Species richness and the temporal stability of biomass production: A new analysis of recent biodiversity experiments

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Abstract

The relationship between biological diversity and ecological stability has fascinated ecologists for decades. Determining the generality of this relationship, and discovering the mechanisms that underlie it, are vitally important for ecosystem management. Here, we investigate how species richness affects the temporal stability of biomass production by re-analyzing 27 recent biodiversity experiments conducted with primary producers. We find that, in grasslands, increasing species richness stabilizes whole-community biomass but destabilizes the dynamics of constituent populations. Community biomass is stabilized because species richness impacts mean biomass more strongly than its variance. In algal communities, species richness has a minimal effect on community stability because richness affects the mean and variance of biomass nearly equally. Using a new measure of synchrony among species, we find that for both grasslands and algae, temporal correlations in species biomass are lower when species are grown together in polyculture than when grown alone in monoculture. These results suggest that interspecific interactions tend to stabilize community biomass in diverse communities. Contrary to prevailing theory, we found no evidence that species' responses to environmental variation in monoculture predicted the strength of diversity's stabilizing effect. Together, these results deepen our understanding of when and why increasing species richness stabilizes community biomass.

Introduction

Are ecosystems that are biologically more diverse also more stable? If so, why? And if not, why not? These questions have fascinated ecologists for generations, both because of the fundamental scientific challenges that they pose and their deep implications for ecosystem management, where sustainability and reduced risk are often primary goals. Today, the specter of rapid biodiversity loss from ecosystems adds urgency to the effort to understand and to articulate the relationship between biological diversity and the different components of ecological stability (Hooper et al., 2005; Ives & Carpenter, 2007; Cardinale et al., 2012).

The history of the diversity-stability debate is long and has been reviewed in depth elsewhere (McCann 2000; Griffin et al. 2009); we summarize this history only briefly here. Early attempts to determine how biodiversity impacts ecological stability relied mostly on verbal arguments and anecdote. This work suggested that more complex ecological communities with a greater number of species and trophic linkages tend to be more stable in the face of environmental perturbations (MacArthur 1955; Elton 1958; Hutchinson 1959; Margalef 1969). Although conclusions from these early studies initially gained broad acceptance because of their intuitive appeal, those conclusions were subsequently challenged both on the grounds that supporting experimental data were sparse (McNaughton 1977), and by mathematical models that demonstrated that more complex communities were less likely to exhibit stable, equilibrium dynamics (May 1974).

This collision of seemingly contradictory results forced researchers to think more deeply about the cause of these contradictions. Some emphasized that 'biological diversity' (or complexity) and 'ecological stability' were both expansive concepts that encompassed a range of definitions, and that loose and imprecise usage of these terms obscured important distinctions among their different meanings (Pimm 1984). Indeed, recent mathematical theory has shown how distinct yet interrelated associations between the many facets of diversity and stability can give rise to a multitude of different relationships (Ives & Carpenter, 2007). Others have stressed that the impact of species diversity on stability may vary between levels of ecological organization (Tilman 1996; Tilman 1999). For example, research focused on the relationship between terrestrial plant species richness and temporal variation in biomass production has led to a growing consensus that increasing species richness stabilizes the biomass of whole communities (Cottingham et al. 2001; Hector et al. 2010; Campbell et al. 2011). However, the impact of species richness on population-level stability is ambiguous. While theory and some empirical work suggests that increasing species richness should destabilize population-level biomass (Ives et al. 1999; Tilman 1999), others have found the reverse to be true (e.g., Steiner et al. 2005; Vogt et al. 2006), and one recent synthesis found sufficient variation among studies to defy generalization (Jiang & Pu, 2009).

Despite progress, our understanding of diversity-stability relationships remains hampered by an inability to decipher underlying mechanisms (Cardinale et al. 2012; de Mazancourt et al. 2013). For example, compensatory dynamics, whereby increases [decreases] in the density of one species are offset by decreases [increases] in the density of another species, are generally thought to provide a proximate explanation for species richness's stabilizing effect on community biomass (Gonzalez & Loreau [2009] provide a review, but see Houlahan et al. 2007 for a dissenting view). However, the ultimate mechanism driving these compensatory dynamics has yet to be resolved. One proposed mechanism is interspecific competition, in which fluctuations in the densities of one species lead directly to countervailing fluctuations in the densities of competing species (Tilman et al., 1998; Lehman & Tilman, 2000). Others have argued that diversity stabilizes communities by introducing species that respond differently to varying environmental conditions (Doak et al., 1998; Ives et al., 2000; Loreau & de Mazancourt, 2013), leading to the prediction that diversity's stabilizing effect should be strongest when communities consist of species that respond independently to changing environments. So far, discussion about mechanisms has been primarily theoretical, as empirical support for one or multiple mechanisms has been elusive (but see de Mazancourt et al., 2013 for a recent exception).

Here, we re-analyze data from 27 recent biodiversity vs. ecosystem function (BEF) experiments to ask how diversity impacts the temporal stability of population and community-level biomass production in competitive communities. BEF experiments consist of replicated communities (alternatively described as species assemblages or mixtures) constructed by randomly selecting member species from an experimental species pool, most often using easily manipulated species groups such as herbaceous plants, algae, or microbes (Loreau et al. 2002). As this field of research has matured, some experiments have been run long enough to quantify how differences in species richness impact temporal variation among primary producers (e.g., Tilman, 1996; Tilman et al., 2006; Hector et al., 2010; Reich et al., 2012).

Our analysis of these experiments is motivated by several questions that have yet to be resolved by any experiments individually, or by data syntheses conducted to date. First, how can the effect of species richness on whole-community biomass production be 'unpacked' into diversity's simultaneous effects on the mean and variance of productivity? Second, do these 27 experiments show that species richness has any consistent, repeatable impact on population-level stability? Third, do species interactions contribute to the compensatory dynamics that stabilize whole-community biomass? And fourth, is diversity's effect on community-level stability strongest when species responses to environmental fluctuations are most dissimilar? The analysis of these latter two questions is enabled by the development of a new metric for quantifying the correlation among a group of species across different levels of species richness.

The remainder of this paper is structured unconventionally. First, the data sets and general strategy for the analysis are described. Then, four separate analyses are presented. Because the analyses build upon one another progressively, methods and results are presented together for each individual analysis before progressing to the next. A discussion concludes.

Data

To select data for this study, we began with data compiled for Cardinale et al. (2013). In brief, those data were chosen using the following steps (full details of the selection procedure and data are available in Cardinale et al. 2013). First, a list of BEF experiments was compiled from several recent meta-analyses (Jiang and Pu 2009; Campbell et al. 2011; Cardinale et al. 2011). From that list, we identified all studies that: (a) experimentally manipulated species richness of primary producers, (b) included single-species monocultures, (c) measured biomass production at least three time points, and (d) retained individual data for all experimental units (as opposed to treatment means). Additionally, we included both the Jena experiment, for which full data have only recently been made available (Weigelt et al. 2010), and more recent data updates from two on-going experiments (Isbell et al. 2009; Reich et al. 2012).

Altogether, we analyzed data from 27 independent experiments associated with 12 separate studies (Table 1; additional information in online appendix A). We counted an experiment as a group of replicate communities subjected to identical manipulations and intended to be compared directly to one another, and a study as an experiment or set of experiments reported in the same article or sequence of related articles. For example, the European BioDEPTH project represents several independent manipulations of plant species richness performed in different countries; yet, these independent experiments were often reported together as a single study (e.g., Hector et al. 2010). Our data included 16 terrestrial grassland experiments (from 8 studies) and 11 laboratory microcosm experiments with freshwater microalgae (from 4 studies). Although these experiments represent only a small fraction of BEF experiments conducted to date, they are the only ones we found that met all the criteria necessary for inclusion in this study.

The measured response variable in grassland experiments was typically aboveground dry biomass per unit area (or, alternatively, percent ground cover), while the response variable in algal experiments was algal wet mass or biovolume per unit volume. Throughout, we refer to the response variable as 'biomass' to simplify presentation. Maximum species richness ranged from 6-60 species (median = 15) for grassland experiments, and from 3-7 species (median = 6) for algal microcosms. Whenever possible, the biomass of unintended, routinely weeded species was removed from whole-community biomass measurements prior to analysis.

Although we strove to select experiments with similar designs, differences among these 27 experiments are numerous and go beyond simple taxonomic distinctions. Several of these differences are noteworthy. First, grassland experiments generally exhibited a marked seasonality, and biomass production was typically measured once near the conclusion of each growing season. Grassland experiments also focused primarily on perennial plants whose average generation time exceeded the annual sampling interval. In contrast, algal experiments performed in laboratory microcosms typically exhibited more continuous (i.e., non-seasonal) population dynamics, and experiments often spanned a dozen or more generations of the included taxa. Second, experiments differed in the extent to which communities were characterized by initial transient dynamics as they progressed from their inoculation densities to their steady-state biomass and community composition. In some algal microcosms (e.g., Fox 2004; Weis et al. 2007), simultaneous exponential growth of all species was the predominant initial dynamic, while in others (e.g., Gonzalez & Descamps-Julien 2004; Zhang & Zhang 2006) sampling began only after exponential growth had waned. In grassland experiments, exponential population growth across multiple growing seasons was rare because of high initial seeding densities; however, community structure in mixtures typically evolved through time as these experiments matured (e.g., Reich et al., 2012). Third, in 8 of 11 algal experiments, growing conditions were tightly controlled and abiotic heterogeneity was minimized (e.g., Fox 2004), while in the other 3 experiments environmental heterogeneity (e.g., fluctuating temperatures) was introduced as part of the experimental design (e.g., Gonzalez & Descamps-Julien 2004). In contrast, in terrestrial grasslands, substantial effort was often made to minimize spatial heterogeneity across plots, although some year-to-year variation in abiotic conditions like temperature or precipitation was inevitable. Finally, terrestrial experiments typically included more species than their aquatic counterparts (Table 1). While the datasets from all 27 experiments were subjected to identical analyses for consistency, the design differences mentioned above must be borne in mind when comparing the results for terrestrial vs. aquatic ecosystems. However, the juxtaposition of the two systems will also hint at new hypotheses about the roles of the mechanisms driving diversity-stability relationships.

Analyses

Metrics and terminology

We focused specifically on the relationship between species richness and the variation and co-variation in the biomass of individual species populations or entire communities (summed biomass of species) through time. Species richness was measured as the number of species initially seeded or inoculated in an experimental unit. Stability of biomass was measured using the coefficient of variation (CV), defined as the ratio of the standard deviation to the mean. CV is a widely used measure for stability (e.g., May 1974; Tilman 1996; Doak et al. 1998) because it provides a standardized measure of variation that is comparable across ecosystems. Increases in CV correspond to decreases in stability, and vice versa. When increasing species richness was associated with decreasing (increasing) CV, we referred to this as a positive (negative) effect of richness on stability.

We quantified the relationship between species richness and the mean, standard deviation (SD) and CV of biomass production using linear-regression slopes on a log-log scale. We log-transformed predictor values (species richness) because species richness levels were often more evenly spaced on a log scale, and thus log-transformation reduces the leverage of the most species-rich treatments. We log-transformed response variables to ensure that predicted values of all quantities would be positive. Lack-of-fit testing indicated that linear regressions on log-log scales provided adequate fits in the large majority of cases (results in online appendix B). Helpfully, log CV can be re-written as the difference between log SD and the log of the mean, which allows the effect of richness on stability to be separated into the effects of richness on average biomass and on unscaled variance (see below).

We also measured the correlation among the biomasses of several species in a group as they fluctuated through time. Depending on the analysis, this group was either species grown separately in monoculture or together in polyculture. A single quantity that measures the overall synchrony among fluctuations of more than two populations has proven elusive (Loreau & de Mazancourt, 2008; Gonzalez & Loreau 2009). For example, the average correlation among n variables can be no less than $-1/(n-1)$ (Willis 1959), and thus the average correlation is poorly suited for comparing groups with differing numbers of species. Others (e.g., Lehman et al., 2000; Mikkelson et al., 2011) have used the sum of the covariances between all pairs of species to measure how species interactions impact synchrony. While summed covariance may be useful for comparing the same group of species under different conditions, it also depends on the number of species and the scale of measurement, and thus is difficult to compare across ecosystems. More recently, Loreau & de Mazancourt (2008) proposed a scale-free metric φ that varies between 0 when species fluctuations are maximally asynchronous (and hence the total biomass is constant) and 1 when species are perfectly synchronized. Loreau & de Mazancourt's φ can also be interpreted as the square of the ratio between the community-wide CV and the weighted CVs of constituent species (Thibaut & Connolly, 2013). While Loreau & de Mazancourt's φ is easy to calculate and intuitive, it suffers from the limitation that independently fluctuating species will generate different values of φ depending on the number of species and the individual species' variances. Consequently, this metric is less useful for our purposes because it does not provide a benchmark that can be used to assess how species interactions influence synchrony in population dynamics.

We developed a new measure of overall synchrony among species that overcomes this limitation. This metric, which we denote η, is the average across species of the correlation between the biomass of each species and the total biomass of all other species in the group. In notation, if Y_i is the biomass of species i in a group of n species, η is written as

$$\eta = \left(1/n\right)\sum_{i} Corr\left(Y_i, \sum_{j\neq i} Y_j\right). \tag{1}$$

This calculation provides an overall measure of synchrony among species biomasses that has appealing properties (proofs in online appendix C). First, similarly to Loreau & de Mazancourt's φ, η ranges from its minimum value of -1 when species are maximally asynchronized (and total biomass is constant) to a maximum of +1 when species are perfectly synchronized. Second, η is centered at 0 when species fluctuate independently, thus providing a useful reference point that enables comparisons to be made across organisms, experiments, or study systems. Online appendix D provides a simulation study that verifies that η reliably measures the overall synhcrony among a group of competing species.

Calculated metrics for all analyses are available in the Dryad Digital Repository, doi: 10.5061/dryad.787rm (Gross & Cardinale 2013).

Analysis 1: Unpacking species richness's impact on community stability into its effects on the mean and variance of community biomass

Methods: We first quantified the association between species richness and the mean, SD and CV of community biomass for each experiment. To do so, we calculated the mean, SD and CV for each experimental unit (e.g., replicate community, plot, jar, etc.) in each experiment, and regressed the log of each response vs. log(species richness). Denote the estimated slopes from each of these linear regressions as $\hat{\beta}_{\mu}$, $\hat{\beta}_{\sigma}$ and $\hat{\beta}_{CV}$, respectively. Conveniently, $\hat{\beta}_{CV} = \hat{\beta}_{\sigma} - \hat{\beta}_{\mu}$, and thus the impact of species richness on community-level stability ($\hat{\beta}_{CV}$) can be separated into the impacts of species richness on the mean and variance of biomass (see online appendix E for an illustration with data). In addition, we plotted $\hat{\beta}_{\sigma}$ vs. $\hat{\beta}_{\mu}$ to graphically summarize diversity's stabilizing effect on community biomass (fig. 1). In this plot, experiments in which species richness stabilizes community biomass ($\hat{\beta}_{CV} < 0$) generate points that fall below a 45° line (where $\hat{\beta}_{CV} = 0$), while experiments in which richness destabilizes community biomass generate points above a 45° line. Moreover, points further away from the 45° line indicate a stronger effect of species richness on community stability.

We also averaged $\hat{\beta}_{\mu}$, $\hat{\beta}_{\sigma}$ and $\hat{\beta}_{CV}$ within terrestrial and algal data sets. Statistical inference for these averages is complicated by the fact that the statistical uncertainty in each estimate differs among experiments (because different experiments may have different levels of replication, etc.). To account for this heterogeneity, we used a two-stage bootstrap resampling process that captured variation both within and among experiments. In the first stage, experiments were resampled with replacement. In the second stage, for each selected experiment, values of $\hat{\beta}_{\mu}$, $\hat{\beta}_{\sigma}$ and $\hat{\beta}_{CV}$ were resampled from their estimated sampling distribution. Statistical inference was based on 10,000 such bootstrap samples.

Results: Increasing species richness stabilized community biomass in terrestrial grasslands, but not in algal microcosms (fig. 2). In grassland experiments, increasing species richness increased mean biomass production in all 16 studies (average over terrestrial experiments $\bar{\hat{\beta}}_{\mu}$ = 0.308, bootstrap s.e. = 0.035, two-tailed bootstrap $p < 0.001$; cf Cardinale et al. 2007). In 12 of 16 experiments, increasing species richness also increased variance, although the statistical significance of the average effect was marginal ($\bar{\hat{\beta}}_{\sigma}$ = 0.124, b.s.e. = 0.061, p = 0.051). Because increasing species richness had a larger effect on mean biomass than its variance, increasing species richness had a positive effect on community stability ($\bar{\hat{\beta}}_{CV}$ = -0.185, b.s.e. = 0.043, $p < 0.001$).

In algal microcosms, however, increasing species richness increased both mean biomass ($\bar{\hat{\beta}}_{\mu}$ = 0.668, b.s.e. = 0.179, $p < 0.001$) and variance ($\bar{\hat{\beta}}_{\sigma}$ = 0.572, b.s.e. = 0.228, p = 0.010) at comparable rates. Thus, no association between species richness and community stability was found ($\bar{\hat{\beta}}_{CV}$ = -0.096, b.s.e. = 0.076, p = 0.21).

Analysis 2: How does species richness impact population-level stability?

Methods: Although theory has suggested that increasing species richness should destabilize the dynamics of individual populations (Tilman 1999), empirical evidence for this pattern has so far been equivocal (e.g., Cottingham et al. 2001; Steiner et al. 2005; Vogt et al. 2006; Jiang & Pu 2009; Campbell et al. 2011). We looked for an impact of species richness on species-level stability by first calculating the CV of each individual species biomass in each monoculture or mixture in which that species occurred. We then averaged these population-level CVs across all species in an experimental unit, using species average biomasses as weights. (Weighted averaging was used because very rare species — especially those near a detection threshold — tended to have large CVs that were likely artifacts of measurement error.) Average population-level CVs were then regressed vs. species richness for each experiment, again using logs of both variables. The slope of this regression quantified the effect of species richness on population-level stability for a single experiment. Statistical inferences for average slopes across experiments were based on a bootstrap similar to analysis 1. This analysis excluded one terrestrial experiment for which species-level data were not available (Table 1).

Results: Increasing species richness destabilized individual populations in 21 of 26 experiments (fig. 3). Differences between terrestrial and aquatic studies were again clear. In all 15 grassland studies, increasing species richness increased population-level CV, with an average regression slope of +0.161 (b.s.e. = 0.028, $p < 0.001$). Among the 9 terrestrial experiments with at least 4 years of data, the effects of species richness on community and population-level stability were strikingly consistent (filled points, fig. 3a; note that 6 of these 9 experiments came from Cedar Creek MN, USA). In contrast, there was no consistent effect of species richness on population-level stability in algal microcosms (average regression slope of -0.011; b.s.e. = 0.72, $p = 0.87$).

Analysis 3: How do species interactions affect correlations among species?

Methods: If, in grasslands, increasing species richness stabilizes community biomass but destabilizes the populations in those communities, then on the whole correlations among species biomasses must decline as species richness increases. Here, we investigated this phenomenon by comparing the synchrony among species in the most species-rich mixtures to the synchrony of those same species grown alone in monoculture. Specifically, for every replicate of the most species-rich mixtures, we used η (eq. 1) to measure the synchrony among species in that replicate mixture. We then used η to measure the synchrony of those same species grown in monoculture (after averaging across replicate monocultures of the same species at each time point when necessary). Each of these two quantities was then averaged across all replicates of the most species-rich mixtures in an experiment. Comparison of the average η's across experiments reveals how interspecific interactions impact temporal correlations among competing species.

This analysis was only possible for the 10 grassland experiments and 11 algal microcosms in which population-level data were available in mixtures, and for which all species in the experiment were grown in monoculture. Statistical inference for averages across experiments was based on a bootstrap similar to analysis 1 and 2, except that here the second stage of the bootstrap entailed re-sampling replicates of the most species-rich mixtures.

Results: Species synchrony in the most species-rich mixtures was lower than the synchrony among the same species grown in monoculture in 20 of 21 experiments (fig. 4; two-tailed sign test $p < 0.001$). This suggests that interspecific interactions reduce correlations among species biomasses. In the most species-rich mixtures, the average value of η was small in grasslands (average across experiments = +0.10, b.s.e. = 0.09, $n = 10$) and moderate in algal microcosms (average across experiments = +0.34, b.s.e. = 0.08, $n = 11$). The average value of η was larger among species in monoculture (average across grassland experiments = +0.50, b.s.e. = 0.09; in algal microcosms = +0.54, b.s.e. = 0.07). Reduced correlations among species were particularly marked in the 7 terrestrial experiments with at least 4 years of data. In these experiments, the average value of η in polycultures was +0.00 (b.s.e. = 0.02), compared to +0.37 (b.s.e. = 0.08) in monocultures. These results show that interspecific interactions generate compensatory dynamics among species.

Analysis 4: Do species responses to environmental fluctuations predict the strength of diversity's effect on community stability?

Methods: Some theory predicts that the effect of species richness on community stability will be strongest when species respond independently to environmental fluctuations, and will be weakest when species responses to environmental fluctuations are strongly positively correlated (Ives et al. 2000). To examine this prediction, we compared species correlations in monoculture to the strength of diversity's effect on community stability. Correlations of species abundance in monoculture are, at best, an indirect measure of the (dis)similarity of species responses to environmental fluctuations. However, direct measures of species responses to the environment were not available for most studies, and model simulation suggests that the synchrony of species abundances when grown alone indicates how similarly species respond to environmental variation (online appendix D). Thus, we quantified the synchrony among species in monoculture by calculating η for the monocultures of all species in an experiment (again after averaging across replicate monocultures of the same species when necessary). We compared this measure to community-level $\hat{\beta}_{CV}$, our measure of the stabilizing effect of species richness on community biomass from analysis 1.

For the 8 algal experiments in which growing conditions were held constant, the correlations among species in monoculture probably have little to do with how similarly those species would respond to changing environments in nature. Even so, to remain consistent with our analysis of the terrestrial data, we subjected all algal experiments with suitable data to the same analysis, although care was taken not to over-interpret our results. This analysis excluded 5 terrestrial studies for which not all species were planted in monoculture.

Results: In both grassland (rank correlation = +0.05, two-tailed asymptotic *t*-test p = 0.88, n = 11) and algal (rank correlation = -0.09, two-tailed asymptotic *t*-test p = 0.80, n = 11) experiments, there was no association between species synchrony in monoculture and community-level $\hat{\beta}_{CV}$ (fig. 5). Thus, the effect of species richness on community stability was not predicted by species correlations in monoculture. This result suggests that independent responses of species to a fluctuating environment did not contribute to increased stability of community biomass in these experiments.

Discussion

This study provides a deep analysis of longer-running biodiversity vs. ecosystem function (BEF) experiments that helps explain why species richness affects the temporal stability of biomass in both individual populations and whole communities. We discuss results for grassland experiments first, before turning to algal microcosms and comparisons between systems. In grasslands, the results here add to the burgeoning evidence that increasing species richness tends to stabilize community biomass (e.g., Tilman 1996; Cottingham et al. 2001; Jiang & Pu 2009; Campbell et al. 2011; Cardinale et al. 2012). However, this analysis extends our understanding in three important ways. First, these results show that the stabilizing effect of species richness on community biomass arises because increasing species richness increases mean biomass by a larger amount than it increases variance, thus increasing stability (fig. 2a). Second, we find clear and consistent evidence that increasing species richness destabilizes individual populations in grasslands (fig. 3a). As discussed above, previous work has led to little agreement regarding diversity's impact on population stability (e.g., Cottingham et al. 2001; Jiang & Pu 2009; Campbell et al. 2011). The pairing of a stabilizing effect of species richness on community biomass with a destabilizing effect on individual populations matches theoretical predictions (Ives et al. 1999; Tilman 1999).

Third, this analysis shows that interspecific competition generates compensatory dynamics in grasslands, and suggests that compensatory dynamics help stabilize community biomass. This latter conclusion follows from three separate findings: (a) richness stabilizes community biomass, (b) species biomasses are less correlated when species are grown together in polyculture (fig. 4a), and (c) similarity among species responses to environmental fluctuations when grown alone as monocultures does not predict the strength of diversity's stabilizing effect (fig. 5a). These findings contradict some prior analyses that have been unable to detect compensatory dynamics in mixtures with more than two species (e.g., Houlahan et al. 2007). However, early work relied heavily on metrics such as summed covariances that are not well suited to quantifying synchrony in multi-species communities (Gonzalez & Loreau, 2009). New measures of species synchrony, such as η from eq. (1), provide a more reliable way to compare correlations across different species mixtures.

Algal systems show strikingly different stability properties than terrestrial grasslands. Chiefly, increasing species richness in aquatic microcosms leads to similar increases in both the mean and variance of community biomass, resulting in a minimal effect on community stability. Species richness also does not have a consistent effect on population-level stability. One qualitatively similar result between grassland and algal systems is that correlations among species biomasses are lower when they are reared in polyculture than when grown alone, although the effect is less dramatic with algae than in grasslands (fig. 4).

It is difficult to determine whether differences between grassland vs. algal experiments are due to any fundamental ecological properties of these taxa or the communities and ecosystems they collectively inhabit, or are simply caused by inevitable design differences in terrestrial vs. microcosm studies. There are, however, select biological differences among the dominant primary producers that hint at underlying ecological explanations. First, in algal studies, species that were more productive in monoculture were also less stable (rank correlation between biomass and CV for monoculture species, averaged across experiments = +0.24, s.e. = 0.15, n = 10). In grasslands, the reverse was true — more productive species were more stable in monoculture (avg. rank correlation = -0.45, s.e. = 0.07, n = 16). Second, algal communities were more strongly dominated by species that were more productive in monoculture (avg. rank correlation between abundance in the most species-rich polycultures vs. abundance in monoculture for algal communities = +0.63, s.e. = 0.09, n = 11; for grassland communities = +0.26, s.e. = 0.08, n = 10). Thus, aquatic communities tended to be dominated by low-stability taxa to an extent not observed in grasslands.

With respect to why this may be so, it has also been suggested that aquatic systems have a simplified physical environment that may reduce the potential for complementary resource use among algae relative to terrestrial plants (Schmidtke et al. 2010). If aquatic systems are, in fact, more spatially homogeneous — either in nature, or just in these experiments — it could explain why more productive but less stable species come to dominate aquatic communities. Although the data currently available do not allow us to explore this possibility definitively, it does underscore how differences in species traits could interact with environmental conditions to impact the diversity-stability relationship.

In grassland systems, the lack of an association between the correlations among species densities in monocultures and the strength of the richness-stability relationship is puzzling (fig. 5a). To the extent that monocultures reflect species' responses to the abiotic environment, this result clashes with the theoretical prediction that the effect of species richness on stability should be controlled by how similarly or dissimilarly species respond to environmental fluctuations (e.g., Ives et al. 2000). There are several possible reasons why data and theory do not align in this case. First, much of the theory relevant to diversity-stability relationships pertains to stability across many generations for systems that have achieved their stochastic steady-state and are buffeted only by small perturbations (May, 1974; Ives et al., 2000; Lehman & Tilman, 2000; Loreau & de Mazancourt, 2013). However, even though some of these grassland experiments are among the longest-running ecological manipulations, most encompass only a few generations of their constituent species, if they incorporate reproduction at all. In contrast, algal experiments often extend for a greater number of generations, albeit with fewer species. Second, this same theory assumes that species' growth rates are determined by the separate and additive effects of species interactions and environmental fluctuations. However, this separation may be too simplistic, as species' perceptions of, and responses to, the environment may be mediated by the presence of other nearby species, in ways that extend beyond mere resource competition (Loreau & de Mazancourt, 2013). For example, in experimental communities of bryophytes, species richness reduces water stress during drought because greater architectural complexity in polycultures traps moisture and enhances microclimate humidity (Mulder et al. 2001). Lastly, recent theoretical work has shown that diversity-stability relationships may be affected by strong over-compensatory density-dependence (Fowler et al. 2012) and also by serial correlation in the environment (so-called "red" noise; Fowler & Ruokolainen 2013). Both of these phenomena may be more amenable to exploration in microcosms that allow multi-generational dynamics and tight control of environmental variables (e.g., Gonzalez & Descamps-Julien 2004). Each of these observations poses new challenges for diversity-stability research, and underscores the value of conducting BEF research across a broad range of taxa and ecological systems.

The disagreement between theory and these experiments suggested by analysis 4 also helps explain why the interpretation of our findings differs from the conclusions of a recent paper by de Mazancourt et al. (2013). That study analyzed four of the grassland biodiversity experiments examined here (van Ruijven & Berendse, 2005; Tilman et al., 2006; Isbell et al., 2009; Weigelt et al., 2010), and concluded that species richness "stabilized communities mainly by increasing community biomass and reducing the strength of demographic stochasticity." Demographic stochasticity may indeed contribute to community stability in these experiments (see below). However, de Mazancourt et al. (2013) based their analysis on a theoretical framework (Ives et al., 2000; Loreau & de Mazancourt, 2013) that does not allow species interactions to impact the variance of community biomass. Therefore, they did not look for, and did not find, an impact of species interactions on community stability, nor did they compare species synchrony in monoculture vs. polyculture. Certainly, the difference between our study and de Mazancourt et al.'s highlights how different theoretical foundations can suggest different analyses that yield different interpretations of similar data. That said, the argument for our approach and interpretation is that the theory that guided de Mazancourt et al.'s analysis rests on assumptions that may not apply to these BEF experiments, as suggested by analysis 4 above. Consequently, we need a deeper (and likely more mechanistic) understanding of how and why species interactions impact community biomass in these experiments before we can predicate their analysis on any single theoretical model.

Finally, in both terrestrial and algal systems, both demographic stochasticity and measurement error may have contributed to decreased population-level stability and decreased synchrony among species in polycultures. Both demographic stochasticity and measurement error introduce variation in the measured abundances of individual species that disproportionately affects small populations. Thus, if the average abundance of a species declines as its number of competitors increases, then both demographic stochasticity and measurement error will inflate the CV of individual populations and will decrease the correlations in measured species abundances as richness increases (de Mazancourt et al., 2013). Of course, demographic stochasticity would impact natural populations in a similar way, albeit only in very small populations. Conversely, measurement error is an artifact that may exaggerate the effects of species richness on population-level stability and interspecific correlations in the analysis of BEF experiments such as these.

To sum up, contemporary BEF experiments in grasslands show compelling evidence that increasing species richness stabilizes community biomass while destabilizing the dynamics of individual populations, at least at the temporal, spatial and taxonomic scales characteristic of those experiments. In contrast, increasing species richness does not stabilize community biomass in algal microcosms, perhaps because experimental algal communities were more strongly dominated by highly productive but less stable species. In grasslands, compensatory dynamics among species promote community stability, regardless of how similarly or dissimilarly those species respond to the environment. Species interactions also moderately reduce correlations among algal species, although the effect is not sufficient to stabilize total community biomass. While the extent to which these findings may pertain to other taxa, trophic levels or spatiotemporal scales remains an open question, they do provide a point of reference from which our understanding may grow.

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Table 1. Included studies and key characteristics thereof

Study and representative citation	no. of experiments	system	response variable	max. species richness	no. of time points
Fox (2004)	5	freshwater microalgae	algal wet mass	7	3
Gonzalez & Descamps-Julien (2004)	3	freshwater microalgae	algal biovolume	6	32
Weis (2007)	2	freshwater microalgae	algal wet mass	3	9
Zhang & Zhang (2006)	1	freshwater microalgae	algal wet mass	5	3
Flombaum & Sala (2008)*	1	terrestrial plants	percent cover	6	3
Hector et al. (2010)†	6	terrestrial plants	aboveground dry mass	8-16	3
Isbell et al. (2009)	1	terrestrial plants	aboveground dry mass	8	10
Reich et al. (2006)	4	terrestrial plants	aboveground dry mass	16	11

Tilman et al. (1996)[‡]	1	terrestrial plants	percent cover	24	7
Tilman et al (2006)	1	terrestrial plants	aboveground dry mass	16	8
van Ruijven & Berendse (2005)	1	terrestrial plants	aboveground dry mass	8	4
Weigelt et al. (2010)[‡]	1	terrestrial plants	aboveground dry mass	60	6

[*] Species-level data not available in mixtures.

[†] Data from Greece and Switzerland not included. Not all species planted in monoculture for Germany, Ireland and Silwood.

[‡] Not all species planted in monoculture.

Figure legends

Figure 1. A graphical summary of the effects of species richness on mean, SD and stability of biomass. The horizontal axis shows $\hat{\beta}_{\mu}$, the least-squares regression slope of log(mean biomass) vs. log(species richness). The vertical axis shows $\hat{\beta}_{\sigma}$, the least-squares regression slope of log(SD of biomass) vs. log(species richness). Because $\hat{\beta}_{CV} = \hat{\beta}_{\sigma} - \hat{\beta}_{\mu}$, the distance that points fall from the 45° (dashed) line is proportional to $\hat{\beta}_{CV}$, the least-squares regression slope of log(CV of biomass yield) vs. log(species richness). Points below the 45° line indicate a stabilizing effect of species richness ($\hat{\beta}_{CV} < 0$), and points above the 45° line indicate a destabilizing effect of species richness ($\hat{\beta}_{CV} > 0$). The perpendicular distance from the 45° line to each data point equals $\hat{\beta}_{CV} \big/ \sqrt{2}$.

Figure 2. Effects of species richness on mean, SD and CV of community biomass for (A) terrestrial and (B) algal-microcosm experiments. In (A), filled plot symbols correspond to experiments with ≥4 time points, and open symbols show experiments with 3 time points.

Figure 3. A comparison of the effects of species richness on population-level CV vs. community-level CV for (A) terrestrial and (B) algal-microcosm experiments. Along both axes, $\hat{\beta}_{CV} < 0$ indicates a positive effect of species richness on stability, and $\hat{\beta}_{CV} > 0$ indicates a negative effect of species richness on stability. The dashed line is a line of equality. In (A), filled plot

symbols correspond to experiments with ≥4 time points, and open symbols show experiments with 3 time points.

Figure 4. Synchrony among species in the most species-rich mixtures vs. synchrony among the same species grown alone in monoculture for (A) terrestrial and (B) algal microcosm studies. Species synchrony is measured using η from eq. (1). The dashed line is a line of equality. In (A), filled plot symbols correspond to experiments with ≥4 time points, and open symbols show experiments with 3 time points.

Figure 5. Strength of the effect of species richness on community stability, as measured by $\hat{\beta}_{CV}$ vs. the similarity in species responses to environmental fluctuations, as measured by the synchrony of species grown in monoculture for (A) terrestrial and (B) algal microcosm studies. Species synchrony is measured using η from eq. (1). In (A), filled plot symbols correspond to experiments with ≥4 time points, and open symbols show experiments with 3 time points. In (B), +'s show experiments in which environmental conditions were intentionally varied, and x's show experiments in which environmental conditions were held constant.

Figure 1.

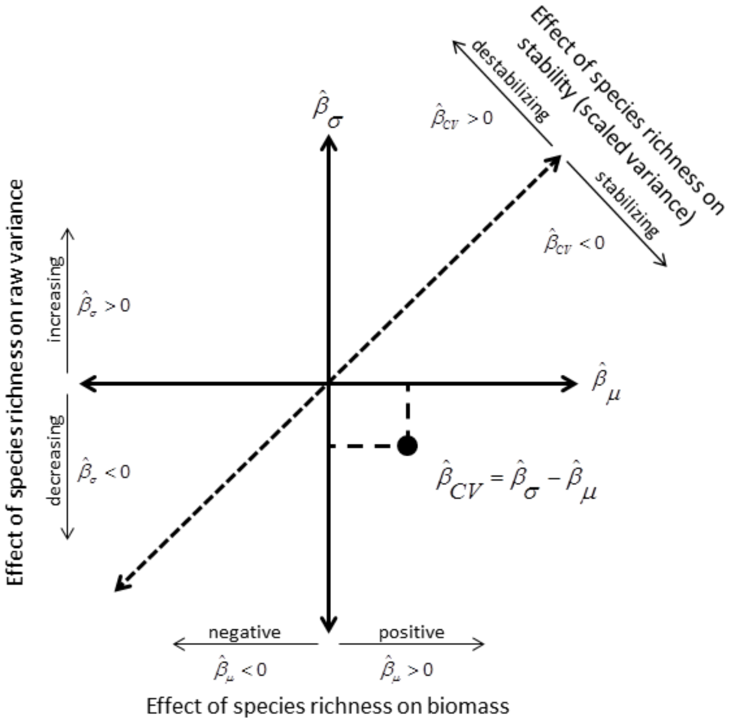

$\hat{\beta}_\sigma$
$\hat{\beta}_\mu$
Effect of species richness on stability (scaled variance)
destabilizing
$\hat{\beta}_{CV} > 0$
stabilizing
$\hat{\beta}_{CV} < 0$
Effect of species richness on raw variance
increasing
$\hat{\beta}_\sigma > 0$
decreasing
$\hat{\beta}_\sigma < 0$
$\hat{\beta}_{CV} = \hat{\beta}_\sigma - \hat{\beta}_\mu$
negative
$\hat{\beta}_\mu < 0$
positive
$\hat{\beta}_\mu > 0$
Effect of species richness on biomass

Figure 2.

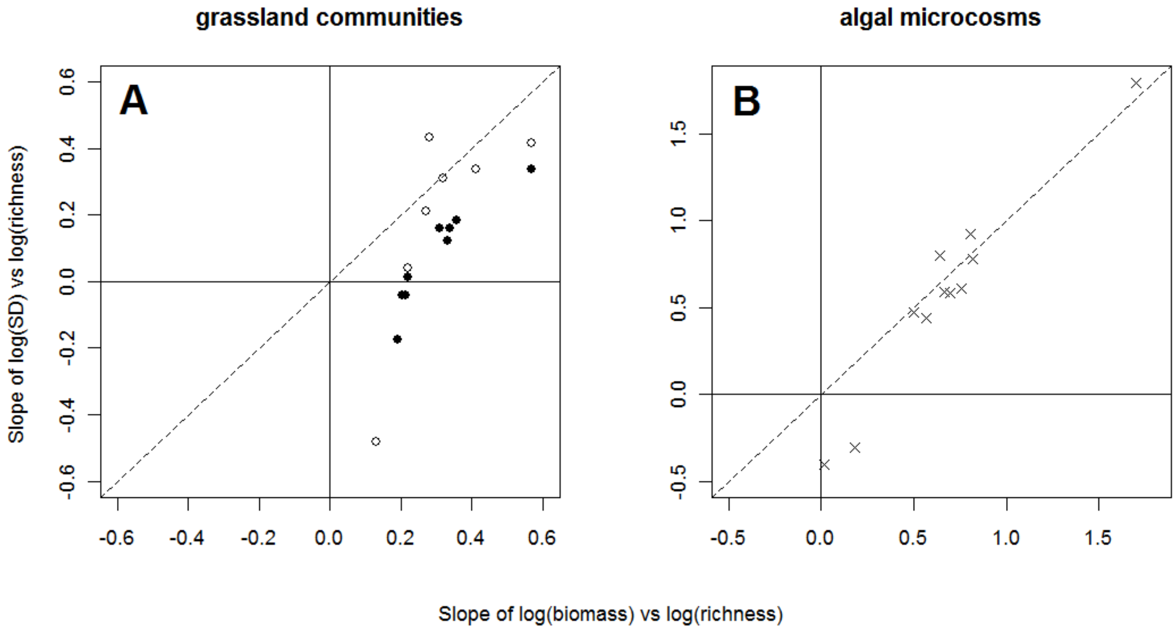

grassland communities
algal microcosms
A
B
Slope of log(SD) vs log(richness)
Slope of log(biomass) vs log(richness)
-0.6
-0.4
-0.2
0.0
0.2
0.4
0.6
-0.5
0.0
0.5
1.0
1.5

Figure 3.

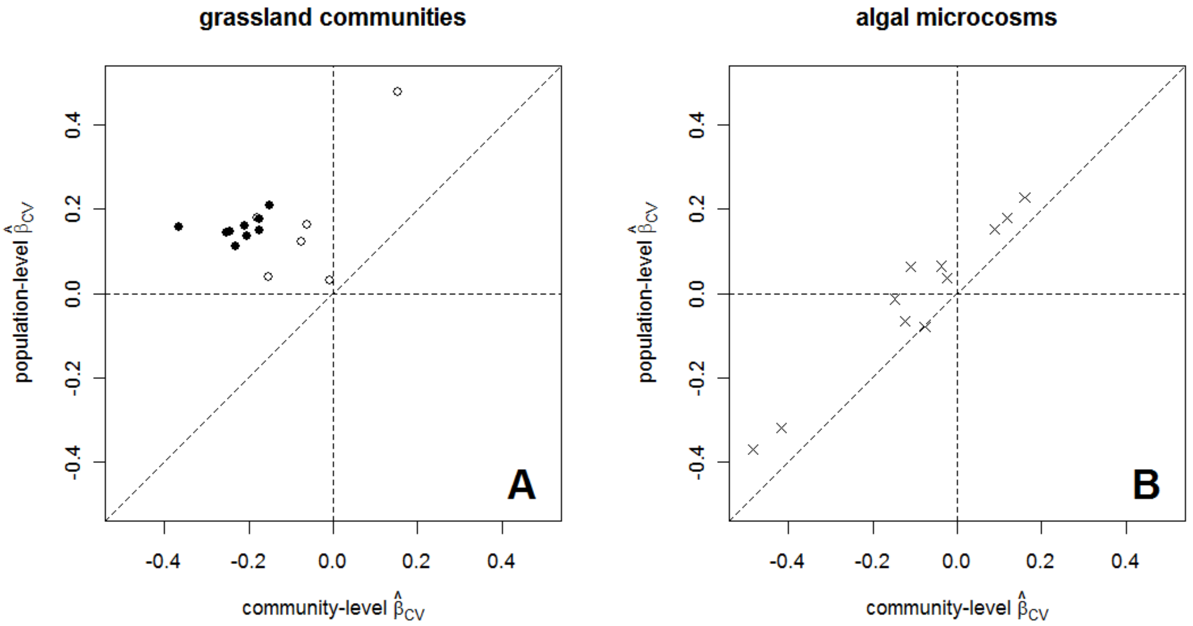

grassland communities
algal microcosms
population-level $\hat{\beta}_{CV}$
community-level $\hat{\beta}_{CV}$
-0.4
-0.2
0.0
0.2
0.4
A
B

Figure 4.

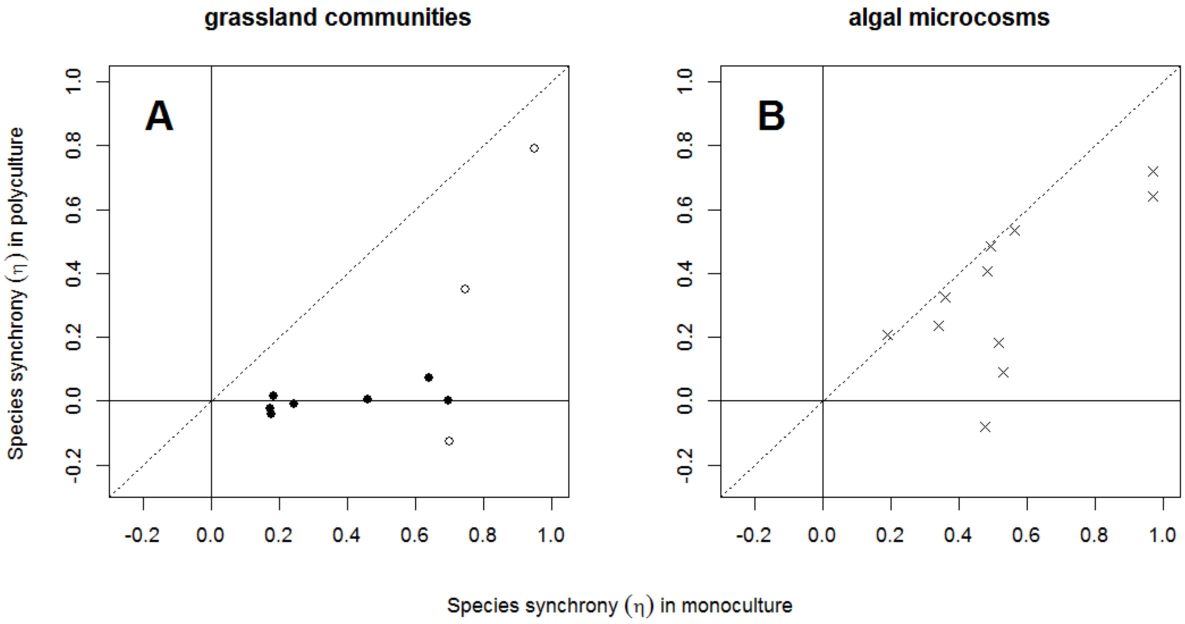
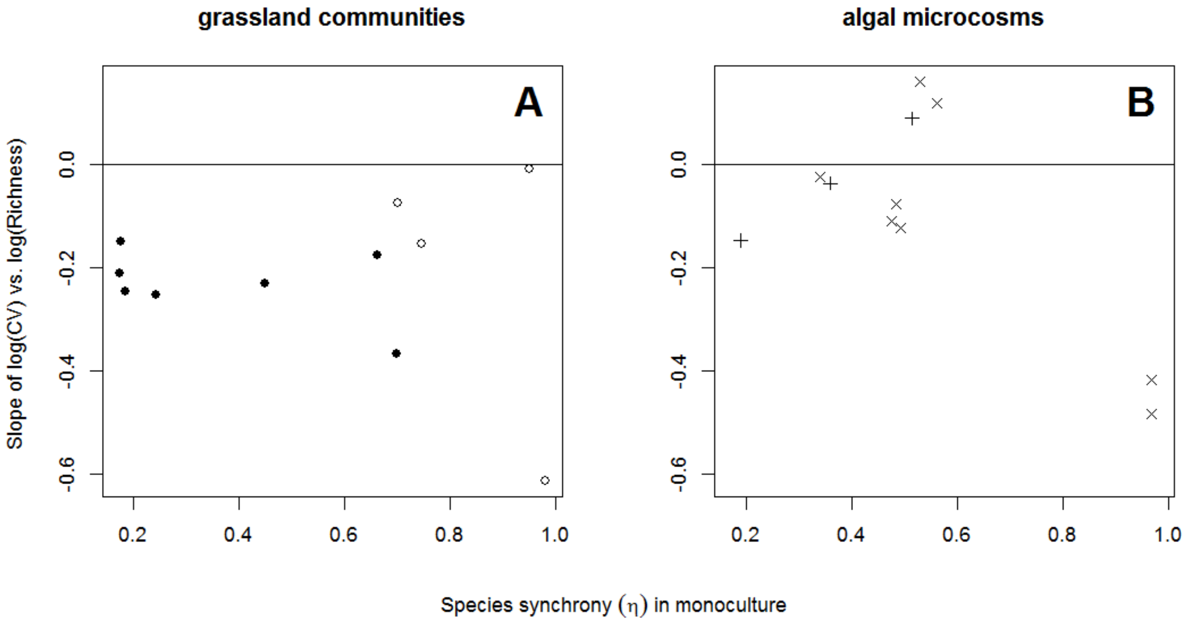

grassland communities
algal microcosms
A
B
Species synchrony (η) in polyculture
Species synchrony (η) in monoculture
-0.2
0.0
0.2
0.4
0.6
0.8
1.0

Figure 5.


grassland communities
algal microcosms
A
B
Slope of log(CV) vs. log(Richness)
0.0
-0.2
-0.4
-0.6
0.2
0.4
0.6
0.8
1.0
Species synchrony (η) in monoculture