Biodiversity simultaneously enhances the production and stability of community biomass, but the effects are independent

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Abstract. To predict the ecological consequences of biodiversity loss, researchers have spent much time and effort quantifying how biological variation affects the magnitude and stability of ecological processes that underlie the functioning of ecosystems. Here we add to this work by looking at how biodiversity jointly impacts two aspects of ecosystem functioning at once: (1) the production of biomass at any single point in time (biomass/area or biomass/volume), and (2) the stability of biomass production through time (the CV of changes in total community biomass through time). While it is often assumed that biodiversity simultaneously enhances both of these aspects of ecosystem functioning, the joint distribution of data describing how species richness regulates productivity and stability has yet to be quantified. Furthermore, analyses have yet to examine how diversity effects on production covary with diversity effects on stability. To overcome these two gaps, we reanalyzed the data from 34 experiments that have manipulated the richness of terrestrial plants or aquatic algae and measured how this aspect of biodiversity affects community biomass at multiple time points. Our reanalysis confirms that biodiversity does indeed simultaneously enhance both the production and stability of biomass in experimental systems, and this is broadly true for terrestrial and aquatic primary producers. However, the strength of diversity effects on biomass production is independent of diversity effects on temporal stability. The independence of effect sizes leads to two important conclusions. First, while it may be generally true that biodiversity enhances both productivity and stability, it is also true that the highest levels of productivity in a diverse community are not associated with the highest levels of stability. Thus, on average, diversity does not maximize the various aspects of ecosystem functioning we might wish to achieve in conservation and management. Second, knowing how biodiversity affects productivity gives no information about how diversity affects stability (or vice versa). Therefore, to predict the ecological changes that occur in ecosystems after extinction, we will need to develop separate mechanistic models for each independent aspect of ecosystem functioning.

Key words: *biodiversity; community biomass; ecosystem functioning; ecosystem stability; productivity; species richness.*

Introduction

Soon after the Convention on Biological Diversity was signed at the 1992 Earth Summit, there was an explosion of interest in how changes in biological diversity might alter the productivity and sustainability of Earth's ecosystems (Mooney et al. 1996). This interest helped stimulate two decades of experimental research in which biologists manipulated the variety of genes, species, or functional traits of organisms in hundreds of types of ecological communities (reviewed by Tilman [1999], Loreau et al. [2001], Naeem [2002], Hooper et al. [2005], and most recently, Cardinale et al. [2012]). As experiments and publications amassed, this body of research became known as the field of Biodiversity and Ecosystem Functioning (BEF), and it grew sufficiently data rich to enter an extended period of synthesis. In the past six years, we have seen at least 13 quantitative data

syntheses summarize how various aspects of biodiversity influence the magnitude of ecosystem functions, such as the production of community biomass (Balvanera et al. 2006, Cardinale et al. 2006, 2007, 2009, 2011, Worm et al. 2006, Stachowicz et al. 2007, Bruno and Cardinale 2008, Cadotte et al. 2008, Schmid et al. 2009, Srivastava et al. 2009, Quijas et al. 2010, Flynn et al. 2011). These syntheses have shown that more diverse communities, whether at the level of genes, species, or functional traits, are generally more efficient at capturing biologically essential resources and, in turn, produce more biomass than less diverse communities. In contrast to the large number of syntheses focused on productivity, comparably few have tallied how biodiversity influences the stability of ecosystems. In part, this may be due to the fact that "stability" has been used to refer to a wide variety of ecological phenomena (e.g., resistance, resilience, alternative states, temporal variation, and so on), and the various facets of stability are not necessarily expected to respond to diversity in the same way (Ives and Carpenter 2008). Even so, several recent papers have summarized a subset of work that has focused on how biodiversity influences variation in community-level properties like biomass through time (Cottingham et al. 2001, Griffin et al. 2009, Jiang and Pu 2009, Hector et al. 2010, Campbell et al. 2011). These syntheses tend to agree that community-level biomass is generally more stable (less variable) through time in diverse communities, and identifying the dominant mechanism(s) has now become the primary focus (Loreau and de Mazancourt 2008).

Given the conclusions of recent syntheses, a widely held perception is that biodiversity not only enhances the production of community biomass, it also reduces variability (increases stability) of biomass through time (as in Fig. 1A). We suspect that many biologists also take this to mean that conservation of biodiversity represents a "win–win" scenario for maximizing and sustaining certain types of ecosystem functions like productivity. But we would argue that such conclusions are premature for at least two reasons. First, although it may not be widely recognized, the studies that have comprised syntheses of how biodiversity impacts productivity tend to have minimal overlap with studies used in syntheses focused on stability. As an example, consider that one of the most recent syntheses on diversity–stability relationships (Jiang and Pu 2009) shared only five studies in common with a recent synthesis on diversity–productivity relationships (Cardinale et al. 2011). The lack of overlap shouldn't necessarily be a surprise given that studies of diversity–stability relationships are often performed by different researchers, working with different organisms and systems than those who examine diversity–productivity relationships. There are exceptions to this, where researchers have analyzed productivity and stability for the same biodiversity experiment; but it is noteworthy that the two diversity effects tend to be reported in

separate publications, which means the literature on diversity–productivity relationships has remained remarkably distinct from the literature on diversity–stability relationships (for example, Hector et al. 1999 and Hector et al. 2010, or Tilman et al. 2001 and Tilman et al. 2006, or Wilsey and Polley 2004 and Isbell et al. 2009). So while it may be a common assumption that biodiversity simultaneously enhances both biomass production and stability, we would argue that this assumption has yet to be explicitly tested or verified as a generality across ecological communities.

Second, and equally important, we are unaware of any analysis that has examined how diversity effects on biomass production covary with diversity effects on stability. Understanding how these two effects covary is fundamental to many conservation and management goals. For example, a common goal in ecosystem management is to achieve high yields that can be sustained through time (e.g., production of crops, wood, fisheries, or carbon sequestration). If biodiversity enhances both the magnitude of biomass production at a given time, and increases the stability of community biomass over time, then conservation of biodiversity may indeed help achieve both goals at once. If, on the other hand, increases in one ecosystem function (productivity) correspond to reductions in another (stability), then we shouldn't necessarily expect conservation to maximize the different aspects of ecosystem functioning at once. To distinguish which of these scenarios is possible, we need to know how diversity effects on biomass production covary with effects on temporal stability.

At least three hypotheses have been proposed to explain how diversity effects on biomass production and stability covary (Fig. 1B). Yachi and Loreau (1999) used statistical models to describe what they called the "insurance effect" of diversity. This effect assumes that the productivity of an ecosystem at any point in time is equal to the biomass of the most productive species. Having higher diversity in the system not only ensures that the most productive species will maximize biomass at any one time, it ensures that biomass is maximized by at least one highly productive species at all times. This causes high biomass to be associated with lower variation (H1 in Fig. 1B). If correct, then we would expect the highest levels of productivity in a diverse community to also be associated with the highest levels of stability.

Ives et al. (2000) used Lotka-Volterra consumer–prey models to develop an alternative prediction that diversity effects on production and stability should be independent of one another because the two effects are driven by different mechanisms. In their models, effects of diversity on production were controlled by the degree of niche partitioning among species, which determined how efficiently communities of organisms capture available resources. In contrast, effects of diversity on temporal stability were controlled by the strength of
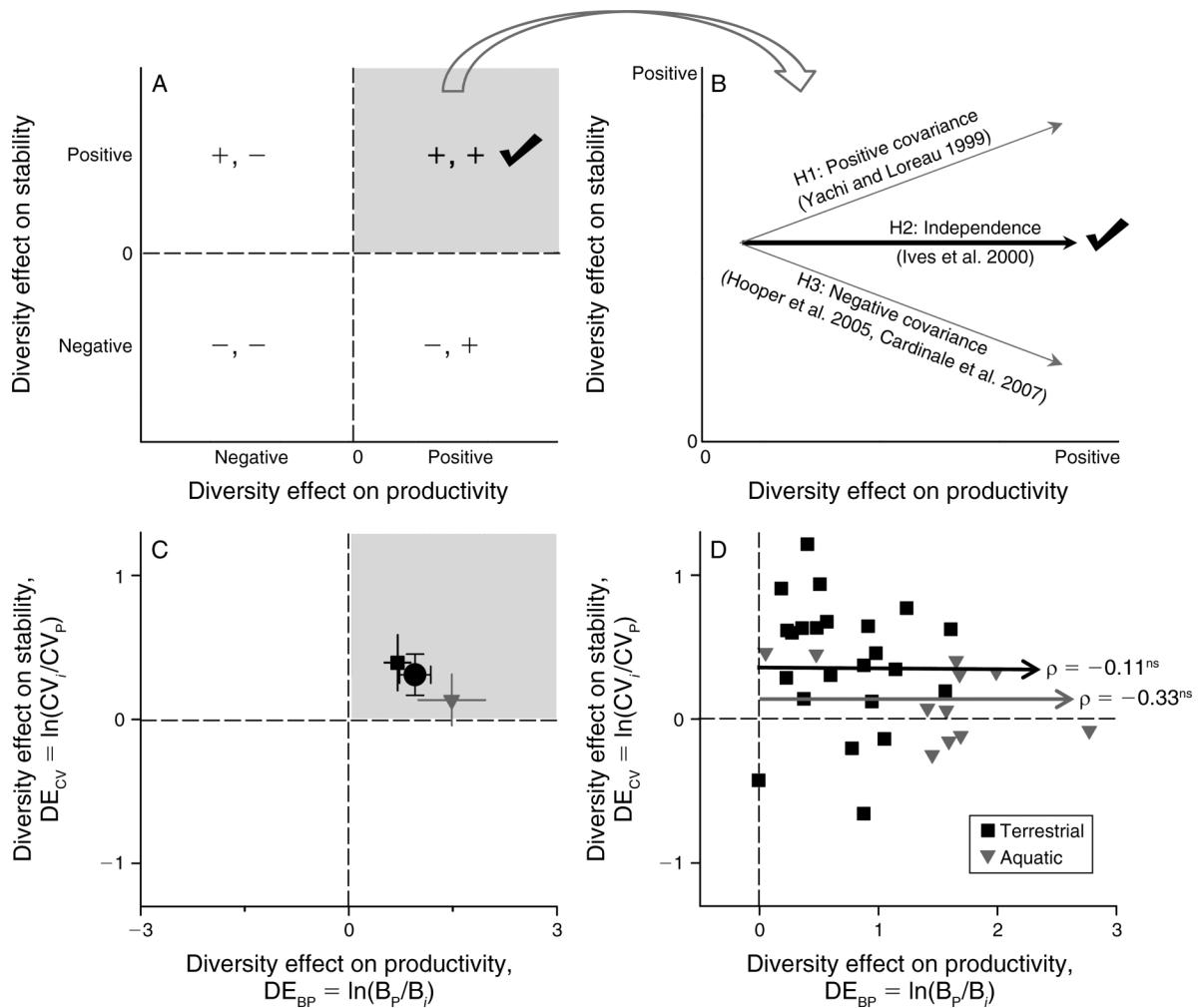
FIG. 1. Effects of biodiversity on the productivity and stability of biomass. In this study we addressed two distinct questions: (A) What is the joint distribution of data describing how biodiversity impacts both the production of biomass, and the stability of biomass through time? (B) How do diversity effects on production covary with the effects of diversity on stability (see *Introduction* for three contrasting predictions)? Check marks signify which hypotheses were supported. Our re-analysis of 34 biodiversity experiments performed with plants and algae shows that (C) producer species richness simultaneously enhances both the production of biomass (x-axis) and the stability of biomass through time (y-axis; see Table 1 for a description of metrics). Data points give the mean effect sizes ±95% confidence intervals for terrestrial (square) and aquatic (triangle) studies, and collectively for all 34 experiments (black circle). Note that studies generally fall within quadrant 1, corresponding to the upper right of panel A. Our re-analysis also shows that (D) diversity effects on biomass production are independent of diversity effects on temporal stability. Each data point gives results for one experiment (N = 23 terrestrial, 11 aquatic). Spearman rank correlations (ρ) illustrate the covariance between the magnitude of the two diversity effects (i.e., correlation between x and y data points); "ns" indicates not significant.

correlations in species responses to environmental variability, which determined the magnitude of compensatory dynamics among species through time. The independence of mechanisms ensured that diversity effects on production were not correlated with diversity effects on stability. When this is true, diversity will not necessarily lead to the highest joint values of productivity and stability, even if diversity tends to have positive effects on both aspects of functioning.

Lastly, some have argued that diversity effects on production should be negatively correlated with its effects on stability. This argument is based on the

assumption that both effects are controlled by the degree of niche partitioning among species, but niche partitioning leads to an inherent trade-off in the two functions (Hooper et al. 2005, Cardinale et al. 2007). When niche partitioning is large, diversity has a strong impact on productivity because diverse communities use available resources efficiently. Yet, because niche partitioning reduces competitive interactions, it also reduces the potential for compensatory dynamics among species that can stabilize community biomass through time. Conversely, when niche partitioning is low (high resource use overlap), diversity has little impact on

productivity. But because competition is strong, diverse communities have greater potential for compensatory dynamics that stabilize biomass. If correct, we would expect that stronger effects of diversity on productivity would be associated with weaker effects on stability (and vice versa). This could be true even when diversity effects on each ecosystem functioning are generally positive.

Here we reanalyzed data from 34 experiments that allowed us to address two questions (represented pictorially in Fig. 1A, B). First, we asked "What is the joint distribution of data that describes how producer species richness simultaneously impacts the production and stability of community biomass?" As we will show, our reanalysis confirms what many researchers already suspect, that biodiversity simultaneously enhances both the productivity and stability of ecosystems (corresponding to quadrant 1, Fig. 1A). We then used the data to ask "How do effects of diversity on biomass production covary with diversity effects on stability?" Our analyses show that diversity effects on productivity are independent of diversity effects on temporal stability (corresponding to H2 in Fig. 1B). The implications of diversity effects being independent are important. While biodiversity may enhance both productivity and stability, the highest levels of productivity in a diverse community will not, as a general rule, be associated with the highest levels of stability. These results emphasize that knowing the effect of biodiversity on productivity provides no information about the impacts of diversity loss on stability (or vice versa), which also means that predicting the ecological consequences of diversity loss will require us to develop separate mechanistic models for each aspect of ecosystem function.

METHODS

Selection of studies

Our study was based on a reanalysis of experiments that had manipulated the richness of plants or algae in field or laboratory settings and measured the production of community biomass (i.e., summed across species) at multiple time points. To identify these studies, we began with a search of the data set that was collated by Cardinale et al. (2011), which summarized manipulations of species richness that had been reported in 192 peer-reviewed papers through 2009. From this data set, we extracted records that met the following criteria: (1) Study must have manipulated the richness of primary producers (plants or algae) and measured some aspect of biomass production (mass/m^2 or mass/L, or percent cover) at two or more time points. (2) Study must have a complete data set in which metrics of biomass production and stability could be calculated for each experimental unit (field plot, greenhouse pot, laboratory aquaria, and so on). Studies for which only treatment means were available were excluded due to the potential bias in estimating variance from summarized data. (3)

Studies must have data for focal species grown alone in monoculture, as several calculations in our analyses require estimates of species-specific variances.

In addition to the Cardinale et al. (2011) data set, we examined all references in recent summaries of diversity–stability relationships by Jiang and Pu (2009), and the subsequent extension by Campbell et al. (2011). In total, 34 independent manipulations of biodiversity met the criteria above. Twenty-three of these experiments were performed in terrestrial grasslands using herbaceous plants, all of which were field studies where manipulations and measurements were taken in open plots. Eleven of the experiments focused on various types of freshwater algae, all of which were performed in controlled laboratory microcosms like bottles or test-tubes. These experiments were reported in 13 "studies," which represent different papers that report the results of multiple independent manipulations of biodiversity (for example, the BIODEPTH study represents $N = 8$ independent biodiversity experiments that were run concurrently in different European countries). The final list of studies included in our analyses is provided in the Supplement.

"Across-experiment" analysis

In our first set of analyses, we treated each of the 34 experiments as a single observation in statistical models that examined how diversity effects on productivity relate to diversity effects on stability across all studies. We began by calculating two standardized effect sizes for each experiment (Table 1 gives a summary of these metrics). First, we calculated the diversity effect on biomass production, DE$_{BP}$, as the log response ratio $\ln(B_P/B_i)$, where B_P is the average biomass production across sampling times for the most diverse polyculture used in an experiment (calculated separately for each experimental unit and then averaged across replicate units), and B_i is the median value of the time-averaged biomass for species grown alone in monoculture. DE$_{BP}$ is a dimensionless ratio that gives the proportional change in productivity between the highest and lowest levels of diversity manipulated in an experiment (mono- and polycultures). Values >0 indicate that the most diverse polycultures produce more biomass than the median monoculture. To obtain estimates of B_i for each monoculture, we calculated the time-averaged biomass for each experimental unit and then averaged across replicates to obtain a species-level estimate. We then used the median as the measure of central tendency for these species-level estimates because occasionally there were species that had high estimates of biomass when grown alone (that is, $B_i > 2$ SD's from the mean, which also leads to skewed CV$_i$'s). However, our final conclusions do not depend on the particular measure of central tendency used since median, and mean values of B_i were highly correlated across experiments ($r = 0.98$). In contrast to data distributions for monocultures, we found no evidence of strong skew for values of B_P,

TABLE 1. Description of metrics and effect sizes calculated for each data set used in our meta-analysis.

Variable	Description	Symbol
A) Metrics		
Monoculture biomass production	The median (across species) of the average (across sampling times) biomass in monocultures. For each monoculture plot, we calculated the average biomass across sampling times, and then averaged these across all replicate monocultures for each species. We then took the median value across all species.	B_i
Polyculture biomass production	The average (across replicates) of the average (across sampling times) biomass in the most diverse polyculture. For each replicate experimental unit, we calculated the average biomass across sampling occasions and then averaged the temporal means across all replicate polycultures.	B_P
Monoculture stability though time	The median (across species) CV (across sampling times) of biomass in monocultures. For each monoculture plot, we calculated the CV of biomass across sampling occasions as the ratio of the standard deviation to the mean. We then averaged values across replicates for a given species, and finally took the median value across the species.	CV_i
Polyculture stability through time	The average (across plots) of the CV (across sampling time) of biomass in polyculture. For each polyculture plot, we calculated the CV of biomass across sampling times as the ratio of the standard deviation to the mean, and then averaged these across all replicate polycultures.	CV_P
B) Effect sizes		
Diversity effect on biomass production	Log response ratio, $\ln(B_P/B_i)$. Values >0 indicate the polycultures produce more biomass than the typical monoculture.	DE_{BP}
Diversity effect on stability through time	Log response ratio, $\ln(CV_i/CV_P)$. Values >0 indicate that biomass in polycultures is more stable through time (less variable) when standardized by biomass.	DE_{CV}

suggesting the mean was a good measure of central tendency for the polycultures.

Second, we calculated the effect of diversity on the stability of biomass through time as the log response ratio of the coefficients of variation, $DE_{CV} = \ln(CV_i/CV_P)$. The numerator, CV_i, was equal to the median (across species) CV of biomass in monocultures. For each monoculture experimental unit, we calculated the CV of biomass as the ratio of the standard deviation (across sampling times) to the average biomass. We then averaged values across replicates for a given species, and then took the median value across species. While we used the median value of CV_i, across species to deal with occasional skew in the data sets (i.e., select species were occasionally highly variable [stable]), our conclusions did not depend on the measure of central tendency, as the mean and median values of CV_i were highly correlated across experiments ($r = 0.97$). The denominator, CV_P, was the mean (across plots) of the CV (across sampling times) of biomass in each replicate polyculture plot. For each polyculture plot, we calculated the CV as the ratio of the standard deviation of biomass (across sampling times) to the mean, and then averaged these across all replicate polycultures. Values of $DE_{CV} > 0$ indicate that biomass in polycultures is more stable (less variable) through time.

After calculating the two diversity effect sizes, we performed three analyses on the data set. First, we examined the *distribution of effect sizes* by using t tests to determine whether DE_{BP} and DE_{CV} were significantly different from zero for the full set of 34 experiments. We

then examined the *covariance among diversity effect sizes* in two ways: (1) by calculating Spearman rank correlations between DE_{BP} and DE_{CV}, and (2) by modeling the diversity effect sizes as functions of one another using mixed model ANOVAs of the form $DE_{CV} = \mu + DE_{BP} + \tau_i + b_i + \varepsilon_i$, where μ is the grand mean, τ_i is a fixed categorical effect of ecosystem type (terrestrial or aquatic), b_i is the random effect of study i (independent and identically distributed $N[0, \sigma_b^2]$), and ε_i is the residual error. Finally, to more closely examine the underlying nature of correlations between DE_{BP} and DE_{CV}, we quantified the biomass–variance scaling relationships that describe how stability scales with mean biomass in mono- and polycultures. If effects of species richness on biomass and stability are independent, then variance of biomass through time should scale as the square of mean biomass. This expectation derives from the fact that, when scaling any random variable X with finite mean m and variance σ^2 by a constant k, the mean and variance of kX are km and $k^2\sigma^2$, respectively. On a log–log plot, this should translate to a linear relationship between km and $k^2\sigma^2$ with a slope $= 2$. To test for this relationship, we used mixed-model ANOVA's of the form $v_j = \mu + b_j + r_j + \tau_j + \varepsilon$ where v_j is the $\log_{10}$-transformed variance in biomass through time for study j (SD_P^2 for polycultures, or median SD_i^2 for monocultures), μ is the grand mean, b_j is the $\log_{10}$-transformed estimate of mean biomass (B_P for polycultures, median B_i for monocultures), r_j is the effect of species richness (mono- vs. polycultures), τ_j is the

random effect of study j, and ε is the residual unexplained variation.

It is worth noting here that our analyses focused on the extreme levels of diversity used in experiments (mono- vs. maximum richness polycultures). One could justifiably argue that much more information could be gleaned by also examining trends at the intermediate levels of diversity. Aside from the fact that presentation of data for all levels of richness of 34 studies would be difficult, if not unmanageable, we would also point out two justifications for our analyses as stated. First, diversity–function relationships are known to fit well to positive, decelerating functions (e.g., Michaelis-Menten, log, power), which means the strongest diversity effects generally occur at the highest levels of richness (Schmid et al. 2009, Cardinale et al. 2011). Thus, if we don't see joint distributions and quantifiable covariance for this subset of data, then they are not likely to exist. Second, the metrics we use here are the same as those that have been widely used to analyze diversity effects on productivity and stability in prior analyses (e.g., Cardinale et al. 2006, Jiang and Pu 2009). Consistency helps ensure that our analyses and conclusions are directly comparable to prior publications that have focused on these same data sets. We do, however, recognize that one potential limitation of our approach is that variation in the maximum levels of diversity used in experiments (range = 3–32 species) could drive variation in diversity effect sizes. Therefore, we statistically controlled for the maximum richness as a covariate in each of our *across-experiment* analyses.

"Within-experiment" analysis

The advantage of the "across-experiment" analysis is it has potential to reveal trends that are general across all experiments in the data set. The weakness is that there are potentially differences among experiments (e.g., time, location, the size and composition of species pools, and so on) that cannot be statistically controlled for, but which could influence the response variables of interest (e.g., productivity and stability). The best way to determine if conclusions from the across-experiment analyses are robust is to perform comparable analyses for individual experiments and assess if data lead to the same conclusions.

To complement our analyses of the 34 experiments, we performed supplemental analyses that examined trends within a select subset of experiments. For this purpose, we focused on six experiments, including the four experiments that are part of the Reich et al. (2001) BioCon manipulations of plant richness in factorial combination of nitrogen $\times$ CO$_2$ enrichment, the Isbell et al. (2009) summary of Wilsey and Polley's (2004) plant diversity experiment, and Tilman et al.'s "big" biodiversity experiment (E120) at Cedar Creek Ecosystem Science Reserve (Tilman et al. 2001). We focused on this subset of studies because (1) they have the longest time series of any studies in our data set (6–10 years), and (2)

they are the only data sets available that had measures of biomass for each individual species in every experimental unit, which is required for the within-experiment analysis.

For each of these studies, we calculated DE$_{BP}$ and DE$_{CV}$ as described above in the across-experiment analyses except that estimates were made for each of the individual polyculture plots in the experiment (not averaged across plots, as in the across-experiment analyses). For each included polyculture plot we calculated the biomass production B_P and coefficient of variation CV$_P$ as described in Table 1, and the biomass and variance of the same species from the polyculture when grown alone in monoculture (B_i and CV$_i$, as in Table 1). From this, we calculated a diversity effect on the production of each of the polyculture plots DE$_{BP}$, and an effect on stability DE$_{CV}$. For Reich et al.'s BioCon experiments (2001) and Tilman et al.'s E120 experiment (2001), we used polyculture plots from the richness treatment with the second-most species, because species composition varied considerably more among these plots than it did among replicates of the most species-rich treatment. For Isbell et al. (2009), species composition among replicates from the most diverse treatment were less similar, and so we used data from both the most and second-most species rich treatments. We examined the distribution of effect sizes using t tests, and the covariance among effect sizes with rank correlations and mixed models.

RESULTS

Across-experiment analysis

The overall distribution of log ratios indicated that producer diversity simultaneously enhanced both the production of biomass and stability of biomass through time (Fig. 1C, note black circle in quadrant 1, which gives the mean effect sizes ±95% confidence intervals). The effect of plant or algal richness on biomass production was significantly greater than zero ($t = 8.58$, df = 33, $P < 0.01$ for a t test) with a log ratio of 0.96 ± 0.11 SEM. This indicates that the most species-rich assemblages used in experiments have achieved $e^{0.96} = 2.61\times$ more biomass than the median of the same species grown in monoculture. This estimate is higher than what has previously been reported in a review covering many more studies ($e^{0.36} = 1.43\times$; Cardinale et al. 2011), and probably reflects the fact that experiments which run longer tend to show larger effects of species richness on biomass production (Cardinale et al. 2007, Fargione et al. 2007, Reich et al. 2012). We found no evidence to suggest the effect size was influenced by differences in the highest levels of richness used among studies ($P = 0.71$ for a linear regression).

The effect of producer richness on the stability of biomass through time was also greater than zero ($t = 4.39$, df = 33, $P < 0.01$ for a t test), with an average log response ratio of 0.31 ± 0.07 SEM. Thus, the most species rich assemblages used in experiments to date
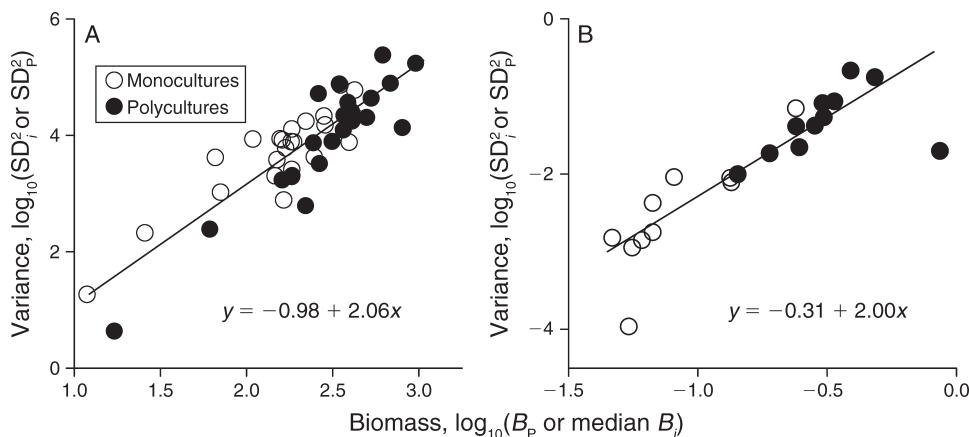
FIG. 2. Biomass–variance scaling relationships in (A) terrestrial and (B) aquatic ecosystems. In these graphs, there are two data points per experiment: one for monocultures (open circles) and one for polycultures (solid circle). Regressions give results from a general linear mixed model (described in *Methods*). All data used to generate this figure are given in the Supplement in the file *Data for across study analyses*. See Table 1 for clarification of abbreviations and units.

have been $e^{0.31} = 1.36\times$ more stable (i.e., a lower coefficient of variation) than the median of those same species grown in monoculture. Effects of producer diversity on stability were slightly higher for terrestrial than aquatic systems (Fig. 1C, compare squares to triangles), though this difference was marginally non-significant ($F_{1,32} = 3.12$, $P = 0.09$). Once again, there was no evidence that the effect size was influenced by differences in the highest levels of richness used among studies ($P = 0.35$ for a linear regression).

When all data points were considered together (both terrestrial and aquatic), there was a marginally nonsignificant negative rank correlation between the effect of diversity on production and the effect of diversity on stability ($\rho = -0.33$, $P = 0.06$). However, this weak negative correlation was driven entirely by a difference in effect sizes among ecosystems, with aquatic studies as a whole having higher effects on productivity and lower effects on stability (Fig. 1D, compare squares to triangles). When separate correlations were run by ecosystem type, the rank correlations between effect sizes were definitively nonsignificant for both terrestrial ($\rho = -0.11$, $P = 0.62$) and aquatic systems ($\rho = -0.33$, $P = 0.33$). Results of the mixed-model ANOVA's (see *Methods*) also supported the conclusion that effect sizes were independent. When we modeled DE_{CV} as a function of DE_{BP}, we found that DE_{CV} was independent of DE_{BP} ($P = 0.39$), and that dependence of DE_{CV} on DE_{BP} was the same for both ecosystem types ($P = 0.83$ for the interaction term). When we similarly modeled DE_{BP} as a function of DE_{CV}, we found that DE_{BP} differed among ecosystems ($P = 0.04$), but that DE_{BP} was independent of DE_{CV} ($P = 0.36$). Dependence of DE_{BP} on DE_{CV} was again the same for both ecosystem types ($P = 0.36$ for the interaction term).

Independence of the two diversity effect sizes was further supported by the biomass–variance scaling relationships (Fig. 2). If effects of species richness on

biomass and stability are independent, then variance of biomass through time should scale as the square of mean biomass. This expectation derives from the fact that, when scaling any random variable X with finite mean m and variance σ^2 by a constant k, the mean and variance of kX are km and $k^2\sigma^2$, respectively. On a log–log plot, this should translate to a linear relationship between km and $k^2\sigma^2$ with a slope of 2. For terrestrial ecosystems, variance scaled with mean biomass as $\log_{10}(\sigma^2) = -0.98 + 2.06 \times \log_{10}(m)$, with a 95% confidence interval for the slope of 1.72 to 2.40 (Fig. 2A). For aquatic ecosystems, variance scaled as $\log_{10}(\sigma^2) = -0.31 + 2.00 \times \log_{10}(m)$, with a 95% confidence interval for the slope of 1.43 to 2.57 (Fig. 2B).

Within-experiment analysis

Analyses of trends within individual experiments corroborated patterns and conclusions from the across-experiment analyses. In all six experiments, more diverse communities were simultaneously more productive and more stable (Fig. 3, black circles give the mean effect sizes ±95% confidence intervals). But even while diversity enhanced both productivity and stability, there was never a significant rank correlation between the two effect sizes (Fig. 3). Thus, both sets of analyses (across and within experiment) show that (1) biodiversity simultaneously enhances both the productivity and stability of ecosystems, but (2) diversity effects on productivity are independent of diversity effects on temporal stability.

DISCUSSION

Over the past two decades, ecologists have made great strides in understanding how biodiversity influences various aspects of ecosystem functioning. While studies have historically taken a univariate perspective and examined each facet of ecosystem functioning individually, recent work has started to build on this
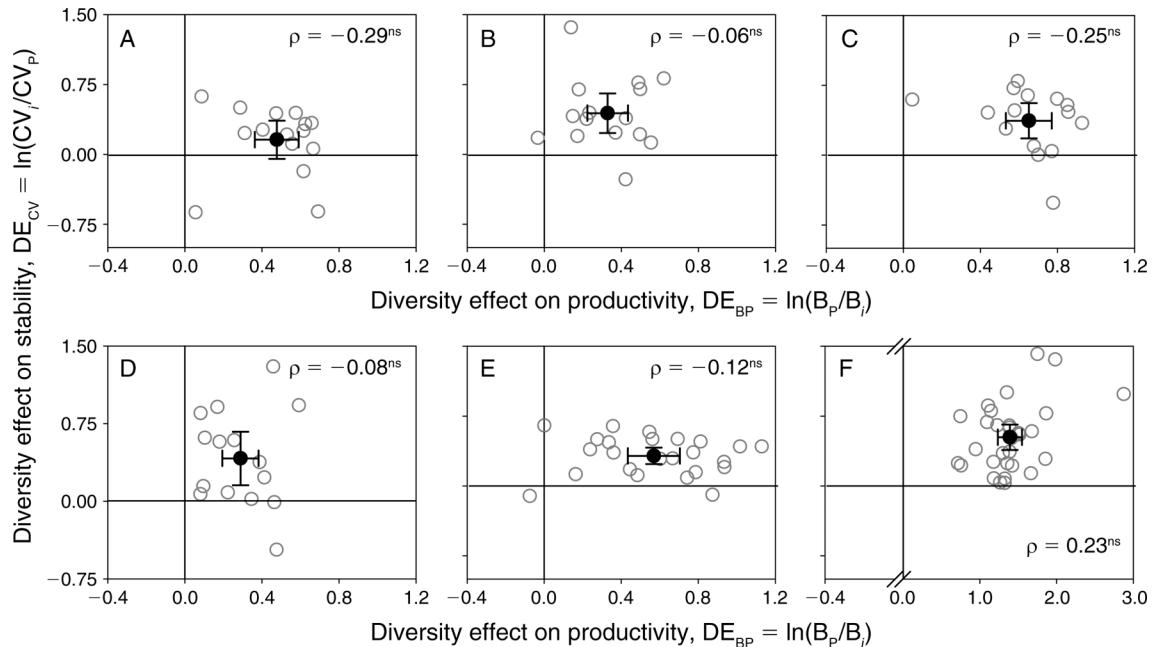
FIG. 3. Empirical relationship between the effect of producer diversity on production (x-axis) and the effect of diversity on stability (y-axis) for six representative experiments. The x-axis in each plot gives the log ratio of biomass in any single experimental unit (e.g., a field plot) containing the most diverse polyculture relative to the same species grown in monoculture. The y-axis gives the log ratio of the coefficients of variation in any single experimental unit (e.g., a field plot) containing the most diverse polyculture relative to the same species grown in monoculture. Solid black circles give the mean effect sizes $\pm 95\%$ confidence interval for all experimental units, and Spearman rank correlations (ρ) illustrate the covariance between the magnitude of the two diversity effects ("ns" indicates not significant). All data used to generate this figure are given in the Supplement in the file *Data for within study analyses* and come from the following sources: (A) Reich et al. (2001), BioCon E141 (ambient nitrogen, ambient CO_2); (B) Reich et al. (2001), BioCon E141 (enriched nitrogen, ambient CO_2); (C) Reich et al. (2001), BioCon E141 (ambient nitrogen, enriched CO_2); (D) Reich et al. (2001), BioCon E141 (enriched nitrogen, enriched CO_2); (E) Isbell et al. (2009); and (F) Tilman et al. (2001), Biodiversity II E120 experiment.

foundation by exploring how biodiversity simultaneously influences different aspects of ecosystem function that might not all respond to changes in the diversity in the same way (Hector and Bagchi 2007, Gamfeldt et al. 2008, Zavaleta et al. 2010, Isbell et al. 2011, Maestre et al. 2012). Our work here falls squarely within that same goal of exploring how diversity jointly impacts two aspects of ecosystems functioning (productivity and stability) that may, or may not respond to diversity loss similarly. We reanalyzed data from 34 experimental manipulations of plant and algal diversity and found that (1) biodiversity of primary producers simultaneously enhances both the production and stability of biomass in ecosystems; however, (2) diversity effects on productivity are independent of diversity effects on temporal stability. The first of these results, showing that biodiversity simultaneously enhances both the magnitude and stability of biomass production, is something that many researchers probably already assume is true. However, to our knowledge, ours is the first explicit attempt to quantify the joint distribution of data describing how species richness regulates productivity and stability, and to assess the consistency of this joint distribution across many different communities of primary producers.

The second result of our paper, showing that the size of the richness effect on biomass is independent of the size of the effect on stability, is more novel, but also more difficult to understand. Even so, its implications for how we interpret the effects of biodiversity on the functioning of ecosystems are important. Even while diversity may generally enhance productivity and stability, this does not necessarily mean that biodiversity will generally cause ecosystems to have the highest levels of both of aspects of ecosystem functioning at once. This is not to say that select combinations of species can't generate high levels of productivity and stability, or that diverse communities in certain ecosystems won't achieve high productivity and stability. Rather, it simply says that (as a general rule) the highest levels of productivity in a diverse community are not associated with the highest levels of stability. This result contrasts starkly with the predictions of several conceptual and theoretical models.

For example, Yachi and Loreau (1999) predicted that effects of biodiversity on productivity and stability should covary positively with one another. This prediction was based on a set of phenomenolgcial models that made rather strict assumptions about the most productive species dominating biomass of a

community at every point in time, even if the dominant species changed through time as a result of environmental variation. Our analyses show no evidence of positive covariance between diversity effects on production and stability. There was no indication of positive covariance in the across-experiment analyses (Fig. 1D), and only one of the within-experiment analyses showed even a hint of a positive correlation (Fig. 3F; Tilman et al.'s E120 experiment [2001]); yet even that was not statistically significant.

Our results also do not support the idea that there is any type of trade-off between biodiversity effects on productivity and stability. Several authors have outlined qualitative arguments that diversity effects on production should correlate negatively with effects on stability because both depend, in differing ways, on niche partitioning (Hooper et al. 2005, Cardinale et al. 2007). As niche partitioning maximizes productivity by increasing resource use efficiency, higher niche partitioning decrease stability by reducing the competitive interactions among species that generate compensatory dynamics. In contrast to the prediction of this hypothesis, neither terrestrial nor aquatic studies showed any significant correlation between effect sizes (Fig. 1D), and there were no significant negative correlations among effect sizes in any of the six within-experiment analyses (Fig. 3A–F).

For the experimental systems of grasslands and algal microcosms analyzed here, the balance of evidence is most consistent with the prediction of Ives et al. (2000). Ives et al. (2000) used Lotka-Volterra models to show that diversity effects on productivity are independent of diversity effects on stability. In their models, diversity effects on production were controlled by the degree of niche partitioning among species, whereas diversity effects on temporal stability were instead controlled by the strength of correlations in species responses to environmental variability. The independence of mechanisms ensured that diversity effects on production were not correlated with diversity effects on stability. While the results of our analyses are consistent with the prediction that independent mechanisms operate to control diversity's effect on productivity vs. stability, it is important to note that the data collected in most biodiversity–ecosystem function studies do not allow for rigorous tests of underlying mechanisms, and are insufficient to directly link patterns to any theoretical model. For example, species-specific responses to environmental variability are often thought to generate negative covariance in population densities that help stabilize community biomass (Doak et al. 1998, Ives et al. 2000, Gonzalez and Loreau 2009, Loreau 2010). However, negative covariances can also result from interspecific competitive interactions (Tilman et al. 1998, Lehman and Tilman 2000). The data collected in most experiments does not allow one to separate the role of species interactions from independent responses to a fluctuating environment (Loreau and de Mazancourt

2008), and thus, future studies will need to be redesigned to partition covariance into its contributing biological mechanisms.

Identifying the mechanisms by which species richness increases community biomass production has also been an enduring problem for biodiversity–ecosystem function studies (see Cardinale et al. 2011 for a review). While many have claimed that biodiversity increases productivity through "niche partitioning" or some type of positive species interaction, these claims are usually derived from one of two sources. Many claims stem from qualitative interpretations of species natural histories or differences in functional traits; unfalsifiable narratives that are always subject to alternative explanations. Other claims stem from post hoc statistical analyses of experimental data (Loreau and Hector 2001) that partition diversity effects into categories commonly called "complementarity" and "selection" effects. Complementarity represents that portion of a diversity effect (increased biomass in polyculture) that cannot be explained by any single species (selection effects), and is often interpreted as a measure of niche partitioning or facilitation based on the original authors interpretation. But subsequent work has clearly demonstrated that such post hoc statistical tests do not correspond to any known biological mechanism per se (Petchey 2003, Hooper and Dukes 2004, Cardinale et al. 2007), and the fact that 40% of past measures of complementarity have proven to be negative emphasizes that the common biological interpretation of this metric is fundamentally flawed (Cardinale et al. 2011). Recent work has made some progress on testing for select mechanisms by which biodiversity might enhance community biomass production, such as those that have attempted to quantify niche partitioning more directly by measuring the strength of frequency dependent growth rates (so-called "advantage when rare" [Chesson 2000, Adler et al. 2007]), quantifying the ratio of intra- to interspecific interaction strengths (Weis et al. 2007), fitting experimental data to models of niche overlap (Northfield et al. 2010), and experimentally removing niche opportunities that are presumed to exist (Cardinale 2011). As more studies like these amass, we may soon be in a position to verify the general mechanisms by which diversity influences biomass production.

Our findings have a number of important implications for the conservation and management of biodiversity. First, our work suggests that the impacts of biodiversity loss on different aspects of ecosystem functioning may exhibit an inherent level of unpredictability. For the studies reviewed here, the effect of diversity on productivity contained no information about the effect of diversity stability, and vice versa. This implies that extinction might generate large reductions in productivity and small changes in stability, large reductions in stability but small changes in productivity, large changes in both productivity and stability, and so on. In fact, our work emphasizes that diversity effects on various facets

of ecosystem functioning need not be correlated. Therefore, if we are to understand and predict the variety of ecological changes that occur in ecosystems after extinction, we are going to need to develop separate predictive models for each of these mechanistically independent aspects of ecosystem functioning.

If we are to develop predictive models, then we also need research that better elucidates the biological mechanisms by which diversity affects productivity and stability. The independent effects of diversity on these two functions suggest that the mechanisms behind diversity–production and diversity–stability relationships are also distinct. If we fail to understand how these mechanisms operate, then meeting conservation goals to sustain ecosystem productivity risks failure, or could even run counter to management goals. These risks are particularly important when we consider that enhancing productivity or stability is only a "desired" state in certain management scenarios, such as in agriculture or select forms of forestry where the goal is often to maximize a particular product, and do so sustainably through time. In other scenarios, boosting productivity and stability is not the desired goal (e.g., high biomass associated with nutrient pollution and eutrophication). With a mechanistic understanding in hand, we will be better equipped to use conservation of biodiversity as one of many potential management tools to achieve desired levels of productivity and stability of ecosystem functions and services.

LITERATURE CITED

Adler, P. B., J. HilleRisLambers, and J. M. Levine. 2007. A niche for neutrality. Ecology Letters 10:95–104.

Balvanera, P., A. B. Pfisterer, N. Buchmann, J. S. He, T. Nakashizuka, D. Raffaelli, and B. Schmid. 2006. Quantifying the evidence for biodiversity effects on ecosystem functioning and services. Ecology Letters 9:1146–1156.

Bruno, J. F., and B. J. Cardinale. 2008. Cascading effects of predator richness. Frontiers in Ecology and the Environment 6:539–546.

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.

Campbell, V., G. Murphy, and T. N. Romanuk. 2011. Experimental design and the outcome and interpretation of diversity-stability relations. Oikos 120:399–408.

Cardinale, B. J. 2011. Biodiversity improves water quality through niche partitioning. Nature 472:86–89.

Cardinale, B. J., E. Duffy, D. Srivastava, M. Loreau, M. Thomas, and M. Emmerson. 2009. Towards a food-web perspective on biodiversity and ecosystem functioning. Pages 105–120 in S. Naeem, D. Bunker, M. Loreau, A. Hector, and C. Perring, editors. Biodiversity and human impacts. Oxford University Press, Oxford, UK.

Cardinale, B. J., et al. 2012. Biodiversity loss and its impact on humanity. Nature 486:59–67.

Cardinale, B. J., K. L. Matulich, D. U. Hooper, J. E. Byrnes, E. Duffy, L. Gamfeldt, P. Balvanera, M. I. O'Connor, and A. Gonzalez. 2011. The functional role of producer diversity in ecosystems. American Journal of Botany 98:572–592.

Cardinale, B. J., D. S. Srivastava, J. E. 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.

Cardinale, B. J., J. P. Wright, M. W. Cadotte, I. T. Carroll, A. Hector, D. S. Srivastava, M. Loreau, and J. J. Weis. 2007. Impacts of plant diversity on biomass production increase through time due to complementary resource use: A meta-analysis. Proceedings of the National Academy of Sciences USA 104:18123–18128.

Chesson, P. 2000. General theory of competitive coexistence in spatially-varying environments. Theoretical Population Biology 58:211–237.

Cottingham, K. L., B. L. Brown, and J. T. Lennon. 2001. Biodiversity may regulate the temporal variability of ecological systems. Ecology Letters 4:72–85.

Doak, D. F., D. Bigger, E. K. Harding, M. A. Marvier, R. E. O'Malley, and D. Thomson. 1998. The statistical inevitability of stability-diversity relationships in community ecology. American Naturalist 151:264–276.

Fargione, J., D. Tilman, R. Dybzinski, J. H. R. Lambers, C. Clark, W. S. Harpole, J. M. H. Knops, P. B. Reich, and M. Loreau. 2007. From selection to complementarity: shifts in the causes of biodiversity-productivity relationships in a long-term biodiversity experiment. Proceedings of the Royal Society of London B 274:871–876.

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.

Gamfeldt, L., H. Hillebrand, and P. R. Jonsson. 2008. Multiple functions increase the importance of biodiversity for overall ecosystem functioning. Ecology 89:1223–1231.

Gonzalez, A., and M. Loreau. 2009. The causes and consequences of compensatory dynamics in ecological communities. Annual Review of Ecology, Evolution, and Systematics 40:393–414.

Griffin, J. N., E. O'Gorman, M. C. Emmerson, S. R. Jenkins, A. Klein, M. Loreau, and A. Symstad. 2009. Biodiversity and the stability of ecosystem functioning. Pages 78–93 in S. Naeem, D. Bunker, M. Loreau, A. Hector, and C. Perring, editors. Biodiversity and human impacts. Oxford University Press, Oxford, UK.

Hector, A., and R. Bagchi. 2007. Biodiversity and ecosystem multifunctionality. Nature 448:188–190.

Hector, A., et al. 2010. General stabilizing effects of plant diversity on grassland productivity through population asynchrony and overyielding. Ecology 91:2213–2220.

Hector, A., et al.. 1999. Plant diversity and productivity experiments in European grasslands. Science 286:1123–1127.

Hooper, D. U., et al. 2005. Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. Ecological Monographs 75:3–35.

Hooper, D. U., and J. S. Dukes. 2004. Overyielding among plant functional groups in a long-term experiment. Ecology Letters 7:95–105.

Isbell, F., et al. 2011. High plant diversity is needed to maintain ecosystem services. Nature 477:199–202.

Isbell, F. I., H. W. Polley, and B. J. Wilsey. 2009. Biodiversity, productivity and the temporal stability of productivity: patterns and processes. Ecology Letters 12:443–451.

Ives, A. R., and S. R. Carpenter. 2008. Stability and diversity of ecosystems. Science 317:58–62.

Ives, A. R., J. L. Klug, and K. Gross. 2000. Stability and species richness in complex communities. Ecology Letters 3:399–411.

Jiang, L., and Z. C. Pu. 2009. Different effects of species diversity on temporal stability in single-trophic and multi-trophic communities. American Naturalist 174:651–659.

Lehman, C. L., and D. Tilman. 2000. Biodiversity, stability, and productivity in competitive communities. American Naturalist 156:534–552.

Loreau, M. 2010. From populations to ecosystems: theoretical foundations for a new ecological synthesis. Princeton University Press, Princeton, New Jersey, USA.

Loreau, M., and C. de Mazancourt. 2008. Species synchrony and its drivers: Neutral and nonneutral community dynamics in fluctuating environments. American Naturalist 172:E48–E66.

Loreau, M., and A. Hector. 2001. Partitioning selection and complementarity in biodiversity experiments. Nature 412:72–76.

Loreau, M., et al. 2001. Biodiversity and ecosystem functioning: Current knowledge and future challenges. Science 294:804–808.

Maestre, F. T., et al. 2012. Plant species richness and ecosystem multifunctionality in global drylands. Science 335:214–218.

Mooney, H. A., International Council of Scientific Unions. Scientific Committee on Problems of the Environment, and United Nations Environment Programme. 1996. Functional roles of biodiversity: a global perspective. Wiley, Chichester, New York, New York, USA.

Naeem, S. 2002. Ecosystem consequences of biodiversity loss: The evolution of a paradigm. Ecology 83:1537–1552.

Northfield, T. D., G. B. Snyder, A. R. Ives, and W. E. Snyder. 2010. Niche saturation reveals resource partitioning among consumers. Ecology Letters 13:338–348.

Petchey, O. L. 2003. Integrating methods that investigate how complementarity influences ecosystem functioning. Oikos 101:323–330.

Quijas, S., B. Schmid, and P. Balvanera. 2010. Plant diversity enhances provision of ecosystem services: A new synthesis. Basic and Applied Ecology 11:582–593.

Reich, P. B., et al. 2001. Plant diversity enhances ecosystem responses to elevated CO_2 and nitrogen deposition. Nature 410:809–812.

Reich, P. B., D. Tilman, F. Isbell, K. Mueller, S. E. Hobbie, D. F. B. Flynn, and N. Eisenhauer. 2012. Impacts of biodiversity loss escalate through time as redundancy fades. Science 336:589–592.

Schmid, B., P. Balvanera, B. J. Cardinale, J. Godbold, A. B. Pfisterer, D. Raffaelli, M. Solan, and D. S. Srivastava. 2009. Consequences of species loss for ecosystem functioning: a meta-analysis of data from biodiversity experiments. Pages 14–29 in S. Naeem, D. Bunker, M. Loreau, A. Hector, and C. Perring, editors. Biodiversity and human impacts. Oxford University Press, Oxford, UK.

Srivastava, D. S., B. J. Cardinale, A. L. Downing, J. E. Duffy, C. Jouseau, M. Sankaran, and J. P. Wright. 2009. Diversity has stronger top-down than bottom-up effects on decomposition. Ecology 90:1073–1083.

Stachowicz, J., J. F. Bruno, and J. E. Duffy. 2007. Understanding the effects of marine biodiversity on communities and ecosystems. Annual Review of Ecology, Evolution, and Systematics 38:739–766.

Tilman, D. 1999. The ecological consequences of changes in biodiversity: a search for general principles. Ecology 80:1455–1474.

Tilman, D., C. L. Lehman, and C. E. Bristow. 1998. Diversity-stability relationships: Statistical inevitability or ecological consequence? American Naturalist 151:277–282.

Tilman, D., P. B. Reich, and J. M. H. Knops. 2006. Biodiversity and ecosystem stability in a decade-long grassland experiment. Nature 441:629–632.

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.

Weis, J. J., B. J. Cardinale, K. J. Forshay, and A. R. Ives. 2007. Effects of species diversity on community biomass production change over the course of succession. Ecology 88:929–939.

Wilsey, B. J., and H. W. Polley. 2004. Realistically low species evenness does not alter grassland species-richness-productivity relationships. Ecology 85:2693–2700.

Worm, B., et al. 2006. Impacts of biodiversity loss on ocean ecosystem services. Science 314:787–790.

Yachi, S., and M. Loreau. 1999. Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis. Proceedings of the National Academy of Sciences USA 96:1463–1468.

Zavaleta, E. S., J. R. Pasari, K. B. Hulvey, and G. D. Tilman. 2010. Sustaining multiple ecosystem functions in grassland communities requires higher biodiversity. Proceedings of the National Academy of Sciences USA 107:1443–1446.

SUPPLEMENTAL MATERIAL

Supplement

Summarized data for the across-study analyses presented in Fig. 1, and within-study analyses presented in Fig. 3 (*Ecological Archives* E094-155-S1).