Evolutionary history and the effect of biodiversity on plant productivity

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Loss of biological diversity because of extinction is one of the most pronounced changes to the global environment. For several decades, researchers have tried to understand how changes in biodiversity might impact biomass production by examining how biomass correlates with a number of biodiversity metrics (especially the number of species and functional groups). This body of research has focused on species with the implicit assumption that they are independent entities. However, functional and ecological similarities are shaped by patterns of common ancestry, such that distantly related species might contribute more to production than close relatives, perhaps by increasing niche breadth. Here, we analyze 2 decades of experiments performed in grassland ecosystems throughout the world and examine whether the evolutionary relationships among the species comprising a community predict how biodiversity impacts plant biomass production. We show that the amount of phylogenetic diversity within communities explained significantly more variation in plant community biomass than other measures of diversity, such as the number of species or functional groups. Our results reveal how evolutionary history can provide critical information for understanding, predicting, and potentially ameliorating the effects of biodiversity loss and should serve as an impetus for new biodiversity experiments.

community ecology | ecosystem function | phylogenetic diversity | biodiversity experiments | metaanalysis

The modern era has come to be defined as a period of rapid environmental change. One of the most prominent changes taking place globally is a reduction in the number of genes, species, and functional groups of organisms that comprise the biological diversity of natural and managed communities. Widespread loss of biodiversity has prompted scientists from an increasing number of disciplines to begin studying the social, economic, and environmental impacts of diversity change (1–5). For example, seminal experiments in the 1990s suggested that species loss might reduce the amount of biomass produced by plants (6–9), possibly translating to a loss of important ecological services such as the ability of natural habitats to absorb CO_2 from the atmosphere. These experiments stimulated 2 decades of research detailing the functional role of plant diversity in ecosystems. Recent summaries of this body of research have confirmed that systems with fewer species generally produce less biomass than those with more species (10–14).

However, why changes in the number of species cause ecosystems to be less productive is still not entirely clear. Is it because less diverse communities tend to be missing genes, metabolic pathways, or traits that would otherwise allow a more complete utilization of local conditions (4, 15)? To answer this question would require that researchers quantify the biological traits that drive resource use and biomass production. However, because a multitude of traits are potentially associated with the ecological differences among species that drive patterns of resource use, knowing the evolutionary relationships of the members of a community can serve to quantify patterns of trait diversity (16).

Here, we present results from a formal metaanalysis of experiments performed in locations around the world to show that phylogenetic diversity is the single best predictor of how community biomass is altered by changes in species diversity. Our dataset is derived from 29 experiments that manipulated the number of species of terrestrial angiosperms in experimental plots, pots, or garden beds in fields or greenhouses and then measured the impacts of plant species number on the production of plant biomass [for a summary of studies used, see supporting information (SI) Table S1]. For each of the experimental units that contained more than one species for which constituent monocultures were measured, we standardized the diversity "effect size" of the biomass produced in a polyculture to the mean of the constituent species in monoculture, as the log response ratio (LR_{mean}; see *Materials and Methods*). The pool of species used includes 177 taxa that span all major functional groups of grassland ecosystem plants (C3 and C4 graminoids, legumes, etc.). We calculated not only the number of species in a plot, but also the number of functional groups (for functional group definitions, see *Materials and Methods*) and the amount of phylogenetic diversity in a community (PD_C) in a plot (Fig. 1). PD_C measures the magnitude of the divergences among species that have evolved since a common ancestor, calculated as the sum of phylogenetic branch lengths separating species on a phylogeny. We estimated the phylogenetic relationships among species by using Bayesian inference with Ultrametric rate smoothing for 143 of the 177 species for which nucleotide sequences from 4 genes (*5.8s*, *atpb*, *matk*, and *rbcl*) were available in GenBank [National Center for Biotechnology Information (www.ncbi.nlm.nih.gov); for details, including support metrics, and for comparisons with other phylogenetic methods, see *SI Text* and Figs. S1 and S2]. We were able to estimate PD_C in 78% of all experimental polycultures (i.e., 1,315 experimental units).

Results and Discussion

Similar to prior summaries (6, 12, 17), our analyses confirm that both the number of species and the number of plant functional groups in an experiment are significant predictors of plant biomass production (Table 1, Model A, and Fig. 2 *A* and *B*). The finding of our analysis is that phylogenetic diversity is also a highly significant predictor of biomass production (Table 1, Model A, Fig. 2*C*). Given that we have data on the number of plant species, the number of plant functional groups, and the phylogenetic diversity in an experimental unit, it is possible to ask which of these metrics of biological diversity best explains variation in biomass production among experimental commu-

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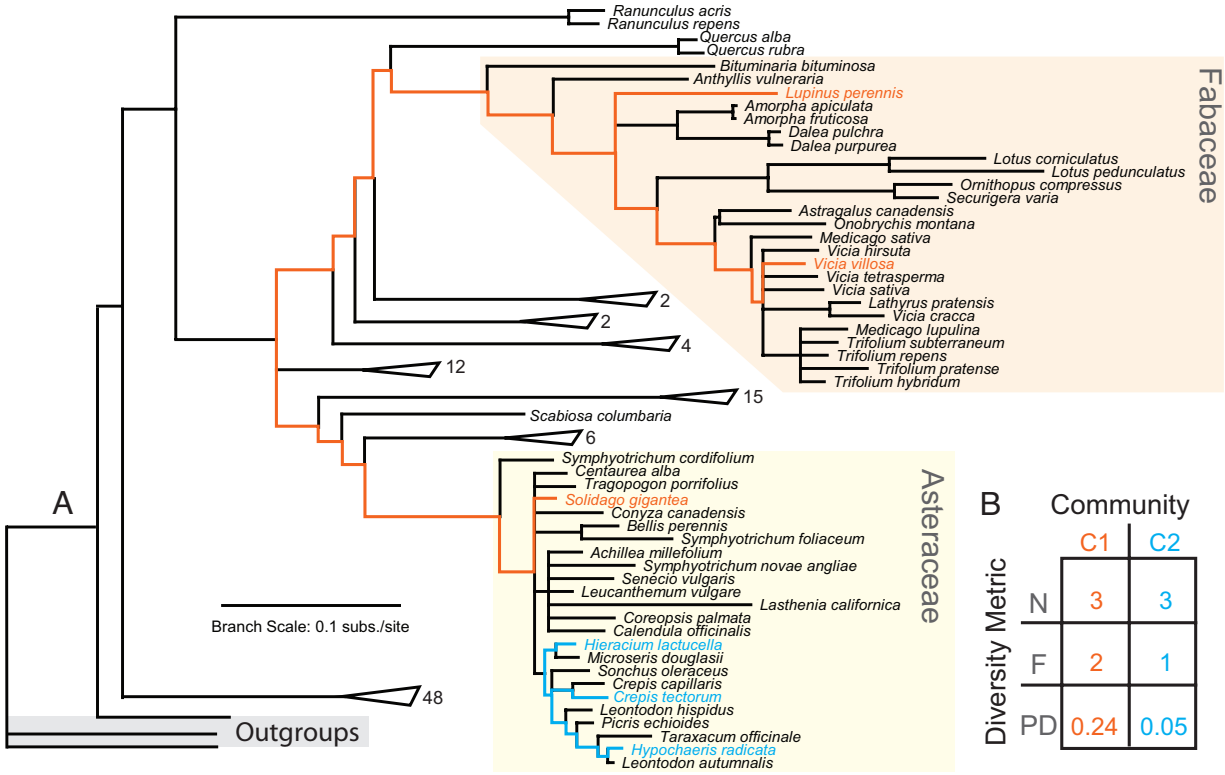

Fig. 1. Summary of phylogenetic results. (*A*) Illustrated is the majority rule consensus from a Bayesian MCMC search, with several clades collapsed because of space considerations. Triangles represent collapsed clades, with numbers of species per clade indicated. Two clades (Fabaceae and Asteraceae) representing different functional groups are highlighted for illustrating different biodiversity metrics. Details of phylogenetic analyses and results, including support values, are presented in the *Materials and Methods* and the *SI Text*. (*B*) Biodiversity can be measured in a number of ways, including the number of species in a community (N), the number of trait-based functional groups (F), or the total phylogenetic diversity (PD_C) representing the members of a community. PD_C is calculated as the sum of branch lengths leading to all members of a community, and two examples are shown using orange and blue branches. The number of species and functional groups often give little information about the underlying phylogeny describing the evolutionary history of a group of species. In 2 hypothetical communities, C1 and C2, the number of species is the same, but variation exists in the number of functional groups and the calculated PD_C.

nities. Such information would potentially be useful for conservation and management where it is often beneficial to predict how community composition affects ecologically important processes. When we compared single-variable models that included the different measures of diversity as explanatory variables, PD_C was a significantly better predictor of variation in plant biomass than either the number of species or functional groups (Table 1, Model A).

When productivity was modeled as a function of species number (the form of diversity directly manipulated in these studies), PD_C, and their two-way interaction, we found that PD_C was not only a significant predictor of plant biomass, but that there was a highly significant interaction between species number and PD_C (Table 1, Model B). Thus, the impact of plant species number on biomass in past experiments is at least partially explained by the amount of phylogenetic diversity represented in an experimental unit. Further, because PD_C and species number are positively correlated (Fig. 2*D*), we examined the impacts of PD_C on production within species number treatments. We found that the effects of PD_C on production were most pronounced at lower numbers of species where studies typically included many different combinations of species (2 species: $F_{1,439} = 4.813$, $P = 0.029$; 4 species: $F_{1,277} = 10.435$, $P = 0.001$), whereas the impacts of PD_C became less pronounced at higher levels of diversity (6 species: $F_{1,106} = 0.026$, $P = 0.873$; 8 species: $F_{1,90} = 3.077$, $P = 0.083$), probably because researchers tended to use far fewer combinations of species, resulting in less variation in PD_C.

The number of functional groups of plants was also significantly related to PD_C among species within experimental units ($F_{1,1262} = 1016.61$, $P < 0.0001$, also see Fig. S3). This relationship raises the possibility that the explanatory value of PD_C might simply be a result of its correlation to the number of functional groups. However, when we ran a mixed effects model that included a hierarchical effect of the number of functional groups used in an experiment and the effects PD_C, species number and the species number–PD_C interaction, PD_C and the interaction were both significant predictors of plant community biomass (Table 1, Model C). Thus, given that controlling for the effect of the number of functional groups does not diminish the productivity–PD_C relationship, we conclude that existing definitions of functional groups are too coarse and do not correspond well to true functional trait differences in communities (also see ref. 18).

Although the R^2_{pseudo} (see *Materials and Methods*) values from the mixed effects models ranged from 0.181 to 0.211 (Table 1), individual experiments were highly variable in the amount of variation explained. The within-experiment R^2 for the effect of species number on biomass ranged from <0.001 to 0.62, and ranged from 0.01 to 0.69 for PD_C and 0.03 to 0.78 for the full model, including species number, PD_C, and their interaction. Although there are strong overall effects of PD_C and species number on community biomass production, environmental or experimental context seems to be a major factor determining the magnitude of these effects within individual experiments. However, the explanatory power of PD_C appeared unchanged even after we accounted for the fact that a small number of species are

Table 1. Results of linear mixed effects models predicting the log response ratio of biomass production to three measures of biodiversity

Models and variables	*F*	*df*	*P* value	R^2_{pseudo}	Log likelihood	AIC	Akaike weight
A: Single variable with Exp as random effect							
Spp	90.443	1,262	<0.0001	0.184	−1057.728	2,123.456	3.97×10^{-6}
FG	65.469	1,262	<0.0001	0.181	−1067.760	2,143.521	1.74×10^{-10}
PD_C	112.31	1,262	<0.0001	0.206	−1045.291	2,098.582	≈1.0
B: Multivariable with Exp as random effect							
Spp + PD_c + Spp*PD_c				0.210	−1049.218	2,110.436	
Spp	0.449	1,260	0.5028				
PD_C	112.77	1,260	<0.0001				
Spp*PD_C	6.492	1,260	0.0110				
C: Multivariable with FG as random effect nested in Exp							
Spp + PD_C + Spp*PD_C				0.211	−1048.977	2,111.954	
Spp	0.402	1,220	0.5261				
PD_C	98.154	1,220	<0.0001				
Spp*PD_C	5.905	1,220	0.0152				

Spp is the number of species in an experimental unit; FG is the number of functional groups, and PD_C is phylogenetic diversity calculated from the Bayesian Inference with Ultrametric rate-smoothing phylogeny. Results Model A are for single-variable, fixed-effect models with experiment (Exp) included as a random effect. Model B is a model with Spp and PD_C, and their interaction is with the Exp random effect. Model C is the two-variable model with FG as a random effect nested within Exp. Akaike weights can be interpreted as the probability that model *i* is the best fit to the observed data among a set of models (54).

widely used in experiments, and the prevalence of just a few species could dictate the results. When we excluded species found in >10% of experimental units ($n = 14$ species) and reran the analyses, none of our conclusions was altered (see Table S2). The results were also robust to five commonly used methods used to estimate phylogenies (see *SI Text*), and regardless of which phylogeny was used to estimate PD_C, phylogenetic diversity was always a superior predictor of community biomass production compared with the number of species or functional groups included in diversity experiments, indicating that our conclusions

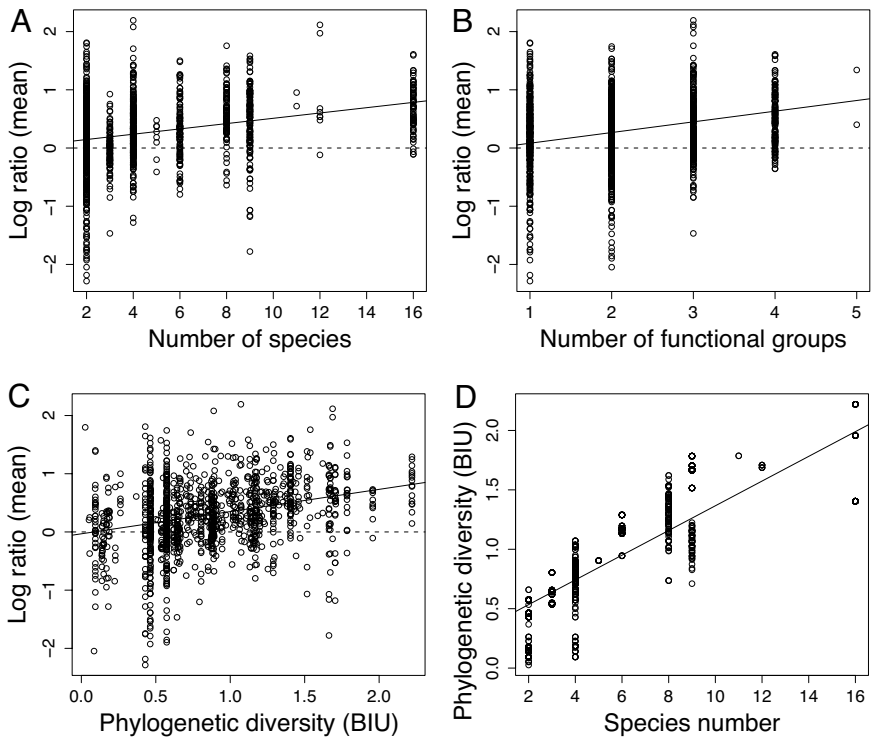

Fig. 2. The proportional difference between polyculture biomass and mean biomass of species monocultures [log ratio (mean)] is positively related to: the number of species (*A*), the number of plant functional groups (*B*), and plot phylogenetic diversity based on Bayesian Inference with Ultrametric rate smoothing (*C*). (*D*) Significant relationship between the number of species and phylogenetic diversity. The linear fits come from single-variable mixed-effects models (Table 1, Model A), and the dashed lines represent the case where polyculture biomass equals mean monoculture biomass.

are not sensitive to minor differences in estimates of PD_C caused by using different phylogenetic methods (see *SI Text*).

Data and analyses presented here show that when controlled experiments simulate changes in species diversity, changes in community biomass are greater for groups of plant species that have a distant common ancestor than for groups that share a recent common ancestor. However, it is not yet clear why increasing phylogenetic diversity results in increased plant community biomass (but see ref. 19). Some research suggests that phylogenetic relatedness is an indicator of the ecological uniqueness of species and a predictor of patterns of competitive coexistence (20–24; but see ref. 25). For example, it has long been assumed, and sometimes demonstrated, that within a habitat type, the amount of ecological differentiation among species is proportional to the amount of evolutionary and genetic divergence (26). Ecological differentiation can result in reduced resource use overlap between species, allowing species to stably coexist together (e.g., niche partitioning). These ecologically differentiated species could potentially complement each other in their resource use by differentially capturing resources in space and/or time. Greater niche and trait differences could, in turn, translate to higher production of biomass (4, 15, 19, 21, 27).

If this interpretation is correct, then future work should be able to map variation in niche differences (or plant traits that confer such differences) onto our phylogenies and find strong correspondence. However, until the time that such datasets exist, we suggest that phylogenetic diversity may be a useful biodiversity metric for predicting the ecological consequences of modern diversity change and for scaling from organism physiology to ecosystem processes (28). This tool may prove especially useful in the world's ecosystems where organisms are too large (e.g., rainforests), the systems too vast (e.g., plankton of the open ocean and the taxa of the ocean floor), or population sizes already too small (endangered species) to allow manipulative biodiversity experiments.

Materials and Methods

Obtaining and Standardizing Data. We used recent reviews and metaanalyses of biodiversity and ecosystem studies (4, 10, 12, 13) to identify 29 experiments that have experimentally manipulated the diversity of 3 or more terrestrial plant species in greenhouse or field settings. Most of these experiments were performed by using seasonal systems where most above-ground biomass has a yearly senescence phase. We obtained data on the species composition and community-level biomass in each experimental pot or plots used in these 29 studies by using data presented in the original publication, online data repositories, or directly from the principal investigators of the experiments (refs. 7, 17, 29–37; see Table S1 and Fig. S4 for a summary of experiments). Our dataset included a total of 177 species of angiosperms that are inhabitants of ecosystems found throughout the world (see *SI Text*).

We used two complementary metrics to characterize diversity effects on the production of biomass in each plot or pot (10, 12, 38). The first metric characterizes the net diversity effect size. It is estimated as the log ratio: $LR_{mean} = \ln(y_{ip}/y_{\bar{m}})$, which gives the proportional difference between biomass production (y) of a polyculture (p) and the mean biomass of those same species in monoculture ($\bar{m}$) in experiment i. The second metric gives the proportional difference in biomass production (y) of a polyculture (p) and the biomass of the maximum producing monoculture ($\hat{m}$) in experiment i, $LR_{max} = \ln(y_{ip}/y_{\hat{m}})$. This metric characterizes the amount of ''transgressive overyielding'' in a community, which occurs when a diverse polyculture produces more biomass than even its single most productive species. The main text of this article focuses on the net diversity effect size, LR_{mean}, whereas results for LR_{max} are reported in the *SI Text*, Table S3, and Fig. S6.

Because these two metrics require information about the biomass that species achieve individually in monoculture, a number of polyculture plots could not be included in our analyses. This was true for two principal reasons. First, some experiments did not include monocultures of all species in the experimental design, which meant that only a subset of polycultures could be included in our analyses (e.g., 7, 30, 36). Second, in a subset of experiments, unintentional species were sown into plots (37). These additions created 2-species polycultures in place of the intended single-species monocultures. In either case, adequate monoculture estimates could not be calculated for all species in 310 plots, which were excluded from our analyses.

Constructing the Phylogeny. The 177 species recorded in these experiments included mainly herbaceous angiosperms (both monocots and eudicots), with experimenters explicitly focusing on species that mimic herbaceous grassland-type communities. We pooled all 177 species together to construct a master phylogeny. We used two methods to construct this phylogeny: (*i*) by using the angiosperm supertree (39); and (*ii*) from molecular data where we estimated a phylogeny from either (*i*) maximum likelihood or (*ii*) Bayesian inference analyses, and for the final two phylogenies we further used Ultrametric rate smoothing on the two molecular phylogenies.

Angiosperm supertree. We constructed this phylogeny by using the Davies *et al.* (39) supertree and generated a phylogeny for our species list by using Phylomatic (40). We then used the BLADJ procedure in Phylocom 3.40 (41) to scale branch lengths by using known node ages. For angiosperms, we used the divergence times estimated by Wikstrom *et al.* (42). Therefore, our estimates of phylogenetic distance from the supertree are in millions of years.

Molecular phylogenies. For each of the 177 species, we searched GenBank (43) for 4 gene sequences commonly used in published angiosperm phylogenies: *atpb*, *matk*, *rbcl*, and *5.8s*. Of the 177 species, 110 had at least 1 gene represented in GenBank. For a further 33 species, we used gene sequences for a congeneric relative only if there were not any other congeners used in the experimental plots. We also included 3 representatives of early diverging lineages as outgroup species, including *Amborella trichopoda*, *Magnolia grandiflora*, and *Nymphaea odorata*. For these 148 species we aligned sequences by using MUSCLE (44). We then selected best-fit models of nucleotide substitution for each gene by using the Akaike Information Criterion, as implemented in Modeltest and MrModeltest (45, 46).

Maximum likelihood phylogeny from gene sequences. Using the aligned sequences and the estimated models of nucleotide substitution, we estimated a maximum likelihood phylogeny by using the PHYML algorithm with a BIONJ starting tree (47, 48). To assess nodal support on maximum likelihood phylogenies, we report Approximate Likelihood Ratio Test (aLRT) scores, which have been shown to correlate with ML bootstrap scores but require much less computational time (48).

Bayesian phylogeny from gene sequences. We conducted partitioned Bayesian Inference, estimating the posterior probability distribution of all possible phylogenies by using Metropolis Coupled Markov Chain Monte Carlo (MCMCMC), as implemented in MrBayes (49, 50). Four independent Markov Chains were run, each with 3 heated chains for 100 million generations. To monitor possible convergence of the separate MCMC runs, we tracked the standard deviation of split frequencies (SDSF), which was 0.022 at the end of the analysis. We sampled the runs every 10,000 generations and used a burnin of 70 million steps to generate a majority rule consensus tree that was used to calculate PD_C. The Bayesian phylogeny is shown in Fig. S1.

Maximum likelihood and Bayesian trees with Ultrametric rate smoothing. We created two additional phylogenies that represent estimated divergence times based on Ultrametric transformations of the maximum likelihood and Bayesian phylogenetic analyses described above. We performed nonparametric rate smoothing (51) on both phylogenies.

Calculating Phylogenetic Diversity. We calculated the phylogenetic diversity of plant species sown together in each experimental unit as total phylogenetic branch lengths connecting species together by using script provided by T. Jonathan Davies run in R 2.6.2 (R Development Core Team, www.R-project.org). The results are provided in the *SI Text*.

Another PD metric, Faith's PD (52) or phylogenetic diversity, is identical to ours except that it calculates PD including the root node of a larger regional phylogeny. Faith's PD then is a measure of the proportion of evolutionary history represented within a local community. Our measure, PD_C, simply calculates the phylogenetic distance connecting all members of a community together without considering a larger regional phylogeny. We calculated PD_C for plots that had all resident species included in all phylogenies, to compare results among the different phylogenetic methods; therefore, the species included in the supertree phylogeny mirror those for the molecular phylogeny.

In the main text, we present only the results from one phylogenetic analysis (Bayesian inference with Ultrametric rate smoothing; see *SI Text* for results from other phylogenetic methods) because estimates of PD_C depended very little on the specific method of phylogenetic analysis. This finding is evidenced by a high correlation of PD_C values calculated with trees resulting from five different phylogenetic methods (for all, $r > 0.912$, $P < 0.01$; see Fig. S2). We chose to present the Bayesian tree in particular because Bayesian search algorithms represent a more thorough exploration of parameter space than maximum-likelihood methods, likely optimizing tree topology and branch

lengths better. We also chose to use the Ultrametric version of the Bayesian tree because present-day taxa are assumed to be equally divergent from the shared ancestor.

Assigning Functional Groups. To assign species to plant functional groups we used the classifications provided by individual researchers for their own experiments (17, 34, 36, 37), which generally organized plants into nitrogen fixers (Fabaceae), woody species, C3 graminoids, C4 graminoids, and nonnitrogen-fixing forbs. To standardize the classification of graminoids, we used a single source (53) to determine C3–C4 status. We then enumerated the number of functional groups within experimental plots.

Statistical Analysis. Our analyses focused on comparing the relative importance of seven potential predictors of LR_{mean}, including species number, the number of plant functional groups, and the five PD_C estimates from different phylogenetic methods. For each predictor we ran single variable mixed effects models of the general form:

$$y_i = \beta_o + \beta_1 x_1 + b_i + \varepsilon_i, \qquad [1]$$

where y_i is the LR_{mean} value in a plot in experiment i, β_o is the intercept, β_1 is the coefficient associated with the fixed effect variable x_i (either species number, PD_C, or functional group number), b_i is the coefficient of the random effect (experiment), and the error term, ε_i, is the remaining variation. Parameters in all mixed-effects models were estimated by using restricted likelihood estimation (54). Individual models were compared by using log-likelihood values, Akaike Information Criterion (AIC), and the Akaike weight, which gives the likelihood that model i explains the most variation in an observed data given a set of candidate models (55). We also calculated pseudo-R^2 values by regressing model-fitted response values to the observed response variable. Twenty-one statistical outliers (of 1,315) were excluded from our analyses. These were identified from Bonferroni 2-sided tests on Studentized residuals.

Species number, PD_C, and their interaction were then combined into the single mixed-effects model:

$$y_i = \beta_o + \beta_{sp} x_{sp} + \beta_{PD} x_{PD} + \beta_{spxPD} x_{sp} x_{PD} + b_i + \varepsilon_i. \qquad [2]$$

With this model we tested the assumption that the predictor variables were fixed effects, as in a standard mixed-effects model, vs. whether heterogeneous results necessitate allowing β estimates to vary among experiments. To test this assumption, we fit models with random effects for both the intercept and the slope estimates for either species number or PD_C nested within experiment and compared these models with the corresponding one where the intercept and slope were modeled as fixed effects (54). Fixed independent-variable models (i.e., single β) were most parsimonious for both richness and PD_C (likelihood ratios: 2.995, $P = 0.2236$; 4.091, $P = 0.1293$, respectively).

Although we know that functional groups are predictors of LR_{mean}, we also know that functional groupings generally have a phylogenetic signal (28). Also, from the data it is apparent that the number of functional groups in a plot is correlated with the average PD_C in that plot (see Fig. S3). Therefore, because not all experiments explicitly manipulated the number of plant functional groups, we included the number of functional groups, j, as a random effect nested hierarchically within experiment. The model is:

$$y_{ij} = \beta_o + \beta_{sp} x_{sp} + \beta_{PD} x_{PD} + \beta_{spxPD} x_{sp} x_{PD} + b_i + b_{i,j} + \varepsilon_{ij}, \qquad [3]$$

where y_{ij} is the LR_{mean} value in a plot in experiment i with j functional groups, β_o is the intercept, β_{sp} is the slope of the effect of species number, β_{PC} is the slope of the PD_C effect, and $\beta_{sp\times PD}$ is the slope of the effect of the interaction between species number and PD_C. b_i is the coefficient of the random effect of experiment i, b_{ij} is the coefficient of the random effect of j number of functional groups nested with experiment i, and the error term, ε_{ij}, is the remaining variation. Because of the apparent colinearity between predictors, we preformed a ridge regression (e.g., 56) on the full model and found no significant change in parameter estimation with an estimated Hoerl–Kennard–Baldwin parameter of 2.315.

Finally, species varied in the number of plots in which they occurred (see Fig. S5), and commonly used species could have a disproportionate effect on the results. Therefore, we created n data subsets corresponding to the n species found in >10% of plots. In each data subset, all plots containing common species n_i were removed. We reran the statistical analyses and compared these results with the full dataset to determine whether species n_i had a disproportionate effect on the results (see *SI Text*). All analyses were run by using *R* 2.6.2 (R Development Core Team, www.R-project.org).

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