LETTER

Mechanisms contributing to stability in ecosystem function depend on the environmental context

Emily Grman,[1,2]* Jennifer A. Lau,[1,2] Donald R. Schoolmaster, Jr.[2] and Katherine L. Gross[1,2]

[1]*Plant Biology Department, Michigan State University, East Lansing, MI 48824, USA*

[2]*W. K. Kellogg Biological Station, Michigan State University, Hickory Corners, MI 49060, USA*

*Correspondence: E-mail: grmanemi@msu.edu

Abstract

Stability in ecosystem function is an important but poorly understood phenomenon. Anthropogenic perturbations alter communities, but how they change stability and the strength of stabilizing mechanisms is not clear. We examined temporal stability (invariability) in aboveground productivity in replicated 18-year time series of experimentally perturbed grassland plant communities. We found that disturbed annual-dominated communities were more stable than undisturbed perennial communities, coincident with increases in the stabilizing effect of mean–variance scaling. We also found that nitrogen-fertilized communities maintained stability despite losses in species richness, probably because of increased compensatory dynamics and increased dominance by particularly stable dominant species. Among our communities, slight variation in diversity was not the strongest mechanism driving differences in stability. Instead, our study suggests that decreases in individual species variabilities and increases in the relative abundance of stable dominant species may help maintain stability in the functioning of ecosystems confronted with eutrophication, disturbance, and other global changes.

Keywords

Compensatory dynamics, diversity, dominance, evenness, fertilization, LTER, portfolio effect, stability, Taylor power law.

Ecology Letters (2010) **13**: 1400–1410

INTRODUCTION

Despite large fluctuations in environmental conditions, ecosystems often maintain relatively stable levels of function. However, stability varies widely among natural communities (Fang *et al.* 2001; Knapp & Smith 2001) and the reasons for this variation are not well understood. Degradation of ecosystems may reduce their capacity to provide stable levels of function (McCann 2000; Kremen 2005). Understanding the drivers of stability in ecosystem function across diverse community types, especially communities faced with anthropogenic change, has thus become a critical challenge for ecologists.

Community ecologists have focused on the role that species interactions, diversity, and functional traits play in maintaining stability in ecosystem function. Changes in those aspects of community structure are thought to influence both the level of stability exhibited by an ecosystem and the primary mechanisms promoting stability. Communities can reorganize in response to perturbations, changing their structure, composition, and diversity (Hooper *et al.* 2005). For example, nitrogen-fertilized grassland communities typically experience reductions in species richness (Suding *et al.* 2005), increases in dominance (Hillebrand *et al.* 2008), and shifts in the functional traits of the persistent species (Suding *et al.* 2005). Frequent soil disturbances can shift community composition towards species with shorter lifespans that regenerate readily from the seedbank. It is not known how these complex changes in community composition, and thus changes in the strength of stabilizing mechanisms, will map onto changes in the stability of ecosystem function. To predict how environmental perturbations such as eutrophication and disturbance will affect stability in ecosystem function, we must experimentally perturb communities but allow natural reassembly processes to reconstruct those communities. We can then examine how stability and the strength of the stabilizing mechanisms vary among those perturbed communities.

Among hypothesized stabilizing mechanisms, species diversity has been intensively studied and found to both enhance ecosystem function and stabilize function through

space or time (Hooper *et al.* 2005; Jiang & Pu 2009). Anthropogenic perturbations that decrease diversity may therefore decrease stability in ecosystem function. For example, nitrogen additions to Minnesota grasslands led to decreases in species richness and decreases in stability (Tilman & Downing 1994), among other changes in community structure and dynamics (Huston 1997). However, other stabilizing mechanisms could possibly increase with these complex changes in communities in response to perturbation. Thus ecosystem stability might not always be reduced when species richness is reduced by perturbation.

Species interactions can generate a suite of stabilizing mechanisms. Compensatory dynamics exist when increases in the abundance of one species are associated with decreases in the abundance of another species. These negatively correlated fluctuations in species abundances can promote stability because species may overlap in the ecosystem functions they provide. However, the existence and strength of compensatory dynamics may vary widely across environments and communities (Micheli *et al.* 1999; Tilman 1999; Valone & Hoffman 2003; Caldeira *et al.* 2005; Steiner 2005; Steiner *et al.* 2005; Romanuk *et al.* 2006; Tilman *et al.* 2006; Zhang & Zhang 2006; Houlahan *et al.* 2007; Valone & Barber 2008; Gonzalez & Loreau 2009). Compensatory dynamics could be driven by a variety of mechanisms, including competition or negatively correlated responses to environmental drivers (Schluter 1984; Micheli *et al.* 1999). Facilitation or positively correlated responses to environmental drivers are thought to weaken compensatory dynamics (Houlahan *et al.* 2007). By altering the relative importance of competition and facilitation (Callaway *et al.* 2002) or by selecting for species that may be more or less sensitive to abiotic drivers such as moisture or temperature (Ives *et al.* 1999), human-caused changes in environmental conditions could alter the stabilizing effect of compensatory dynamics.

Mean–variance rescaling is another mechanism that could stabilize ecosystem function (Cottingham *et al.* 2001). Less abundant species are less variable. This mean–variance scaling relationship, summarized by Taylor's power law (Taylor 1961), seems to be a ubiquitous trait of communities, for as-yet unknown reasons (Kendal 1995). The slope of this scaling relationship, z, determines the strength of this stabilizing mechanism (Tilman *et al.* 1998). This slope is known to vary widely across communities (Taylor 1961; Downing 1979; Cottingham *et al.* 2001), but variation in the relative importance of this stabilizing effect is not well understood.

Dominance, on the other hand, is well known to vary with environmental conditions, but the role of dominance in stabilizing ecosystem function is less well known (Hillebrand *et al.* 2008). Dominance is a function of both the distribution of species relative abundances (evenness)

and species richness (Smith & Wilson 1996). It is therefore conceptually, but not necessarily empirically, related to species evenness. Evenness of species abundances is thought to increase stability through enhancing effective diversity and allowing compensatory dynamics and the mean–variance scaling effect to stabilize communities (Doak *et al.* 1998; Cottingham *et al.* 2001). This suggests that higher dominance might be expected to decrease stability because it is associated with reduced species richness and evenness. However, one study found no effect of evenness on stability (Isbell *et al.* 2009) and several studies have found that dominant species have greater stability than subordinate species (Leps 2004; Steiner *et al.* 2005; Polley *et al.* 2007). Increasing the relative abundance of these particularly stable species might enhance ecosystem stability in a manner analogous to the sampling effect (Huston 1997; Tilman 1999), where the inclusion of high-functioning species increases total ecosystem function. It is not clear whether the stabilizing effect of stable dominant species outweighs the destabilizing effect of the reduced diversity that is typically associated with increased dominance. Perturbations that increase dominance might thus increase or decrease stability.

Manipulative experiments have tested the effectiveness of these hypothesized drivers of stability (e.g. Isbell *et al.* 2009; Tilman *et al.* 2006). However, those manipulative experiments necessarily constrain the ability of ecosystems to reorganize and provide stability in ecosystem function via some other stabilizing mechanism. To test for differences in stability and the drivers of stability across grassland communities experiencing two common types of anthropogenic perturbation, we analysed data on plant species aboveground biomasses from a replicated long-term disturbance and fertilization experiment. Fertilization, intentional or inadvertent via atmospheric deposition, affects the structure of plant communities in a variety of habitats globally (Suding *et al.* 2005). The disturbance treatment led to communities dominated by species with very different traits: annual plants in annually tilled plots and perennial plants in neighbouring untilled areas. The treatments thus allow us to test for the effects on stability of two critically important, widespread anthropogenic perturbations. We then tested for differences among the communities in the prevalence of four related mechanisms predicted to influence stability in ecosystem function: (1) species diversity, (2) compensatory dynamics, (3) mean–variance scaling, and (4) dominance. We asked two main questions. First, does stability in aboveground biomass production depend on fertilization or differ between annual and perennial communities? Second, does the strength of those stabilizing mechanisms differ with fertilization or between tilled annual and untilled perennial communities?

MATERIALS AND METHODS

The data

We analysed data from a long-term disturbance and fertilization experiment established in the successional communities of the Long-Term Ecological Research Project at the W.K. Kellogg Biological Station of Michigan State University in southwestern Michigan, USA (42°24′N, 85°24′W). The site received about 890 mm of precipitation per year; mean annual temperature was 9.7 °C. Six replicate old-field communities were allowed to establish in a former agricultural field in 1989. A two by two split plot experiment (fertilization within disturbance) was initiated in each of six replicate blocks in 1990. The disturbance treatment has been maintained by annually moldboard or chisel plowing and then disking a 20 m × 30 m area at the north end of each plot in early May or June. This annual tillage treatment set up two distinct community types: annual species dominated the areas receiving annual tillage and, since 1991, perennials have come to dominate the untilled areas (Huberty *et al.* 1998). Within these annual and perennial communities, two 5 m × 5 m plots were delineated and 12.3 g N m^{-2} was applied as granular ammonium nitrate to one plot in each community in mid-June. All plots have been burned in the spring in two out of 3 years (when weather conditions permit) since 1997 to maintain herb-dominated old-fields. Aboveground biomass was harvested annually from a 1-m^2 (2 m × 0.5 m) area located in the central 3 m × 3 m of each plot. The perennial communities were harvested in early August when they have reached peak biomass. The annual communities were typically harvested in late August when the plants are setting seed. The location of the harvested area was shifted each year to avoid harvesting the same area in successive years. Biomass was clipped at ground level and live and standing biomass was sorted to species, dried, and weighed to the nearest 0.01 g. Huberty *et al.* (1998) provide additional details on sampling methods and site conditions. Gross & Emery (2007) describe community compositional convergence through time among the six replicate untilled, unfertilized communities. In the first 2 years of the experiment (1990 and 1991), multiple harvests using smaller plots (0.3 m^2) were taken; we omitted duplicate biomass harvests within a year, choosing the late July or early August harvest date from each year. We omitted biomass of unidentified species. We analysed data from all six replicates for an 18-year (1990–2007) time series of species aboveground biomass for each of the four communities (annually tilled fertilized, annually tilled unfertilized, untilled perennial fertilized, untilled perennial unfertilized). We first tested for differences in stability across communities, then tested for variation in the strength of our four stabilizing mechanisms (species

diversity, compensatory dynamics, mean–variance scaling, and the stability of dominant species) across communities, as described below.

Analysis of treatment effects on stability, compensatory dynamics, species richness, evenness, dominance, and productivity

We measured the stability in aboveground productivity of each plot through time by calculating the temporal mean divided by the temporal standard deviation (Tilman 1999; Lehman & Tilman 2000). Repeating the analysis with the SD[log(biomass)] (Cottingham *et al.* 2001) gave qualitatively similar results. We calculated plot species richness by averaging (over years) the number of species present in each plot. For each plot in each year, we calculated Simpson's dominance index (Smith & Wilson 1996) to understand the proportion of total biomass contributed by dominant species. We then averaged dominance values over time to estimate a plot's dominance. We calculated evenness as $(1/D)$/SR, where SR is plot species richness and D is Simpson's dominance index, then averaged evenness values through time to estimate a plot's evenness. To examine compensatory dynamics, we calculated the sum of species covariances through time for each plot (Tilman 1999; Houlahan *et al.* 2007).

To determine how stability, species richness, the sum of species covariances, dominance, evenness, mean aboveground productivity, log(variance in aboveground productivity), and the sum of species variances differed among the communities, we conducted split-plot ANOVA. All models included a random block (plot) effect, with tillage split within block and fertilization split within tillage. Patterns of temporal autocorrelation in aboveground biomass were very minor in our dataset: the unfertilized perennial community had marginally significant positive autocorrelation at lag one, but we detected no significant autocorrelation in the other communities. Detrending (Tilman *et al.* 2006) was not necessary: in a first-order autoregressive model that accounted for our minor autocorrelation structure (Crawley 2007), year had a statistically significant ($F_{1,400} = 6.47$, $P = 0.011$) but biologically insignificant effect on total plot productivity, increasing total aboveground biomass by 6.5 g yr^{-1} in all four communities. If not reported, terms and interactions were non-significant in ANCOVA and ANOVA models ($P > 0.05$).

Analysis of statistical significance of compensatory dynamics

To determine whether the compensatory dynamics we detected using the sum of species covariances were statistically significant, we used the variance ratio (Schluter 1984). The variance ratio was calculated as the ratio of the

variance of community biomass to the sum of the variances of species biomasses. That is, given data x_i, where x is the biomass of species i, temporal variance ratios were calculated as

$$vr = \frac{\text{var}\left(\sum_{i}^{n} x_i\right)}{\sum_{i}^{n} \text{var}(x_i)} \qquad (1)$$

Because

$$\text{var}\left(\sum_{i} x_i\right) = \sum_{i} \text{var}(x_i) + 2 \sum_{i \neq k} \text{cov}(x_i, x_k), \qquad (2)$$

the variance ratio equals one if the biomass of species vary independently from each other. The variance ratio is greater than one if positive species covariances predominate, and is less than one if negative species covariances predominate, indicating compensatory dynamics. To test whether variance ratios were significantly less than one, we used phase-scrambling randomization because temporal variance ratios can be influenced by temporal autocorrelation in species abundances (Solow & Duplisea 2007). This method generates random time series to simulate the null hypothesis of independently varying species abundances while preserving the patterns of temporal autocorrelation in species dynamics. The phase-scrambling randomization allowed us to test whether observed temporal variance ratios were significantly different from a null hypothesis of independently varying (uncorrelated) species biomass, indicating whether compensatory dynamics were statistically significant.

Analysis of the mean–variance scaling relationship and dominant species stability

To investigate the mean–variance scaling relationship, we calculated the temporal mean and temporal variance of each species' biomass within each replicate plot. We then conducted ANCOVA, using tillage, fertilization, log(mean), treatment by log(mean) interactions, and a random block factor to predict log(variance). A significant interaction between fertilization and log(mean), or between tillage and log(mean), would indicate that the treatments affected the mean–variance scaling relationship. We used each species' residual from this regression to estimate its relative stability; a large negative residual indicated that a species was more stable. To test for a relationship between dominance and stability, we calculated Pearson's correlation coefficients between species relative abundances and these residuals. To determine whether correlations were significant, we calculated correlation coefficients from 10 000 random assignments of species' relative abundances to residuals, then tested our observed correlation against this null distribution.

We performed all the statistics and calculations in R 2.10.1 (2009–12–14, R Foundation for Statistical Computing, Vienna, Austria), except that we used Matlab 7.6 (R2008a, The MathWorks, Inc., Natick, MA, USA) for the phase-scrambling randomization.

RESULTS

Temporal stability in total aboveground biomass was greater in annually tilled plant communities, dominated by annual species, than in mid-successional old-fields, dominated by herbaceous perennial species, upon both visual inspection (Fig. 1) and when calculating temporal stability as mean/standard deviation (Fig. 2; $F_{1,5} = 14.29$, $P = 0.013$). Long-term nitrogen fertilization, however, had no effect on the stability of aboveground biomass ($F_{1,10} = 1.09$, $P = 0.32$). The components of our measure of stability, the mean and variance of total aboveground productivity, also varied in response to the treatments (Fig. 2). Fertilization increased both the mean ($F_{1,10} = 66.79$, $P < 0.001$) and the variance ($F_{1,10} = 71.61$, $P < 0.001$), resulting in equal stability in fertilized and unfertilized communities. Annual communities, when compared with perennial, had equivalent means ($F_{1,5} = 0.06$, $P = 0.81$) and smaller variances ($F_{1,5} = 6.05$, $P = 0.057$; interaction $F_{1,10} = 5.72$, $P = 0.04$), resulting in increased stability in annual communities. To understand the drivers of stability in these old-fields, we investigated four hypotheses: species richness,
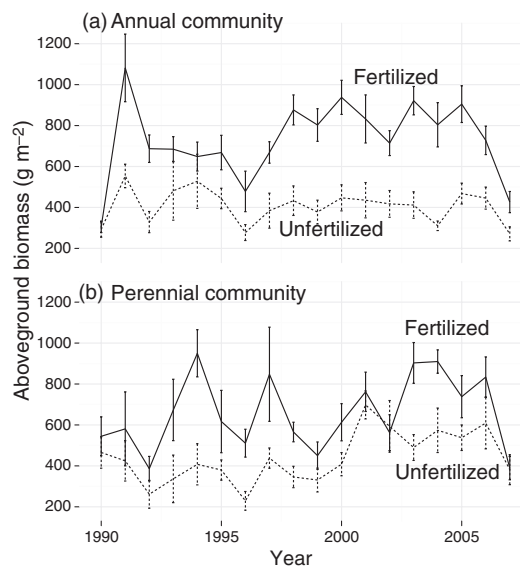
Figure 1 Mean aboveground biomass in each year of the 18-year time series, plotted with one standard error (bars) in annually tilled, annual-dominated (a) and untilled, perennial-dominated (b) old-field plant communities. Solid lines indicate fertilized communities, dashed lines are unfertilized communities.
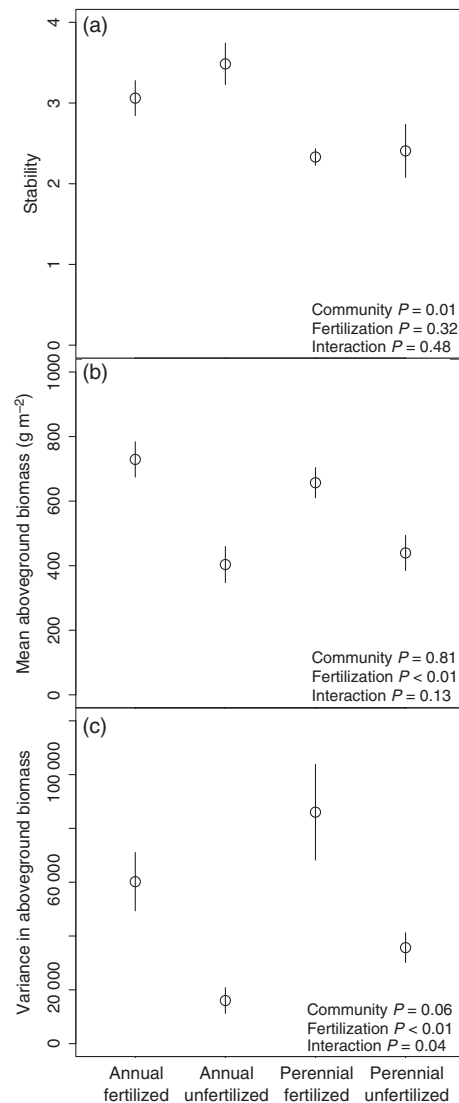
Figure 2 Temporal stability (a), calculated as mean/standard deviation and its components parts, mean aboveground biomass (b) and variance in aboveground biomass (c) in fertilized and unfertilized tilled annual and untilled perennial plant communities (mean of six replicate plots ± one standard error).

Figure 3 The effect of fertilization on species richness (a), evenness (b), and Simpson's dominance index (c) in tilled annual and untilled perennial communities (means and standard errors).

compensatory dynamics, mean–variance scaling, and the stability of dominant species.

Species diversity

We found approximately equivalent species richness in annual (10 species per m^2) and perennial (11 species per m^2) communities (Fig. 3a; $F_{1,5} = 2.13$, $P = 0.2$). Fertilization reduced species richness from 12 to 10 species per m^2 ($F_{1,10} = 20.71$, $P = 0.001$). In contrast, species evenness did not respond to fertilization (Fig. 3b; $F_{1,10} = 0.56$, $P = 0.47$) and did not differ between annual and perennial
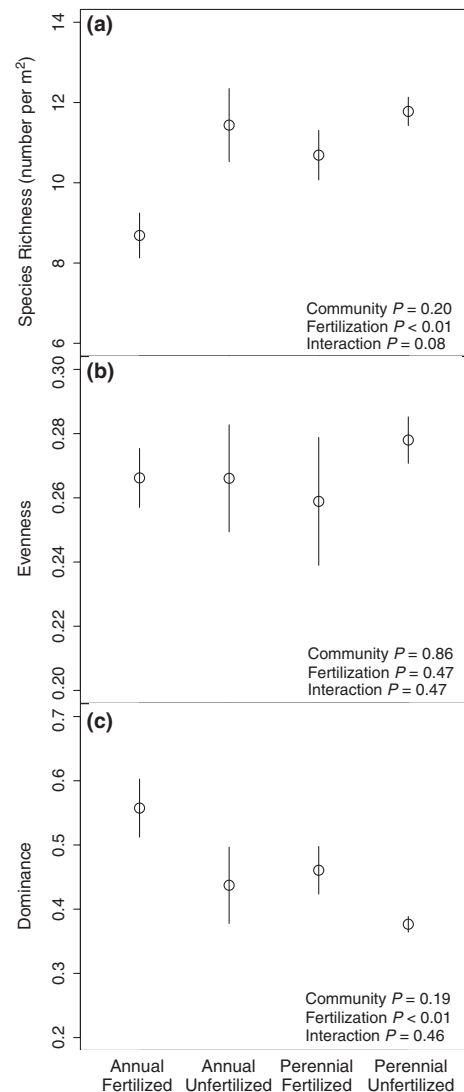
communities ($F_{1,5} = 0.03$, $P = 0.86$). Patterns of species diversity differences among treatments were largely consistent through time [see Fig. S1(a–d) in Supporting Information].

Compensatory dynamics

In all four treatments, variance ratios were less than the 95% confidence limits of simulated variance ratios, indicating that species covaried negatively and compensatory dynamics were present (Fig. 4a). The sum of species covariances did not differ between annual and perennial communities (Fig. 4b; $F_{1,5} = 0.18$, $P = 0.69$), indicating that compensatory dynamics were equally strong in both communities.
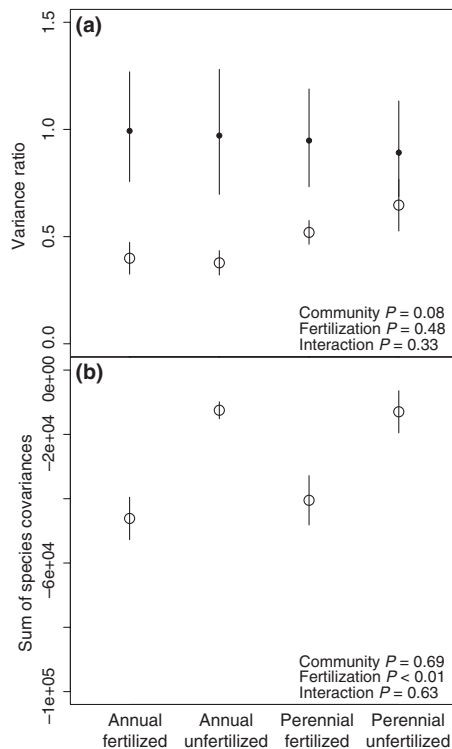
Figure 4 Compensatory dynamics, measured as the variance ratio [large dots in (a)] and as the sum of individual species covariances (b) in fertilized and unfertilized annual and perennial plant communities (means and standard errors). Small dots with error bars in (a) indicate the mean and 95% confidence intervals of a null model (simulated variance ratios with independently varying species).

However, fertilization made the sum of species covariances more negative ($F_{1,10} = 24.62$, $P = 0.006$), indicating stronger compensatory dynamics in fertilized communities.

Mean–variance scaling

We found a greater scaling coefficient (larger slope) in untilled perennial ($z = 1.83$) than in tilled annual ($z = 1.77$) communities (Fig. 5; ANCOVA log(mean) × community interaction $F_{1,796} = 18.56$, $P < 0.001$). The slope did not differ between fertilized and unfertilized treatments [ANCOVA log(mean) × fertilization $F_{1,796} = 3.44$, $P = 0.06$]. The intercept of the relationship was smaller in annual than perennial communities ($F_{1,5} = 783.45$, $P < 0.001$) and smaller with fertilization ($F_{1,10} = 241.91$, $P < 0.001$) but this has no known biological interpretation.

Dominance and stability of dominant species

Fertilization increased dominance (Fig. 3c; $F_{1,10} = 19.20$, $P = 0.001$), but dominance was equivalent in annual and
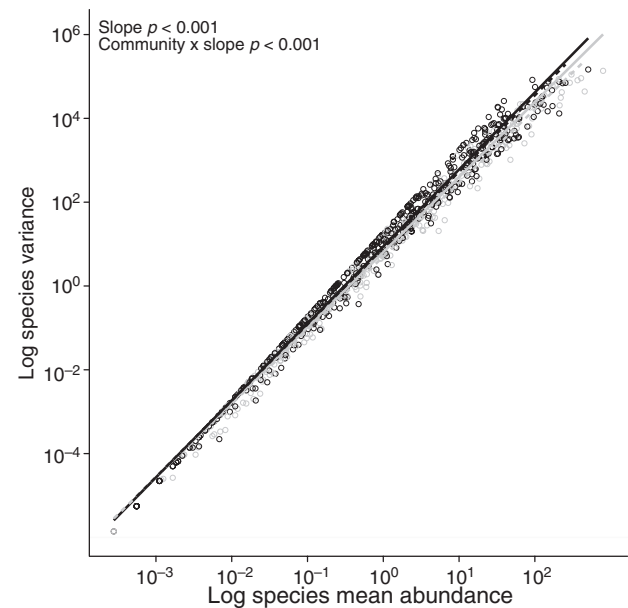

Figure 5 Mean–variance scaling relationships in fertilized (dashed line) and unfertilized (solid line) annual and perennial communities. The slope of the scaling relationship was greater in perennial (black) than in annual (gray) communities. There was no difference between the relationship in fertilized and unfertilized communities, so dashed and solid lines overlap.

perennial communities ($F_{1,5} = 2.33$, $P = 0.19$). These results were consistent through time (Fig. S1(e–f)). In annual communities, the dominant species in five out of six plots was *Setaria faberi*; this species was dominant in almost every year in those plots (Fig. S2). Across all six replicates, the dominant species contributed 50% of the total aboveground biomass in fertilized annual communities, but only 38% in unfertilized annual communities. In perennial communities, fertilization caused *Solidago canadensis* to dominate in five of six replicates in almost every year (Fig. S2); averaged across years and replicates, the dominant made up 34% of total aboveground biomass. In unfertilized perennial communities, on the other hand, four of six replicates had unique dominant species (*S. canadensis*, *Phleum pratense*, *Aster pilosus*, and *Elymus repens*), the identity of each plot's dominant was not consistent through time (Fig. S2), and the dominant in each plot, averaged over years, contributed less than 30% of total biomass. Species relative abundances were significantly negatively correlated with their residuals from the Taylor power relationship (Fig. 5), indicating that dominant species were more stable than subordinate species (Fig. 6; $P < 0.001$ in all four communities). Although dominants were more stable than subordinates, they did still vary through time (Fig. 5) and did exhibit negative covariances with other species (data not shown).
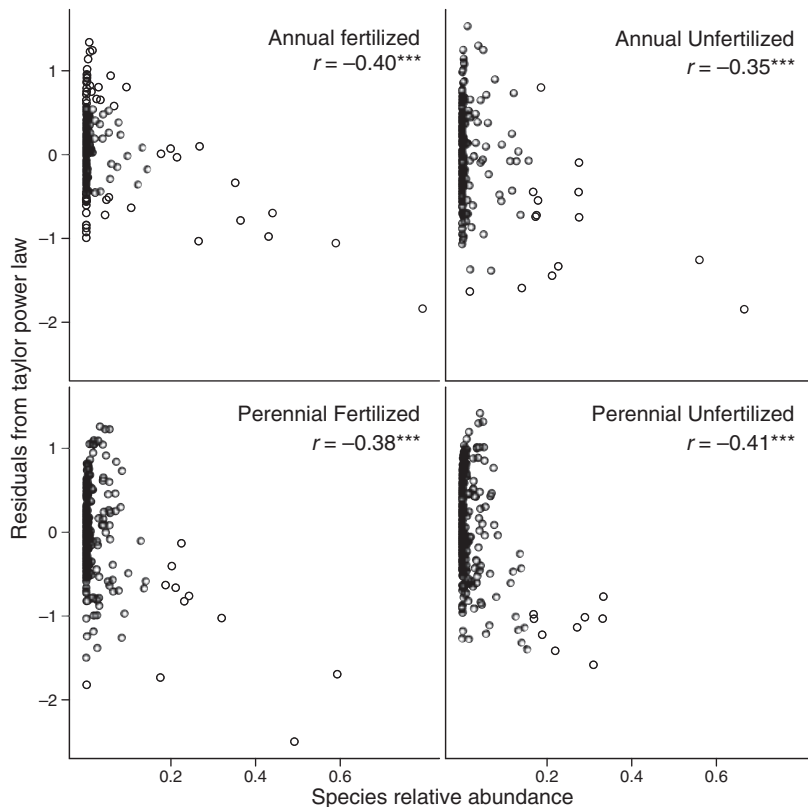
Figure 6 The relationship between species dominance (high relative abundance) and species relative stability (standardized residuals from Taylor's power law regression shown in Fig. 5). Stars with correlation coefficients indicate a significant negative correlation after a permutation test.

DISCUSSION

We found that two common anthropogenic perturbations, disturbance and eutrophication, altered both stability in ecosystem function and the mechanisms promoting stability. Annual disturbance, leading to dominance by annual plant communities, led to increased stability in production of aboveground biomass. Fertilization, on the other hand, had no effect on temporal stability of aboveground productivity. We investigated multiple hypothesized stabilizing mechanisms to determine the cause of this greater stability in annual plant communities with surprising results.

Diversity

Many ecologists have wondered whether human perturbations to ecosystems will drive a loss of stability in function via losses in diversity (Tilman 1999; Hooper *et al.* 2005; Kremen 2005; Jiang & Pu 2009). However, we observed only small changes in diversity in response to drastic annual disturbance (tillage), which resulted in conversion to an annual-dominated community and reduced species richness by one. We also saw small changes in diversity in response to high levels of nitrogen application, which nearly doubled aboveground productivity and reduced species richness by two. Previous analyses on this dataset indicate that the

species lost to fertilization were likely initially rare, and perennials were marginally more likely to be lost than annuals (Suding *et al.* 2005).

We observed no link between these slight losses in species richness and ecosystem function or stability. Statistically controlling for the changes in diversity among communities did not weaken the differences in stability among communities, and there was no relationship between species richness and stability within a community type (Fig. S3). Neither species richness nor species evenness differed between annual and perennial communities, suggesting that diversity cannot explain the increased stability in the annual communities. Species richness declined slightly with fertilization (by 24% in annual communities and by 9% in perennial communities), but fertilized communities maintained the stability in productivity observed in unfertilized communities. Leps (2004) reported similar results in wet meadows: fertilization reduced species richness but did not significantly reduce stability. Other studies suggest that the effect of fertilization on stability might be mediated, at least in part, through its effect on diversity: if fertilization increases diversity, it tends to increase stability (Steiner *et al.* 2005); if fertilization decreases diversity, it decreases stability (Dodd *et al.* 1994; Tilman 1996); and if controlling for the effects of fertilization on diversity, fertilization does not affect stability (Zhang & Zhang 2006). In our system,

however, effects on diversity were weak and did not explain effects on stability. Thus, other stabilizing mechanisms may be more important in understanding our pattern of greater stability in annual communities and the maintenance of stability in fertilized communities.

Compensatory dynamics

We found evidence of significant compensatory dynamics occurring in all four of the communities we investigated, likely contributing to the stability of our ecosystems (Doak *et al.* 1998; Tilman *et al.* 1998; Ernest & Brown 2001). This result is somewhat surprising, given that several recent studies using similar methods have failed to find evidence for compensatory dynamics (Valone & Hoffman 2003; Houlahan *et al.* 2007; Valone & Barber 2008; but see Ranta *et al.* 2008; Gonzalez & Loreau 2009). The compensatory dynamics we observed could have been driven by negative species interactions such as competition or by negatively correlated species responses to environmental drivers (Schluter 1984; Micheli *et al.* 1999).

We found no difference in the strength of compensatory dynamics between annual and perennial communities, suggesting that variation in the strength of compensatory dynamics did not determine variation in stability across those communities. We might have expected annuals to display more compensatory dynamics. Annuals, which must regenerate each year from seed, might be less tied to the production of previous years than perennials, which resprout from stored belowground reserves, leaving annuals more free to respond to climatic variability. On the other hand, perennials may have had greater growth potential because of those stored reserves, and thus greater potential to respond to good years and yet maintain production in bad years (Knapp & Smith 2001). The strength of competition could vary across community types, driving differences in compensatory dynamics, but we did not detect this. Successional processes could also cause negative species covariances, as early successional species are absent when later successional species are present. For the first 1–2 years, annuals dominated our perennial communities (Huberty *et al.* 1998); the decline in annuals and the increase in perennials in these plots should have driven strong negative species covariances. However, our annual communities also experienced species shifts through time, dominated initially by annual forbs and later by annual grasses. We repeated the analyses omitting the first 10 years of succession (using data 1999–2007), after which time species composition was more stable (Figs S1 and S4; Gross & Emery 2007), and again found no difference in compensatory dynamics between annuals and perennials. Houlahan *et al.* (2007) found that only three of 41 communities (all perennial plants: trees at Hubbard Brook, herbaceous plants at Cedar Creek, and

Sonoran herbaceous plants) exhibited more negative species covariances than expected. However, their study included few annual plant datasets and no experimentally disturbed communities. Our result suggests that disturbed annuals and undisturbed perennials are equally likely to exhibit compensatory dynamics.

Interestingly, we did detect stronger compensatory dynamics in response to fertilization, suggesting that fertilization might have caused species to be more vulnerable to environmental fluctuations or more strongly competing. This occurred despite largely similar community composition in fertilized and unfertilized plots, except for the loss of a few rare species (Fig. S4; Suding *et al.* 2005). This increase in compensatory dynamics could have balanced the loss in stability caused by the reduction in species richness in fertilized communities. One study in aquatic microcosms also detected stronger negative species covariances with higher nutrients (Zhang & Zhang 2006), but another found no effect (Romanuk *et al.* 2006). Given the difficulty in detecting compensatory dynamics at the appropriate temporal (Gonzalez & Loreau 2009) and spatial (Houlahan *et al.* 2007) scales, it is perhaps not surprising that generalizations about the community types likely to exhibit compensatory dynamics have been elusive.

Mean–variance scaling relationships

We found evidence of greater impact of another stabilizing mechanism in annually disturbed, annual-dominated communities: a smaller mean–variance scaling exponent indicating less variable species abundances. This scaling exponent is derived from Taylor's power law $\sigma^2 = c\mu^z$, where c and z are constants, σ^2 is the variance in species abundance, and μ is mean species abundance (Taylor 1961). A species' log variance increases with its log mean abundance with slope z. Species characterized by higher values of z will be more variable, at a given abundance, than species with a lower z. Because of statistical averaging, our annual community composed of relatively stable species (lower z) should be more stable than our perennial community composed of an equal number of more variable species (higher z). Mean–variance scaling is thus a likely mechanism driving greater stability in productivity in our annual communities.

We found that when matched for abundance, species in the tilled, annual-dominated communities were less variable than perennials in the untilled communities. This result raises questions about the drivers of variation in the slope of the mean–variance scaling relationship. Why would annual species be more stable than perennials? A biologically mechanistic explanation for Taylor's power law has been elusive, but the dispersal traits of the organisms, the geometry of space filling, interspecific interactions, correlations among species responses to environmental

fluctuations, or differences in population growth rates could be involved (Kendal 1995; Tilman 1999; Yamamura 2000; Kilpatrick & Ives 2003). Leps (2004) found increases in the slope with fertilization and suggests that in his system, fertilization removed nutrient limitation, causing species to become water limited and thus more responsive to interannual variation in rainfall. This idea seems unlikely to explain our result that annuals varied less in productivity than perennials: annuals, with shallower root systems, would seem likely to be more responsive to rainfall variation, not less responsive. Annual communities experienced more subtle species shifts during succession than perennial communities, but this difference between communities would not have caused the observed pattern. In the perennial communities, early successional species, initially abundant but lost through succession, would have had a low mean abundance but high variance. This would have driven up the *y*-intercept of the Taylor power law but not affected the slope, the opposite pattern of what we observed. Alternatively, tillage could have influenced mean–variance scaling directly, perhaps through altering the spatial distribution of individuals or resources. The biological mechanism driving differences in the mean–variance scaling relationship between annual and perennial communities remains an open question.

Stability of dominant species

In contrast to the expectation that decreasing evenness should decrease stability (Doak *et al.* 1998), we found that greater dominance in fertilized plots contributed to the maintenance of stability in ecosystem function in those plots, despite losses in species richness. Interestingly, we also saw greater consistency in the identity of the dominant in fertilized communities (Fig. S2). Annual communities also tended to have higher dominance, but this was not significant. In all four community types, dominant species were more stable than subordinates, although they did vary through time. This greater stability in dominants than subordinates, observed here and in other empirical studies (Bai *et al.* 2004; Leps 2004; Steiner *et al.* 2005; Polley *et al.* 2007), violates theoretical assumptions of equal stability among species and could explain why empirical results differ from expectations. Greater abundance of particularly stable species should increase ecosystem stability, just as particularly high-functioning species should increase ecosystem function (Huston 1997; Tilman 1999). However, in a study where dominant species were not the most stable, higher dominance (lower evenness) was not related to greater stability (Isbell *et al.* 2009), suggesting that the relative stability of dominant species may determine whether evenness can affect ecosystem stability. Links between the abundance and relative stability of dominant species and increased ecosystem stability, whether because of individual species relative stability or for other reasons (this study; Leps 2004; Steiner *et al.* 2005; Polley *et al.* 2007), reinforce the importance of dominant species on ecosystem function (Grime 1998; Smith & Knapp 2003; Bai *et al.* 2004; Hillebrand *et al.* 2008).

CONCLUSION

The capacity of communities to shift in composition and structure in response to environmental perturbations complicates our understanding of how those perturbations will affect stability and the strength of stabilizing mechanisms. Increases in the strength of one stabilizing mechanism could compensate for losses in another, driven by complex changes in community structure, composition, and diversity. In our system, annual tillage drove grassland communities to be dominated by annual species. Those annual species exhibited a different mean–variance scaling relationship than the perennial species which dominated untilled communities, allowing annual-dominated communities to exhibit greater stability. Our result raises the interesting question of whether annual disturbance caused this result directly or indirectly via selection for an annual life-history.

We also saw community reorganization in response to annual addition of an important limiting resource (nitrogen). Fertilized communities lost rare species (Suding *et al.* 2005) and experienced increases in the abundance of the dominant species, although community composition was not sharply distinct from unfertilized communities (Fig. S4). These fertilized communities maintained equal stability by increased compensatory dynamics among the fewer remaining species. Increases in abundance of the relatively stable dominant species also contributed to the maintenance of stability. We have been unable to assess whether overyielding, another hypothesized stabilizing mechanism, affects stability differently in our four communities because of limitations imposed by the experimental design, but other studies have shown that it can be important (Lehman & Tilman 2000; Valone & Hoffman 2003; Isbell *et al.* 2009; Jiang & Pu 2009).

Anthropogenic perturbations can have dramatic effects on the structure of ecosystems, but the causal relationships among perturbations, community structure, and stability in ecosystem function are unknown. In at least some communities, species richness, species evenness, dominance, the stability of individual species, the portfolio effect, mean–variance scaling, compensatory dynamics, and overyielding have all been associated with greater stability (Cottingham *et al.* 2001; Polley *et al.* 2007; Isbell *et al.* 2009; Jiang & Pu 2009). However, quantifying the relative contributions of the different mechanisms, especially in ecosystems

reorganizing in response to natural or anthropogenic perturbations, is an essential next step. This task remains an important challenge for ecologists.

REFERENCES

Bai, Y., Han, Z., Wu, J., Chen, Z. & Li, L. (2004). Ecosystem stability and compensatory effects in the Inner Mongolia grassland. *Nature*, 431, 181–184.

Caldeira, M.C., Hector, A., Loreau, M. & Pereira, J.S. (2005). Species richness, temporal variability and resistance of biomass production in a Mediterranean grassland. *Oikos*, 110, 115–123.

Callaway, R.M., Brooker, R.W., Choler, P., Kikvidze, Z., Lortie, C.J., Michalet, R. *et al.* (2002). Positive interactions among alpine plants increase with stress. *Nature*, 417, 844–848.

Cottingham, K.L., Brown, B.L. & Lennon, J.T. (2001). Biodiversity may regulate the temporal variability of ecological systems. *Ecol. Lett.*, 4, 72–85.

Crawley, M.J. (2007). *The R Book*. John Wiley and Sons Ltd, West Sussex.

Doak, D.F., Bigger, D., Harding, E.K., Marvier, M.A., O'Malley, R.E. & Thomson, D. (1998). The statistical inevitability of stability-diversity relationships in community ecology. *Am. Nat.*, 151, 264–276.

Dodd, M.E., Silvertown, J., McConway, K., Potts, J. & Crawley, M. (1994). Stability in the plant communities of the Park Grass Experiment: the relationships between species richness, soil pH and biomass variability. *Philos. Trans. R Soc. Lond. B*, 346, 185–193.

Downing, J.A. (1979). Aggregation, transformation, and the design of benthos sampling programs. *J. Fish. Res. Board Can.*, 36, 1454–1463.

Ernest, S.K.M. & Brown, J.H. (2001). Homeostasis and compensation: the role of species and resources in ecosystem stability. *Ecology*, 82, 2118–2132.

Fang, J., Piao, S., Tang, Z., Peng, C. & Ji, W. (2001). Interannual variablity in net primary production and precipitation. *Science*, 293, 1723a.

Gonzalez, A. & Loreau, M. (2009). The causes and consequences of compensatory dynamics in ecological communities. *Annu. Rev. Ecol. Syst.*, 40, 393–414.

Grime, J.P. (1998). Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *J. Ecol.*, 86, 902–910.

Gross, K.L. & Emery, S.M. (2007). Succession and restoration in Michigan old field communities. In: *Old Fields: Dynamics and Restoration of Abandoned Farmland* (eds Cramer, V.A. & Hobbs, R.J.). Island Press, Washington, D.C, pp. 162–179.

Hillebrand, H., Bennett, D.M. & Cadotte, M.W. (2008). Consequences of dominance: a review of evenness effects on local and regional ecosystem processes. *Ecology*, 89, 1510–1520.

Hooper, D.U., Chapin, F.S., III, Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S. *et al.* (2005). Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol. Monogr.*, 75, 3–35.

Houlahan, J.E., Currie, D.J., Cottenie, K., Cummings, G.S., Ernest, S.K.M., Findlay, C.S. *et al.* (2007). Compensatory dynamics are rare in natural ecological communities. *Proc. Natl Acad. Sci. USA*, 104, 3273–3277.

Huberty, L.E., Gross, K.L. & Miller, C.J. (1998). Effects of nitrogen addition on successional dynamics and species diversity in Michigan old-fields. *J. Ecol.*, 86, 794–803.

Huston, M.A. (1997). Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia*, 110, 449–460.

Isbell, F.I., Polley, H.W. & Wilsey, B.J. (2009). Biodiversity, productivity and the temporal stability of productivity: patterns and processes. *Ecol. Lett.*, 12, 443–451.

Ives, A.R., Gross, K. & Klug, J.L. (1999). Stability and variability in competitive communities. *Science*, 286, 542–544.

Jiang, L. & Pu, Z. (2009). Different effects of species diversity on temporal stability in single-trophic and multitrophic communities. *Am. Nat.*, 174, 651–659.

Kendal, W.S. (1995). A probabilistic model for the variance to mean power law in ecology. *Ecol. Modell.*, 80, 293–297.

Kilpatrick, A.M. & Ives, A.R. (2003). Species interactions can explain Taylor's power law for ecological time series. *Nature*, 422, 65–68.

Knapp, A.K. & Smith, M.D. (2001). Variation among biomes in temporal dynamics of aboveground primary productivity. *Science*, 291, 481–484.

Kremen, C. (2005). Managing ecosystem services: what do we need to know about their ecology? *Ecol. Lett.*, 8, 468–479.

Lehman, C.L. & Tilman, D. (2000). Biodiversity, stability, and productivity in competitive communities. *Am. Nat.*, 156, 534–552.

Leps, J. (2004). Variability in population and community biomass in a grassland community affected by environmental productivity and diversity. *Oikos*, 107, 64–71.

McCann, K.S. (2000). The diversity-stability debate. *Nature*, 405, 228–233.

Micheli, F., Cottingham, K.L., Bascompte, J., Bjornstad, O.N., Eckert, G.L., Fischer, J.M. *et al.* (1999). The dual nature of community variability. *Oikos*, 85, 161–169.

Polley, H.W., Wilsey, B.J. & Derner, J.D. (2007). Dominant species constrain effects of species diversity on temporal variability in biomass production of tallgrass prairie. *Oikos*, 116, 2044–2052.

Ranta, E., Kaitala, V., Fowler, M.S., Laakso, J., Ruokolainen, L. & O'Hara, R. (2008). Detecting compensatory dynamics in competitive communities under environmental forcing. *Oikos*, 117, 1907–1911.

Romanuk, T.N., Vogt, R.J. & Kolasa, J. (2006). Nutrient enrichment weakens the stabilizing effect of species richness. *Oikos*, 114, 291–302.

Schluter, D. (1984). A variance test for detecting species associations, with some example applications. *Ecology*, 65, 998–1005.

Smith, M.D. & Knapp, A.K. (2003). Dominant species maintain ecosystem function with non-random species loss. *Ecol. Lett.*, 6, 509–517.

Smith, B. & Wilson, J.B. (1996). A consumer's guide to evenness indices. *Oikos*, 76, 70–82.

Solow, A.R. & Duplisea, D.E. (2007). Testing for compensation in a multi-species community. *Ecosystems*, 10, 1034–1038.

Steiner, C.F. (2005). Temporal stability of pond zooplankton assemblages. *Freshw. Biol.*, 50, 105–112.

Steiner, C.F., Long, Z.T., Krumins, J.A. & Morin, P.J. (2005). Temporal stability of aquatic food webs: partitioning the effects of species diversity, species composition and enrichment. *Ecol. Lett.*, 8, 819–828.

Suding, K.N., Collins, S.L., Gough, L., Clark, C., Cleland, E.E., Gross, K.L. *et al.* (2005). Functional- and abundance-based mechanisms explain diversity loss due to N fertilization. *Proc. Natl Acad. Sci. USA*, 102, 4387–4392.

Taylor, L.R. (1961). Aggregation, variance, and the mean. *Nature*, 189, 732–735.

Tilman, D. (1996). Biodiversity: population versus ecosystem stability. *Ecology*, 77, 350–363.

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

Tilman, D. & Downing, J.A. (1994). Biodiversity and stability in grasslands. *Nature*, 367, 363–365.

Tilman, D., Lehman, C.L. & Bristow, C.E. (1998). Diversity-stability relationships: statistical inevitability or ecological consequence? *Am. Nat.*, 151, 277–282.

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

Valone, T.J. & Barber, N.A. (2008). An empirical evaluation of the insurance hypothesis in diversity-stability models. *Ecology*, 89, 522–531.

Valone, T.J. & Hoffman, C.D. (2003). A mechanistic examination of diversity-stability relationships in annual plant communities. *Oikos*, 103, 519–527.

Yamamura, K. (2000). Colony expansion model for describing the spatial distribution of populations. *Popul. Ecol.*, 42, 161–169.

Zhang, Q.-G. & Zhang, D.-Y. (2006). Resource availability and biodiversity effects on the productivity, temporal variability and resistance of experimental algal communities. *Oikos*, 114, 385–396.

SUPPORTING INFORMATION

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

Figure S1 Changes through time in plot species richness, evenness, and dominance.
Figure S2 Temporal consistency in dominant species identity in each plot.
Figure S3 Relationship between plot species richness and plot stability, within treatments.
Figure S4 Community compositional similarity among fertilized and unfertilized replicate plots, for both annually tilled annual-dominated and untilled perennial-dominated communities.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials are peer-reviewed and may be re-organized for online delivery, but are not copy-edited and typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.