



Plant functional traits improve diversity-based predictions of temporal stability of grassland productivity

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Synthesis The temporal stability of plant production is greater in communities with high than low species richness, but stability also may depend on species abundances and growth-related traits. Annual precipitation varied by greater than a factor of three over 11 years in central Texas, USA leading to large variation in production. Stability was greatest in communities that were not dominated by few species and in which dominant species rooted shallowly, had dense leaves, or responded to the wettest year with a minimal increase in production. Stability may depend as much on species abundances and functional traits as on species richness alone.

Aboveground net primary productivity (ANPP) varies in response to temporal fluctuations in weather. Temporal stability of community ANPP may be increased by increasing plant species richness, but stability often varies at a given richness level implying a dependence on abundances and functional properties of member species. We measured stability in ANPP during 11 years in field plots (Texas, USA) in which we varied the richness and relative abundances of perennial grassland species at planting. We sought to identify species abundance patterns and functional traits linked to the acquisition and processing of essential resources that could be used to improve richness-based predictions of community stability. We postulated that community stability would correlate with abundance-weighted indices of traits that influence plant responses to environmental variation. Annual precipitation varied by a factor of three leading to large inter-annual variation in ANPP. Regression functions with planted and realized richness (species with > 1% of community ANPP during the final four years) explained 32% and 25% of the variance in stability, respectively. Regression models that included richness plus the fraction of community ANPP produced by the two most abundant species in combination with abundance-weighted values of either the fraction of sampled root biomass at 20–45 cm depth, leaf dry matter content (LDMC), or response to greater-than-average precipitation of plants grown in monocultures explained 58–69% (planted richness) and 58–64% (realized richness) of the variance in stability. Stability was greatest in communities that were not strongly dominated by only two species and in which plants rooted shallowly, had high values of LDMC, or responded to the wettest year with a minimal increase in ANPP. Our results indicate that the temporal stability of grassland ANPP may depend as much on species abundances and functional traits linked to plant responses to precipitation variability as on species richness alone.

Many factors can affect temporal variability in primary productivity, including plant functional trait relationships (Huxman et al. 2008), disturbance regimes, and soil fertility (Grman et al. 2010), but productivity often varies in response to temporal fluctuations in weather (Knapp and Smith 2001, Tilman et al. 2006). Various management approaches are used to lessen impacts of weather variability on plant productivity and other economically-important ecosystem functions. For intensively-managed agricultural systems, these approaches include irrigation to reduce effects of drought and adjustments in planting schedules to minimize impacts of adverse temperatures or precipitation patterns. Changing the number (richness), relative abundances (evenness), or identities (functional properties) of plant species

are among the few economically-viable tools available to land managers as a means to reduce fluctuations and increase the temporal stability of productivity in pastures, semi-natural grasslands, and other less-intensively managed ecosystems dominated by perennial plants (Ospina et al. 2012).

Temporal stability of aboveground net primary productivity (ANPP) is calculated as the ratio of the mean (μ) to the standard deviation (σ) of community ANPP (Lehman and Tilman 2000). Results from manipulative experiments have confirmed that greater richness stabilizes production of herbaceous communities (Tilman et al. 2006, Isbell et al. 2009, Hector et al. 2010, Gross et al. unpubl.). Greater richness increases stability by promoting interspecific competition and compensatory dynamics among species

(species interactions; Tilman et al. 1998), increasing the number of species that respond differently to the environment (species responses; Ives et al. 2000), or both (Gross et al. unpubl.). Much of the empirical evidence that richness stabilizes productivity is from experiments with replicated communities created by randomly selecting species from a common pool (biodiversity ecosystem-function experiments, BEF; Tilman et al. 2006, Hector et al. 2010). Results from BEF experiments demonstrate substantial variability in stability at a given richness level that partly reflects the influence of species responses and, by extension, species functional traits on community dynamics. Indeed, stability may be greater in some species mixtures with few species than in some mixtures with many species. The variability in stability that is associated with species composition poses a practical dilemma. What information in lieu of, or in addition to, species richness is required to predict community stability?

There is increasing evidence that primary productivity is governed by the functional trait composition of plant communities, including the distribution and relative abundances of traits among species (Díaz and Cabido 2001, Roscher et al. 2012). Two metrics commonly are used to quantify functional diversity. First, community-aggregated means of trait values are calculated by weighting trait values of each species by the relative abundance of the species in the community, an approach that is theoretically-consistent with Grime's (1998) mass-ratio hypothesis. This abundance-weighted trait index is interpreted as the trait value expected from a random sample of the community (Díaz and Cabido 2001). Secondly, the distribution of trait values among species within a community is calculated as a metric of functional trait diversity or functional dissimilarity (Roscher et al. 2012). Predictions of community stability might be improved by combining data on species richness with information about species abundances and plant functional traits that regulate the responses of plant communities to environmental variability (response traits; Naeem and Wright 2003).

Species functional traits affect stability partly by influencing population growth rates. Community stability should be correlated with the variances in ANPP displayed by species monocultures if stability is determined largely by species growth rates and environmental responses rather than species interactions. To the extent that stability is related to dynamics of species monocultures, we anticipate a correlation between community stability and the functional dissimilarity in, or community-weighted means of, species traits that are linked to growth responses to the environment through the acquisition and processing of carbon and essential elements. For example, per capita reproductive rate varied widely among years in Sonoran Desert annuals with high relative growth rate (RGR), whereas species with low RGR exhibited less inter-annual variability (Huxman et al. 2008). Growth rate or primary productivity often are highly correlated with leaf or plant traits (Garnier et al. 2004, Vile et al. 2006). On the other hand, community stability may not be predictable from functional traits if stability is strongly influenced by factors that lead to greater asynchrony in species fluctuations (Roscher et al. 2011).

Species contributions to stability likely depend on the biotic and abiotic contexts in which they are considered.

For example, the extent to which species environmental responses affect community stability likely depends both on richness levels and the types of species present (Fowler et al. 2012). Species traits that affect environmental responses may be especially important in communities in which there are relatively few species (such as planted pastures) and asynchrony in species responses is limited by species properties or the primary environmental driver of ANPP fluctuations. In particular, we expect stability to depend on species responses to the environment and related functional traits and functional diversity when richness is relatively low and inter-annual variability in ANPP results mainly from change in variables such as precipitation to which most species respond synchronously.

We calculated stability in ANPP during an 11-year period for plots in a grassland BEF study in which the planted richness and evenness of perennial species were varied (Wilsey and Polley 2004, Isbell et al. 2009). Temporal stability of productivity was greater in plots planted with four or eight than two species per m² during the first eight years of this study (Isbell et al. 2009). Here, we test the hypothesis that the temporal stability of community ANPP can be predicted by using species abundances and functional trait diversity or abundance (community)-weighted values of species functional traits in lieu of, or addition to, data on species richness. Quantitative traits that are linked to plant processes have been used to detect the influence of species composition on functional responses (instantaneous or cumulative) of plant communities and ecosystems (Garnier et al. 2004, Roscher et al. 2012), but rarely to characterize the variability or stability of processes. de Mazancourt et al. (2013) recently developed theory to predict community stability using the dynamics of species monocultures, whereas Gross et al. (unpubl.) found that correlations in the temporal dynamics of production among species differed depending on whether species were grown in monocultures or communities. We extend these analyses of relationships between community stability and the environmental responses of species monocultures by linking stability to abundances and functional traits of component species. A practical goal of our analysis is to identify traits that could be used to select species combinations to increase community stability in the face of variability in weather, particularly precipitation.

Methods

Experimental design

We measured the aboveground net primary productivity (ANPP) of mixtures (communities) and monocultures of perennial plant species common to grasslands in central Texas, USA (31°05'N, 97°20'W). Annual precipitation at the site averages 875 mm (91 year record). The final year of this study (2011) was one of severe drought, during which annual precipitation (November through October) was 41% of the mean for the site. Plants for the experiment were grown from seeds in greenhouses in soil taken from the field site. The soil is a Vertisol, the surface 0.4 m of which is composed mostly (55%) of clay. Equal-sized

seedlings were transplanted into 1×1 m field plots (96 plants per plot) on 19–25 April 2001. Plots included 36 species mixtures and 39 monocultures. The species composition of mixtures was determined by random draw from a pool of 13 perennial species. The species pool contained five native C_4 grasses: *Schizachyrium scoparium*, *Sporobolus compositus*, *Bothriochloa laguroides*, *Bouteloua curtipendula*, *Sorghastrum nutans*; three exotic C_4 grasses: *Bothriochloa ischaemum*, *Paspalum dilatatum* and *Panicum coloratum*; one native C_3 grass: *Nassella leucotricha*; and four native C_3 non-leguminous forbs: *Ratibida columnifera*, *Oenothera speciosa*, *Salvia azurea* and *Echinacea purpurea*. Mixture plots were planted to one of three richness levels (two, four or eight species). The species composition of each of the three richness treatments was determined by six random draws. Each richness treatment of a given composition was planted at both high and realistically low species evenness levels. Mixtures assigned to the high evenness treatment were planted with the same number of individuals of each member species. The low evenness treatment was based on a geometric distribution of species (64:32 in two-species mixtures, 51:26:13:6 in four-species mixtures, and 47:24:12:6:3:2:1:1 in eight-species mixtures) with a slope of the rank–abundance relationship (−0.30) that is within the range of values recorded for grasslands in the area (Wilsey and Polley 2004). Three replicate monocultures of each of the 13 species were planted. Treatments were randomly assigned within three blocks, each with 25 plots. Volunteer plants (i.e. weeds) were removed by hand.

ANPP for each plot was estimated annually from 2001 through 2011 near the end of the growing season (autumn) when biomass is near its peak. Peak biomass provides a reasonable estimate of ANPP in this system because aboveground tissues represent current-year growth only (standing tissues are removed at harvest each year) and all species, with the exception of two minor components of mixtures, *Echinacea* and *Nassella*, continue growth until the autumn harvest. Aboveground material was clipped by species, dried to constant mass, and weighed. In order to minimize effects of harvesting on element cycling, harvested material was returned to the plot from which it was removed prior to the next growing season. Plant material was shredded with a wood chipper to simulate effects of late-season mowing before it was returned. No fertilizer was added.

Variability in ANPP

Inter-annual (temporal) stability of community ANPP was calculated across 11 biomass harvests by dividing the mean of ANPP per plot by the standard deviation in productivity among years (μ/σ). Two factors contribute to community variance (and hence to σ), the summed variances of individual species and the summed covariances between species pairs (Doak et al. 1998), the latter assessed using the community-wide synchrony of species fluctuations (Loreau and de Mazancourt 2008). Temporal stability is maximized when species fluctuations are perfectly asynchronous, such that a decrease in ANPP of one species is fully compensated by an increase in production of a second

species. Plot-level synchrony in species biomass production (ϕ_b) was calculated as:

$$\phi_b = \phi_{bT}^2 / (\sum_{i=1}^S \sigma_{bi}^2) \quad (1)$$

where, ϕ_{bT}^2 is the variance in community biomass and σ_{bi} is the standard deviation in biomass of species i in a mixture with S species (Loreau and de Mazancourt 2008).

Precipitation is an important regulator of grassland ANPP in central Texas (Polley et al. 2007). In order to determine how precipitation affected ANPP, we averaged ANPP across all communities or monocultures and regressed means of annual ANPP on precipitation summed for the November through October period each year. We explored impacts of precipitation extremes (wettest and driest years) on ANPP by calculating the relative maximum ((inter-annual maximum – mean)/mean) and relative minimum ((mean – inter-annual minimum)/mean) of ANPP for each plot (Knapp and Smith 2001). Stability likely depends on ANPP responses to precipitation extremes in systems in which plant growth is strongly regulated by water availability.

Aggregated stability indices

Temporal trends in communities depend on how member species respond to environmental fluctuations as modified by interspecific interactions and species demography (de Mazancourt et al. 2013). To the extent that stability is related to dynamics of species monocultures, we anticipate a link between community stability and abundance weighted (aggregated) indices of both the stability components of monocultures and values of species traits. We used data collected from monocultures to calculate 1) an index of each of the three components of community stability (ANPP, species variances, and synchrony) and 2) community-aggregated values of plant traits. These data were used to test the hypothesis that diversity-based predictions of temporal stability can be improved by using abundance-weighted values of species dynamics in monocultures and plant traits linked to potential growth responses to environmental variation.

Indices of the components of community stability were calculated as follows. An index of synchrony was calculated for each mixture by dividing the variance of the annual sum of the ANPP of monocultures of all member species by the squared value of the sum of the standard deviations of ANPP from monocultures (Eq. 1). We calculated community-aggregated indices of the mean and variance of ANPP ($ANPP_{agg}$ and Var_{agg}) for each mixture by weighting values of the mean and variance of the ANPP of monocultures of member species by the relative contribution of each species to community productivity over the 11-year period, then summing weighted values across species (Garnier et al. 2004, Díaz et al. 2007). Note that the value of Var_{agg} differs from the value calculated using weighted values of ANPP (weighted variance). Aggregated indices for each community were calculated using data from all member species. The fraction of community ANPP produced by the two most abundant (dominant) species is termed $fANPP_{dom}$.

Aggregated values of several leaf and plant traits or response indices ($trait_{agg}$) also were calculated for each

community. Traits considered included: 1) specific leaf area (SLA), the ratio of leaf area to leaf dry mass, 2) leaf dry matter content (LDMC), the dry mass of a leaf divided by its saturated fresh weight, 3) maximum height, 4) the fraction of sampled root biomass (0–45 cm depth) recovered at 20–45 cm depth (fRoot20_45), 5) the relative minimum of monoculture ANPP (Rel_min), and 6) the relative maximum of monoculture ANPP (Rel_max), the latter indicative of the relative ANPP response to the wettest year. Community-aggregated trait values represent the trait values expected from a random sample of the community. SLA, LDMC and height were measured in monocultures during the period of peak growth (June) in 2010 using methods suggested by Cornelissen et al. (2003). Root biomass was measured in autumn of 2001 and 2002 by extracting live roots from two 4.2-cm diameter soil cores from each monoculture plot (Wilsey and Polley 2006).

Functional trait diversity

Functional trait diversity was calculated based on the quadratic entropy of Rao (1982; FD_Q). We calculated FD_Q for each of the six leaf or plant traits measured (FD_{trait}). We multiplied the squared difference between values of a given trait for a given pair of species by the product of the relative contribution of each species to community ANPP. This process was repeated for all possible species pairs per community. FD_Q is the sum of these pairwise differences between species, each weighted by the product of the species relative abundances. Values of each trait were standardized to the range 0–1 prior to calculations. FD_Q is interpreted as the average trait difference between two randomly selected individuals in a given community (Botta-Dukát 2005).

Statistical analyses

We used an analysis of variance (ANOVA) to determine the effect of planted species richness and evenness treatments on community stability. We modeled the treatment structure as a randomized-block split-plot ANOVA with richness effects in the main plot, evenness effects and interactions in the subplot, and $\text{rep}(\text{block} \times \text{richness})$ as the error term. The analysis was confined to plots in which two or more species were retained after 11 years ($n = 28$). Data from 8 of the 12 plots planted to two species were excluded because one of the two planted species (*Echinacea*, *Oenothera*, or *Paspalum*) became locally extinct during years 2–7. Satterthwaite's formula was used to calculate the degrees of freedom for statistical tests because the number of observations differed among planted richness treatments. We used regression analyses, including residual or sequential multiple regression (Graham 2003), to examine relationships between ANPP and precipitation and between community stability and the following variables: planted and realized richness, monoculture-based indices of stability components, and aggregated values and the FD_Q of functional traits. Realized richness is defined as the number of species per mixture that each contributed >1% of community ANPP during the final four years (2008–2011). Traditional multiple regression models do not account for

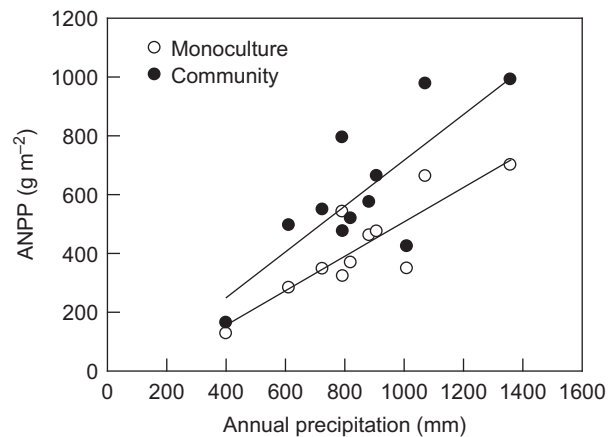


Figure 1. Relationships between aboveground net primary productivity (ANPP) of species monocultures or communities (mixtures) and annual precipitation during 11 years. Lines are linear regression fits to data for monocultures ($\text{ANPP} = -78.39 + 0.59 \times \text{precipitation}$, $r^2 = 0.72$, $p = 0.0006$, $n = 11$ species) and communities ($\text{ANPP} = -62.66 + 0.78 \times \text{precipitation}$, $r^2 = 0.59$, $p = 0.003$, $n = 28$). ANPP for monocultures was calculated by averaging data from three plots per species. All plants in monocultures of two species (*Echinacea*, *Oenothera*) died between the second and eighth years of the experiment. Data for these species were excluded.

the shared contributions of predictor variables that covary or are collinear. In sequential regression, variables deemed to be functionally more important than others are assigned priority over shared contributions. SAS (SAS Inst.) was used for all statistical analyses.

Results

Precipitation as a driver of ANPP variability

During the 11 years of this experiment, annual precipitation varied by greater than a factor of three (range = 400–1359 mm) leading to large inter-annual variation in ANPP for both species monocultures and communities (Fig. 1). The ANPP of both communities and monocultures was a positive, linear function of precipitation summed from November through October of each year. The slope of the linear ANPP–precipitation relationship was significantly greater on average for communities than monocultures (0.78 vs 0.59 g m^{-2} per mm of precipitation; $F_{(1,18)} = 0.02$, $p > 0.75$). As a consequence, the absolute advantage in ANPP of communities over monocultures increased as precipitation increased. There was no relationship between ANPP and the number of years into the experiment (year effect) after accounting for the precipitation effect ($p = 0.10$ – 0.13).

Because ANPP responded strongly to variability in precipitation, temporal stability of monocultures was lowest for species that responded to the wettest year with a large increase in ANPP. The relative maximum of ANPP was greatest for *Sorghastrum* (1.97), followed by *Ratibida*, and *Schizachyrium* (1.83 and 1.71, respectively) and least for *Bothriochloa laguroides* and *Bouteloua* (0.37 and 0.63,

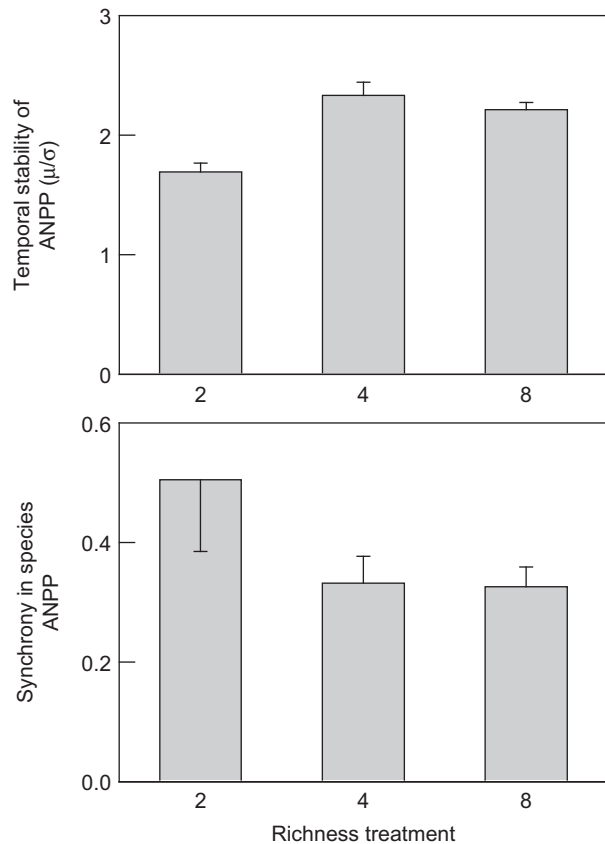


Figure 2. Temporal stability of community ANPP (μ/σ) and plot-level synchrony in species ANPP (variance in community ANPP/the square of the sum of the σ in ANPP of component species) in plots planted with two, four or eight grassland species ($n = 4, 12$ and 12 , respectively). Bars indicate 1 SE.

respectively). The relative maxima of monocultures, in turn, were a positive linear function of the fraction of root mass at 20–45 cm depth ($\text{Rel_max} = -0.10 + 3.90 \times \text{fRoot20_45}$; $r^2 = 0.44$, $p = 0.02$, $n = 11$).

Community stability

Temporal stability differed by a factor of two among communities (range 1.5–3.1), was greater on average in communities planted to four and eight than two species although differences between richness treatments were not significant ($p = 0.13$, Fig. 2), and varied as a quadratic function of planted richness ($\text{stability} = 0.596 + 0.670 \times \text{richness} - 0.058 \times \text{richness}^2$; $r^2 = 0.32$, $p = 0.003$) and exponential function of realized richness ($\text{stability} = 2.4007 \times (1 - e^{(-0.8184 \times \text{richness})})$; $r^2 = 0.25$, $p = 0.006$). Species richness declined with time, but differences in richness persisted between planted treatments. Realized richness varied from 2–6 species and averaged 2.0, 2.9 and 4.4 species in plots planted to two, four and eight species. Conversely, species evenness treatments converged during the first two growing seasons (Wilsey and Polley 2004). Evenness treatment did not significantly influence stability ($p = 0.69$).

Stability will increase as community ANPP increases provided that the σ of productivity does not increase by a similar or greater fraction and will be greater in communities in

which species vary asynchronously through time. Mean ANPP increased proportionately more than did the σ of productivity among communities (Table 1, among community components), leading to a slight increase in temporal stability at high ANPP. The temporal stability of communities increased linearly as synchrony declined. Synchrony was greater (Fig. 2) and ANPP was smaller (not shown), on average, in mixtures planted to two than four and eight species, but linear and quadratic regression relationships between synchrony and richness were not significant ($p > 0.12$).

Each of the three components of community stability, mean ANPP, the sum of species variances, and species synchrony, was positively correlated with a related index calculated with data from monocultures (Table 1, communities vs stability indices from monocultures). Values for aggregated (abundance-weighted) stability components calculated using monoculture data closely mirrored observed values for two components of community stability, ANPP and the sum of species variances (ratio of observed value to index value = 1.1 and 1.2, respectively). On the other hand, species synchrony in communities (ϕ_b) averaged 50% of the synchrony in ANPP of component monocultures (ϕ_{bM}).

Stability, aggregated trait values and functional diversity

Regression analyses indicated that the fraction of community ANPP produced by the two most abundant species ($\text{fANPP}_{\text{dom}}$) plus community-aggregated values of either the relative maxima ($\text{Rel_max}_{\text{agg}}$), the fraction of sampled root biomass at 20–45 cm depth ($\text{fRoot20_45}_{\text{agg}}$), or the LDMC (LDMC_{agg}) of species grown in monocultures explained 57%, 49% and 42% of the variance in community stability, respectively (Table 1, communities vs plant traits). Community-aggregated values of other traits explained a lesser fraction of the variance in community stability when combined in regression with $\text{fANPP}_{\text{dom}}$ (not shown). Stability was positively correlated with LDMC_{agg} and negatively correlated with each of the other three variables retained in regression models. Stability thus was highest in communities that were not strongly dominated by only two species and in which member species rooted shallowly, had high values of LDMC, or responded to the wettest year with a minimal increase in ANPP when grown in monoculture. Values of $\text{Rel_max}_{\text{agg}}$, $\text{fRoot20_45}_{\text{agg}}$, and LDMC_{agg} were correlated ($p = 0.0001$ – 0.14 for pairwise comparisons). The $\text{Rel_max}_{\text{agg}}$ also was negatively correlated with means of community ANPP ($r^2 = 0.31$, $p = 0.001$), whereas $\text{fANPP}_{\text{dom}}$ was positively correlated with species synchrony in mixtures ($r^2 = 0.33$, $p = 0.001$, $n = 28$). The $\text{fANPP}_{\text{dom}}$ of communities was not significantly correlated with species evenness calculated using mean ANPP per species over 11 years ($p = 0.21$).

Regression equations that included $\text{fANPP}_{\text{dom}}$ and FD_Q calculated using a single plant trait explained a similar or lesser fraction of the variance in community stability than equations in which the trait was modeled as an aggregated value (Table 1; communities vs plant traits). Values of functional diversity calculated using the relative maximum

Table 1. Best regression models for relationships among community stability (μ/σ) and 1) its components, mean ANPP (μ), the standard deviation of community ANPP (σ), and species synchrony (ϕ_b) [among community components], 2) indices of stability components calculated using monoculture data [communities vs stability indices from monocultures], or 3) species richness, abundances, or traits [communities vs plant traits].

Dependent variable	Independent variable(s)	Slope	Intercept	r ²	p-value
Among community components					
Community ANPP (g m ⁻²)	Community σ	0.34	73.43	0.67	<0.0001
Community stability (μ/σ)	Species synchrony (ϕ_b)	-0.81	2.48	0.13	0.05
Communities vs stability indices from monocultures					
Community ANPP (g m ⁻²)	ANPP _{agg}	0.73	164.77	0.66	<0.0001
Community variance (σ^2)	Var _{agg}	0.68	42.12	0.20	0.02
Species synchrony in communities (ϕ_b)	Synchrony of monocultures (ϕ_{bM})	0.76	-0.17	0.39	0.0002
Communities vs plant traits					
<i>Two-variable models</i>					
Community stability (μ/σ)	fANPP _{dom} + Rel_max _{agg}	-1.67/-0.44	4.12	0.57	<0.0001
Community stability (μ/σ)	fANPP _{dom} + fRoot20_45 _{agg}	-1.84/-1.91	4.38	0.49	0.0002
Community stability (μ/σ)	fANPP _{dom} + LDMC _{agg}	-1.88/0.002	3.15	0.42	0.001
Community stability (μ/σ)	fANPP _{dom} + FD_Rmax	-1.95/-1.80	3.93	0.49	0.0002
Community stability (μ/σ)	fANPP _{dom} + FD_Root	-1.89/-2.81	3.86	0.48	0.0003
Community stability (μ/σ)	fANPP _{dom} + FD_LDMC	-1.65/7.44	3.50	0.44	0.0007
<i>Three-variable models</i>					
Community stability (μ/σ)	S _p + S _p ² + r_fANPP _{dom} + Rel_max _{agg}	0.25/-0.022/-2.07/-0.43	2.08	0.69	<0.0001
Community stability (μ/σ)	S _p + S _p ² + r_fANPP _{dom} + fRoot20_45 _{agg}	0.38/-0.035/-2.15/-2.77	2.03	0.69	<0.0001
Community stability (μ/σ)	S _p + S _p ² + r_fANPP _{dom} + LDMC _{agg}	0.46/-0.039/-1.87/0.0015	0.60	0.58	0.0003
Community stability (μ/σ)	S _{r,a} × S _{r,b} + r_fANPP _{dom} + Rel_max _{agg}	11.64/1.83/-2.10/-0.39	-8.92	0.64	<0.0001
Community stability (μ/σ)	S _{r,a} × S _{r,b} + r_fANPP _{dom} + fRoot20_45 _{agg}	6.93/1.54/-2.36/-1.73	-4.08	0.58	0.0004
Community stability (μ/σ)	S _{r,a} × S _{r,b} + r_fANPP _{dom} + LDMC _{agg}	385.9/3.42/-2.06/0.002	-384.4	0.58	0.0003

The stability components calculated using monoculture data include the temporal synchrony of monocultures (ϕ_{bM}) and values for ANPP and the sum of species variances in monocultures (divided by 1000) aggregated at the community level by weighting species values by species relative abundances in communities (ANPP_{agg}, Var_{agg}). Species richness/abundances and traits include planted and realized richness (S_p, S_r), the fraction of community ANPP produced by the two most abundant species (fANPP_{dom}), community-aggregated values and functional trait diversity of the relative maximum of member species (FD_Rmax; Rel_max_{agg}), the fraction of sampled root biomass at 20–45 cm depth (FD_Root; fRoot20_45_{agg}), and leaf dry matter content (FD_LDMC; LDMC_{agg} - mg g⁻¹). Multiple regression analyses were used to model community stability (Communities vs plant traits) as a quadratic function of S_p (S_p, S_p²) or exponential function of S_r [a(1 - e^(-b × S_r)); S_{r,a}, S_{r,b}] and as linear functions of aggregated trait values, functional trait diversity and fANPP_{dom} or r_fANPP_{dom} (variance in fANPP_{dom} not explained by richness).

(FD_Rmax), fraction of root biomass at 20–45 cm depth (FD_Root), and LDMC (FD_LDMC) were correlated (p = 0.0001 to 0.07 for pairwise comparisons). Stability was positively linked to community variation in LDMC and negatively linked to FD_Root and FD_Rmax.

The fANPP_{dom} was not correlated with aggregated trait values (p = 0.26–0.47) or FD_Rmax or FD_Root (p = 0.56–0.80), but was a negative linear function of both planted and realized richness (r² = 0.31 and 0.45, respectively, p < 0.0001). Because fANPP_{dom} and richness were correlated, these two potential predictors of stability exhibited a shared contribution to changes in stability. We modeled effects of planted and realized richness on stability using a sequential regression model in which the variance shared by richness and fANPP_{dom} was assigned to richness. Stability was modeled as a quadratic function of planted richness or exponential function of realized richness and as linear functions of aggregated trait values and residuals from a regression of fANPP_{dom} on richness (r_fANPP_{dom}), where r_fANPP_{dom} represents variance in fANPP_{dom} not explained by planted or realized richness. Including richness in regression models with r_fANPP_{dom} and aggregated trait values explained an additional 12–20% (planted richness) or 7–16% (realized richness) of variance in community stability (Table 1, communities vs

plant traits). Regression models that included planted (or realized) richness, r_fANPP_{dom}, and either Rel_max_{agg}, fRoot20_45_{agg}, or LDMC_{agg} explained 69% (64%), 69% (58%) and 58% (58%) of the variance in community stability, respectively. Regression fits were not improved by adding FD_Q derived from individual traits (not shown).

Discussion

The temporal stability of ANPP varied by a factor of two among grassland communities planted with two, four or eight species in response to a maximum three-fold change in annual precipitation. Stability increased with richness and was greatest in communities that were not strongly dominated by only two species and in which species rooted shallowly, had high values of LDMC, or responded to the wettest year with a minimal increase in ANPP when grown in monoculture. Our analysis extends the demonstration by de Mazancourt et al. (2013) that the stability of community biomass can be predicted from the dynamics of species monocultures by identifying the influence of species relative abundances (fANPP_{dom}) and functional traits on community stability. Our results indicate that the temporal stability of grassland ANPP may depend as much on species

abundance patterns and functional traits linked to plant responses to precipitation variability as on species richness.

The stability of grassland ANPP in the face of precipitation variability depended on species relative abundances as well as functional traits. The greater was the combined abundance of the two dominant species in communities ($fANPP_{dom}$), the greater was the similarity (synchrony) in species responses to environmental variability and the smaller was temporal stability. Interspecific competition is thought to enhance stability by facilitating compensatory dynamics, such that an increase in the production of one or more species is offset by a decrease in production of other species (Tilman et al. 1998, Lehman and Tilman 2000). Interspecific competition likely declines and intraspecific interactions increase in importance as community biomass is increasingly concentrated in few species. In general, dominance and the frequency of intraspecific interactions should also decrease as richness increases.

Communities may be stabilized by adding species that respond differently than current members to environmental fluctuations (Ives et al. 2000). The positive correlation observed between species synchrony in grassland communities and the synchrony among member species when grown in monocultures is consistent with the view that stability was greater in communities with species that responded differently to precipitation variability. On the other hand, species synchrony in communities (ϕ_b) averaged 50% of the synchrony of species monocultures (ϕ_{bM}), evidence that interspecific interactions reduced species correlations in mixtures and increased community stability (Gross et al. unpubl.). Of the variables included in our regression analyses of community stability, $fANPP_{dom}$ rather than aggregated trait values correlated most strongly with ϕ_b . Synchrony in communities may be difficult to predict from species traits or the environmental responses of monocultures alone.

Communities may be stabilized by species that respond relatively little to environmental fluctuations (Lepš 2004, Polley et al. 2007, Derner et al. 2011, Sasaki and Lauenroth 2011). This effect, wherein stable species contribute to stable communities, is consistent with evidence that ecosystem processes often depend more on species identity and specifically, the functional traits of dominant species, than diversity per se (Grime 1998, Griffin et al. 2009, Roscher et al. 2012). In our experiment, stability was greatest in communities dominated by species that responded to the wettest year with the smallest relative increase in production. A species' environmental response, like its potential productivity, is an intrinsic, functional property (de Mazancourt et al. 2013) that is related to plant traits (Díaz and Cabido 2001). ANPP was comparably insensitive to high precipitation in species that rooted shallowly and had high values of LDMC, the latter often taken as an indication of leaf tissue density. Species that root shallowly will have limited access to water that percolates through the upper 20 cm of soil during wet years. On the other hand LDMC often is negatively correlated to plant relative growth rate (Reich et al. 1992), implying that LDMC will correlate negatively with the ANPP response to favorable growth conditions. LDMC and the fraction of sampled root biomass at 20–45 cm depth constitute functional response traits (Díaz and Cabido 2001, Naeem and

Wright 2003), species traits that regulate the response of plant communities to variability in precipitation.

Stability in ANPP was determined by trait values of the dominant contributors to community productivity. Trait distribution (functional diversity) apparently played a complementary role, but did not improve the prediction of stability after we accounted for effects of community-weighted mean traits. Roscher et al. (2012) found that community productivity was better explained by traits of dominant species than functional diversity.

Stability may not have correlated as strongly with species relative abundances and traits had diversity effects been more strongly expressed in this experiment. An underlying assumption of our attempt to predict community stability from the abundance and traits of species is that stability is determined more by species environmental responses than species interactions. Greater richness increases community stability partly by promoting interspecific competition and compensatory dynamics among species (Tilman et al. 1998, Gross et al. unpubl.). The greater is the contribution of competition-caused compensation to community stability, the weaker will be the link between stability and the traits or monoculture dynamics of member species. On the other hand, greater richness need not weaken trait-based predictions of community dynamics if richness serves mainly to increase the number of species that respond differently to the environment (Doak et al. 1998, Ives et al. 2000).

Rarely have quantitative traits that are linked to plant processes been used to characterize the variability or stability of processes. We demonstrate that community stability may be predicted from species traits and species relative abundances in communities, at least in the specific case in which richness is relatively low and variability in ANPP is caused by fluctuation in precipitation. Precipitation variability is a widely-recognized driver of variability in grassland ANPP (Paruelo et al. 1999, Knapp and Smith 2001, Huxman et al. 2004). We anticipate that a trait-based approach to predicting stability will be especially useful when plant communities are dominated by few species of a single growth type and inter-annual variability in ANPP results mainly from fluctuations in a single environmental variable such as precipitation. Our results indicate that the temporal stability of grassland ANPP may depend as much on species abundance patterns and functional traits linked to plant responses to precipitation variability as on species richness.

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