

Explaining maximum variation in productivity requires phylogenetic diversity and single functional traits

JIAJIA LIU,¹ XINXIN ZHANG,² FEIFAN SONG,² SHURONG ZHOU,^{1,6} MARC W. CADOTTE,^{3,4} AND COREY J. A. BRADSHAW⁵

¹Ministry of Education Key Laboratory for Biodiversity Science and Ecological Engineering, School of Life Sciences, Fudan University, 220 Handan Road, Shanghai 200433 People's Republic of China

²State Key Laboratory of Grassland Agro-ecosystems, School of Life Sciences, Lanzhou University, Lanzhou 730000 People's Republic of China

³Department of Biological Sciences, University of Toronto–Scarborough, 1265 Military Trail, Toronto, Ontario M1C 1A4 Canada

⁴Department of Ecology and Evolutionary Biology, University of Toronto, 25 Wilcocks Street, Toronto, Ontario M5S 3B2 Canada

⁵The Environment Institute and School of Earth and Environmental Sciences, University of Adelaide, South Australia 5005 Australia

Abstract. Many community experiments have shown a positive relationship between plant biodiversity and community productivity, with biodiversity measured in multiple ways based on taxonomy, function, and phylogeny. Whether these different measures of biodiversity and their interactions explain variation in productivity in natural assemblages has rarely been tested. In a removal experiment using natural alpine assemblages in the Tibetan Plateau, we manipulated species richness and functional diversity to examine how different measures of biodiversity predict aboveground biomass production. We combined different biodiversity measures (functional, phylogenetic, richness, evenness) in generalized linear models to determine which combinations provided the most parsimonious explanations of variation in biomass production. Although multivariate functional diversity indices alone consistently explained more variation in productivity than other single measures, phylogenetic diversity and plant height represented the most parsimonious combination. In natural assemblages, single metrics alone cannot fully explain ecosystem function. Instead, a combination of phylogenetic diversity and traits with weak or no phylogenetic signal is required to explain the effects of biodiversity loss on ecosystem function.

Key words: alpine meadow; biodiversity; biodiversity–productivity relationship; community phylogeny; functional diversity; functional traits; resilience; richness; Tibetan Plateau.

INTRODUCTION

As human endeavors continue to compromise the delivery of ecosystem services around the world, a critical task for scientists is to determine the degree to which changes in biological diversity affect how ecosystems function. The central prediction is that communities with more species can exploit more of the available resources (e.g., water, nutrients, pollinators, fungal symbionts, etc.), thus converting more of the total resource pool into biomass production, i.e., productivity (Tilman et al. 2001, Cardinale et al. 2006, Cadotte et al. 2009).

Complicating our understanding of how biodiversity affects ecosystems is that “biodiversity” itself can be quantified in many different ways (Redding and Mooers 2006, Tucker and Cadotte 2013). The simplest measure, species richness, has repeatedly been shown to correlate with biomass production (Tilman et al. 2001, Cardinale et al. 2006, Zhang et al. 2012). However, species richness generally explains only a small component of the variance in community production (Cardinale et al.

2006). This implies that species composition and their interactions are also important for determining community productivity (Tilman et al. 1997, Petermann et al. 2008), and that measures like richness cannot account for the differences or similarities in species' ecologies (Cadotte et al. 2011).

There have been two important advances in the past decade to move beyond counts of species for such questions. The first is a trait-based approach that uses measured functional traits to quantify species diversity in terms of single or multivariate traits (Walker et al. 1999, Petchey and Gaston 2002). While trait-based measures have provided important insights into community diversity and ecosystem function (Cadotte et al. 2011), they are limited by the traits that are measured, implicit assumptions about how trait differences translate into ecological differences, and proper methods to combine multiple traits (Cadotte et al. 2013). The alternative approach has been to use phylogenetic distances, where the idea is that the dissimilarity in phenotypes and by proxy, ecological function, is correlated with evolutionary divergence times (Harvey and Pagel 1991, Cadotte et al. 2009, Cavender-Bares et al. 2009). Community phylogenetic ecology has made great progress in bridging community ecology and

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⁶ Corresponding author. E-mail: zhshrong@fudan.edu.cn

evolutionary ecology in recent years (Webb et al. 2002, Cavender-Bares et al. 2009, Mouquet et al. 2012), namely because of the reduced costs and time of sequencing large numbers of genes, and the availability of species-level phylogenies. Yet phylogenetic approaches have their own limitations, such as how best to quantify phylogenetic relationships in a single metric and determining how phylogenetic distances correspond to real ecological differences, especially when the traits that are important to species demographic rates rapidly diverge or converge on the community phylogenetic tree (Cadotte et al. 2013). There are several metrics that capture phylogenetic information, including summing branches, average distances among co-occurring species, deviations in phylogenetic variance-covariance matrices, and entropic measures (Faith 1994, Webb et al. 2002, Helmus et al. 2007, Cadotte et al. 2010).

Several recent studies have attempted to evaluate the relative power of these approaches to explain variation in productivity of plant communities. In some cases, phylogenetic diversity appears to explain variation in biomass production better than species richness and functional groupings (Maherali and Klironomos 2007, Cadotte et al. 2008), whereas in others, functional and phylogenetic diversity demonstrate similar explanatory power (Flynn et al. 2011). We know that different diversity measures can explain a substantial amount of the variation in productivity in experimental settings, where a large range in phylogenetic relationships or trait variation has been explicitly designed (Cadotte et al. 2009). However, there is a remaining question as to whether such patterns occur in natural settings where phylogenetic relationships and trait variation might be more limited. This is an important question because natural communities are assembled by a combination of deterministic and stochastic processes that might influence the type of species that can persist locally (Weiher et al. 1998). By contrast, synthetically assembled communities start with a list of species comprising a subset of the local species pool that are often chosen for their particular characters to create different levels of species richness. Since natural assembly processes have selected species based on their functional traits and ecological similarity, do measures that quantify these still explain variation in function in natural communities?

To address these questions, we developed a diversity-productivity experiment in alpine meadows of the Tibetan Plateau where we manipulated the naturally occurring species, functional and phylogenetic diversity in replicated removal treatments. The advantage of a removal approach is that it more realistically mimics natural community composition and its assembly mechanisms, representing a potentially useful expectation for broader-scale degradation of plant communities (Diaz et al. 2003, Zavaleta and Hulvey 2004, McLaren and Turkington 2010). In addition to measuring species richness and evenness, we calculated a suite of single and

multivariate functional diversity metrics, as well as several phylogenetic metrics, based on both maximum-likelihood and Bayesian phylogenetic estimation. Taking a multi-model comparative approach, we assess the relative contribution of single metrics and various combinations of multivariate indices to predict over 77% of the variance in biomass production in this species-rich alpine community—a heretofore-unprecedented explanatory power in the diversity-productivity relationship in natural systems.

MATERIALS AND METHODS

Study site

We established our study site on a southeast-facing meadow of near-regular topography (little slope) in the eastern Tibetan Plateau (101°53' E, 35°58' N) at approximately 3500 m elevation (see Plate 1). The climate is humid-alpine with a mean annual rainfall of 620 mm, most of which falls during summer. Mean annual temperature is 1.2°C, with averages of -10.7°C in January and 11.7°C in July. The average annual number of frost days is >270, and there is a mean of <150 growing degree-days per year. The soil is typical for alpine meadows and about 80 cm deep on average (Gong 1999). The plant community is dominated by a few graminoids of the genera *Poa*, *Kobresia*, *Elymus*, and *Stipa*, and by various dicots such as *Trollius*, *Anemone*, *Aconitum*, *Ligularia*, *Saussurea*, *Pedicularis*, *Potentilla*, and *Gentiana* (Liu et al. 2013). The dominant animals observed in the area include livestock (e.g., yaks, horses), marmots (*Marmota himalayana*), zokor (*Myospalax* spp.), and various ant species.

We established a 50 × 50 m permanent area in July 2009 with fencing, permitting grazing only in winter. In June 2011, we regularly arranged 85 circle plots of 1 m diameter in the area (10 of which were assigned as alternate controls without rare species), with at least 3 m between the nearest edges of adjacent plots. Due to their different physical, reproductive, and dispersal attributes, we classified all the species we found in the plots into one of the four taxonomic groups: Poaceae and Cyperaceae (A), Asteraceae (B), Fabaceae (C), and others (D) (Appendix: Table A1). We then considered all possible combinations of these four groups as treatments, by removing the aboveground material for each species belonging to specific groups twice per year. This provided a total of $2^4 - 1 = 15$ treatments (ABCD, ABC, ABD, BCD, ACD, AB, AC, AD, BC, BD, CD, A, B, C, D) assigned randomly to a plot and replicated five times each (75 plots). For 10 additional plots, we removed all rare species (defined as having a relative abundance <5% of the total).

We recorded species composition and abundance in a circular subplot of 50-cm diameter measured from the center of each plot at the peak of the growing season in August of 2011 and 2012. We used the data collected in 2012 in all the analyses such that the remaining species compensate the removal of biomass in two years. From

the abundance and richness data, we also calculated Shannon's evenness index (H')

$$H' = \sum_{i=1}^S \frac{n_i}{N} \log_e \left(\frac{n_i}{N} \right)$$

for a total of N individuals of S species, each of abundance n , using the function "diversity" in the vegan library of the R statistical software package (Oksanen et al. 2013). We then harvested all the stems in each subplot at ground level, dried and weighed them to 0.1 mg to estimate biomass production (productivity).

Trait data

We measured five plant traits generally considered important for plant competition or dispersal abilities: maximum plant height (cm), leaf nitrogen content and phosphorus content (mg/g), per capita seed mass (mg), and specific leaf area (cm²/g) (Walker et al. 1999, Flynn et al. 2011). We measured mature and undamaged leaves of 50 randomly selected individuals per species to estimate leaf area to the nearest 0.001 cm² using an Epson-V200 scanner (Epson, Beijing, China) and image analysis software (ImageJ; *available online*).⁷ We measured leaf dry mass and nitrogen and phosphorus content (expressed as mg/g) from leaves collected from the same individuals. We collected 100 mature seeds for each species from the study area and nearby meadows, air-dried and weighed them to estimate average seed mass of each species. We recorded maximum and mean plant height of 50 randomly selected individuals from each species in the area.

Community phylogenies

An exhaustive description of the methods for DNA extraction, amplification, and sequencing are provided in Kress et al. (2010), but we briefly describe the phylogenetic inference methods here. For the 54 species recorded in our study, we aligned the rbcL and matK sequences using MUSCLE (Edgar 2004) and concatenated matK to the rbcL to construct an entire matrix. We substituted missing rbcL or matK sequences for nine species with sequences from congeneric representatives in GenBank. We then selected top-ranked maximum likelihood models of nucleotide substitution for each gene using Akaike's information criterion, as implemented in the function "modelTest" in the phangorn library (Schliep 2011) in R (R Core Team 2013). Using the aligned sequences and the best-fit models of nucleotide substitution, we estimated a maximum-likelihood phylogeny using PhyML 3.0 (Guindon et al. 2010) with the starting tree estimated from the best-fit maximum likelihood model. To assess nodal support on maximum likelihood phylogenies, we ran 500 bootstrap replicates (see Fig. A1 for tree structure). We also

constructed a Bayesian phylogeny as an alternative using MrBayes3.2 (Ronquist and Huelsenbeck 2003), because both Bayesian posterior probabilities and maximum likelihood bootstraps could differentially supply potential upper and lower bounds of node reliability (Douady et al. 2003), and potentially support different topologies depending on the shape of the likelihood distributions. We chose a representative of an early-diverging angiosperm lineage *Amborella trichopoda* to serve as the outgroup and to root both of the maximum-likelihood and Bayesian phylogenies. We then used a semi-parametric rate-smoothing method to transform the phylogeny to an ultrametric tree using the "chronos" function with parameter value 1 in the R ape library (Paradis et al. 2004).

From these phylogenies, we calculated several measures of phylogenetic diversity: Faith's PD, which sums total phylogenetic branch lengths (Faith 1992); mean pairwise distance (MPD), which is the average distance separating all pairs of species on the phylogenetic tree (Webb et al. 2002); and an entropic measure (H_{ed}) that quantifies the distribution of evolutionary distinctiveness (Cadotte et al. 2010; see Appendix: Table A2 for the other measures of diversity).

Multivariate functional trait diversity metrics

In addition to considering the different trait variables separately, we calculated seven multivariate trait diversity metrics to choose accurate and consistent indices. These measures of functional diversity are listed in Table A2. Functional diversity (FD) estimates net species' similarity or differences as branch lengths from a functional dendrogram based on a multivariate distance matrix. To calculate FD, we rescaled the traits to have a mean of zero and variance of one (Cadotte et al. 2009). We then calculated a Euclidean distance matrix and did a hierarchical clustering on this matrix to calculate FD as the total branch lengths connecting community members. For FAD, we used the traits scaled to mean = 0 and variance = 1 and calculated a Euclidean distance matrix. We then summed the distances for all species in the community. Other functional metrics can be found in Table A2.

Phylogenetic signal in individual functional traits

We used function "phylosignal" in the picante library (Kembel et al. 2010) in R (R Core Team 2013) to calculate phylogenetically independent contrasts for each of the individual functional traits based on the maximum-likelihood and Bayesian phylogenetic trees. The function calculates the phylogenetic K statistic and estimates the probability of generating the same signal based on 1000 randomizations relative to the observed variance (Blomberg et al. 2003).

Generalized linear models

To determine the most parsimonious relationships between productivity (biomass production) and the

⁷ <http://rsb.info.nih.gov/ij>

TABLE 1. Generalized linear model (GLM) results for biomass production as a function of several factors.

Model	LL	k	AIC _c	Δ AIC _c	wAIC _c	DE
$\sim H_{\text{ed}} + H_{\text{max}}$	-271.463	3	551.497	0.000	0.574	77.7
$\sim \text{PD} + H_{\text{max}}$	-271.856	3	552.283	0.786	0.388	77.5
$\sim S + H_{\text{max}}$	-274.217	3	557.006	5.509	0.037	76.0
$\sim \text{MPD} + H_{\text{max}}$	-277.387	3	563.345	11.848	0.002	74.0
$\sim H' + H_{\text{max}}$	-280.501	3	569.574	18.077	<0.001	71.7
$\sim H_{\text{ed}} + N + \text{SM}$	-285.986	4	582.841	31.344	<0.001	67.4
$\sim S + N + \text{SM}$	-286.326	4	583.521	32.024	<0.001	67.1
$\sim H_{\text{ed}} + N + \text{SM} + \text{SLA}$	-285.980	5	585.195	33.698	<0.001	67.4
$\sim S + N + \text{SM} + \text{SLA}$	-286.273	5	585.782	34.285	<0.001	67.1
$\sim H' + N + \text{SM}$	-289.698	4	590.266	38.770	<0.001	64.0

Notes: Factors are number of species (S), Shannon's evenness (H') and phylogenetic diversity (PD, phylogenetic diversity; MPD, mean pairwise distance; and H_{ed} , evolutionary distinctiveness), and various community-level means of single functional traits (H_{max} , maximum plant height; P , leaf phosphorus content; N , leaf nitrogen content, SM, mean seed mass; and SLA, specific leaf area) or multivariate functional trait indices (FD, functional diversity; FAD, functional attribute diversity). Values are shown for the estimated number of model parameters (k), maximum log-likelihood (LL), the information-theoretic Akaike's information criterion corrected for small samples (AIC_c), change in AIC_c relative to the top-ranked model (Δ AIC_c), AIC_c weight (wAIC_c, model probability), and the percentage of deviance explained (DE) as a measure of the model's goodness-of-fit. The top 10 models are listed; the full table is shown in Appendix: Table A4.

various phylogenetic, trait, abundance and richness data, we constructed a series of generalized linear models using the "glm" function in the stats library in R to account for non-Gaussian error distributions and non-linear relationships. We validated the use of a gamma distribution of model residuals based on the normalized scores of standardized residual deviance (Q - Q plots). We evaluated model support using Akaike's information criterion corrected for small sample sizes (AIC_c; Burnham and Anderson 2002, 2004). We also used the percentage of deviance explained in the response variable (DE) as a measure of the model's goodness-of-fit.

There were 20 different biodiversity variables used in this analysis (Appendix: Table A2), and we aimed to identify the most parsimonious models explaining patterns of biomass production. To remove redundant predictors, we first grouped all variables into three categories: (1) species richness, (2) phylogenetic diversity metrics, and (3) functional diversity metrics; then we searched for the relatively better-ranked single-variable models in each group where annual productivity was regressed against each biodiversity metric and compared to the explanatory ability of these models using Akaike's information criterion weights. Variables we used in model construction are listed in Table A2. In addition, we averaged all measured traits at the community-level as single functional traits in our models.

Because of the strong correlation between most biodiversity indices (Spearman's $\rho > 0.3$; Appendix: Table A3) and because multivariate functional indices are derived from the same trait data, we avoided including more than one of these like indices in any one model. Then we constructed models with all remaining combinations of selected variables to search for the most parsimonious ones (simplest models explaining the most variation in productivity).

Assumption checks

We tested whether the number of groups removed affected the biomass of the others. We found that apart from the Asteraceae, the number of groups removed had no effect on the total biomass of each taxonomic category (Appendix: Fig. A2). We included two checks on our assumptions regarding the plausibility of the maximum-likelihood phylogenetic tree (Appendix: Fig. A1), and the influence of rare species on our biodiversity indices based on the potential role of rare species in the maintenance of ecosystem function and community phylogenetic structure (Lyons and Schwartz 2001, Mi et al. 2012). For the first, we included a new phylogenetic diversity measure based on the Bayesian phylogenetic tree (Appendix: Fig. A1) to assess its influence on model rankings. Second, we replaced the five control plots (ABCD) with the 10 plots where rare species were removed, thus increasing the number of plots tested to 80.

RESULTS

There were strong relationships among most of the raw indices, especially between species richness (S), evenness (H'), the multivariate functional diversity indices, and phylogenetic diversity indices (Appendix: Fig. A3, Table A3).

Of the 68 generalized linear models constructed (including the intercept-only model), those including single functional traits vastly outperformed multivariate functional trait indices based on the model rankings (Table 1; Appendix: Table A4), despite the single-trait models having many more parameters than the multivariate-trait models. The most parsimonious model (wAIC_c=0.574) included evolutionary distinctiveness (H_{ed}) and maximum plant height, accounting for >77% of the deviance explained in productivity (Table 1, Fig. 1), with leaf nitrogen and phosphorus content, mean seed mass, and specific leaf area having little additional explanatory power in terms of deviance explained (Table 1).

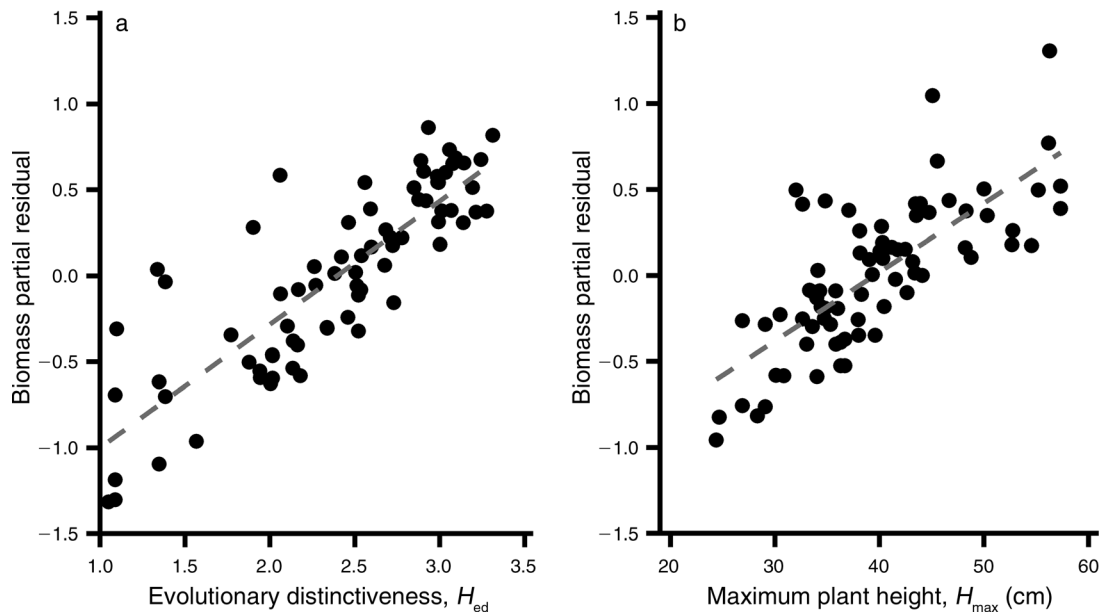


FIG. 1. Partial residual plots of the best-supported variables combined in the generalized linear models to predict variation in biomass production: (a) evolutionary distinctiveness (H_{ed}) based on a maximum-likelihood phylogeny and (b) community-level mean of maximum plant height (H_{max}). Dashed lines are linear regression lines.

Substituting the 10 control (ABCD) plots with rare species removed for the five original control plots resulted in a largely equivalent model ranking and deviance explained (Table A5), although removing rare species reduced phylogenetic diversity (PD) compared to that of the control (ABCD). Likewise, substituting the Bayesian phylogenetic tree-based phylogenetic diversity (PD) for the maximum likelihood-based PD did not weaken its role in explaining variation in biomass production; we found nearly identical model ranking and explanatory power given the strong correlation between PD determined using both methods (Fig. A4).

We found evidence for a weak phylogenetic signal in maximum plant height and possibly leaf phosphorus

content, but not in leaf nitrogen, seed mass or specific leaf area (Table 2). However, when we tested for the signal using the Bayesian phylogenetic tree, evidence for the effects disappeared, again demonstrating that they were weak or unimportant. Plotting the mean maximum plant height for each of the main taxonomic treatment groups, there is some evidence that individuals from the Poaceae and Cyperaceae species were relatively and marginally taller (Fig. 2).

DISCUSSION

While the results from experiments that synthetically assemble communities have added to our knowledge of biodiversity effects on productivity, until now we have

TABLE 2. Maximum-likelihood and Bayesian phylogenetically independent contrasts to determine whether individual functional traits demonstrated a phylogenetic signal.

Trait	K	$\hat{\sigma}_{obs}^2$	$\hat{\sigma}_{rand}^2$	P	Z
Maximum likelihood					
H_{max}	0.0853	5 692.4	214 846 657.9	0.003	-0.5705
P	0.0037	5.7	7 706.1	0.041	-0.2760
N	0.0001	9 544.1	356 503.9	0.124	-0.8031
SLA	0.0000	3 503 371 792.0	3 024 260 021.0	0.683	0.1274
SM	0.0004	29 999.6	3 551 560.0	0.273	-0.2076
Bayesian					
H_{max}	0.0939	5 213.5	10 085.7	0.308	-0.6004
P	0.0709	0.3	0.5	0.683	-0.2343
N	0.1443	6.8	19.9	0.040	-1.1622
SLA	0.0568	135 670.4	158 433.6	0.492	-0.2680
SM	0.3475	31.4	251.6	0.086	-0.4570

Note: Values are shown for K , the phylogenetic K statistic; $\hat{\sigma}_{obs}^2$, the observed phylogenetically independent contrasts (PIC) variance; $\hat{\sigma}_{rand}^2$, the randomized PIC variance; P , the probability of randomly generated variance relative to observed variance; and Z , the observed vs. random variance Z score.



PLATE 1. An alpine meadow near Maqu, Gansu Province, People's Republic of China. The small black dots in the upper region are yaks (*Bos grunniens*). Photo credit: C. J. A. Bradshaw.

understood little about how different forms of biodiversity influence ecosystem function in natural assemblages. Experimenters generally select species to manipulate gradients of biodiversity (Cadotte 2013), with little or no connection to the mechanisms that actually assemble communities. Our results reveal that not only does biodiversity strongly influence productivity in natural assemblages (Flombaum and Sala 2008), phylogenetic diversity and traits with no or weak phylogenetic signals were all required to explain maximum variation in productivity.

In our system, multivariate functional diversity as a single predictor slightly outperformed other multivariate predictors when considered in isolation, which is consistent with previous studies (Petchey et al. 2004, Cadotte et al. 2009). This is not surprising because we expected that trait differences should influence ecological differences, and higher trait diversity means more access to limited resources. However, when compared to individual traits, the multivariate functional diversity predictors were always outranked by phylogenetic diversity and some combination of single functional traits. This suggests that phylogenetic diversity possibly captures some component of the influence of unmeasured functional traits such as those associated with roots or herbivores, or perhaps our method for estimating multivariate functional diversity is suboptimal. However, functionally important traits that have diverged are also necessary to compensate for the loss of information in phylogenetic measures of biodiversity. In other words, there was no single biodiversity measure

that adequately summarized biodiversity, and several dimensions were required to predict the largest component of variation in productivity.

Our result that Shannon's evenness outperformed simple species richness as a predictor of productivity corroborates meta-analytical and experimental evidence that it is a superior predictor of productivity even at multiple spatial scales (Zhang et al. 2012). The reason for the additional influence of abundance might be due to the mechanism of both intra- and inter-specific density feedbacks resulting from biotic interactions

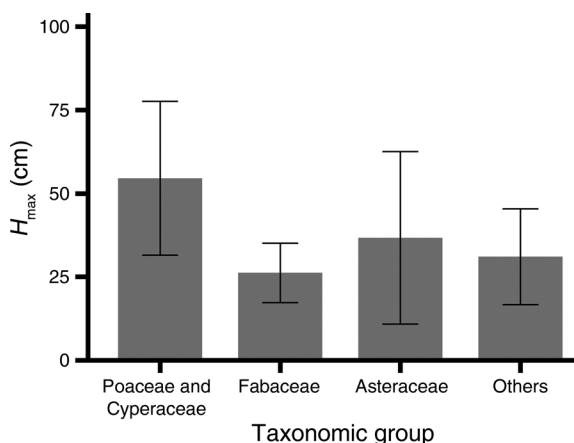


FIG. 2. Maximum plant height (H_{\max} ; mean \pm SD) per experimental taxonomic group. Evidence for a phylogenetic signal in this trait (see *Results*) appears to arise from the larger maximum height of species within the Poaceae and Cyperaceae.

within communities (Hillebrand et al. 2008). Indeed, the functional traits of dominant species can play an important role in determining ecosystem processes. For example, Roscher et al. (2012) showed that community-weighted means of trait values, which quantify the dominant traits in a community, accounted for up to 80% of explained variance in the biomass of an experimentally planted community.

Investigations of the biodiversity–productivity relationship in natural systems have tended to produce inconclusive or inconsistent results, predicting either stronger effects of biodiversity on productivity relative to “artificial” ecosystems (Flombaum and Sala 2008), or no relationship at all (Grace et al. 2007). This contrasts with most experimental evidence that generally supports the positive relationship between biodiversity and productivity (Tilman et al. 1996, Hector et al. 1999, Cadotte et al. 2009), and the possible higher explanatory power of phylogenetic diversity compared to species richness and functional diversity (Cadotte et al. 2009). While our analyses generally agree with previous findings, our study has the advantages of both sown experiments and natural investigations (Diaz et al. 2003). On the one hand, the biodiversity–productivity experiment we manipulated maintains the naturally occurring species assemblage, their abundances and spatial positions, which is lacking in sown experiments. On the other, we manipulated gradients in species richness, functional diversity, and phylogenetic diversity through taxonomic group removal, demonstrating a convincing relationship between different biodiversity metrics and community production in a homogeneous habitat.

Here, certain plots had entire families removed, thus mimicking deep phylogenetic divisions. However, examining the tree structure for both phylogenies demonstrated reasonable balance according to standardized Colless' I ($I = 1.052$, $P = 0.076$ and $I = 0.868$, $P = 0.136$ for the maximum-likelihood and Bayesian trees, respectively). Hence, our phylogenies did have the characteristics of deep divisions (strong internal branching) based on their relative balance, which is predicted to result in strong richness–phylogenetic-diversity relationships (Rodrigues et al. 2005, Tucker and Cadotte 2013). This congruence makes richness an appropriate surrogate for phylogenetic diversity in this and other communities (Polasky et al. 2001, Tôrres and Diniz-Filho 2004).

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LITERATURE CITED

- Blomberg, S. P., T. Garland, Jr., and A. R. Ives. 2003. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* 57:717–745.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.
- Burnham, K. P., and D. R. Anderson. 2004. Understanding AIC and BIC in model selection. *Sociological Methods and Research* 33:261–304.
- Cadotte, M., C. H. Albert, and S. C. Walker. 2013. The ecology of differences: assessing community assembly with trait and evolutionary distances. *Ecology Letters* 16:1234–1244.
- Cadotte, M. W. 2013. Experimental evidence that evolutionarily diverse assemblages result in higher productivity. *Proceedings of the National Academy of Sciences USA* 110:8996–9000.
- Cadotte, M. W., B. J. Cardinale, and T. H. Oakley. 2008. Evolutionary history and the effect of biodiversity on plant productivity. *Proceedings of the National Academy of Sciences USA* 105:17012–17017.
- Cadotte, M. W., K. Carscadden, and N. Mirotchnick. 2011. Beyond species: functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology* 48:1079–1087.
- Cadotte, M. W., J. Cavender-Bares, D. Tilman, and T. H. Oakley. 2009. Using phylogenetic, functional and trait diversity to understand patterns of plant community productivity. *PLoS ONE* 4:e5695.
- Cadotte, M. W., T. Jonathan Davies, J. Regetz, S. W. Kembel, E. Cleland, and T. H. Oakley. 2010. Phylogenetic diversity metrics for ecological communities: integrating species richness, abundance and evolutionary history. *Ecology Letters* 13:96–105.
- Cardinale, B. J., D. S. Srivastava, J. Emmett Duffy, J. P. Wright, A. L. Downing, M. Sankaran, and C. Jouseau. 2006. Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature* 443:989–992.
- Cavender-Bares, J., K. H. Kozak, P. V. A. Fine, and S. W. Kembel. 2009. The merging of community ecology and phylogenetic biology. *Ecology Letters* 12:693–715.
- Diaz, S., A. J. Symstad, F. Stuart Chapin, III, D. A. Wardle, and L. F. Huenneke. 2003. Functional diversity revealed by removal experiments. *Trends in Ecology and Evolution* 18:140–146.
- Douady, C. J., F. Delsuc, Y. Boucher, W. F. Doolittle, and E. J. P. Douzery. 2003. Comparison of Bayesian and maximum likelihood bootstrap measures of phylogenetic reliability. *Molecular Biology and Evolution* 20:248–254.
- Edgar, R. C. 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* 32:1792–1797.
- Faith, D. P. 1992. Conservation evaluation and phylogenetic diversity. *Biological Conservation* 61:1–10.
- Faith, D. P. 1994. Phylogenetic pattern and the quantification of organismal biodiversity. *Philosophical Transactions: Biological Sciences* 345:45–58.
- Flombaum, P., and O. E. Sala. 2008. Higher effect of plant species diversity on productivity in natural than artificial ecosystems. *Proceedings of the National Academy of Sciences USA* 105:6087–6090.
- Flynn, D. F. B., N. Mirotchnick, M. Jain, M. I. Palmer, and S. Naeem. 2011. Functional and phylogenetic diversity as predictors of biodiversity–ecosystem-function relationships. *Ecology* 92:1573–1581.
- Gong, Z. T. 1999. Chinese soil taxonomy: theories, methods and applications. Science Press, Beijing, China.
- Grace, J. B., et al. 2007. Does species diversity limit productivity in natural grassland communities? *Ecology Letters* 10:680–689.
- Guindon, S., J. F. Dufayard, V. Lefort, M. Anisimova, W. Hordijk, and O. Gascuel. 2010. New algorithms and methods to estimate maximum-likelihood phylogenies: assessing the performance of PhyML 3.0. *Systematic Biology* 59:307–321.

- Harvey, P. H., and M. Pagel. 1991. *The comparative method in evolutionary biology*. Oxford University Press, Oxford, UK.
- Hector, A., et al. 1999. Plant diversity and productivity experiments in European grasslands. *Science* 286:1123–1127.
- Helmus, M. R., T. J. Bland, K. W. Christopher, and R. I. Anthony. 2007. Phylogenetic measures of biodiversity. *American Naturalist* 169:E68–E83.
- Hillebrand, H., D. M. Bennett, and M. W. Cadotte. 2008. Consequences of dominance: a review of evenness effects on local land and regional ecosystem processes. *Ecology* 89:1510–1520.
- Kembel, S. W., P. D. Cowan, M. R. Helmus, W. K. Cornwell, H. Morlon, D. D. Ackerly, S. P. Blomberg, and C. O. Webb. 2010. Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* 26:1463–1464.
- Kress, W. J., D. L. Erickson, N. G. Swenson, J. Thompson, M. Uriarte, and J. K. Zimmerman. 2010. Advances in the use of DNA barcodes to build a community phylogeny for tropical trees in a Puerto Rican Forest Dynamics plot. *PLoS ONE* 5:e15409.
- Liu, J., D. Wu, X. Peng, S. Zhou, and C. J. A. Bradshaw. 2013. Exogenous and endogenous determinants of spatial aggregation patterns in Tibetan Plateau meadow vegetation. *Journal of Plant Ecology* 6:277–285.
- Lyons, K. G., and M. W. Schwartz. 2001. Rare species loss alters ecosystem function–invasion resistance. *Ecology Letters* 4:358–365.
- Maherali, H., and J. N. Klironomos. 2007. Influence of phylogeny on fungal community assembly and ecosystem functioning. *Science* 316:1746–1748.
- McLaren, J. R., and R. Turkington. 2010. Ecosystem properties determined by plant functional group identity. *Journal of Ecology* 98:459–469.
- Mi, X., et al. 2012. The contribution of rare species to community phylogenetic diversity across a global network of forest plots. *American Naturalist* 180:E17–E30.
- Mouquet, N., et al. 2012. Ecophylogenetics: advances and perspectives. *Biological Reviews* 87:769–785.
- Oksanen, J., et al. 2013. vegan: community ecology package. R package version 2.0-10. <http://cran.r-project.org/web/packages/vegan/>
- Paradis, E., J. Claude, and K. Strimmer. 2004. APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* 20:289–290.
- Petchey, O. L., and K. J. Gaston. 2002. Functional diversity (FD), species richness and community composition. *Ecology Letters* 5:402–411.
- Petchey, O. L., A. Hector, and K. J. Gaston. 2004. How do different measures of functional diversity perform? *Ecology* 85:847–857.
- Petermann, J. S., A. J. F. Fergus, L. A. Turnbull, and B. Schmid. 2008. Janzen-Connell effects are widespread and strong enough to maintain diversity in grasslands. *Ecology* 89:2399–2406.
- Polasky, S., B. Csuti, C. A. Vossler, and S. M. Meyers. 2001. A comparison of taxonomic distinctness versus richness as criteria for setting conservation priorities for North American birds. *Biological Conservation* 97:99–105.
- R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.r-project.org
- Redding, D. W., and A. Ø. Mooers. 2006. Incorporating evolutionary measures into conservation prioritization. *Conservation Biology* 20:1670–1678.
- Rodrigues, A. S. L., T. M. Brooks, and K. J. Gaston. 2005. Integrating phylogenetic diversity in the selection of priority areas for conservation: does it make a difference? Pages 101–119 in A. Purvis, J. L. Gittleman, and T. Brooks, editors. *Phylogeny and conservation*. Cambridge University Press, Cambridge, UK.
- Ronquist, F., and J. P. Huelsenbeck. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19:1572–1574.
- Roscher, C., J. Schumacher, M. Gubsch, A. Lipowsky, A. Weigelt, N. Buchmann, B. Schmid, and E.-D. Schulze. 2012. Using plant functional traits to explain diversity–productivity relationships. *PLoS ONE* 7:e36760.
- Schliep, K. P. 2011. phangorn: phylogenetic analysis in R. *Bioinformatics* 27:592–593.
- Tilman, D., J. Knops, D. Wedin, P. Reich, M. Ritchie, and E. Siemann. 1997. The influence of functional diversity and composition on ecosystem processes. *Science* 277:1300–1302.
- Tilman, D., P. B. Reich, J. Knops, D. Wedin, T. Mielke, and C. Lehman. 2001. Diversity and productivity in a long-term grassland experiment. *Science* 294:843–845.
- Tilman, D., D. Wedin, and J. Knops. 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature* 379:718–720.
- Tórres, N. M., and J. A. F. Diniz-Filho. 2004. Phylogenetic autocorrelation and evolutionary diversity of Carnivora (Mammalia) in Conservation Units of the New World. *Genetics and Molecular Biology* 27:511–516.
- Tucker, C. M., and M. W. Cadotte. 2013. Unifying measures of biodiversity: understanding when richness and phylogenetic diversity should be congruent. *Diversity and Distributions* 19:845–854.
- Walker, B., A. Kinzig, and J. Langridge. 1999. Plant attribute diversity, resilience, and ecosystem function: the nature and significance of dominant and minor species. *Ecosystems* 2:95–113.
- Webb, C. O., D. D. Ackerly, M. A. McPeck, and M. J. Donoghue. 2002. Phylogenies and community ecology. *Annual Review of Ecology and Systematics* 33:475–505.
- Weiher, E., G. D. P. Clarke, and P. A. Keddy. 1998. Community assembly rules, morphological dispersion, and the coexistence of plant species. *Oikos* 81:309–322.
- Zavaleta, E. S., and K. B. Hulvey. 2004. Realistic species losses disproportionately reduce grassland resistance to biological invaders. *Science* 306:1175–1177.
- Zhang, Y., H. Y. H. Chen, and P. B. Reich. 2012. Forest productivity increases with evenness, species richness and trait variation: a global meta-analysis. *Journal of Ecology* 100:742–749.

SUPPLEMENTAL MATERIAL

Ecological Archives

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