

## LETTER

# Invaded grassland communities have altered stability-maintenance mechanisms but equal stability compared to native communities

Brian J. Wilsey,<sup>1\*</sup> Pedram P. Daneshgar,<sup>2</sup> Kirsten Hofmocker<sup>1</sup> and H. Wayne Polley<sup>3</sup>

## Abstract

Theory predicts that stability should increase with diversity via several mechanisms. We tested predictions in a 5-year experiment that compared low-diversity exotic to high-diversity native plant mixtures under two irrigation treatments. The study included both wet and dry years. Variation in biomass across years (CV) was 50% lower in mixtures than monocultures of both native and exotic species. Growth among species was more asynchronous and overyielding values were greater during and after a drought in native than exotic mixtures. Mean-variance slopes indicated strong portfolio effects in both community types, but the intercept was higher for exotics than for natives, suggesting that exotics were inherently more variable than native species. However, this failed to result in higher CV's in exotic communities because species that heavily dominated plots tended to have lower than expected variance. Results indicate that diversity-stability mechanisms are altered in invaded systems compared to native ones they replaced.

## Keywords

Diversity-stability relationship, dominant species, evenness, grassland, invasive species, overyielding, population synchrony, portfolio effect, sampling effect.

*Ecology Letters* (2014) **17**: 92–100

## INTRODUCTION

Ecologists have long been interested in whether species diversity is related to ecosystem stability (reviewed by McNaughton 1993). Early debates centered on whether populations or communities should be the focus of studies, and results were found to be variable depending on the measure used (Ives & Carpenter 2007). These apparently conflicting views have been somewhat settled by pointing out that there are several aspects of stability that can have different relationships with diversity, and that populations can be unstable in cases in which community stability is high (Tilman 1999; Ives & Carpenter 2007).

Plant communities are considered to be stable when they have low variability in primary production over time (Loreau 2010). Much of the recent work on this topic has focused on mechanisms behind relationships between species diversity and temporal stability, the inverse of temporal variation in productivity [e.g.  $1/\text{CV}$  with  $\text{CV} = (\text{SD}/\text{mean}) \times 100$ ]. Reductions in species diversity are predicted to cause declines in stability by increasing the temporal SD or by decreasing the mean. Reductions may reduce stability by reducing: (1) Overyielding, (2) asynchrony in species temporal growth patterns, (3) the likelihood that communities contain species with positive responses to environmental changes over time ('portfolio effect'); and by (4) increasing the impact of dominant species (e.g. Ives & Carpenter 2007; Loreau 2010). These mechanisms

may work independently or in concert to affect stability. If these mechanisms are operating, then diversity declines should result in communities that have lower resistance or slower recovery to extreme events, and ultimately, higher CV in biomass production over time. However, these mechanistic hypotheses have rarely been tested because of the long-term nature of the data sets required (Hooper *et al.* 2005; Ives & Carpenter 2007; Cardinale *et al.* 2013).

Mechanisms behind stability have been assessed in a variety of ways. Overyielding can lead to higher mean biomass, which can lead to lowered CV by increasing the denominator. Overyielding occurs when species' yields are higher in mixture compared to their expected values from monocultures (Loreau 2010). This could be especially important for species with abundances that could approach zero in low productivity years, leading to local extinction (Isbell *et al.* 2009a,b; de Mazancourt *et al.* 2013). Synchrony/asynchrony can be based on measures of species' covariance or with indices that look at how temporal variances of species correspond across time periods. If species abundances or biomass rise and fall together, then synchrony is high and this should cause variability at the community level to be higher (McNaughton 1977; Bai *et al.* 2004; Loreau & de Mazancourt 2008). The portfolio effect is present when slopes of  $\log(\text{SD}) \times \log(\text{mean})$  are  $> 1$  and  $< 2$  (Tilman 1999). This can occur with or without other mechanisms operating. The dominant species effect can be assessed by measuring the level of dominance, and

<sup>1</sup>Department of Ecology, Evolution and Organismal Biology, Iowa State University, 253 Bessey Hall, Ames, IA, 50011, USA

<sup>2</sup>Department of Biology, Monmouth University, 400 Cedar Avenue, West Long Branch, NJ, 07764, USA

<sup>3</sup>Grassland, Soil and Water Research Laboratory, USDA-ARS, Temple, TX, 76502, USA

\*Correspondence: E-mail: bwilsey@iastate.edu

then by comparing responses of dominant species over time (Grime 1998; Lepš 2004; Polley *et al.* 2007; Grman *et al.* 2010). This will be especially important in situations where high dominance arises (lowering evenness, Thibault and Connolly 2013) and when species selected for as dominance rises have low temporal variance. This could reduce diversity without lowering stability.

Here, we test whether these mechanisms are altered by the increasingly common situation of species-diverse native grassland communities being replaced by novel exotic-dominated communities of low diversity. In other words, we are testing whether stability is reduced with a realistic diversity decline due to biotic exchanges. Humans are moving plant and animal species among continents at unprecedented rates. Exotic species were commonly planted in pastures and rangelands, and exotic species have often moved from their place of introduction to form mixed native-exotic or almost pure exotic communities in formerly plowed areas. Many pastures in the U.S. are planted to exotic species exclusively (Isbell & Wilsey 2011). As a result, exotic (or 'introduced' or 'alien' or 'invasive') plants are common or even dominant in many areas (MacDougall *et al.* 2013). For example, sampling of 42 sites along a latitudinal gradient from Minnesota to Texas, USA revealed that exotic species contributed 0–30% of biomass in prairie remnants and 68–100% of biomass in formerly plowed areas (Martin *et al.* 2013). Central Texas grasslands consist of 79–97% exotic plant biomass (Wilsey *et al.* 2011), whereas unplowed native dominated sites had 1–26% exotic plant biomass. Plant species in central Texas grasslands originated from a variety of continents (Wilsey *et al.* 2011), do not have an evolutionary history of interaction (Wilsey *et al.* 2009), and are thus considered to be 'novel systems' (Hobbs *et al.* 2006; Mascaro *et al.* 2012). Novel (exotic) grasslands were predicted to have lowered species diversity and reduced niche partitioning compared to native grasslands, and previous studies supported these predictions (Wilsey *et al.* 2009, 2011; Daneshgar *et al.* 2013). Here, we test the prediction that lower diversity will reduce stability by weakening stability-promoting mechanisms in exotic compared to native dominated communities. These effects are predicted to be enhanced under altered climate regimes (i.e. with summer irrigation).

Using the MEND (Maintenance of exotic vs. native diversity) field experiment in Central Texas, we compared native and exotic species using a unique paired-species approach in a common environment to determine if the species themselves are causing differences in species diversity and functional group proportions found in observational studies (e.g. Wilsey *et al.* 2011; Mascaro *et al.* 2012). Experimental plots with identical initial plant densities, functional group proportions, and species diversity have been sampled over 5 years. The strength of this site for testing hypotheses is that the exotic species are from multiple continents (i.e., without an evolutionary history of interacting) and community changes occur relatively rapidly compared to more northern areas. Exotic communities developed reduced species diversity, increased temporal niche overlap, lower proportions of  $C_3$  species, and altered microbial communities compared to native communities (Wilsey *et al.* 2011; Daneshgar *et al.* 2013; Martin *et al.* 2013; Hofmocker, K.S., Gibbons, S.M., Hargreaves, S.K., Wilsey, B.J. & Gilbert,

J.A., unpublished). Differences were found under ambient rainfall levels and in an increased precipitation treatment (Wilsey *et al.* 2011). Thus, this is an excellent model system for studying the effects of non-random species loss due to reduced niche partitioning, addressing recent calls for more studies on realistic losses (Cardinale *et al.* 2012; Naeem *et al.* 2012; Tilman *et al.* 2012). We tested the hypotheses that: (1) variability in biomass across time periods will be higher in low-diversity exotic than in high-diversity native communities, (2) differences in overyielding, species asynchrony, portfolio, and dominant species effects will explain anticipated differences in stability of native and exotic communities and (3) native-exotic differences will vary depending on whether plots receive a summer rainfall treatment. We found that exotic and native communities had similar stabilities, but that they achieved this stability by different mechanisms.

## METHODS

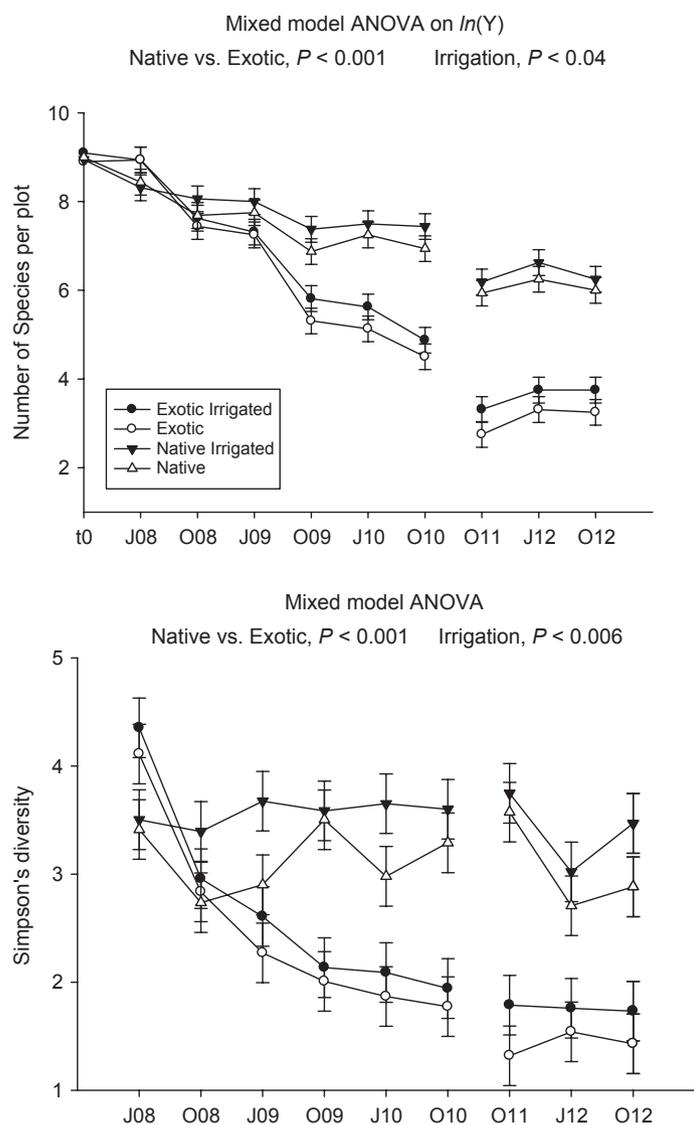
### MEND (Maintenance of Exotic vs. Native Diversity) Irrigation Experiment

We tested these hypotheses in pure native and exotic experimental communities in central Texas. The site receives 878 mm of precipitation per year in a bimodal pattern with a large peak in the spring and a smaller peak in the fall. Soils are Vertisol usterts. The common garden experiment was established in 2007–2008 using 36 widely-distributed native and exotic grassland species. All exotic species used were intentionally introduced by humans for erosion control, as forage plants, or as ornamentals (Wilsey *et al.* 2011). We are comparing native and exotic species in all native or all exotic mixtures ( $n = 32$  mixtures per block,  $n = 2$  blocks), and in monoculture (36 species, 144 plots) in  $1 \times 1$  m plots (see Wilsey *et al.* 2011 for further details). Exotic-native treatments (origin) were crossed with summer irrigation treatments (0 mm or 128 mm added in eight increments of 16 mm from July 15 to August 15). The summer irrigation treatment alters the amount as well as the bimodal nature of rainfall within years. Within each origin  $\times$  irrigation treatment, we included 4 random draws for each 9-species mixture with two replicates in each of two replicate blocks ( $2 \times 2 \times 4 \times 2 \times 2 = 64$ ), and monocultures of all 36 species used (irrigated or not, with  $n = 2$  blocks, 144 in total, Fig. S1 and Table S1).

Plots have been sampled twice per year for five growing seasons (excluding the June 2011 sampling date), including an especially wet year (2010) and an unprecedented drought year in 2011. Due to the bimodal nature of rainfall, there are two distinct growth periods of early and late in the growing season. Therefore, we sampled biomass twice annually with non-destructive estimates of aboveground plant biomass using point intercept sampling in June and October of each growing season, with concurrent estimates of species richness and diversity. Point intercept data were converted to biomass with regression equations, which have an average  $r^2$  of 0.89 across species (Wilsey *et al.* 2011). Gravimetric soil moisture, which was measured each summer (Wilsey *et al.* 2011), established that irrigated plots had 67% greater soil moisture during the water limited period of irrigation. We previously documented

**Table 1** ANOVA results (*F*, *P* values) for species richness (*S*), diversity (Simpson's 1/*D*), and stability measures (overyielding, synchrony of growth across species  $\phi$ ), CV across all nine dates, CV across all five October dates, and CV's between mixtures and average monocultures (test of richness) for native and exotic plots (origin) and non-irrigated and summer irrigated (Irrig) plots during the 5-year study.

d.f.	Term	$\ln(S)$	1/ <i>D</i>	overyielding	$\phi$	CV	CV-Oct.	$\ln(\text{MonoCV}/\text{MixCV})$	$\ln(\text{Biomass})$
	Block								
1,7	Origin (N vs. E)	45.1, <0.01	32.0, <0.01	7.0, 0.034	7.0, 0.03	0.5, 0.51	0.1, 0.78	0.2, 0.66	0.8, 0.41
1,7	Irrig. (Non vs. Irrig)	6.7, 0.036	14.9, <0.01	5.9, 0.046	1.3, 0.29	0.4, 0.52	0.03, 0.87	4.7, 0.06	0.5, 0.51
1,7	Origin $\times$ Irrig.	1.2, 0.305	0.9, 0.369	3.3, 0.115	0.8, 0.41	3.6, 0.10	1.2, 0.31	1.8, 0.23	4.0, 0.09
8,510	Time	123.2, <0.01	14.8, <0.01	6.8, <0.01					309.1, <0.01
8,510	Origin $\times$ Time	37.3, <0.01	13.5, <0.01	9.6, <0.01					3.1, <0.01
8,510	Irrig $\times$ Time	0.7, 0.691	0.4, 0.934	1.3, 0.234					1.2, 0.31
8,510	Origin $\times$ Irrig $\times$ Time	0.4, 0.946	0.4, 0.937	0.8, 0.560					0.8, 0.60



**Figure 1** Plant species richness (left) and diversity (right, Simpson's  $1/\sum p_i^2$ ) in the MEND irrigation experiment. A drought occurred in 2011 and plots were not sampled in June.

much lower diversity and higher temporal niche overlap in exotic than native communities (Wilsey *et al.* 2011).

Variability was quantified with the CV ( $\text{SD}/\text{mean} \times 100$ ) of aboveground biomass across: (1) all nine time periods (twice

yearly, with June 2011 not being sampled) and (2) with only the October dates across the 5 years. The latter analysis was done to make results comparable to studies that include only peak biomass. A test of species richness on CV was conducted for each treatment by comparing the CV of mixtures and monocultures (i.e., 1 vs. higher richness of mixtures) using log response ratios [ $\ln(\text{mixture CV}/\text{mean monoculture CV})$ ]. The portfolio effect was tested with regression of  $\ln(\text{SD})$  and  $\ln(\text{mean})$  according to the power law of Taylor (1961) using ordinary least squares. Overyielding was estimated from biomass data of each species in mixture compared to their corresponding monocultures using log response ratios [ $\ln(\text{mixture yield}/\text{mean of monocultures of species present})$ ], using only species present in each plot. We previously partitioned overyielding into selection and complementarity effects (Wilsey *et al.* 2009, 2011). Results supported the hypothesis that the complementarity effect was more pronounced, and the selection effect was less pronounced in native than in exotic communities. Species synchrony was quantified with the metric of Loreau & de Mazancourt (2008):

$$\phi_b = \frac{\sigma_{b_T}^2}{\left(\sum_{i=1}^S \sigma_{b_i}\right)^2},$$

where  $\sigma_{b_T}^2$  is the variance in mixture biomass and  $\sigma_{b_i}$  is the standard deviation in biomass of species *i* in a mixture with *S* species. This metric is bounded by 1 when species are completely synchronous and 0 when species growth rates are completely asynchronous. In other words, it is a measure of synchrony. In our data set, local extinction due to interspecific interactions led to negative correlations between species that mimicked asynchronous growth in the first 2 years. This does not affect estimates of biomass CV, but it can affect asynchrony. This is probably common to most Biodiversity-Ecosystem function data sets, as many plots lose species over time (e.g. Zavaleta & Hulvey 2004; Spehn *et al.* 2005; Isbell *et al.* 2009a,b). To minimize this effect, we calculated synchrony with data from years 3–5 of the experiment after species diversity had stabilized (Fig. 1, bottom panel).

### Statistical analyses

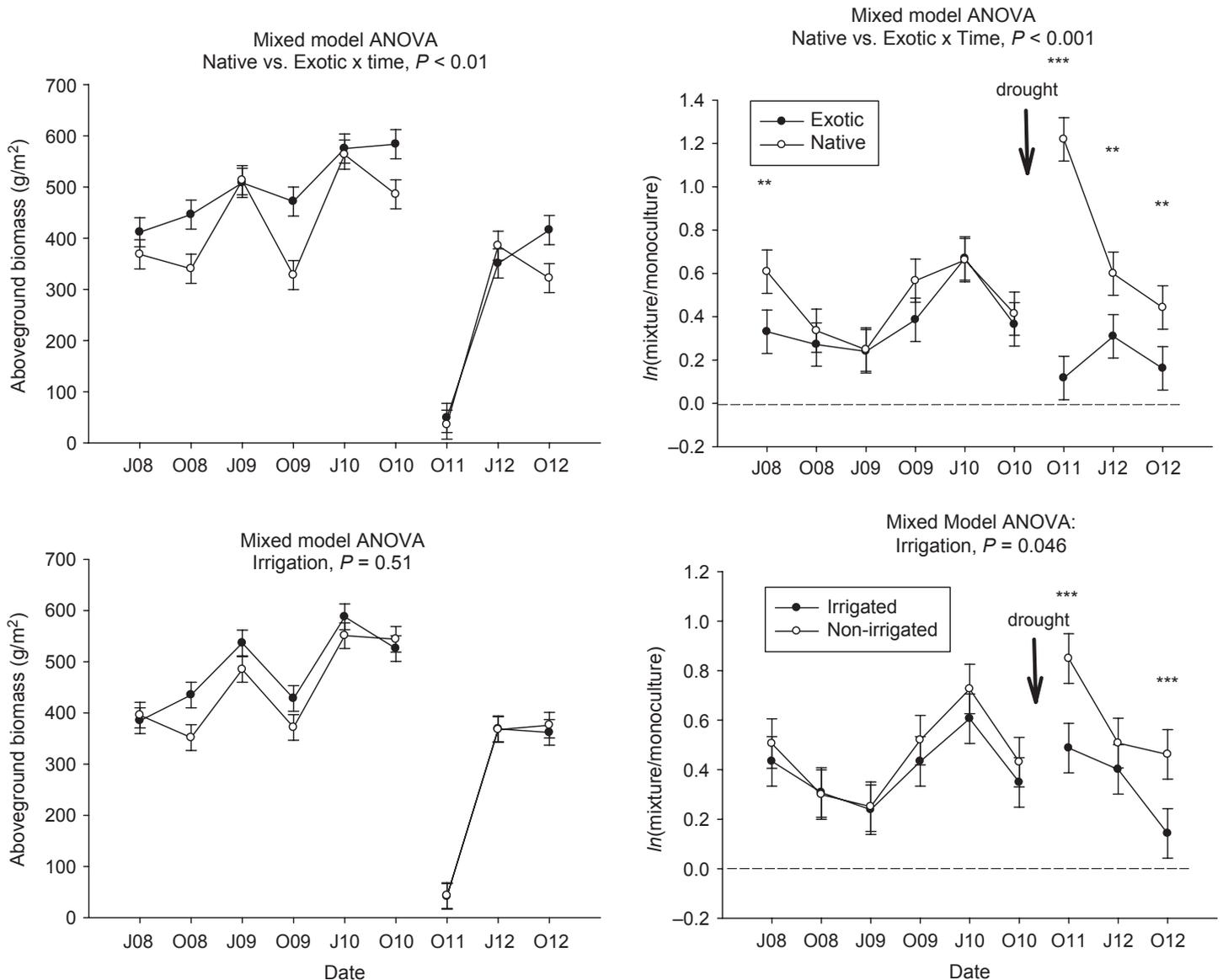
Species synchrony and CV among treatments were analyzed with a mixed model ANOVA (PROC MIXED in SAS), with origin (native vs. exotic) and irrigation as fixed effects, and block,

draw (block) and its interactions as random effects. Species richness, diversity, aboveground biomass and overyielding were analyzed with the same model with repeated measures, with the SLICE function for tests within years. Richness effects on CV (i.e., testing mixtures vs. monocultures) were tested by comparing ratios between  $\ln(\text{mixture CV}/\text{mean CV})$  for species in the plot across treatments. In a few cases, the species failed to persist beyond the first sampling period (e.g. *Trifolium repens*), so no CV could be calculated for those monocultures. These cases were not included in the richness CV calculations. Relationships between  $\ln(\text{var})$  and  $\ln(\text{mean})$  were analyzed with ordinary least-squares regression using PROC REG and GLM (SAS 9.2) and plotted with Sigmaplot (SPSS) across all time periods. Dominant species (defined as

the species with the highest relative biomass or  $p_i$ ) were identified in plots and then compared to the regression line with paired t-tests to test the effects of dominant species (Polley *et al.* 2007). To test how CV was related to mechanistic measures across draws within native and exotic communities, we used SEM. Relationships between CV and asynchrony, overyielding, and dominant species [CV of the species with the highest  $p_i$  (dominant species) during 2012] were tested with SEM using AMOS software (SPSS, IBM, NY, USA).

## RESULTS

Precipitation was a significant predictor of peak biomass in October over the 5-year time frame in non-irrigated plots, and



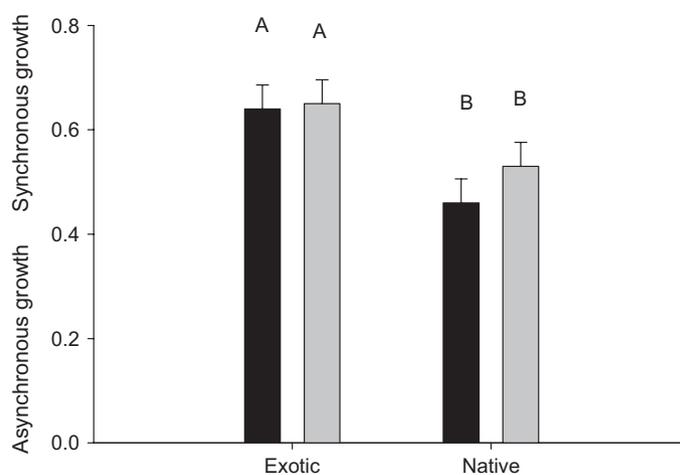
**Figure 2** Aboveground biomass (left panels) and overyielding (right panels, log response ratios between mixtures and monocultures, mean  $\pm$  SE) in June and October of each year in exotic and native communities (top), and between irrigated and non-irrigated treatments (bottom) in MEND plots. Irrigated plots were watered with 128 mm from July 15–August 15 each year starting in 2008. A major drought occurred in 2011 and biomass was not sampled in June of that year. Dotted line in right panels denotes no difference between mixture yields and expected yields from monocultures, and \*\*\* denotes  $P < 0.01$  and \*\*  $P < 0.05$  within years.

the data set included years that were drier and wetter than average. Peak biomass could be predicted by the equation  $y = -65.3 + 0.50$  (precipitation in mm), with an  $r^2 = 0.81$ ,  $P = 0.039$  ( $n = 5$ ). In irrigated plots, peak biomass was non-significantly related to precipitation according to  $y = -54.2 + 0.44$  (precipitation in mm),  $r^2 = 0.60$ ,  $P = 0.126$ . The drought year (2011) was clearly exceptional in that precipitation and peak biomass were much lower than other years (Fig. 2), and 2010 was well above average. Precipitation was 630.7, 785.9, 1165.6, 362.0, 1056.6 mm per year (October through September to correspond to the growing season) for year 1, 2, 3, the drought year 4, and 5. Thus, there was meaningful variation in environmental conditions during the 5 year period of the experiment.

Species richness and Simpson's diversity were both higher in native communities than exotic communities (Fig. 1, Table 1), but this was not associated with higher biomass CV. In contrast to our prediction from hypothesis 1, there was no difference in biomass CV across all time periods between exotic and native communities ( $P > 0.51$ , Fig. S2). Differences were consistent across irrigation treatments ( $P > 0.52$ ) with no interaction between origin and irrigation (CV means 44.1, 47.6, 49.3, 47.6 for exotic non-irrigated, exotic irrigated, native non-irrigated, native irrigated, SE = 2.8,  $F_{1,7} = 3.6$ ,  $P = 0.10$ ). There was also no significant difference in biomass CV when only October dates were used in the analysis. There was no difference between native and exotic communities [native mean = 60.6, exotic mean = 59.3 (SE = 3.0),  $F_{1,7} = 0.09$ ,  $P = 0.78$ ] nor between irrigated and non-irrigated plots (non-irrigated mean = 59.8, irrigated mean = 61.0,  $F_{1,7} = 0.03$ ,  $P = 0.87$ , interaction,  $F_{1,7} = 1.22$ ,  $P = 0.31$ ).

We did find a significant decrease in biomass CV with increased species richness (i.e., between monocultures and mixtures), but the difference was similar between native and exotic treatments. Biomass variation across years was much lower in mixtures than in monocultures of both exotics (CVs of 0.46 vs. 1.03) and natives (0.49 vs. 0.91). The log response ratio  $\ln(CV_{mixture}/CV_{monoculture})$  was not different between native and exotic communities ( $P > 0.66$ , interaction  $P > 0.23$ ), but was higher in irrigated plots than in non-irrigated plots ( $F_{1,7} = 4.7$ ,  $P = 0.06$ ). In other words, non-irrigated plots had smaller differences in CV between mixtures and monocultures than irrigated plots.

Native and exotic mixtures achieved this stability by different mechanisms, however. Native communities had less synchronous growth, greater overyielding during and after the drought, and less variable species than exotic communities (Fig. 3, Table 1). Growth among species was less synchronous in native communities (0.499) than exotic communities (0.644) ( $F_{1,7} = 6.95$ ,  $P = 0.03$ ). Overyielding values were higher on average in native communities ( $F_{1,7} = 6.96$ ,  $P = 0.033$ ), and were higher without irrigation ( $F_{1,7} = 5.9$ ,  $P = 0.046$ , Fig. 2). Perhaps most interestingly, the native-exotic difference in overyielding was enhanced greatly with the onset of the drought in 2011, during which native mixtures yielded  $e^{1.2} = 3.3$  times higher than the average monoculture (Fig. 2, Origin x Time,  $P < 0.0001$ ). This value was much higher than the 1.1 times higher value in exotic mixtures (Origin x Time,  $F_{7,450} = 10.3$ ,  $P < 0.0001$ ). This native-exotic difference then



**Figure 3** Synchrony/Asynchrony in growth among species ( $\phi$ ) in all exotic vs. all native species communities with (Irrigated, black bars) or without (Non-Irrigated, gray bars) summer irrigation.

persisted through the two sampling periods following the drought. Portfolio slopes averaged 1.61 (SE = 0.020) for exotics and 1.65 (SE = 0.021) for natives, suggesting strong effects in both community types ( $r^2 = 0.959$  and  $0.957$  for exotics and natives, respectively, Fig. S3). The intercept was significantly higher for exotics (1.56, SE = 0.061) than for natives (0.99, SE = 0.070), indicating that exotics were inherently more variable than native species than native species overall (test of intercepts,  $t = 14.2$ ,  $P < 0.001$ ). However, the greater intercept of the variance-mean relationship failed to result in higher CV's in exotic communities because species that heavily dominated plots (lowering evenness) tended to have lower than expected variance ( $P < 0.01$ , Table 2). Exotic plots had much higher dominance ( $0.78 \pm 0.04$  SE, using the Berger-Parker measure, or  $p_i$  of the most abundant species) than native plots ( $0.48 \pm 0.04$  SE,  $F_{1,7} = 30.8$ ,  $P < 0.001$ ). A list of

**Table 2** Species that dominated plots in 2012 (i.e., had highest  $p_i$ , mean  $p_i$  for exotics 0.78, range of 0.45–0.99, mean  $p_i$  of 0.48 for natives, range 0.35–0.81) and their deviation from expected variance. FG's are C<sub>4</sub>G = C<sub>4</sub> grasses, C<sub>3</sub>G = C<sub>3</sub> grasses, C<sub>3</sub>F = C<sub>3</sub> forbs

Species	FG	no. plots	mean (g)	deviation	$t$	Ho = 0, $P$ value
Exotic dominant species						
<i>Panicum coloratum</i>	C <sub>4</sub> G	18	276.2	-0.263	-3.63	0.002
<i>Sorghum halepense</i>	C <sub>4</sub> G	8	110.3	-0.324	-2.77	0.012
<i>Eragrostis curvula</i>	C <sub>4</sub> G	3	120.5	-0.023	-0.29	0.777
<i>Cynodon dactylon</i>	C <sub>4</sub> G	2	12.5	-0.846	-4.93	<0.001
<i>Bothriochloa ischaemum</i>	C <sub>4</sub> G	1	20.1	-0.197	-2.39	0.025
Total		32				
Native dominant species						
<i>Eriochloa sericea</i>	C <sub>4</sub> G	13	117.7	-0.540	-9.87	<0.001
<i>Ratibida columnifera</i>	C <sub>4</sub> F	6	152.4	0.486	5.25	<0.001
<i>Elymus canadensis</i>	C <sub>3</sub> G	5	94.8	0.541	5.75	<0.001
<i>Sorghastrum nutans</i>	C <sub>4</sub> G	5	54.4	0.081	0.48	0.634
<i>Nasella leucotricha</i>	C <sub>3</sub> G	2	57.0	0.406	3.29	0.005
<i>Vernonia baldwinii</i>	C <sub>4</sub> F	1	18.8	0.357	2.89	0.012
Total		32				

species that dominated at least one exotic mixture included five  $C_4$  grasses (Table 2). They ranged from species that typically had high biomass (*Panicum coloratum*, *Sorghum halepense*, *Eragrostis curvula*) to species that typically had low biomass in mixture (*Cynodon dactylon*, *Bothriochloa ischaemum*), yet they all tended to have lower variability than the average exotic species. An exception to the rule was *Eragrostis curvula*, which dominated three of the 32 plots. It had high biomass in early years, and lower biomass in later years (i.e., higher variance than other dominant species). Dominant native species were not less variable than average with four species significantly more variable than average, one with average variability, and one species significantly less variable than average (Table 2). Thus, in general, exotic species were more variable than native species, but the species that increased in relative abundance to eventually strongly dominate exotic communities tended to have much lower than average variance. This led to similar biomass CV's over time between native and exotic communities.

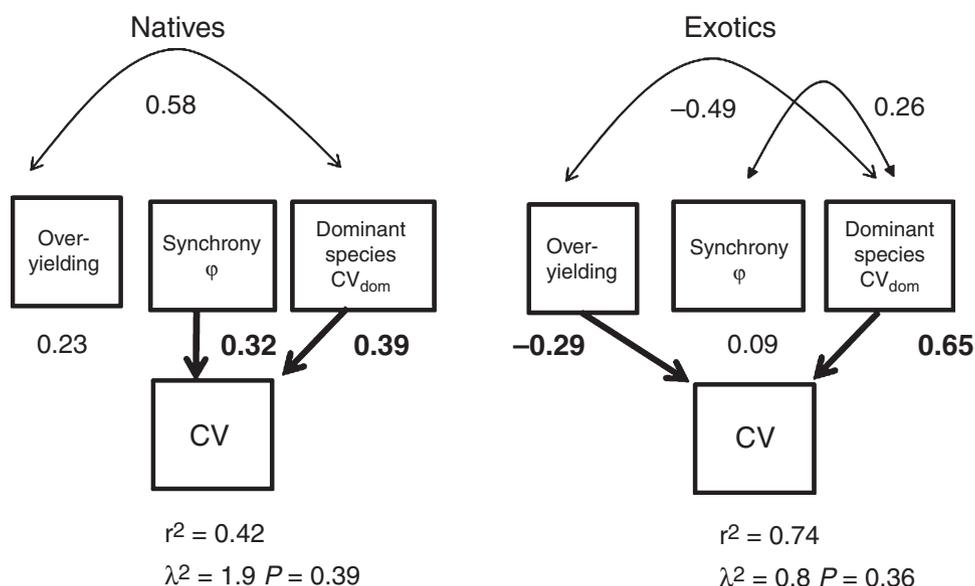
These tests all compared means between native and exotic and irrigated and non-irrigated treatments. We also tested how variables were related to each other across draws within native and exotic communities to test whether high CV was associated with these mechanistic variables at this level. The mechanistic variables that explained biomass CV across mixtures differed greatly between native and exotic communities (Fig. 4). In native communities, synchrony ( $P = 0.018$ ) and the CV of the dominant species ( $P = 0.02$ ) were both positively related to mixture CV's, whereas overyielding was not a significant predictor ( $P = 0.168$ ). In other words, biomass CV significantly increased as species growth became less asynchronous across native mixtures. In exotic communities, biomass CV was much more strongly related to the dominant species ( $P < 0.001$ ), and weakly related to overyielding ( $P = 0.006$ )

across mixtures. It was not significantly related to synchrony ( $P = 0.344$ ). These measures together accounted for 40% of the variance in native CV and 74% of exotic CV's.

## DISCUSSION

We tested for reductions in stability with diversity declines due to the replacement of native, presumably coevolved communities, with novel exotic-dominated communities. Open grasslands with  $C_4$  grasses have been present in the southern Plains for at least 7 million years (Edwards *et al.* 2010), and current communities have persisted since the last ice age 12 000 years ago. Exotic communities have assembled in the last fifteen decades or less. Results indicate that, although there were similar levels of stability (i.e., CV's) and responses to species richness (log-response ratios of monocultures vs. mixtures) between native and exotic communities, the community types achieved stability through vastly different mechanisms. In native communities, stability was associated with asynchronous growth among species, whereas in the exotic communities, stability resulted because strongly dominant species were stable. These native-exotic differences were consistent across the two irrigation treatments.

The literature on how grassland stability is related to species diversity is generally supportive of positive relationships between the two variables (e.g. McNaughton 1993; Tilman *et al.* 2006; Isbell *et al.* 2009a,b; Loreau 2010; Roscher *et al.* 2011; Cardinale *et al.* 2013; de Mazancourt *et al.* 2013), but exceptions to the rule are prevalent and variability exists in the mechanistic variables underlying relationships. No relationship or negative relationships were found between diversity and stability by Sasaki & Lauenroth (2011) in blue grama grasslands, by Polley *et al.* (2007) in comparisons of restored vs. remnant grasslands, by Sankaran & McNaughton (1999)



**Figure 4** Relationships between stability maintenance mechanisms (mean overyielding; asynchrony from 2010–2012; monoculture CV of dominant species, i.e., the species with highest relative biomass) and biomass CV over five years in native vs. exotic communities. Arrows denote significant relationships ( $P < 0.05$ ).

for compositional stability, and by Grman *et al.* (2010) in annual vs. perennial old fields. A meta-analytic study of the asynchrony hypothesis found that it was less common than expected, especially in arid systems (Houlihan *et al.* 2007). Our approach suggests a possible explanation for these disparate results. We originally predicted that positive relationships between diversity and stability would only be found in situations where niche partitioning is important in regulating community structure and dominant species effects are less important. Niche partitioning would be associated with ecological differences among species in a community given sufficient time for assembly (Sankaran & McNaughton 1999). This should be most prominent in well established, relict areas that are dominated by native species. Previously, we found that the complementarity effect was greater (Wilsey *et al.* 2011) and the selection effect was weaker in native than comparable exotic communities (Wilsey *et al.* 2009). Species in native communities had lower temporal niche overlap than exotic communities (Wilsey *et al.* 2011; Martin *et al.* 2013). Results reported here suggest that native species, on average, strongly benefited by being in a mixture (i.e., they overyielded) during and after the drought period. However, these mechanisms were not associated with having higher stability compared to the exotic communities. Heavily degraded systems, such as agricultural systems where there has been strong human selection for plants with targeted traits (Gravuer *et al.* 2008), and assemblages of species without a history of interaction are predicted to lack niche partitioning and have stronger dominant species effects. This would lead to reductions in species richness and evenness without concomitant decreases in ecosystem stability in the many cases where dominant species are more stable than subordinate species. Thus, different mechanisms can be operating to achieve equal levels of stability. This framework should be tested by comparing other native vs. novel community types in a variety of systems during the emerging 'Anthropocene'.

Exotic communities typically had very low evenness (high dominance), an aspect that was missing in native communities. This had important implications for exotic communities, because dominant species tended to have lower than average temporal variability. This enabled exotic communities to have similar amounts of stability compared to native communities with even fewer species present. The reduction in growth asynchrony in exotic communities that was associated with high dominance is consistent with theoretical predictions of Doak *et al.* (1998), Hillebrand *et al.* (2008) and Thibaut & Connolly (2013). When evenness is very low, the stability of the dominant species will over-ride any effects of subordinate species (McNaughton 1977; Grime 1998). The greater growth synchrony among species in exotic communities is evidence that human-induced shifts from native to exotic dominated-communities is altering the mechanisms thought to underlie diversity-stability relationships. But surprisingly, reductions in this mechanism did not lead to greater variability. Importantly, we found that the dominance by species with high stability in exotic communities was sufficiently large enough to offset the native advantages of asynchrony and lower average variability among species.

The finding that the species that became dominant in exotic grassland communities had lower than average variance is relevant for the persistence of these communities on the landscape. There is growing awareness that exotic systems are not ephemeral (Ellis & Ramankutty 2008; Hobbs *et al.* 2013). Exotic species establish in pastures planted by humans (Isbell & Wilsey 2011), are common in areas with high N-deposition (Suding *et al.* 2005; Isbell *et al.* 2013) and self-assemble into exotic-dominated communities in many areas that are disturbed by humans (Hobbs *et al.* 2006; Wilsey *et al.* 2009; Mascaro *et al.* 2012). One might have predicted that exotics are ephemeral on the landscape, and will eventually be replaced by native species given sufficient time and a stressful event or two as predicted by the 'reckless invader' hypothesis of Alpert (2006), as they sometimes are in forested systems (Meiners 2007). The ephemeral nature of these novel communities would have been supported by evidence that exotic communities are highly variable over time, with major declines in biomass during droughts, and large peaks during rainy years. Low temporal stability is predicted to be associated with low persistence, and persistence is a key long term measure of stability (Donohue *et al.* 2013; Huang *et al.* 2013; Roscher *et al.* 2013). Other than losing a few species and becoming even more simplified during the drought, exotic communities were surprisingly stable over time. Dominance by a single species might be highly unstable and vulnerable to pest outbreaks, causing stability to plummet over a longer time frame. This will be tested with further monitoring of the plots. However, in the 5-year time frame of the current study, there were several exotic species that became dominant (usually grasses), and dominant species identity changed from plot to plot. This suggests that these (multiple) exotic species may be highly temporally stable and persistent on the grassland landscape without a severe intrinsic disturbance (Tognetti *et al.* 2010; MacDougall *et al.* 2013). That is, they may be here to stay, and more study of novel ecosystems is warranted.

#### ACKNOWLEDGEMENTS

This work was partially funded by the US-NSF DEB-0639417. We thank Katherine Jones and Chis Kolodziejczyk for help in the field, and four anonymous reviewers for comments on an earlier version of the manuscript.

#### REFERENCES

- Alpert, P. (2006). The advantages and disadvantages of being introduced. *Biol. Invasions*, 8, 1523–1534.
- Bai, Y., Han, X., Wu, J., Chen, Z. & Li, L. (2004). Ecosystem stability and compensatory effects in the Inner Mongolia grassland. *Nature*, 431, 181–184.
- Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P. *et al.* (2012). Biodiversity loss and its impact on humanity. *Nature*, 486, 59–67.
- Cardinale, B.J., Gross, K., Fritschie, K., Flombaum, P., Fox, J., Rixen, C. *et al.* (2013). Can producer diversity simultaneously increase the productivity and stability of ecosystems? A meta-analysis of 34 experiments. *Ecology*, 94, 1697–1707.

- Daneshgar, P.P., Polley, H.W. & Wilsey, B.J. (2013). Simple plant traits explain functional group diversity decline in novel grassland communities of Texas. *Plant Ecol.*, 214, 231–241.
- 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.
- Donohue, I., Petchey, O.L., Montoya, J.M., Jackson, A.L., McNally, L., Viana, M. *et al.* (2013). On the dimensionality of ecological stability. *Ecol. Lett.*, 16, 421–429.
- Edwards, E.J., Osborne, C.P., Strömberg, C.A.E. & Smith, S.A. and the C4 Grasses Consortium. (2010). The origins of C<sub>4</sub> grasslands: integrating evolutionary and ecosystem science. *Science*, 328, 587–591.
- Ellis, E.C. & Ramankutty, N. (2008). Putting people in the map: anthropogenic biomes of the world. *Front. Ecol. Environ.*, 6, 439–447.
- Gravuer, K., Sullivan, J.J., Williams, P.A. & Duncan, R.P. (2008). Strong human association with plant invasion success for *Trifolium* introductions to New Zealand. *PNAS*, 105, 6344–6349.
- Grime, J.P. (1998). Benefits of plant diversity in ecosystems: immediate, filter and founder effects. *J. Ecol.*, 86, 902–910.
- Grman, E., Lau, J.A., Schoolmaster, D.R. & Gross, K.L. (2010). Mechanisms contributing to stability in ecosystem function depend on the environmental context. *Ecol. Lett.*, 13, 1400–1410.
- 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.
- Hobbs, R.J., Arico, S., Aronson, J., Baron, J.S., Bridgewater, P., Cramer, V.A. *et al.* (2006). Novel ecosystems: theoretical and management aspects of the new ecological world order. *Glob. Ecol. Biogeogr.*, 15, 1–7.
- Hobbs, R.J., Higgs, E.S. & Hall, C.M. (2013). *Novel Ecosystems*. John Wiley & Sons Ltd, Chichester, UK.
- Hooper, D.U., Chapin, F.S., 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., Cotterie, K., Ernest, S.K.M., Findlay, C.S., Fuhlendorf, S.D. *et al.* (2007). Compensatory dynamics are rare in natural ecological communities. *PNAS*, 104, 3273–3277.
- Huang, Y., Martin, L.M., Isbell, F.I. & Wilsey, B.J. (2013). Is community persistence related to species diversity at planting? A test with tallgrass prairie species in a long-term field experiment. *Basic Appl. Ecol.*, 14, 199–207.
- Isbell, F.I. & Wilsey, B.J. (2011). Increasing native, but not exotic, biodiversity enhances ecosystem functioning in ungrazed and intensely grazed grasslands. *Oecologia*, 165, 771–781.
- Isbell, F.I., Polley, H.W. & Wilsey, B.J. (2009a). Biodiversity, productivity, and the temporal stability of productivity: patterns and processes. *Ecol. Lett.*, 12, 443–451.
- Isbell, F.I., Polley, H.W. & Wilsey, B.J. (2009b). Species interaction mechanisms maintain grassland plant species diversity. *Ecology*, 90, 1821–1830.
- Isbell, F., Tilman, D., Polasky, S., Binder, S. & Hawthorne, P. (2013). Low biodiversity state persists two decades after cessation of nutrient enrichment. *Ecol. Lett.*, 16, 454–460.
- Ives, A.R. & Carpenter, S.R. (2007). Stability and diversity of ecosystems. *Science*, 317, 58–62.
- Lepš, J. (2004). Variability in population and community biomass in a grassland community affected by environmental productivity and diversity. *Oikos*, 107, 64–71.
- Loreau, M. (2010). *From Populations to Ecosystems: Theoretical Foundations for a New Ecological Synthesis*. Princeton University Press, Princeton, USA.
- Loreau, M. & de Mazancourt, C. (2008). Species synchrony and its drivers: neutral and nonneutral community dynamics in fluctuating environments. *Am. Nat.*, 172, E48–E66.
- MacDougall, A.S., McCann, K.S., Gellner, G. & Turkington, R. (2013). Diversity loss with persistent human disturbance increases vulnerability to ecosystem collapse. *Nature*, 494, 86–90.
- Martin, L.M., Polley, H.W., Daneshgar, P.P., Harris, M.A. & Wilsey, B.J. (2013). Biodiversity, photosynthetic mode, and ecosystem services differ between native and novel ecosystems. *Oecologia*, in press.
- Mascaro, J., Hughes, R.F. & Schnitzer, S.A. (2012). Novel forests maintain ecosystem processes after the decline of native tree species. *Ecol. Monogr.*, 82, 221–238.
- de Mazancourt, C., Isbell, F., Larocque, A., Berendse, F., De Luca, E., Haegeman, B. *et al.* (2013). Predicting ecosystem stability from community composition and biodiversity. *Ecol. Lett.*, 16, 617–625.
- McNaughton, S.J. (1977). Diversity and stability of ecological communities: a comment on the role of empiricism in ecology. *Am. Nat.*, 111, 515–525.
- McNaughton, S.J. (1993). Biodiversity and stability of grazing ecosystems. In: *Biodiversity and Ecosystem Function*. (eds Schulze, E.-D., Mooney, H.A.). Springer-Verlag, Berlin, pp. 361–383.
- Meiners, S.J. (2007). Native and exotic plant species exhibit similar population dynamics during succession. *Ecology*, 88, 1098–1104.
- Naem, S., Duffy, J.E. & Zavaleta, E. (2012). The functions of biological diversity in an age of extinction. *Science*, 336, 1401–1405.
- 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.
- Roscher, C., Weigelt, A., Proulx, R., Marquard, E., Schumacher, J., Weisser, W.W. *et al.* (2011). Identifying population- and community-level mechanisms of diversity–stability relationships in experimental grasslands. *J. Ecol.*, 99, 1460–1469.
- Roscher, C., Ferbus, A.J.F., Petermann, J.S., Buchmann, N., Schmid, B. & Schulz, E.D. (2013). What happens to the sown species if a biodiversity experiment is not weeded? *Basic Appl. Ecology*, 14, 187–198.
- Sankaran, M. & McNaughton, S.J. (1999). Determinants of biodiversity regulate compositional stability of communities. *Nature*, 401, 691–693.
- Sasaki, T. & Lauenroth, W.K. (2011). Dominant species, rather than diversity, regulates temporal stability of plant communities. *Oecologia*, 166, 761–768.
- Spehn, E.M., Hector, A., Joshi, J., Scherer-Lorenzen, M., Schmid, B., Bazeley-White, E. *et al.* (2005). Ecosystem effects of biodiversity manipulations in European grasslands. *Ecol. Monogr.*, 75, 37–63.
- 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. *PNAS*, 102, 4387–4392.
- Taylor, L.R. (1961). Aggregation, variance and the mean. *Nature*, 189, 732–735.
- Thibaut, L.M. & Connolly, S.R. (2013). Understanding diversity-stability relationships: towards a unified model of portfolio effects. *Ecol. Lett.*, 16, 140–150.
- Tilman, D. (1999). The ecological consequences of changes in biodiversity: a search for general principles. *Ecology*, 80, 1455–1474.
- Tilman, D., Reich, P.B. & Knops, J.M.H. (2006). Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature*, 441, 629–632.
- Tilman, D., Reich, P.B. & Isbell, F. (2012). Biodiversity impacts ecosystem productivity as much as resources, disturbance, or herbivory. *PNAS*, 109, 10394–10397.
- Tognetti, P.M., Chaneton, E.J., Omacini, M., Trebino, H.J. & León, R.J.C. (2010). Exotic vs. native plant dominance over 20 years of old-field succession on set-aside farmland in Argentina. *Biol. Conserv.*, 143, 2494–2503.
- Wilsey, B.J., Teaschner, T.B., Daneshgar, P.P., Isbell, F.I. & Polley, H.W. (2009). Biodiversity maintenance mechanisms differ between native and novel exotic-dominated communities. *Ecol. Lett.*, 12, 432–442.
- Wilsey, B.J., Daneshgar, P.P. & Polley, H.W. (2011). Biodiversity, phenology and temporal niche differences between native- and novel exotic-dominated grasslands. *Persp. Plant Ecol. Evol. Systemat.*, 13, 265–276.
- Zavaleta, E.S. & Hulvey, K.B. (2004). Realistic species losses disproportionately reduce grassland resistance to biological invaders. *Science*, 306, 1175–1177.

**SUPPORTING INFORMATION**

Additional Supporting Information may be downloaded via the online version of this article at Wiley Online Library ([www.ecologyletters.com](http://www.ecologyletters.com)).

Editor, Elsa Cleland

Manuscript received 15 July 2013

First decision made 14 August 2013

Second decision made 3 October 2013

Manuscript accepted 7 October 2013