COMMUNITY PHYLOGENETICS AND ECOSYSTEM FUNCTIONING

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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Summary

1. Hundreds of experiments have now manipulated species richness (SR) of various groups of organisms and examined how this aspect of biological diversity influences ecosystem functioning. Ecologists have recently expanded this field to look at whether phylogenetic diversity (PD) among species, often quantified as the sum of branch lengths on a molecular phylogeny leading to all species in a community, also predicts ecological function. Some have hypothesized that phylogenetic divergence should be a superior predictor of ecological function than SR because evolutionary relatedness represents the degree of ecological and functional differentiation among species. But studies to date have provided mixed support for this hypothesis.

2. Here, we reanalyse data from 16 experiments that have manipulated plant SR in grassland ecosystems and examined the impact on above-ground biomass production over multiple time points. Using a new molecular phylogeny of the plant species used in these experiments, we quantified how the PD of plants impacts average community biomass production as well as the stability of community biomass production through time.

3. Using four complementary analyses, we show that, after statistically controlling for variation in SR, PD (the sum of branches in a molecular phylogenetic tree connecting all species in a community) is neither related to mean community biomass nor to the temporal stability of biomass. These results run counter to past claims. However, after controlling for SR, PD was

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positively related to variation in community biomass over time due to an increase in the variances of individual species, but this relationship was not strong enough to influence community stability.

4. In contrast to the non-significant relationships between PD, biomass and stability, our analyses show that SR *per se* tends to increase the mean biomass production of plant communities, after controlling for PD. The relationship between SR and temporal variation in community biomass was either positive, non-significant or negative depending on which analysis was used. However, the increases in community biomass with SR, independently of PD, always led to increased stability. These results suggest that PD is no better as a predictor of ecosystem functioning than SR.

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

Introduction

Over the past few decades, ecologists have completed hundreds of experiments exploring how the variety of life forms influences the fluxes of carbon and cycling of elements that control how ecosystems 'function' (Schulze & Mooney 1993; Tilman & Downing 1994). To date, the field of biodiversity and ecosystem functioning (BEF) has been dominated by studies that used species richness (SR) as their sole measure of biodiversity (Loreau *et al.* 2001; Hooper *et al.* 2005; Cardinale *et al.* 2011). However, ecologists have recently begun to explore how other aspects of diversity like genetic and trait variation can influence the functioning of ecosystems and begun to ask whether certain measures of diversity are better predictors of ecosystem functioning than others (Diaz & Cabido 2001; Petchey & Gaston 2006; Cadotte, Cardinale & Oakley 2008; Cadotte, Dinnage & Tilman 2012). One form of diversity that has received a growing amount of attention is phylogenetic diversity (PD). PD is a measure of how much evolutionary divergence has occurred among the species in a community, often measured as the cumulative branch length differences that separate species on their molecular phylogeny. There are several reasons why ecologists have become interested in using PD to predict ecosystem-level processes. First, this interest is part of a general trend to understand contemporary ecological patterns by looking at the evolutionary history of organisms in a community (Webb *et al.* 2002; Johnson & Stinchcombe 2007). As in the field of 'community phylogenetics', researchers in the field of BEF have begun to think about how ecological and evolutionary processes might interact to control the functioning of ecosystems. Secondly and more importantly, ecologists have been enticed by the simplicity of using phylogenetics to predict ecological function. While it

is difficult and time consuming to run manipulative experiments of SR and equally difficult to identify and measure the myriad of species traits that control the functioning of ecosystems, getting genetic information needed to characterize species relationships and thus to measure PD has become an increasingly straightforward task.

The ability to use PD to predict ecological function is predicated on a sequence of assumptions that have rarely been tested directly, especially in an integrated fashion. The first assumption is that the biological traits that control ecological functions show a phylogenetic signal, meaning they tend to be more similar among closely related species than between distantly related species (Prinzing *et al.* 2001; Losos 2008; Wiens *et al.* 2010; Cavender-Bares & Reich 2012). The second assumption is that, when traits do show a phylogenetic signal, the trait variation leads to functional differentiation among species. The third and final assumption is that such functional differentiation enhances the productivity or stability of an entire community. Productivity might be enhanced if, for example, expression of a greater variety of traits allows species to better exploit all of the available resources (Tilman, Lehman & Thompson 1997; Loreau 2004; Reich *et al.* 2012; Srivastava *et al.* 2012). To date, the influence of PD on ecosystem functioning has been explored in just 12 studies that we know of, and these span a relatively small number of systems (Table 1). Eight of these have found a positive relationship between PD and various aspects of ecosystem functioning, one found a negative relationship, and three showed either mixed results or more complex nonlinear relationships. In the instances where PD was positively related to ecosystem functioning, it tended to explain only a small fraction more of the variation than SR (Cadotte, Cardinale & Oakley 2008; Cadotte *et al.* 2009; Cadotte 2013; but see Paquette & Messier 2011; Cadotte, Dinnage

Table 1. List of existing experimental studies exploring the relationship between evolutionary relatedness and ecosystem functioning. The table presents the reference study (authors and year of publication), the study organism, the number of species (#spp) and communities (plots, #comm) included in the study, the metric of evolutionary relatedness, the ecosystem function that has been measured, the number of time points and the sign of the effect of evolutionary relatedness on ecosystem functioning

	Study	Study organism	#spp/#comm	Evolutionary relatedness metric	Ecosystem function	Number of time points	Effect sign	Notes
1	Maherali & Klironomos (2007)	Fungi	NA	Family richness	Plant biomass	1	Positive	
2	Cadotte, Cardinale & Oakley (2008)	Terrestrial angiosperms	143/1315	Total phylogenetic branch lengths	Biomass (LR mean)	1	Positive $P < 0.0001$	Review of 29 experiments
3	Cadotte et al. (2009)	Terrestrial angiosperms	31/150	Total phylogenetic branch lengths	Biomass	Long-term averaged biomass	Positive $P < 0.0001$	
4	Flynn et al. (2011)	Terrestrial angiosperms	174/1088	Total phylogenetic branch lengths	Biomass (LR mean)	1	Positive $P < 0.0001$	Review of 29 experiments
5	Cadotte & Strauss (2011)	Terrestrial angiosperms	60/NA	Total phylogenetic branch lengths/ other	Biomass	1	For PD: positive $P = 0.0002$ in 1998 no effect $P = 0.629$ in 2001/both years no effect of MNND	Two sampling dates (1998 and 2001)
6	Paquette & Messier (2011)	Trees (temperate forests/boreal forests)	NA	Total phylogenetic branch lengths/ PSV	Annual above-ground biomass increment	1	Positive $P < 0.0001$	
7	Jousset et al. (2011)	Bacteria	8/95	Average of genetic distances between genotypes	Lag phase/growth rate/carrying capacity	1	Mixed (depending on resource complexity)	Genotypes of a species
8	Cadotte, Dinnage & Tilman (2012)	Terrestrial angiosperms	31/150	Total phylogenetic branch lengths/ MNTD/MPD/ others	Average productivity/ stability of above-ground biomass	15 (1996–2010)	Positive $P < 0.001$/ positive $P < 0.001$	
9	Venail et al. (2013)	Green algae	9/36	Total phylogenetic branch lengths	Biomass/temporal stability	10	Negative $P < 0.05$/ negative $P < 0.05$	SR fixed to 2
10	Cadotte 2013;	Terrestrial angiosperms	17/100	Total phylogenetic branch lengths/ MNTD/MPD/ others	Biomass	1	Positive $P < 0.001$	
11	Venail & Vives (2013)	Bacteria	12/60	Mean pairwise distance	Productivity	1	Positive $P < 0.05$	SR fixed to 2 and 4
12	Pu et al. (2014)	Protists	12/9	Sum of lengths of the branches connecting species	Biomass/temporal stability	21	U shape for biomass/for stability ANOVA: positive $P < 0.05$, linear: positive marginal $P = 0.067$	SR fixed to three

NA, non-available; SR, species richness.

& Tilman 2012). Nonetheless, authors of these studies tend to strongly advocate for the importance of phylogentic diversity (PD) for ecosystem functioning.

Many studies have also shown that diverse communities have more temporally stable biomass production than less diverse communities. In most cases, the temporal stability of community biomass production is commonly measured as the inverse of its coefficient of variation over time (Tilman 1999; Jiang & Pu 2009; Hector *et al.* 2010; Campbell, Murphy & Romanuk 2011), which is the biomass of the community averaged over time divided by its standard deviation through time. The standard deviation of community biomass can be influenced by changes in variances of individual species' biomasses as well as by changes in the synchrony of species' biomass fluctuations over time. Thus, diversity can influence temporal community biomass stability through the average biomass production of the community or through individual species' biomasses (e.g. their synchrony). Higher community biomass, lower sum of species variances and more asynchronized fluctuations of species' biomasses would increase community stability. Assuming communities with higher PD result in the expression of a greater variety of traits allowing species to better exploit resources, it can be predicted that the average community biomass will increase with PD. Similarly, a greater variety of traits (assumed to be represented by a higher PD) should allow communities to show a greater array of compensatory dynamics (Tilman 1999; Hector *et al.* 2010; Violle *et al.* 2011; Cadotte, Dinnage & Tilman 2012; Verdu, Gomez-Aparicio & Valiente-Banuet 2012), reducing the standard deviation of community biomass over time. Overall, the temporal stability of community biomass, measured as the average community biomass divided by its standard deviation, is expected to increase as PD increases. To date, only three studies have explored the influence of PD on the temporal stability of ecosystem function (Table 1). One found a positive effect of PD on the stability of plant biomass in grasslands (Cadotte, Dinnage & Tilman 2012), one found a negative effect on the stability of algal biomass in microcosms (Venail *et al.* 2013), and one found a nonlinear (*U*-shaped) relationship between PD and the stability of protists' biomass in microcosms (Pu *et al.* 2014). The relatively small number of studies and their equivocal results suggest more comprehensive studies are needed.

Here, we reanalyse data from 16 biodiversity experiments using grassland plants to better assess how PD influences the production of biomass and its stability over time. Twelve of the studies used here are a subset of the 29 studies used by Cadotte, Cardinale & Oakley (2008) to examine how PD impacts biomass production, and all 16 studies are the same studies whose time series were used by Cardinale *et al.* (2011) and Gross *et al.* (2014) to examine how SR influences the stability of biomass production through time. The primary advance of our study is that we use four different complementary analytical methods to separate the effects of PD and SR on community produc-

tivity and stability. These two forms of diversity are inherently correlated since a greater number of species almost always correlates with greater summed genetic divergence on a phylogeny. However, this correlation has not been adequately dealt with in prior studies and, as we will show, our analyses lead to several modified conclusions about the role of species vs. PD in ecosystem functioning.

Materials and methods

DATA

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

MOLECULAR PHYLOGENY

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

To estimate the evolutionary relatedness among species in a plot, we used PD, defined as the total phylogenetic distance among two or more species (Faith 1992; Cadotte, Cardinale & Oakley

2008). Thus, the PD of an assemblage (plot) is influenced both by the number of species and by their level of evolutionary relatedness. PD is inversely proportional to the evolutionary relatedness of the species, thus the more distantly related a set of species becomes, the higher the PD will be. We used Picante in R (Kembel *et al.* 2010) to calculate different PD metrics including PD (Cadotte, Cardinale & Oakley 2008), mean phylogenetic distance (MPD; Webb, Ackerly & Kembel 2008), mean nearest taxon distance (MNTD; Webb, Ackerly & Kembel 2008) and phylogenetic species variability (PSV; Helmus *et al.* 2007) for each plot (data available in dryad). We assessed the sensitivity of our estimates of PD to different phylogenies by comparing our values with those obtained using a recently published plant phylogeny (Zanne *et al.* 2014). That phylogeny, like ours, is based on a maximum likelihood analysis of GenBank data. The Zanne *et al.* tree used seven gene regions from GenBank, so there is substantial overlap of primary data with our phylogeny. The Zanne *et al.* analysis differs from ours in that those authors constrained major clades (families and orders), partitioned data by gene regions and smoothed their tree using divergence time estimates.

PRODUCTIVITY AND STABILITY

We focus on the influence of biodiversity on both (i) the production and (ii) temporal stability of biomass produced by mixtures of grassland plant species grown in polyculture. At each time point, community biomass production was estimated as the sum of the biomass produced by all the species in a plot. Then, we averaged community (plot) biomass over time. Most estimates of biomass production in the data sets are in units of mass per area; however, two studies used estimates of aerial plant coverage instead (studies 12 and 15, Table S1, Supporting information). For consistency with previous data synthesis (Cardinale *et al.* 2011; Gross *et al.* 2014), we did not transform the data from these two studies.

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

$$\text{Stability} = \frac{\bar{x}}{\text{sd}}. \qquad \text{eqn 1}$$

Thus, community stability can be influenced both by changes in the average biomass production (numerator of eqn 1) or by changes in the temporal standard deviation of biomass production (denominator of eqn 1). The standard deviation can be further decomposed into the sum of population-level variances and the co-variances among species' biomasses through time. The covariance in species biomasses is frequently used as a measure of the degree of synchrony in the temporal variation of species' population responses (Jiang & Pu 2009). However, when more than two species are present in an assemblage, it is now known that covariance is an inappropriate measure of species synchrony because the covariance depends on both the number of species and the synchrony among them (Loreau & de Mazancourt 2008, 2013). This limitation has hindered interpretation of what most contributes to stability and has led to efforts to develop new metrics of species synchrony (Loreau & de Mazancourt 2008; Gross *et al.* 2014). Here, we used the most recent metric developed by Gross *et al.* (2014), which measures synchrony among species' biomasses as the average correlation between the biomass of each species (Y_i) and the total biomass of all other species in the group ($\sum_{j \neq i} Y_j$).

$$\text{Synchrony} = \left(\frac{1}{n}\right) \sum_i \text{corr}\left(Y_i, \Sigma_{j \neq i} Y_j\right). \qquad \text{eqn 2}$$

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

To summarize, in our analyses, we used PD and SR as explanatory variables. Stability and its different components (average biomass and standard deviation, eqn 1) as well as the sum of variances and synchrony (eqn 2) were used as response (dependent) variables.

STATISTICAL ANALYSES

Within the full data set we assembled, which contains 824 experimental plots spread across 16 studies, measures of PD and SR were highly correlated with one another (Fig. 1a, $r = 0.90$). This high degree of correlation is not surprising given that PD is not only influenced by the branch lengths separating species on a phylogeny (i.e. their relatedness), but also by the number of species being considered. Importantly, these 16 experiments were not originally designed to produce a wide range of PD values or to manipulate PD independently of SR. Therefore, the high degree of correlation leads to statistical problems of multicollinearity in many forms of data analyses, making it difficult to draw robust conclusions about the influence of PD *per se*, or SR *per se* on biomass production and stability.

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

Type 1 analysis

In this analysis (Fig. 1a), we quantified the effect of PD on community stability, community biomass production (eqn 1), standard deviation, sum of variances and the synchrony metric (eqn 2) within levels of SR (i.e. holding SR constant). The original data set included species assemblages that spanned a wide array of planted SR levels (from 2 to 60). However, we focused on richness levels 2, 3, 4, 6, 8, 9, 11, 12 and 16 species (for 716 plots in total) because these were the richness levels for which multiple studies were represented, and each level of richness had multiple values of PD (i.e. different species compositions). For each study and within each SR level, we calculated the correlation between PD and each of five response variables: (i) temporally averaged community-level biomass (biomass summed across all species in a plot at each time point, then averaged over time; numerator in right side of eqn 1), (ii) the temporal standard deviation of community biomass (denominator in right side of eqn 1), (iii) the community-level temporal stability of biomass (left side of eqn 1), (iv) the summed variances of individual species' biomasses and (v) population-level temporal synchrony (as in eqn 2). Correlation coefficients were weighted by the number of plots in each study to reduce the influence of poorly replicated studies. We normalized the distribution of data using Fisher's z-algorithm (Z_r; Balvanera *et al.* 2006) to test whether for each of the five response variables the weighted/normalized correlation coefficients (Z_r) were significantly different from zero using double-tailed t-tests.

Type 2 analysis

Unlike the type 1 analysis where we were able to analyse the impact of PD on production and stability with SR held constant, a directly comparable analysis looking at the effects of SR with PD held constant is not straightforward. This is because PD represents a continuous measure that cannot be binned into categories in the same way SR can. Nevertheless, in our type 2 analysis
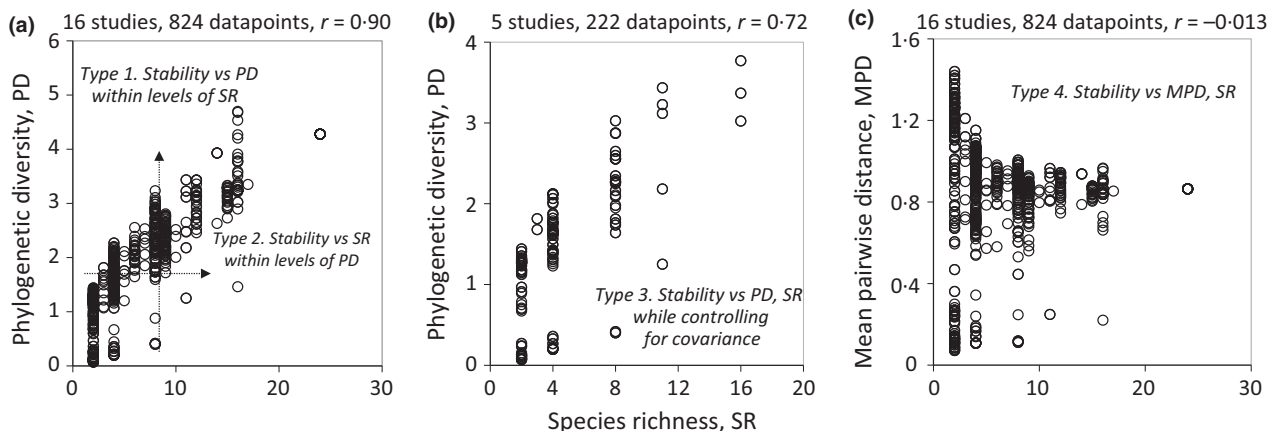
Fig. 1. The relationship between species richness (SR) and phylogenetic diversity (PD) or (MPD) for the grassland studies used in this data synthesis. (a) For the full data set with 824 data points (plots) from 16 independent studies (experiments), PD and SR are very highly correlated ($r = 0.90$; plots with SR = 60 are not shown in the graph). This leads to problems of multicollinearity that make it difficult to separate the effects of PD on community stability from those of SR in any multivariate analyses. Because of this, we performed four complementary types of analyses. For type 1 analysis, we analysed the impacts of PD on stability within levels of SR, (i.e. to analyse effects of PD, while holding SR constant). In the type 2 analysis, we did the opposite and identified 1417 contrasts where plots within a study had very similar values of PD, but differed in SR. While it was not possible to hold PD statistically 'constant', these contrasts offered the closest approximation. (b) In the type 3 analysis, we used five of the 16 studies where PD and SR had the lowest correlations ($r \leq 0.80$; studies 5, 6, 9, 13 and 14 from Table 2), which allowed us to perform more traditional multivariate analyses on this subset of data while accounting for the covariance among explanatory variables. (c) In the type 4, we used an alternative metric of PD (mean pairwise distance, MPD), which is independent of SR ($r = -0.013$, plots with SR = 60 are not shown), allowing us to include the full data set (824 plots). See text for further explanation.

(Fig. 1a), we were able to identify a large number of experimental plots that were relatively similar in values of PD, but which had differing levels of SR. For each study, we compared every plot to every other plot in the study. We found a total of 1417 pairs of plots, with each pair belonging to the same study where PD differed by <10%, but for which SR differed. When compared to random sampling of plots, these paired contrasts represent a highly constrained range of variation in PD, and come as close as is reasonably possible to holding PD constant while allowing SR to vary (Fig. S3, Supporting information). For each of these 1417 pair-wise contrasts, we calculated the log ratios of community biomass and stability, $\ln(Y_{high\ richness}/Y_{low\ richness})$, where Y represents: (i) total plot biomass, (ii) standard deviation of biomass, (iii) temporal stability of biomass through time or (iv) the sum of variances for the high vs. the low SR plot within each pair. Positive log ratios indicate that the more species community either: produces more biomass, has a higher standard deviation in biomass through time, is more stable than the less speciose community or has more variable species. We used two-tailed *t*-tests to evaluate whether log ratios for each metric were different from zero. We could not establish log ratios for synchrony because synchrony can have negative values and it is not possible to calculate a logarithm of negative values.

Type 3 analysis

In this analysis, we used structural equation modelling (SEM) to summarize data from five experiments (studies 5, 6, 9, 13 and 14 in Table S1, Supporting information) where the species pools used led to relatively low correlation coefficients relating PD and SR (Fig. 1b, $N = 5$ studies, $r = 0.72$ using 222 experimental plots). While these five studies represent but a subset of available data, the correlations between PD and SR in all other studies were well above 0.8, rendering them unusable in any attempts to statistically control for covariance among SR and PD in a single analysis. However, for this subset of five studies, it was possible to statistically control for the covariance between SR and PD. In turn, the SEM

allowed us to calculate the partial regression coefficients that represent the unique coefficients relating both PD and SR to community biomass and the standard deviation of biomass through time. We did not incorporate the sum of variances and synchrony into type 3 analyses because clear causal pathways have yet to be established.

Type 4 analysis

In type 1, 2 and 3 analyses, we used PD as a metric of PD, which is the metric used in most previously published studies (eight out of 12 listed in Table 1 used it). However, other metrics of evolutionary relatedness have been developed; among the more common are the mean pairwise distance (MPD), MNTD (Webb, Ackerly & Kembel 2008) and PSV (Helmus *et al.* 2007). Some of these have been proposed to be less correlated to SR than PD (Figs 1c and S4, Supporting information) and would, in principle, reduce statistical problems related to multicollinearity. However, there are concerns about more advanced metrics like MPD and MNTD because they count each branch of the phylogenetic tree multiple times depending on the number of species in a plot (e.g. in a plot with *n* species each branch is counted *n*–1 times). We complemented our three other types of analyses with type 4 analysis that used linear mixed effect (LME) models to explore the impact of SR and MPD on all five-dependent variables: stability, average biomass, standard deviation, sum of variances and synchrony. Analysis using MNTD and PSV would lead to the same results given their strong correlation with MPD (Fig. S2, Supporting information). All our LME models also included 'study' as random effects.

Results

PHYLOGENY

The topology of the phylogeny of grassland plants included in the current study (Fig. S1, Supporting information) is

very similar to a previous study that used similar methods ($\rho = 0.947$, $P < 0.001$; Cadotte, Cardinale & Oakley 2008). As expected, we found support for two major ingroup clades, Poales and eudicots. Forty-one nodes are supported by 100% bootstrap values. Twenty nodes showed lower than 50% bootstrap support, suggesting uncertainty in these nodes. In previous studies (e.g. Cadotte, Cardinale & Oakley 2008), sensitivity analyses using different phylogenetic approaches indicated that correlations between PD and other variables were very minimally affected by differences in tree topology. Again, we found very similar values of PD based on our new tree compared to values obtained with a recently published tree that used different (but overlapping) primary data and made different assumptions (Zanne *et al.* 2014, Fig. S2, Supporting information). Values for the four different PD metrics assuming the two different phylogenetic analyses for each community are available in dryad.

TYPE 1 ANALYSIS: EFFECT OF PD WITHIN RICHNESS LEVELS

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

TYPE 2 ANALYSIS: EFFECT OF SR WITHIN PD BINS

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

TYPE 3 ANALYSIS: EFFECT OF PD AND SR AFTER ACCOUNTING FOR THEIR COVARIANCE

After accounting for the covariance between SR and PD in the five experiments with the lowest correlations (mean
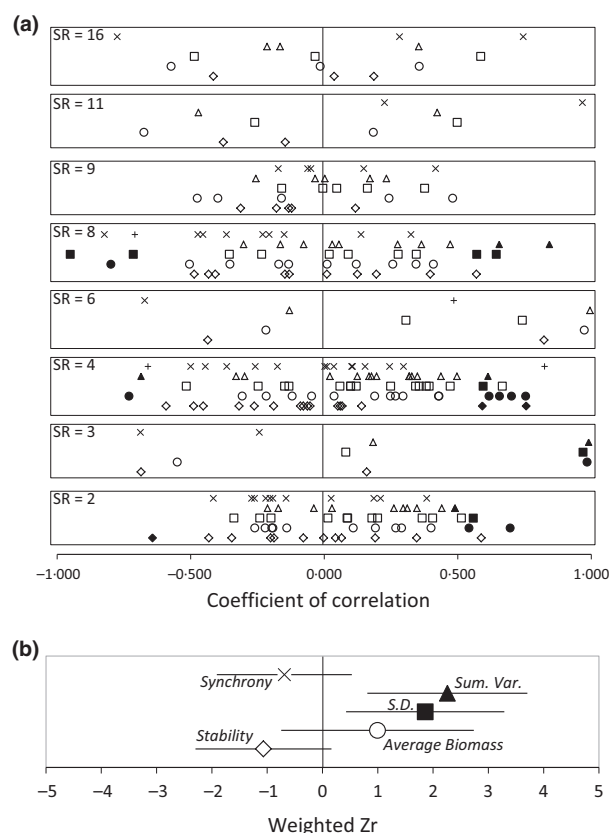

Fig. 2. The effect of PD (PD) on stability and its different components, while holding species richness (SR) constant. (a) Coefficients of correlation relating PD to stability (diamonds), as well as the two components contributing to stability: average biomass (circles) and standard deviation (squares), and to sum of species variances (sum.var., triangles) and synchrony (crosses). Each data point represents the correlation for one individual study. Results are presented for each species richness level (SR, vertical axis) so that conclusions can be drawn about the influence of PD, without confounding changes in SR. Filled data points and plus signs represent studies where correlation coefficient values were significant ($P < 0.05$). (b) Overall weighted and normalized average coefficients of correlation (Weighted Z_r, see text for details) between PD and each component of temporal community stability including all the species richness levels. The sign of overall Z_r represents the overall shape of the relationship between PD and each component (either positive, neutral or negative). Horizontal bars represent 95% confidence intervals. Filled symbols represent overall Z_r values that are significantly different from zero.

$r = 0.72$, $P < 0.05$, $n = 222$), a path analysis suggested that SR was positively associated with mean plot biomass ($r = 0.39$, $P < 0.01$) and with the standard deviation of biomass over time ($r = 0.20$, $P < 0.05$, Fig. 4). Therefore, there were positive indirect effects of SR on community stability that were mediated through the increase in biomass ($r = 0.30$, $P < 0.01$) and variance ($r = -0.21$, $P < 0.01$, Table S3, Supporting information). In contrast, PD was not associated with the standard deviation of biomass over time ($r = 0.10$, $P > 0.05$) or with any change in the mean community biomass ($r = 0.003$, $P > 0.05$, Fig. 4). Therefore, there were no indirect effects of PD on
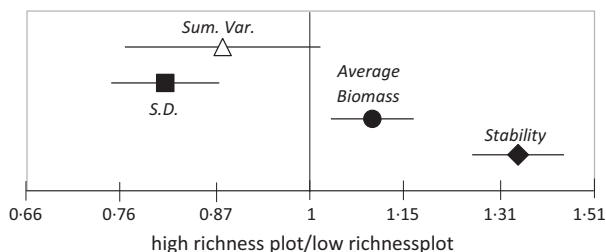
Fig. 3. The effect of species richness (SR) on stability and its different components, while holding PD (PD) constant. For the 1417 contrasts used in type 2 analysis, we further calculated the log ratios for community stability, average community biomass, standard deviation of biomass (SD) and sum of variances of individual species' biomass (sum.var.) in plots through time for higher vs. lower species richness. Positive log ratios for stability and biomass indicate that more speciose communities are more stable and produce more biomass than less speciose ones. Negative log ratios for SD indicate that the biomass of more speciose communities has lower temporal variation than the biomass of less speciose communities. Data points are the mean and 95% confidence intervals. Note than synchrony is not represented because it is not possible to estimate log ratios on negative values.
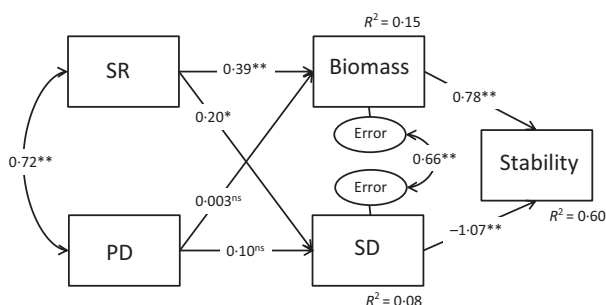

Fig. 4. Results of a structural equations model (SEM) showing the joint effects of species richness (SR) and PD (PD) on stability. The SEM that used data from five studies ($n = 222$ data points, $\chi^2 = 1.19$, d.f. = 2, $P = 0.55$) where the correlation between SR and PD was ≤ 0.8. The reduced correlation of the subdata set allowed us to explicitly model the covariance between SR and PD and then examine the partial regression coefficients (showed as values above the paths) relating both explanatory factors to community biomass (biomass) and the SD of biomass through time. Lines with single headed arrows represent causal pathways, whereas lines with double headed arrows represent covarying variables. Community biomass and the SD of biomass through time are the two components of stability. Significance is indicated by asterisks: *for $P < 0.05$, ** for $P < 0.01$, *ns* for non-significant. See also Table S3 (Supporting information) for more details.

community stability via biomass ($r = 0.002$, $P > 0.05$) or variance ($r = -0.11$, $P > 0.05$, Table S3, Supporting information).

TYPE 4 ANALYSIS: EFFECT OF MPD AND SR

Linear mixed effect models with SR, MPD, both as fixed effects) and study (as random effect) on the five different dependent variables revealed a positive effect of SR on stability, average biomass, standard deviation (SD) and

synchrony, but no effect on the sum of species variances (sum. var., Table S4, Supporting information). PD (measured as MPD) had positive effects on SD driven by a positive effect on the sum of species variances, but had no effect on stability, average biomass or synchrony.

SUMMARY OF RESULTS

Table 2 summarizes results of the different types of analyses, which were consistent in showing a positive relationship between SR and biomass production after controlling for PD. Analyses disagreed in how SR influences the standard deviation of biomass through time. Type 2 analysis showed a negative influence of SR on SD, but with an absence of effect on the sum of variances. Type 3 showed a positive effect on SD, whereas type 4 showed no effect on SD, with type 4 also revealing no effect on the sum of species variances but a positive effect of SR on synchrony. Ultimately all the analyses converged in showing that SR has a positive influence on community biomass stability via the increase in average community biomass.

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

Discussion

Here, we reanalysed data from 16 experiments that manipulated plant SR in grassland ecosystems to examine how SR and PD influence mean community biomass and its temporal stability. The primary advance of our study was to use a variety of analyses that attempt to control for the inherent positive covariance between SR and PD so that we could try to tease apart their effects. Consistent with the results of many individual studies (e.g. almost all of those referenced in Table 1, among others) and prior data syntheses (e.g. Balvanera *et al.* 2006; Cardinale *et al.* 2006, 2011; Cadotte, Cardinale & Oakley 2008; Flynn *et al.* 2011; Gross *et al.* 2014), our analyses confirmed that plant communities composed of more species tend to produce greater community-level biomass and to be more stable over time. This result held true even after controlling for variation in the PD of species, suggesting that the impact of SR on biomass production and temporal stability cannot be explained fully by differences in PD among communities.

Although our analyses confirmed prior conclusions about the positive effect of SR on community biomass production and stability after controlling for variation in PD, the reverse was not true. We found no evidence that, after

Table 2. Summary of the results of the four different analyses performed to establish the effects of either species richness (SR) or phylogenetic diversity (PD or MPD) on the temporal stability of community biomass, average community biomass production, the standard deviation (SD), the sum of individual species variances (sum.var.) and their temporal synchrony. Effects of diversity could be positive (+), null (0) or negative (−). Type numbers represent different statistical analyses (see text for explanation)

	Species richness			Phylogenetic diversity (PD or MPD)		
	Type 2	Type 3	Type 4	Type 1	Type 3	Type 4
Stability	+	+	+	0	0	0
Biomass	+	+	+	0	0	0
SD	−	+	0	+	0	+
Sum.var.	0	N.A.[1]	0	+	N.A.[1]	+
Synchrony	N.A.[2]	N.A.[1]	+	0	N.A.[1]	0

Type 1 to type 3 analyses used PD as metric of phylogenetic diversity, whereas type 4 used MPD which is independent of SR. Some results are not available (N.A.) either because: [1]a structural equation model including sum.var. and synchrony would be too complex or [2]synchrony can have negative values, making it impossible to calculate logarithms. Cases with positive effects are shown in grey for visual clarity.

controlling for variation in SR, PD was related to community biomass production or its temporal stability in grasslands. Despite this absence of any effect on the average community biomass and stability, two of our analyses revealed a positive effect of PD on the standard deviation (SD) of community biomass. Examination of the sum of species variances and synchrony components suggests that the increase in community biomass SD was driven by an increase in the sum of individual species variances and not by changes in the synchrony of their fluctuations. This suggests that closely related species share low biomass variation over time, but these similarities vanish as species become less related, providing some evidence of a phylogenetic signal in the temporal variation of species' biomass. A recent study by Godoy, Kraft & Levine (2014) found that fitness differences among annual plants were higher and much more variable between distantly than closely related species, suggesting that the outcome of competition should be more variable between more distantly related species. It is possible that such increased competitive variability with increasing PD lead to an increase in biomass variability over time. Though, the observed increase in the sum of variances with PD could also be due to a higher probability of the presence of species with higher biomass variability in plots with higher PD (i.e. sampling effect).

Our general conclusion about the lack of effect of PD on community biomass differs from the conclusions of two previous data syntheses (Cadotte, Cardinale & Oakley 2008; Flynn *et al.* 2011). Cadotte, Cardinale & Oakley (2008) summarized data from 29 experiments that manipulated richness of terrestrial angiosperms and asked whether PD could explain variation in a standardized diversity 'effect size' (the log ratio of biomass in a polyculture/the mean biomass of the constituent species in monoculture). The authors concluded that 'the amount of PD within communities explained significantly more variation in plant community biomass than other measures of diversity, such as the number of species or functional groups'. In an attempt to deal with the strong covariance between SR and PD, Cadotte, Cardinale & Oakley (2008) examined how

PD related to diversity effect sizes within levels of SR. They found that PD was only related to diversity effects at the lowest levels of richness (i.e. 2 and 4 species) and suggested this was because researchers tended to use fewer species combinations at high levels of richness (i.e. 6 and 8 species), resulting in less variation in PD.

The study by Cadotte, Cardinale & Oakley (2008) differs from ours in several aspects. First, only 12 of the studies included in our analyses overlapped with those included in their data set. This is because we only included studies providing community biomass for at least three different time points so that we could quantify temporal stability. Secondly, the phylogenetic trees used to calculate the PD within plots in our study and the Cadotte, Cardinale & Oakley 2008 study were though similar but not exactly the same. Thirdly, the response variables used in our studies were different; we used the mean biomass across time series, as opposed to a log response ratio at a single time point used in Cadotte *et al.*'s study. Finally, the statistical analyses also differed among studies. Cadotte *et al.* used LME models with SR and PD as explanatory variables despite the fact these two variables were strongly correlated. In our study, to avoid the problems related to covariance of the explanatory variables, we calculated correlation coefficients between PD and community biomass at each level of SR and for each individual study. Then, we weighted and averaged the correlation coefficients among studies and richness levels.

In order to determine which of these four factors were responsible for the discrepancies in the results among both studies, we collated a data set that contained the explanatory (i.e. PD) and dependent variables (i.e. community biomass) from both studies. This resulted in an overlapping data set that included 318 plots. We tested the effect of switching the two metrics of PD, the two measures of community biomass and the two statistical analyses from both studies by performing a series of permutations using the collated data set (see Data S1, Supporting information). The permutations revealed that the conclusions from both studies about the effect of PD on community biomass (i.e.

positive for *Cadotte et al.*'s and no effect for this study) differed because they focused on different measures of community biomass and used different statistical approaches. This is not surprising, given that both studies were answering different questions related to the role of PD as a predictor of community biomass as we explained before. We consider that for the purposes of our study, which was to separate the effects of SR and PD, the statistical approach based on coefficients of correlations is more appropriate because it avoids problems due to collinearity between SR and PD. Moreover, the lack of effect of PD (as PD) on community biomass was confirmed by a LME models using MPD as the explanatory variable. While useful for addressing questions related to the effect of diversity on ecosystem functioning, log ratios open the possibility that the observed differences in community biomass are due to differences in the monoculture biomasses of the constituent species, which seemed to be the case here (see Data S1, Supporting information). For instance, having monocultures with lower average biomass would result in higher community biomass if estimated as log ratios. Thus, to allow a clearer interpretation of the differences in biomass among communities, we preferred to directly analyse raw community biomass.

Our results also deviate from the conclusions of another prominent data synthesis by Flynn *et al.* (2011), who added measures of functional diversity (i.e. trait variation among plant species on the phylogeny) to Cadotte *et al.*'s data set and tested to see whether functional diversity was a superior predictor of biomass production than PD. The authors ran a variety of models comparing the explanatory power of PD alone, functional diversity alone, both together, as well as in combination with SR. They concluded that a model containing only PD was the most likely explanation of variation in plant biomass among plots (see Table 2 in their paper). But Flynn *et al.* did not statistically control for the covariance between SR and PD when drawing their conclusions. Because none of their linear mixed models (Table 2 in Flynn *et al.* 2011) accounted for covariance among variables, nor did any of their multivariate analyses (see the structural equations models presented in their Fig. 3 and their Appendix), we cannot judge how their findings relate to our own. While our results do not directly contradict previous findings, given that we were addressing related but different questions, the contrast in our conclusions leads us to believe that former statements about the strong impacts of PD on community biomass may have been partly driven by the strong correlation between PD and SR. When we control for the collinearity between SR and PD, the residual effects of PD on community biomass are non-significant.

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

The use of PD as a predictor of ecosystem functioning assumes that evolutionary distance and ecological differentiation are positively related, with close relatives being ecologically more similar than distant relatives (i.e. phylogenetic signal; Losos 2008; Wiens *et al.* 2010). There are currently divergent positions on whether or not the evolutionary relatedness among modern species is a reasonable proxy for ecological similarity (Prinzing *et al.* 2001; Freckleton, Harvey & Pagel 2002; Johnson & Stinchcombe 2007; Losos 2008; Wiens *et al.* 2010; Cavender-Bares & Reich 2012; Narwani *et al.* 2013; Kelly, Grenyer & Scotland 2014; Venail *et al.* 2014; Muükemüller *et al.* in press). Moreover, in order to positively influence ecosystem functioning, more phylogenetically diverse communities need to somehow maximize resource partitioning (i.e. niche complementarity) or to enhance facilitation, thus leading to greater resource use efficiency compared to less diverse communities. Similarly, to ensure ecosystem functioning in the face of changing conditions (i.e. to increase temporal or spatial stability), phylogenetically diverse communities may generate negative covariances in population dynamics by either increasing competitive interactions (Godoy, Kraft & Levine 2014) or by ensuring that species' responses to the environment are independent (Venail *et al.* 2013). Our analyses suggest that the phylogenetic relatedness of species, beyond its covariance with SR, may not be a good predictor of ecosystem functioning (at least when this is measured as biomass production) with one possible explanation being the lack of phylogenetic signal in traits related to biomass production. This would suggest that, across the suites of species used in these experiments, functional complementarity between species did not increase with increasing PD between them.

More broadly, our result suggest that if standard diversity metrics based on species numbers (e.g. SR) were to be replaced by alternative metrics based on genetic differentiation (e.g. PD), caution would be needed when inferring ecosystem functioning because there may be functionally important trait differences among species that are not simply explained in full by phylogenetic relatedness (Kelly, Grenyer & Scotland 2014). While maximizing PD (Vane-Wright, Humphries & Williams 1991; Faith 1992, 1994; Winter, Devictor & Schweiger 2013) might seem to be a promising way to maximize functional diversity and thus ecosystem functioning, management recommendations that suggest conservation of evolutionarily distinct species will lead to higher functional diversity and more stable communities are not well supported by the data explored in this study.

Data accessibility

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Supporting Information

Additional Supporting information may be found in the online version of this article:

Fig. S1. Phylogenetic relationship of the 141 plant species used in the current analysis and two outgroups (*Magnolia grandiflora* and *Amborella trichopoda*).

Fig. S2. Comparison of the four PD measures estimated with the phylogenetic tree developed in the current study (Fig. S1, *x*-axis) and a recently published mega-tree (Zane *et al*. 2014, *y*-axis).

Fig. S3. For the Type 2 analysis we attempted to hold PD relatively constant and examine the impacts of species richness (SR) on community stability, biomass production, and the S.D. of biomass production through time.

Fig. S4. Correlations between five different metrics of biodiversity: species richness (SR).

Table S1. List of the 16 studies included in this data synthesis presenting the reference study (authors and year of publication) with the name of the project and details on different treatments when available in parenthesis, the geographic location of the original study (locality or state and country), the number of time points over which biomass was measured and the total number of plots with different species compositions.

Table S2. GenBank Accession numbers for genes used in phylogenetic analyses.

Table S3. Detailed results of the structural equation model (Type 3 analysis, Fig. 4) exploring the effect of PD (PD) and species richness (SR) on average community biomass (biom) and standard deviation (SD) as components of community stability (stab).

Table S4. Results of linear models linking PD (mean phylogenetic distance, MPD) and species richness (SR) to stability, average biomass, standard deviation (SD), sum of species variances (sum. var.) and synchrony (called Type 4 analysis in main text).

Data S1. The current data-synthesis suggests that, after correcting for species richness, PD is not a good predictor of community biomass (see Summary Table 2 in main document).

Table S5. Summary of the results of a permutation exercise about the effect of PD on community biomass.