  
190 of individual species in polycultures (which is necessary for certain calculations of  
191 stability). Only sixteen studies met all four of these criteria (**Table S1**). All the data used in  
192 the current analysis are available in dryad (<http://datadryad.org/>).

193

194 *Molecular phylogeny*

195 We estimated phylogenetic relationships of 141 plant species used in the experimental plots  
196 plus two outgroups (*Magnolia grandiflora* and *Amborella trichopoda*, **Fig. S1**). For this,  
197 we used publicly available genetic data from 6 gene sequences commonly used in  
198 angiosperm phylogenetics: *matk*, *rbcl*, *ndhf*, *its1*, *its2*, and *5.8s*. All but 14 species had  
199 publicly available genetic data from at least one of the target genes. To represent each  
200 species that had none of these genes available (*Amorpha canadensis*, *Anemone cylindrica*,  
201 *Bothriochloa laguroides*, *Conyza albida*, *Dalea villosa*, *Medicago varia*, *Mulinum*  
202 *spinosum*, *Nassella leucotricha*, *Pimpinella major*, *Poa ligularis*, *Salvia azurea*,  
203 *Sporobolus compositus*, *Stipa speciosa*, *Symphotrichum oolentangiense*), we randomly  
204 chose a representative congener with target genes publicly available (*Amorpha fruticosa*,  
205 *Anemone patens*, *Bothriochloa insculpta*, *Conyza gouanii*, *Dalea brachystachya*, *Medicago*  
206 *sativa*, *Mulinum chillanense*, *Nassella pampagrandensis*, *Pimpinella betsileensis*, *Poa*  
207 *sichotensis*, *Salvia przewalskii*, *Sporobolus atrovirens*, *Stipa stenophylla*, *Symphotrichum*  
208 *ericoides*). Accession numbers for all genes used are reported in **Table S2**. We aligned all  
209 sequences of each gene using MUSCLE (Edgar 2004). We concatenated all genes using  
210 phyloclatenator (Oakley *et al.* 2014) and estimated a maximum likelihood phylogeny using  
211 RAxML (Stamatakis & Ott 2008), along with 100 bootstrap pseudoreplications to gauge  
212 nodal support. We conducted all phylogenetic analyses in the Osiris package (Oakley *et al.*  
213 2014) of Galaxy, which allows us to easily share all data and analyses with a web link  
214 (<http://galaxy-dev.cnsi.ucsb.edu/osiris/u/ostratodd/h/plant-pd-venail>).

215 To estimate the evolutionary relatedness among species in a plot we used  
216 phylogenetic diversity, defined as the total phylogenetic distance among two or more  
217 species (Faith 1992, Cadotte *et al.* 2008). Thus, the phylogenetic diversity of an assemblage  
218 (plot) is influenced both by the number of species and by their level of evolutionary  
219 relatedness. Phylogenetic diversity is inversely proportional to the evolutionary relatedness  
220 of the species, thus the more distantly related a set of species becomes, the higher the  
221 phylogenetic diversity will be. We used Picante in R (Kembel *et al.* 2010) to calculate  
222 different phylogenetic diversity metrics including phylogenetic distance (PD, Cadotte *et al.*  
223 2008), mean phylogenetic distance (MPD, Webb *et al.* 2008), mean nearest taxon distance  
224 (MNTD, Webb *et al.* 2008) and phylogenetic species variability (PSV, Helmus *et al.* 2007)  
225 for each plot (data available in dryad). We assessed the sensitivity of our estimates of  
226 phylogenetic diversity to different phylogenies by comparing our values with those  
227 obtained using a recently published plant phylogeny (Zanne *et al.* 2014). That phylogeny,  
228 like ours, is based on a Maximum Likelihood analysis of GenBank data. The Zanne *et al.*  
229 tree used seven gene regions from GenBank, so there is substantial overlap of primary data  
230 with our phylogeny. The Zanne *et al.* analysis differs from ours in that those authors  
231 constrained major clades (families and orders), partitioned data by gene regions, and  
232 smoothed their tree using divergence time estimates.

### 233 *Productivity & Stability*

234 We focus on the influence of biodiversity on both 1) the production and 2) temporal  
235 stability of biomass produced by mixtures of grassland plant species grown in polyculture.  
236 At each time point community biomass production was estimated as the sum of the biomass  
237 produced by all the species in a plot. Then, we averaged community (plot) biomass over

238 time. Most estimates of biomass production in the datasets are in units of mass per area;  
239 however, two studies used estimates of aerial plant coverage instead (studies 12 and 15,  
240 **Table S1**). For consistency with previous data-synthesis (Cardinale *et al.* 2011, Gross *et al.*  
241 2014) we did not transform the data from these two studies.

242 The most commonly used measure of temporal variability in community biomass is  
243 the coefficient of variation (Jiang & Pu 2009, Hector *et al.* 2010, Campbell *et al.* 2011),  
244 which is the standard deviation of community biomass through time scaled to account for  
245 the average biomass of the community. Temporal community stability is then the inverse of  
246 the coefficient of variation:

$$248 \text{ stability} = \frac{\bar{x}}{sd} \quad \text{Equation 1}$$

249  
250 Thus, community stability can be influenced both by changes in the average biomass  
251 production (numerator of **equation 1**) or by changes in the temporal standard deviation of  
252 biomass production (denominator of **equation 1**). The standard deviation can be further  
253 decomposed into the sum of population-level variances and the covariances among species'  
254 biomasses through time. The covariance in species biomasses is frequently used as a  
255 measure of the degree of synchrony in the temporal variation of species' population  
256 responses (Jiang & Pu 2009). However, when more than two species are present in an  
257 assemblage, it is now known that covariance is an inappropriate measure of species  
258 synchrony because the covariance depends on both the number of species and the  
259 synchrony among them (Loreau & de Mazancourt 2008, 2013). This limitation has  
260 hindered interpretation of what most contributes to stability, and has led to efforts to

261 develop new metrics of species synchrony (Loreau & de Mazancourt 2008, Gross *et al.*  
262 2014). Here, we used the most recent metric developed by Gross *et al.* (2014), which  
263 measures synchrony among species' biomasses as the average correlation between the  
264 biomass of each species ( $Y_i$ ) and the total biomass of all other species in the group  
265 ( $\sum_{j \neq i} Y_j$ ).

266

$$267 \text{ synchrony} = \left(\frac{1}{n}\right) \sum_i \text{corr} (Y_i, \sum_{j \neq i} Y_j) \quad \textbf{Equation 2}$$

268

269 A *synchrony* value close to -1 suggests species are maximally asynchronized, a value close  
270 to +1 that species are maximally synchronized and values close to 0 that species fluctuate  
271 independently.

272 To summarize, in our analyses we used phylogenetic diversity and species richness  
273 as explanatory variables. Stability and its different components (average biomass and  
274 standard deviation, **equation 1**) as well as the sum of variances and synchrony (**equation 2**)  
275 were used as response (dependent) variables.

276

### 277 *Statistical Analyses*

278 Within the full dataset we assembled, which contains 824 experimental plots spread across  
279 16 studies, measures of phylogenetic diversity (PD) and species richness (SR) were highly  
280 correlated with one another (**Fig. 1a**,  $r = 0.90$ ). This high degree of correlation is not  
281 surprising given that PD is not only influenced by the branch lengths separating species on  
282 a phylogeny (i.e., their relatedness), but also by the number of species being considered.  
283 Importantly, these 16 experiments were not originally designed to produce a wide range of

284 PD values or to manipulate phylogenetic diversity independently of species richness.  
285 Therefore, the high degree of correlation leads to statistical problems of multi-collinearity  
286 in many forms of data analyses, making it difficult to draw robust conclusions about the  
287 influence of PD per se, or SR per se on biomass production and stability.

288 In an attempt to disentangle the effects of PD and SR on community biomass  
289 production and temporal stability in community biomass, we performed four unique  
290 analyses on this dataset (**Fig. 1**). These are described as follows:

291 *Type 1 analysis:* In this analysis (**Fig. 1a**) we quantified the effect of PD on  
292 community stability, community biomass production (**equation 1**), standard deviation, sum  
293 of variances and the synchrony metric (**equation 2**) within levels of species richness (i.e.,  
294 holding SR constant). The original dataset included species assemblages that spanned a  
295 wide array of planted species richness levels (from 2 to 60). However, we focused on  
296 richness levels 2, 3, 4, 6, 8, 9, 11, 12 and 16 species (for 716 plots in total) because these  
297 were the richness levels for which multiple studies were represented and each level of  
298 richness had multiple values of phylogenetic distance (i.e., different species compositions).  
299 For each study and within each species richness level, we calculated the correlation  
300 between phylogenetic distance (PD) and each of five response variables: 1) temporally  
301 averaged community-level biomass (biomass summed across all species in a plot at each  
302 time point, then averaged over time; numerator in right side of **equation 1**), 2) the temporal  
303 standard deviation of community biomass (denominator in right side of **equation 1**), 3) the  
304 community-level temporal stability of biomass (left side of **equation 1**), 4) the summed  
305 variances of individual species' biomasses and 5) population-level temporal synchrony (as  
306 in **equation 2**). Correlation coefficients were weighted by the number of plots in each  
307 study to reduce the influence of poorly replicated studies. We normalized the distribution of

308 data using Fisher's z-algorithm ( $Z_r$ ; Balvanera *et al.* 2006) to test if for each of the five  
309 response variables the weighted/normalized correlation coefficients ( $Z_r$ ) were significantly  
310 different from zero using double-tailed t-tests.

311 *Type 2 analysis:* Unlike the *type 1 analysis* where we were able to analyze the  
312 impact of phylogenetic diversity (PD) on production and stability with species richness  
313 (SR) held constant, a directly comparable analysis looking at the effects of SR with PD held  
314 constant is not straightforward. This is because PD represents a continuous measure that  
315 cannot be binned into categories in the same way SR can. Nevertheless, in our *type 2*  
316 *analysis* (**Fig. 1a**) we were able to identify a large number of experimental plots that were  
317 relatively similar in values of PD, but which had differing levels of SR. For each study, we  
318 compared every plot to every other plot in the study. We found a total of 1,417 pairs of  
319 plots, with each pair belonging to the same study where PD differed by <10%, but for  
320 which species richness differed. When compared to random sampling of plots, these paired  
321 contrasts represent a highly constrained range of variation in PD, and come as close as is  
322 reasonably possible to holding PD constant while allowing SR to vary (**Fig. S3**). For each  
323 of these 1,417 pair-wise contrasts, we calculated the log ratios of community biomass and  
324 stability,  $\ln(Y_{\text{high richness}}/Y_{\text{low richness}})$ , where Y represents: a) total plot biomass, b) standard  
325 deviation of biomass, c) temporal stability of biomass through time or d) the sum of  
326 variances for the high vs. the low species richness plot within each pair. Positive log ratios  
327 indicate that the more speciose community either: produces more biomass, has a higher  
328 standard deviation in biomass through time, is more stable than the less speciose  
329 community or has more variable species. We used two tailed t-tests to evaluate if log-ratios  
330 for each metric were different from zero. We could not establish log ratios for synchrony

331 because synchrony can have negative values and it is not possible to calculate a logarithm  
332 of negative values.

333 *Type 3 analysis:* In this analysis we used Structural Equation Modelling (SEM) to  
334 summarize data from five experiments (studies 5, 6, 9, 13 and 14 in **Table S1**) where the  
335 species pools used led to relatively low correlation coefficients relating PD and SR (**Fig.**  
336 **1b**,  $N = 5$  studies,  $r = 0.72$  using 222 experimental plots). While these five studies represent  
337 but a subset of available data, the correlations between PD and SR in all other studies were  
338 well above 0.8, rendering them unusable in any attempts to statistically control for  
339 covariance among SR and PD in a single analysis. However, for this subset of five studies,  
340 it was possible to statistically control for the covariance between SR and PD. In turn, the  
341 SEM allowed us to calculate the partial regression coefficients that represent the unique  
342 coefficients relating both PD and SR to community biomass and the standard deviation of  
343 biomass through time. We did not incorporate the sum of variances and synchrony into *type*  
344 3 analyses because clear causal pathways have yet to be established.

345 *Type 4 analysis:* In *type 1, 2 and 3 analysis* we use PD as a metric of phylogenetic  
346 diversity, which is the metric used in most previously published studies (8 out of 12 listed  
347 in **Table 1** used it). However, other metrics of evolutionary relatedness have been  
348 developed; among the more common are the mean pairwise distance (MPD), mean nearest  
349 taxon distance (MNTD, Webb *et al.* 2008) and phylogenetic species variability (PSV,  
350 Helmus *et al.* 2007). Some of these have been proposed to be less correlated to species  
351 richness than PD (**Fig. 1c**, **Fig. S4**) and would, in principle, reduce statistical problems  
352 related to multi-collinearity. However, there are concerns about more advanced metrics like  
353 MPD and MNTD because they count each branch of the phylogenetic tree multiple times  
354 depending on the number of species in a plot (e.g., in a plot with  $n$  species each branch is

355 counted  $n-1$  times). We complemented our three other types of analyses with *type 4*  
356 *analysis* that used linear mixed effect (LME) models to explore the impact of species  
357 richness (SR) and mean pairwise distance (MPD) on all five dependent variables: stability,  
358 average biomass, standard deviation, sum of variances and synchrony. Analysis using  
359 MNTD and PSV would lead to the same results given their strong correlation with MPD  
360 (**Fig. S2**). All our LME models also included “study” as random effects.

361

## 362 **Results**

### 363 *Phylogeny*

364 The topology of the phylogeny of grassland plants included in the current study (**Fig. S1**) is  
365 very similar to a previous study that used similar methods ( $\rho = 0.947$ ,  $p < 0,001$ ; Cadotte *et*  
366 *al.* 2008). As expected, we found support for two major ingroup clades, Poales and  
367 eudicots. Forty-one nodes are supported by 100% bootstrap values. Twenty nodes showed  
368 lower than 50% bootstrap support, suggesting uncertainty in these nodes. In previous  
369 studies (e.g., Cadotte *et al.* 2008) sensitivity analyses using different phylogenetic  
370 approaches indicated that correlations between phylogenetic diversity and other variables  
371 were very minimally affected by differences in tree topology. Again, we found very similar  
372 values of phylogenetic diversity based on our new tree compared to values obtained with a  
373 recently published tree that used different (but overlapping) primary data and made  
374 different assumptions (Zanne *et al.* 2014, **Fig. S2**). Values for the four different  
375 phylogenetic diversity metrics assuming the two different phylogenetic analyses for each  
376 community are available in dryad.

377

378 *Type 1 analysis: effect of PD within richness levels.*

379 For each level of species richness considered, studies showed highly variable effects of  
380 phylogenetic diversity (PD) on stability, average biomass production, standard deviation  
381 (SD), the sum of species variances (sum. var.) and synchrony, ranging from negative to  
382 positive relationships (**Fig. 2a**). Of these, only a limited set of studies had any significant  
383 relationship between PD and community stability or its different components (**Fig. 2a**).  
384 When the correlation coefficients were weighted and averaged across all experiments, there  
385 was a tendency for PD to be negatively related to temporal community stability and  
386 positively related to average community biomass production, though neither of these trends  
387 were significantly different from zero at the  $p = 0.05$  level of significance (**Fig. 2b**). PD  
388 was, however, positively correlated with temporal variation in community biomass (SD  
389 biomass), a trend that was driven by an increase in the summed variance across species,  
390 rather than by a change in the synchrony of species' biomasses through time (**Fig. 2b**).

391

392 *Type 2 analysis: effect of SR within PD bins.*

393 When we performed pair-wise comparisons among plots that differed in SR but had similar  
394 PD (values differing by less than 10%), the temporal stability of biomass and the average  
395 biomass both significantly increased as a function of SR (**Fig. 3**). In contrast, the standard  
396 deviation of community biomass through time (S.D.) was negatively influenced by SR. The  
397 sum of species variances (sum. var.) was not affected by species richness.

398

399 *Type 3 analysis: Effect of PD and SR after accounting for their covariance.*

400 After accounting for the covariance between SR and PD in the five experiments with the  
401 lowest correlations (mean  $r = 0.72$ ,  $p < 0.05$ ,  $n = 222$ ), a path analysis suggested that SR

402 was positively associated with mean plot biomass ( $r = 0.39, p < 0.01$ ) and with the standard  
403 deviation of biomass over time ( $r = 0.20, p < 0.05$ , **Fig. 4**). Therefore, there were positive  
404 indirect effects of SR on community stability that were mediated through the increase in  
405 biomass ( $r = 0.30, p < 0.01$ ) and variance ( $r = -0.21, p < 0.01$ , **Table S3**). In contrast, PD  
406 was not associated with the standard deviation of biomass over time ( $r = 0.10, p > 0.05$ ) or  
407 with any change in the mean community biomass ( $r = 0.003, p > 0.05$ , **Fig. 4**). Therefore,  
408 there were no indirect effects of PD on community stability via biomass ( $r = 0.002, p >$   
409  $0.05$ ) or variance ( $r = -0.11, p > 0.05$ , **Table S3**).

410

411 *Type 4 analysis: Effect of MPD and SR.*

412 Linear mixed effect (LME) models with species richness (SR), mean pairwise distance  
413 (MPD, both as fixed effects) and study (as random effect) on the five different dependent  
414 variables revealed a positive effect of species richness on stability, average biomass,  
415 standard deviation (S.D.) and synchrony, but no effect on the sum of species variances  
416 (sum. var., **Table S4**). Phylogenetic diversity (measured as MPD) had positive effects on  
417 S.D. driven by a positive effect on the sum of species variances, but had no effect on  
418 stability, average biomass or synchrony.

419

420 *Summary of results*

421 **Table 2** summarizes results of the different types of analyses, which were consistent in  
422 showing a positive relationship between species richness (SR) and biomass production after  
423 controlling for phylogenetic diversity. Analyses disagreed in how SR influences the  
424 standard deviation of biomass through time. Type 2 analyses showed a negative influence  
425 of SR on S.D. but with an absence of effect on the sum of variances. Type 3 showed a

426 positive effect on S.D. whereas Type 4 showed no effect on S.D., with type 4 also revealing  
427 no effect on the sum of species variances but a positive effect of SR on synchrony.  
428 Ultimately all the analyses converged in showing that species richness has a positive  
429 influence on community biomass stability, via the increase in average community biomass.

430 Analyses were also consistent in showing that phylogenetic diversity (measured as  
431 PD for type 1-3 analyses, and as MPD for type 4 analysis), after controlling for species  
432 richness, did not explain any significant variation in mean community biomass. While  
433 there was a positive effect of phylogenetic diversity (either as PD in Type 1 and MPD in  
434 Type 4 analysis respectively) on the standard deviation of biomass over time, driven by a  
435 positive effect on the sum of variances but not on synchrony, this was not sufficiently large  
436 to generate a decrease in community stability as PD increased.

437

## 438 **Discussion**

439 Here, we re-analyzed data from sixteen experiments that manipulated plant species richness  
440 in grassland ecosystems to examine how species richness and phylogenetic diversity  
441 influence mean community biomass and its temporal stability. The primary advance of our  
442 study was to use a variety of analyses that attempt to control for the inherent positive  
443 covariance between species richness and phylogenetic diversity so that we could try to  
444 tease apart their effects. Consistent with the results of many individual studies (e.g., almost  
445 all of those referenced in **Table 1**, among others) and prior data syntheses (e.g., Balvanera  
446 *et al.* 2006, Cardinale *et al.* 2006, Cadotte *et al.* 2008, Cardinale *et al.* 2011, Flynn *et al.*  
447 2011, Gross *et al.* 2014), our analyses confirmed that plant communities composed of more  
448 species tend to produce greater community level biomass and to be more stable over time.  
449 This result held true even after controlling for variation in the phylogenetic diversity of

450 species, suggesting that the impact of species richness on biomass production and temporal  
451 stability cannot be explained fully by differences in phylogenetic diversity among  
452 communities.

453         Although our analyses confirmed prior conclusions about the positive effect of  
454 species richness on community biomass production and stability after controlling for  
455 variation in phylogenetic diversity, the reverse was not true. We found no evidence that,  
456 after controlling for variation in species richness, phylogenetic diversity was related to  
457 community biomass production or its temporal stability in grasslands. Despite this absence  
458 of any effect on the average community biomass and stability, two of our analyses revealed  
459 a positive effect of phylogenetic diversity on the standard deviation (S.D.) of community  
460 biomass. Examination of the sum of species variances and synchrony components suggest  
461 that the increase in community biomass standard deviation (S.D.) was driven by an increase  
462 in the sum of individual species variances and not by changes in the synchrony of their  
463 fluctuations. This suggests that closely related species share low biomass variation over  
464 time but these similarities vanish as species become less related, providing some evidence  
465 of a phylogenetic signal in the temporal variation of species' biomass. A recent study by  
466 Godoy *et al.* (2014) found that fitness differences among annual plants were higher and  
467 much more variable between distantly than closely related species, suggesting that the  
468 outcome of competition should be more variable between more distantly related species. It  
469 is possible that such increased competitive variability with increasing phylogenetic  
470 diversity lead to an increase in biomass variability over time. Though, the observed  
471 increase in the sum of variances with PD could also be due to a higher probability of the  
472 presence of species with higher biomass variability in plots with higher phylogenetic  
473 diversity (i.e., sampling effect).

474 Our general conclusion about the lack of effect of phylogenetic diversity on  
475 community biomass differs from the conclusions of two previous data-syntheses (Cadotte  
476 *et al.* 2008, Flynn *et al.* 2011). Cadotte *et al.* (2008) summarized data from 29 experiments  
477 that manipulated richness of terrestrial angiosperms and asked whether phylogenetic  
478 diversity could explain variation in a standardized diversity “effect size” (the log ratio of  
479 biomass in a polyculture / the mean biomass of the constituent species in monoculture). The  
480 authors concluded that “*the amount of phylogenetic diversity within communities explained*  
481 *significantly more variation in plant community biomass than other measures of diversity,*  
482 *such as the number of species or functional groups*”. In an attempt to deal with the strong  
483 covariance between species richness and phylogenetic diversity, Cadotte *et al.* (2008)  
484 examined how phylogenetic diversity related to diversity effect sizes within levels of  
485 species richness. They found that phylogenetic diversity was only related to diversity  
486 effects at the lowest levels of richness (i.e., 2 and 4 species), and suggested this was  
487 because researchers tended to use fewer species combinations at high levels of richness  
488 (i.e., 6 and 8 species), resulting in less variation in phylogenetic diversity.

489 The study by Cadotte *et al.* (2008) differs from ours in several aspects. First, only  
490 twelve of the studies included in our analyses overlapped with those included in their  
491 dataset. This is because we only included studies providing community biomass for at least  
492 three different time-points so that we could quantify temporal stability. Second, the  
493 phylogenetic trees used to calculate the phylogenetic diversity within plots in our study and  
494 the Cadotte *et al.* 2008 study were though similar but not exactly the same. Third, the  
495 response variables used in our studies were different; we used the mean biomass across  
496 time-series, as opposed to a log response ratio at a single time point used in Cadotte *et al.*’s  
497 study. Finally, the statistical analyses also differed among studies. Cadotte *et al.* used linear

498 mixed effect models with species richness and phylogenetic diversity as explanatory  
499 variables despite the fact these two variables were strongly correlated. In our study, to  
500 avoid the problems related to covariance of the explanatory variables, we calculated  
501 correlation coefficients between phylogenetic diversity and community biomass at each  
502 level of species richness and for each individual study. Then we weighted and averaged the  
503 correlation coefficients among studies and richness levels.

504         In order to determine which of these four factors were responsible for the  
505 discrepancies in the results among both studies, we collated a dataset that contained the  
506 explanatory (i.e., phylogenetic diversity) and dependent variables (i.e., community  
507 biomass) from both studies. This resulted in an overlapping dataset that included 318 plots.  
508 We tested the effect of switching the two metrics of phylogenetic diversity, the two  
509 measures of community biomass and the two statistical analyses from both studies by  
510 performing a series of permutations using the collated dataset (see Supplementary Material  
511 **S4**). The permutations revealed that the conclusions from both studies about the effect of  
512 phylogenetic diversity on community biomass (i.e., positive for *Cadotte et al.*'s and no  
513 effect for this study) differed because they focused on different measures of community  
514 biomass and used different statistical approaches. This is not surprising, given that both  
515 studies were answering different questions related to the role of phylogenetic diversity as a  
516 predictor of community biomass as we explained before. We consider that for the purposes  
517 of our study, which was to separate the effects of SR and PD, the statistical approach based  
518 on coefficients of correlations is more appropriate because it avoids problems due to  
519 collinearity between species richness and phylogenetic diversity. Moreover, the lack of  
520 effect of phylogenetic diversity (as PD) on community biomass was confirmed by a linear  
521 mixed effect models using MPD as the explanatory variable. While useful for addressing

522 questions related to the effect of diversity on ecosystem functioning, log ratios open the  
523 possibility that the observed differences in community biomass are due to differences in the  
524 monoculture biomasses of the constituent species, which seemed to be the case here (see  
525 Supplementary Material **S4**). For instance, having monocultures with lower average  
526 biomass would result in higher community biomass if estimated as log ratios. Thus, to  
527 allow a clearer interpretation of the differences in biomass among communities we  
528 preferred to directly analyze raw community biomass.

529         Our results also deviate from the conclusions of another prominent data synthesis  
530 by Flynn *et al.* (2011), who added measures of functional diversity (i.e., trait variation  
531 among plant species on the phylogeny) to Cadotte *et al.*'s dataset and tested to see if  
532 functional diversity was a superior predictor of biomass production than phylogenetic  
533 diversity. The authors ran a variety of models comparing the explanatory power of  
534 phylogenetic diversity alone, functional diversity alone, both together, as well as in  
535 combination with species richness. They concluded that a model containing only  
536 phylogenetic diversity was the most likely explanation of variation in plant biomass among  
537 plots (see Table 2 in their paper). But Flynn *et al.* did not statistically control for the  
538 covariance between species richness and phylogenetic diversity when drawing their  
539 conclusions. Because none of their linear mixed models (Table 2 in Flynn *et al.* 2011)  
540 accounted for covariance among variables, nor did any of their multivariate analyses (see  
541 the Structural Equations models presented in their Figure 3 and their Appendix), we cannot  
542 judge how their findings relate to our own. While our results do not directly contradict  
543 previous findings, given that we were addressing related but different questions, the  
544 contrast in our conclusions leads us to believe that former statements about the strong  
545 impacts of phylogenetic diversity on community biomass may have been partly driven by

546 the strong correlation between phylogenetic diversity and species richness. When we  
547 control for the collinearity between species richness and phylogenetic diversity, the residual  
548 effects of phylogenetic diversity on community biomass are non-significant.

549         The recent incorporation of phylogenetic information into biodiversity-ecosystem  
550 functioning (BEF) studies, and into community ecology research in general, was motivated  
551 at least partially by the relative ease of measuring phylogenetic distances among species  
552 compared to measures of their functional differentiation (Cadotte *et al.* 2008, Srivastava *et*  
553 *al.* 2012). With the increased availability of updated phylogenies, some had hoped that  
554 phylogenetic diversity metrics would summarize information on ecological traits and thus  
555 predict ecosystem function. Our results, showing an absence of effect of phylogenetic  
556 diversity on average community biomass and its temporal stability in grassland  
557 communities, run counter to this expectation.

558         The use of phylogenetic diversity as a predictor of ecosystem functioning assumes  
559 that evolutionary distance and ecological differentiation are positively related, with close  
560 relatives being ecologically more similar than distant relatives (i.e., phylogenetic signal;  
561 Losos 2008, Wiens *et al.* 2010). There are currently divergent positions on whether or not  
562 the evolutionary relatedness among modern species is a reasonable proxy for ecological  
563 similarity (Prinzing *et al.* 2001, Freckleton *et al.* 2002, Johnson & Stinchcombe 2007,  
564 Losos 2008, Wiens *et al.* 2010, Cavender-Bares & Reich 2012, Narwani *et al.* 2013, Kelly  
565 *et al.* 2014, Venail *et al.* 2014, Münkemüller *et al.* in press). Moreover, in order to  
566 positively influence ecosystem functioning, more phylogenetically diverse communities  
567 need to somehow maximize resource partitioning (i.e., niche complementarity) or to  
568 enhance facilitation, thus leading to greater resource use efficiency compared to less  
569 diverse communities. Similarly, to ensure ecosystem functioning in the face of changing

570 conditions (i.e., to increase temporal or spatial stability) phylogenetically diverse  
571 communities may generate negative covariances in population dynamics by either  
572 increasing competitive interactions (Godoy *et al.* 2014) or by ensuring that species'  
573 responses to the environment are independent (Venail *et al.* 2013). Our analyses suggest  
574 that the phylogenetic relatedness of species, beyond its covariance with species richness,  
575 may not be a good predictor of ecosystem functioning (at least when this is measured as  
576 biomass production) with one possible explanation being the lack of phylogenetic signal in  
577 traits related to biomass production. This would suggest that, across the suites of species  
578 used in these experiments, functional complementarity between species did not increase  
579 with increasing phylogenetic distance between them.

580         More broadly, our result suggest that if standard diversity metrics based on species  
581 numbers (e.g., species richness) were to be replaced by alternative metrics based on genetic  
582 differentiation (e.g., phylogenetic diversity), caution would be needed when inferring  
583 ecosystem functioning because there may be functionally important trait differences among  
584 species that are not simply explained in full by phylogenetic relatedness (Kelly *et al.* 2014).  
585 While maximizing phylogenetic diversity (Vane-Wright *et al.* 1991, Faith 1992, 1994,  
586 Winter *et al.* 2013) might seem to be a promising way to maximize functional diversity and  
587 thus ecosystem functioning, management recommendations that suggest conservation of  
588 evolutionarily distinct species will lead to higher functional diversity and more stable  
589 communities are not well supported by the data explored in this study.

590

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734  
735

736 **Figure legends**

737 **Figure 1:** The relationship between species richness (SR) and phylogenetic distance (PD)  
738 or (MPD) for the grassland studies used in this data synthesis. a) For the full dataset with  
739 824 data points (plots) from 16 independent studies (experiments), PD and SR are very  
740 highly correlated ( $r = 0.90$ ; plots with  $SR = 60$  are not shown in the graph). This leads to  
741 problems of multi-collinearity that make it difficult to separate the effects of PD on  
742 community stability from those of SR in any multivariate analyses. Because of this, we  
743 performed four complementary types of analyses. For Type 1 analyses, we analyzed the  
744 impacts of PD on stability within levels of SR, (i.e., to analyze effects of PD whilst holding  
745 SR constant). In the Type 2 analysis, we did the opposite and identified 1417 contrasts  
746 where plots within a study had very similar values of PD, but differed in SR. While it was  
747 not possible to hold PD statistically ‘constant’, these contrasts offered the closest  
748 approximation. b) In the Type 3 analyses, we used five of the 16 studies where PD and SR  
749 had the lowest correlations ( $r \leq 0.80$ ; studies 5, 6, 9, 13 and 14 from Table 2), which  
750 allowed us to perform more traditional multivariate analyses on this subset of data while  
751 accounting for the covariance among explanatory variables. c) In the Type 4, we used an  
752 alternative metric of phylogenetic diversity (mean pairwise distance, MPD), which is  
753 independent of SR ( $r = -0.013$ , plots with  $SR = 60$  are not shown), allowing us to include  
754 the full dataset (824 plots). See text for further explanation.

755

756 **Figure 2:** The effect of phylogenetic diversity (PD) on stability and its different  
757 components, whilst holding species richness (SR) constant. a) Coefficients of correlation  
758 relating phylogenetic diversity (PD) to stability (diamonds), as well as the two components

759 contributing to stability: average biomass (circles) and standard deviation (squares); and to  
760 sum of species variances (sum.var., triangles) and synchrony (crosses). Each data point  
761 represents the correlation for one individual study. Results are presented for each species  
762 richness level (SR, vertical axis) so that conclusions can be drawn about the influence of  
763 PD, without confounding changes in SR. Filled data points and plus signs represent studies  
764 where correlation coefficient values were significant ( $p < 0,05$ ). b) Overall weighted and  
765 normalized average coefficients of correlation (Weighted  $Z_r$ , see text for details) between  
766 phylogenetic diversity (PD) and each component of temporal community stability including  
767 all the species richness levels. The sign of overall  $Z_r$  represents the overall shape of the  
768 relationship between PD and each component (either positive, neutral or negative).  
769 Horizontal bars represent 95% confidence intervals. Filled symbols represent overall  $Z_r$   
770 values that are significantly different from zero.

771

772 **Figure 3:** The effect of species richness (SR) on stability and its different components,  
773 while holding phylogenetic diversity (PD) constant. For the 1417 contrasts used in type 2  
774 analysis, we further calculated the log ratios for community stability, average community  
775 biomass, standard deviation of biomass (S.D.) and sum of variances of individual species'  
776 biomass (sum.var.) in plots through time for higher vs. lower species richness. For a clearer  
777 interpretation of the data the x-axis is presented in a non-log scale. Values higher than one  
778 for stability and average biomass indicate that more speciose communities are more stable  
779 and produce more biomass than less speciose ones. A value lower than one for S.D.  
780 indicates that the biomass of more speciose communities has lower temporal variation than  
781 the biomass of less speciose communities. Data points are the mean and 95% confidence

782 intervals. Note that synchrony is not represented because it is not possible to estimate log  
783 ratios on negative values.

784

785 **Figure 4:** Results of a structural equations model (SEM) showing the joint effects of  
786 species richness (SR) and phylogenetic diversity (PD) on stability. The SEM that used data  
787 from 5 studies ( $n = 222$  data points,  $\chi^2 = 1.19$ ,  $d.f. = 2$ ,  $P = 0.55$ ) where the correlation  
788 between SR and PD was  $\leq 0.8$ . The reduced correlation of the sub dataset allowed us to  
789 explicitly model the covariance between SR and PD and then examine the partial regression  
790 coefficients (showed as values above the paths) relating both explanatory factors to  
791 community biomass (biomass) and the S.D. of biomass through time (SD). Lines with  
792 single headed arrows represent causal pathways whereas lines with double headed arrows  
793 represent co-varying variables. Community biomass and the S.D. of biomass through time  
794 are the two components of stability. Significance is indicated by asterisks: \* for  $p < 0.05$ ,  
795 \*\* for  $p < 0.01$ , *ns* for non-significant. See also Table S3 for more details.

796