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Variability in community productivity—mediating effects of vegetation attributes

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2. Aggregate communities were created by combining patches of spatially distinct communities of perennial plant species from grassland biodiversity experiments in Texas, USA. Interannual variability in above-ground net primary productivity (ANPP) of aggregate communities was analysed as a function of two multiplicative components, mean temporal variability in the ANPP of patches and temporal synchrony in ANPP dynamics among patches. We used regression analyses to determine whether temporal variability in aggregate ANPP and its components were correlated with either species diversity or community-weighted SLA over 5 years.
3. Temporal variability in ANPP of aggregate communities was strongly correlated with temporal variability in patch ANPP. Increasing mean SLA reduced ANPP variability of aggregate communities by increasing mean productivity. Increased temporal changes in patch-scale SLA further reduced temporal variability in aggregate ANPP by reducing effects of precipitation fluctuations on productivity. Conversely, increasing species diversity over the narrow range measured increased temporal variability in aggregate ANPP. High diversity was associated with reduced dominance of temporally stable C4 grasses.
4. Our results implicate means and patch-scale temporal dynamics in community SLA as potential indicators of variability in grassland primary productivity through time.

Keywords
diversity, exotic species, functional trait, grassland, precipitation, spatial scale, specific leaf area, stability

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RESEARCH ARTICLE

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1 | INTRODUCTION

Ecosystem processes vary through time in response to disturbances and environmental fluctuations. Learning to reduce process variability, particularly temporal variability in primary productivity, is a frequent goal of management with clear relevance to sustaining ecosystem services for an expanding human population. Prerequisite to stabilizing productivity is improved understanding of how biological attributes of ecosystems interact with environmental fluctuations to affect temporal variability in plant growth.

At any given spatial scale, temporal variability in productivity, as in other ecosystem processes, is a function of both temporal variability of smaller scale components and temporal synchrony in response among components (Wang & Loreau, 2014, 2016; Figure 1). This variability partitioning approach implies that variability in above-ground net primary productivity (ANPP) of plant communities is positively correlated with both the variability in productivity of component species and similarity in species growth responses to environmental fluctuations through time (synchrony). Similarly, variability in processes at the larger spatial scale of aggregate communities depends on process variability of component communities (patches) and temporal synchrony in processes among patches. Variability in aggregate ANPP is reduced when productivity varies relatively little through time in patches or ANPP responds asynchronously to environmental fluctuations among patches. Aggregate temporal variability will depend primarily on average variability in patch ANPP if patches respond synchronously to fluctuations in the environment. Conversely, aggregate variability will depend at least partly on patch asynchrony if ANPP responds differently to fluctuations among patches.

Temporal variability in ANPP differs among plant communities because communities differ in functional attributes (traits) that mediate the response of productivity to environmental variation (Figure 2). Functional attributes include species richness and diversity (Hautier et al., 2014), the identity and stability of dominant species (Polley, Wilsey, & Derner, 2007; Wilsey, Daneshgar, Hofmockel, & Polley, 2014), and community functional composition or identity (Mouillot, Villéger, Scherer-Lorenzen, & Mason, 2011; Polley, Isbell, & Wilsey, 2013), one index of which is the species abundance-weighted (community-weighted) value of specific leaf area (SLA; leaf area per unit of biomass). Weighted SLA has been shown to correlate with productivity and productivity responses to the environment at the ecosystem scale (Díaz et al., 2007; Garnier et al., 2004; Ma, Baldocchi, Mambelli, & Dawson, 2011; Zheng et al., 2010) and is one component of a suite of community-weighted traits that affected ANPP along a regional water gradient (Wu, Wurst, & Zhang, 2016). Spatial differences in weighted SLA would be expected to reduce ANPP variability of aggregate communities by increasing asynchrony in the ANPP responses of patches. To our knowledge, however, weighted SLA has not been linked explicitly to process variability at different spatial scales. On the other hand, scores of studies have shown that high levels of plant species diversity, as determined by both the number (richness) and relative abundances of species (evenness), are associated with reduced variability and increased stability of ANPP at small spatial scales (e.g. Craven et al., 2016; de Mazancourt et al., 2013; Gross et al., 2014; Hector et al., 2010; Isbell, Polley, & Wilsey, 2009; Tilman, Reich, & Knops, 2006). Diversity is associated with a variety of mechanisms that stabilize productivity. These mechanisms include performance-enhancing effects that increase productivity more than expected based on the productivity of monocultures of component species (overyielding) and buffering effects that decrease temporal variability in productivity (Yachi & Loreau, 1999). Species diversity also may reduce variability at large spatial scales by reducing patch-scale variability and increasing asynchrony (Wang & Loreau, 2016).

Community attributes that affect variability typically also respond to environmental and other drivers of variability (Figure 2). Weighted SLA and diversity, for example, are both “effect” and “response” traits (Lavorel & Garnier, 2002; Suding et al., 2008). SLA and diversity are effect traits in the sense that both attributes are correlated with or influence productivity and productivity responses to environmental variation (Garnier et al., 2004; Hautier et al., 2014; Isbell et al.,

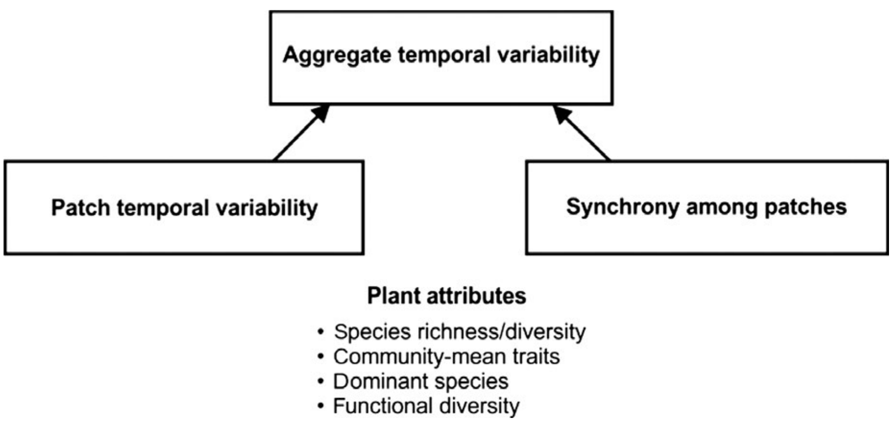

FIGURE 1 Temporal variability in ecosystem processes at any spatial scale (aggregate variability) is a function of temporal variability in processes of spatial components of the aggregate (patch variability) and the extent to which processes respond similarly among components to the factors that cause variability (synchrony in processes among patches). Listed are examples of plant attributes/traits that mediate environmental effects on above-ground net primary productivity (ANPP) variability

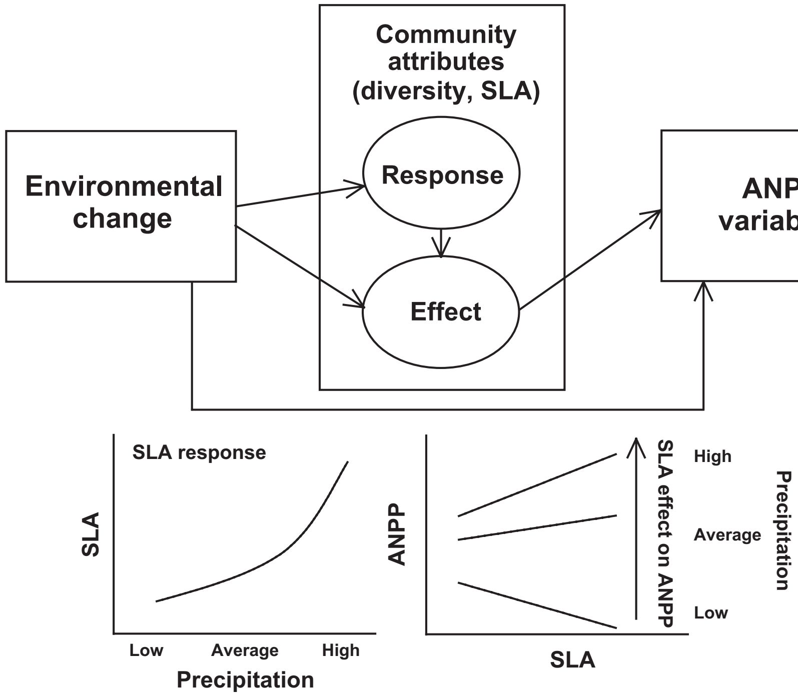

FIGURE 2 Community attributes such as species diversity and abundance-weighted specific leaf area (SLA) mediate the influence of environmental change on variability in above-ground productivity (ANPP) via attribute responses to the environment and temporally variable effects on ANPP. Diversity effects on ANPP may operate via a variety of mechanisms (e.g. overyielding, statistical averaging and asynchrony). Effects of weighted SLA on ANPP-environmental relationships derive from a positive association between SLA and plant growth rate. Graphs in the lower part of the figure illustrate possible impacts of interannual differences in precipitation (i.e. environmental change) on community SLA (SLA response) and slopes of ANPP-SLA relationships (SLA effect on ANPP). Graphs depict trends anticipated when assessed at the aggregate community scale. The figure is adapted from Suding et al. (2008)

2015; Polley, Gibson, Fay, & Wilsey, 2016). SLA and diversity also are community-level response traits, values of which may change in response to environmental drivers of ANPP that alter species composition or abundances (Lavorel & Garnier, 2002; Pfestorf et al., 2013; Wilsey et al., 2014). Attribute effects on productivity will differ among years if ANPP responds more to environmental change in communities with high or low SLA or diversity than the converse, as illustrated in the lower right panel of Figure 2 as interannual variation in the slope of ANPP-SLA regressions. Alternatively, environmental effects on ANPP will be mediated by the SLA or diversity response to the environment, as illustrated in the lower left panel of Figure 2, if the attribute effect on ANPP (e.g. slope of ANPP-attribute regression) remains constant among years. A positive feedback of attributes on ANPP occurs when environmental change both increases attribute values and increases the attribute effect on ANPP by increasing the slope of the ANPP-attribute regression. Such a positive feedback would also amplify the influence of environmental variability on ANPP variability.

We applied the variability partitioning approach (Figure 1) and response–effect framework (Figure 2) to data from experimental grassland communities (patches) that were grown on the same soil type and exposed to the same variation in weather. We address two objectives: (1) determine the contributions of synchrony and mean temporal variability in patch ANPP to temporal variability in aggregate ANPP and (2) investigate links between temporal variability in ANPP and mean and temporal variability in species diversity and weighted SLA. The ANPP of the communities we studied typically fluctuates in response to interannual change in precipitation (Wilsey et al., 2014; Xu, Polley, Hofmockel, & Wilsey, 2017). We tested three predictions. First, we predicted that aggregate variability in ANPP, measured as the square of the temporal CV [$(\delta/\mu)^2$] of ANPP, would be more highly correlated with temporal variability of patches than with synchrony in ANPP among patches (Figure 1). Strong environmental correlations among patches we studied should synchronize the ANPP responses of species in space (Hudson & Cattadori, 1999). Aggregate variability in ANPP correlated more strongly with patch variability than asynchrony in a study of 62 plant communities (Wilcox et al., 2017). Second, we predicted that increasing mean SLA or diversity would reduce temporal variability in aggregate ANPP by increasing the multiyear mean of productivity, as anticipated if ANPP is positively correlated to SLA and diversity during most years (Figure 2; lower right panel). Third, we predicted a positive correlation between the statistical variance (δ^2) in ANPP among years and variances in SLA and diversity. A positive correlation between statistical variances in ANPP and SLA or diversity is anticipated if environmental change during a given year either increases or decreases SLA and diversity, and the slope of ANPP-SLA and ANPP-diversity regressions is similar among years (Figure 2, lower panels). A given change in SLA or diversity will elicit a comparable change in ANPP among years when regression slopes are conserved through time.

2 | MATERIALS AND METHODS

2.1 | Field plots/aggregate communities

We used data from biodiversity ecosystem function (BEF) experiments in central Texas, USA (31°05′N, 97°20′W), to evaluate roles of species diversity and weighted SLA in mediating effects of interannual fluctuations in precipitation on temporal variability of ANPP. Aggregate communities were created by combining 1 × 1 m patches planted with differing mixtures of perennial plant species. We compared aggregate communities composed of a fixed number of patches (21 m^2 in area). ANPP-SLA and ANPP-diversity correlations can be spuriously inflated in comparisons among communities composed of differing numbers of patches when, as here, patch-scale variation in ANPP, SLA and diversity is relatively limited.

Aggregate communities were created from various combinations of patches included in the Evenness-Richness (ER) and Maintenance of Exotic vs. Native Diversity (MEND) experiments. ER and MEND both are two-way factorial experiments applied using a randomized block design. The ER experiment included species evenness (high/low) × species richness (2, 4, 8 species/m^2) treatments (Wilsey & Polley, 2004). MEND included species origin (Native/Exotic) × irrigation (irrigated during summer/not irrigated) treatments (Wilsey, Daneshgar, & Polley, 2011). Equal-sized seedlings of perennial species were transplanted into 1 × 1 m field plots (96 and 72 individuals/m^2 for ER and MEND, respectively). ER included 36 species mixtures in three blocks planted in April 2001. MEND included 64 species mixtures in two blocks, one planted in October 2007 and one planted in March 2008. Volunteer plants were removed by hand. No fertilizer was added to either experiment.

ER mixtures were populated by random draw from a pool of 13 native and exotic perennial species, including five native C_4 grasses, three exotic C_4 grasses, one native C_3 grass and four native C_3 non-leguminous forbs (Isbell et al., 2009; Wilsey & Polley, 2004). Each richness treatment of a given composition was planted at both high and low species evenness levels. Mixtures assigned to the high evenness treatment were planted with the same number of individuals of each member species. Species relative abundances in the low evenness treatment were distributed geometrically (64:32 in 2-species mixtures, 51:26:13:6 in 4-species mixtures and 47:24:12:6:3:2:1:1 in 8-species mixtures).

The species composition of MEND mixtures was determined by random draw from a pool of 18 native or 18 exotic species with the condition that the relative abundances of functional groups of species (C_4 grasses, C_3 grasses, legumes, non-leguminous C_3 forbs) remain constant across mixture patches (Wilsey, Teaschner, Daneshgar, Isbell, & Polley, 2009; Wilsey et al., 2011, 2014). For each random selection of nine native species, we populated one native and one exotic mixture (=draw), the latter by selecting the exotic species that were most closely phylogenetically related to selected natives. Four draws were included in each of the two blocks. Each draw was replicated within each treatment (origin, irrigation) for a total of 32 mixture plots per block (4 draws × 2 origin treatments × 2 irrigation treatments × 2 replicates). Irrigation was applied by hand during the typically dry period of mid-July to mid-August each year at a rate of 128 mm per month. Irrigation was applied as eight events per year of 16 mm each beginning in 2008.

ER and MEND plantings are separated by about 0.5 km on a silty clay soil. Annual precipitation at the site averages 875 mm (91-year record). The year 2011 was one of severe drought during which annual precipitation (November through October) was 41% of the mean for the site.

Before creating aggregate communities, we deleted the four patches with lowest ANPP in which virtually all transplants had died and grouped the remaining 56 ER plus MEND patches into three categories based on the 5-year (2008–2012) average of ANPP (300–420, 421–520, 521–849 g/m^2; n = 18, 20 and 18 for low, medium and high ANPP patch categories, respectively). Forty-two aggregate communities each with 21 patches (slightly > one-third the total number of patches considered) were created by combining patches chosen randomly from each of the three ANPP categories (See Figure S1). To increase the range of ANPP values of aggregate communities, we selected as many as 14 and as few as 0 patches from a given ANPP category. Aggregate communities of all possible permutations of each of the following 3-category groupings of patches: n = 14, 7, 0; 14, 5, 2; 12, 7, 2; 12, 5, 4; 10, 7, 4; 10, 6, 5; and 8, 7, 6 patches per category, were created from low, medium and high ANPP patch categories (n = 7 groupings × 6 permutations/grouping = 42 aggregate communities).

2.2 | Calculation of ANPP, SLA and diversity

ANPP of ER patches was estimated annually by weighing above-ground material that was clipped by species from entire plots near the end of each growing season (October) and dried to constant mass. ANPP of each MEND patch was calculated by summing maximum values of above-ground biomass of each species measured non-destructively in June and October of each year using a point intercept technique (Wilsey et al., 2011). Regression relationships between the number of intercepts per species and species biomass were used to calculate above-ground biomass per species. ANPP and biomass per species were averaged for the two replicates within each treatment (origin, irrigation) and block of MEND that were planted to the same initial species composition and abundances for a total of 32 patches.

Specific leaf area (SLA) was calculated for each species in ER and MEND mixtures from measurements on fully expanded leaves in the upper canopy of each species. We measured the area and dry mass of selected upper leaves collected from plants grown in monocultures of each experiment in June 2010 (ER) and June 2014 (MEND) using methods suggested by Cornelissen et al. (2003). We calculated a community-weighted mean of SLA for each mixture and year by weighting SLA values of each species by the relative abundance of the species in the community (Garnier et al., 2004; Grime, 1998). Abundance-weighted SLA can be thought of as the SLA value most likely to be measured in a random sample from the community (Díaz & Cabido, 2001).

Species diversity was calculated using Simpson's Reciprocal Index (Wang & Loreau, 2016). The ANPP-weighted mean of the diversity of patches in each aggregate community (alpha diversity; α_D) was calculated as follows: $1/\sum_l \omega_l \phi_l$, where $\phi_l = \sum_i p_{il}^2$ and p_{il} is the relative ANPP of species i in patch l and ω_l equals ANPP for patch l divided by ANPP of the aggregate community. Patch-scale variance in diversity for each aggregate community was calculated by squaring the sum of the temporal standard deviation of the diversity of patches i through n $\left[\left(\sum_i^n \delta_{\text{diversity}_i}\right)^2\right]$. Spatiotemporal variation in diversity and weighted SLA reflected both patch differences in species composition at planting and temporal change in species abundances resulting from species interactions as influenced by interannual variation in weather.

2.3 | Calculation of ANPP variability

Following theory developed by Wang and Loreau (2014), we define aggregate (γ) and patch-scale (α) variability in ANPP as the squared coefficient of temporal variation of ANPP at the aggregate (γ_{cv}) and patch spatial scales (α_{cv}), respectively. Both the temporal standard deviation and multiyear mean of aggregate community ANPP are calculated using annual sums of ANPP across the patches that together form the aggregate community. α_{cv} is calculated by squaring the value obtained by dividing the sum of the temporal standard deviations of the ANPP for patches i through n $\left[\left(\sum_i^n \delta\, \alpha_{\text{ANPP}_i}\right)^2\right]$ by the aggregate mean of ANPP (γ_μ). γ_{cv} and α_{cv} are linked by an index of spatial synchrony, φ, which varies between 0 and 1.

$$\gamma_{cv} = \alpha_{cv} \times \varphi, \tag{1}$$

where φ is the ratio of the variance of aggregate ANPP [$(\gamma_\delta)^2$] to the squared value of the sum of the temporal standard deviations of the ANPP of patches $\left[\left(\sum_i^n \delta\, \alpha_{\text{ANPP}_i}\right)^2\right]$. Synchrony ($\varphi$) is a measure of the fraction by which a unit increase in α_{cv} increases γ_{cv}. γ_{cv} is more strongly linked to α_{cv} when temporal dynamics in patch productivity are synchronous than asynchronous (Wang & Loreau, 2014). γ_{cv} and α_{cv} of ANPP may be reduced by increasing mean ANPP, reducing the statistical variance in ANPP or some combination of the two. Temporal variability in ANPP was calculated using ER and MEND data from 2008 to 2012.

2.4 | Statistics

We used regression analyses to assess links between γ_{cv} and α_{cv} and both species diversity and the means and variances in weighted SLA. To determine whether the SLA effect on ANPP differed among years, ANPP and SLA data from all years and 1 × 1 m patches were entered into a separate-slopes regression model (e.g. Hui, Luo, & Katul, 2003). A climatic effect on the ANPP-SLA relationship was detected if the slope of the ANPP-SLA regression differed significantly among one or more years. A separate-slopes regression model also was used to test for interannual change in the diversity effect on ANPP. Bivariate regression was used to determine contributions of precipitation to interannual variation in ANPP-SLA and ANPP-diversity slopes.

3 | RESULTS

3.1 | Precipitation—an environmental driver of ANPP and SLA

ANPP varied among years largely because annual precipitation varied. Mean ANPP of the 56 patches analysed increased as a linear function of precipitation summed from February through July each year (Figure S2). The ANPP-precipitation relationship clearly was defined by reduced ANPP during the drought year of 2011 (precipitation = 18.4 cm). ANPP varied independently of precipitation across the four "non-drought" years (p = .92).

Precipitation increased weighted SLA (SLA response) and altered the SLA effect on ANPP (SLA effect). SLA ranged from 7.5 to 19.5 m^2/kg among patches. The annual mean of patch SLA (n = 56) varied from 13.5 to 14.1 as an exponential function of February–July precipitation (Figure S2). The SLA effect on ANPP differed with precipitation. A regression model in which ANPP-SLA slopes were allowed to vary among years explained 57% of the variance in ANPP among patches (p < .0001, n = 280). Slopes of ANPP-SLA regressions ranged between a drought year low of −17.0 and a high of 23.3 g/m^2 ANPP per m^2/kg change in SLA (M = 7.6 g/m^2 per m^2/kg). Interannual differences in slopes were positively correlated to February through April precipitation (not shown; adj. r^2 = .66, p = .06). For a given increase in SLA, ANPP thus increased more during wet than dry or average precipitation years, indicative of a positive effect of SLA on the ANPP-precipitation response. By contrast, the annual mean of patch diversity (n = 56) varied independently of precipitation (p = .92). Slopes of patch ANPP vs. diversity regressions were significant in only 2 of 5 years (not shown).

3.2 | Partitioning of ANPP variability

ANPP differed between a mean of 305–850 g/m^2 among patches and from 413 to 547 g/m^2 among the 42 aggregate communities analysed. Temporal variability in ANPP at the spatial scale of aggregate communities (γ_{cv}) was strongly positively correlated to temporal variability in ANPP at the spatial scale of the patch (α_{cv}; Figure 3). γ_{cv} also was positively correlated with synchrony (φ), although less strongly so than with α_{cv}.

3.3 | Links between attributes and ANPP variability

Both SLA and diversity mediated precipitation effects on ANPP variability. Unexpectedly, temporal variability in ANPP of both aggregate communities (γ_{cv}) and patches (α_{cv}) was positively correlated to diversity (α_D; Figure 4). Increasing α_D over the narrow range measured increased variability and thereby destabilized productivity by

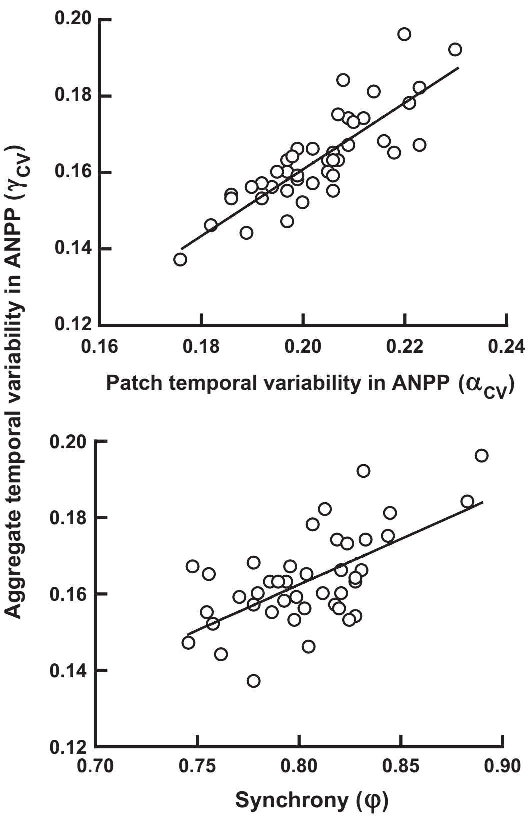

FIGURE 3 Temporal variability in above-ground net primary productivity (ANPP) at the spatial scale of the aggregate community (γ_{cv}) was more strongly correlated with ANPP variability at the patch scale (α_{cv}; adj. r^2 = .69, p < .0001) than with synchrony in ANPP dynamics among patches (φ; adj. r^2 = .38, p < .0001, n = 42). Temporal variability is defined as the squared coefficient of temporal variation. Aggregate communities were created by pooling data from different combinations of grassland patches

reducing the aggregate mean of ANPP (γ_μ; Figure 5). Productivity varied less at low than high diversity apparently because the exotic C_4 grasses (e.g. *Panicum coloratum* L., *Sorghum halepense* (L.) Pers., *Eragrostis curvula* (Schrad.) Nees) that dominated low-diversity patches exhibited both high productivity and low interannual variability (Wilsey et al., 2014). By contrast, both γ_{cv} and α_{cv} decreased as SLA of aggregate communities (γ_{SLA}) increased (Figure 4). γ_{cv} and α_{cv} decreased as γ_{SLA} increased because γ_μ, the denominator in both indices of variability, γ_{cv} [= $(\gamma_\delta/\gamma_\mu)^2$] and α_{cv} $\left[=\left(\left(\sum_i^n \delta\, \alpha_{\mathrm{ANPP}_i}\right)/\gamma_\mu\right)^2\right]$, increased as γ_{SLA} rose (Figure 5). The variance in aggregate ANPP was a positive function of γ_μ when plotted on a log–log scale, with a slope = 1.9 (not shown; adj. r^2 = .78, p < .0001, n = 42). At slopes between 1 and 2, temporal variability in aggregate ANPP declines as mean ANPP increases. Because γ_μ was positively correlated with γ_{SLA}, aggregate communities were stabilized by increasing SLA as predicted.

As also predicted, statistical variance in aggregate ANPP [$(\gamma_\delta)^2$] increased as variance in patch diversity increased $\left[\left(\sum_i^n \delta_{\mathrm{diversity}_i}\right)^2\right]$. But contrary to prediction, $(\gamma_\delta)^2$ either was not correlated with temporal variance in aggregate SLA (p = .46) or was reduced, rather than increased, by heightened interannual variance in the SLA of patches $\left[\left(\sum_i^n \delta_{\mathrm{SLA}_i}\right)^2\text{; Figure 6}\right]$. Inconsistencies in the sign of the response of patch SLA to precipitation contributed to this stabilizing (reduced variance) effect of SLA variability on ANPP. Covariance between SLA and precipitation was negative for 20 of 56 patches (range −0.01 to −15.38; mean covariance across patches = 2.0), rather than positive as expected from the relationship between SLA averages and precipitation (Figure S2). As a result, the positive effect of precipitation on slopes of ANPP-SLA relationships was not consistently reinforced by a precipitation-driven increase in SLA.

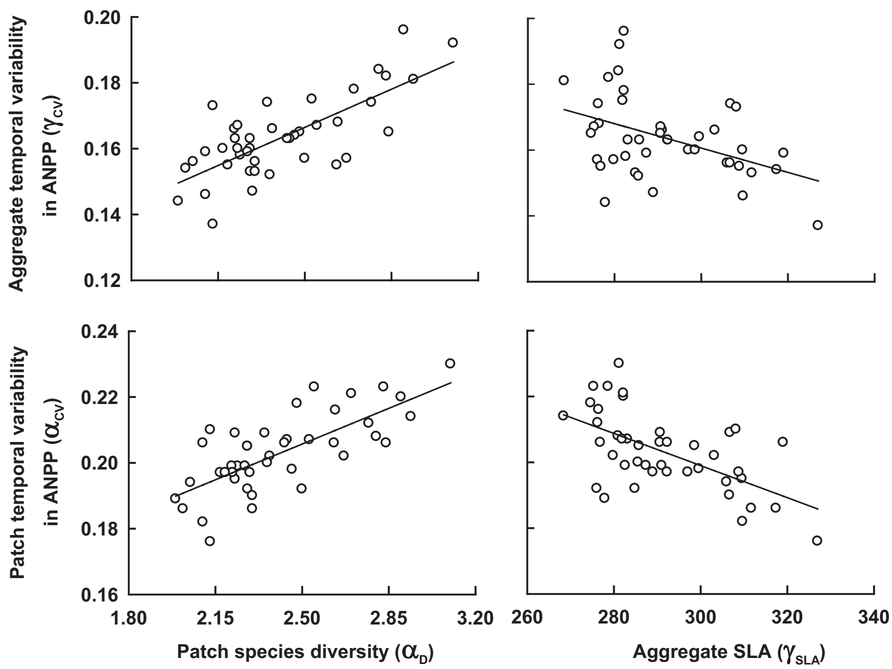

FIGURE 4 Temporal variability in the above-ground net primary productivity (ANPP) of both aggregate communities (γ_{cv}) and patches (α_{cv}) was positively correlated to patch-scale species diversity (α_D; adj. r^2 = .54 and .52, respectively, p < .0001) but negatively correlated to aggregate community specific leaf area (SLA) (γ_{SLA}; adj. r^2 = .17 and .34, p = .004 and < .0001, respectively, n = 42)

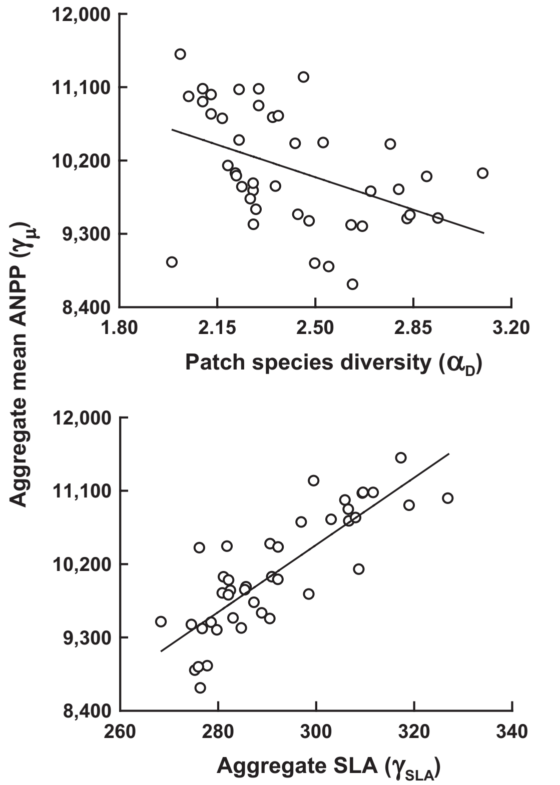

FIGURE 5 The mean of aggregate above-ground net primary productivity (ANPP) (γ_μ) was negatively correlated with patch-scale diversity (α_D; adj. r^2 = .17, p = .004, n = 42) but positively correlated with aggregate specific leaf area (SLA) (γ_{SLA}; adj. r^2 = .68, p < .0001)

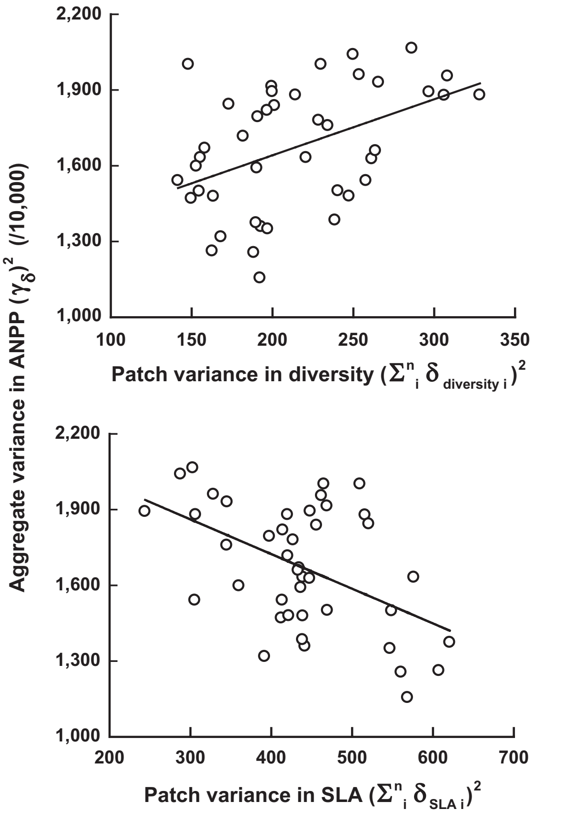

FIGURE 6 The temporal variance in above-ground net primary productivity (ANPP) of aggregate communities [$(\gamma_\delta)^2$] was positively correlated to temporal variance in the diversity of component patches [$\left(\sum_i^n \delta_{\text{diversity}_i}\right)^2$; adj. r^2 = .18, p = .003, n = 42] but negatively correlated to temporal variance in patch specific leaf area (SLA) [$\left(\sum_i^n \delta_{\text{SLA}_i}\right)^2$; adj. r^2 = .22, p = .001]

4 | DISCUSSION

Our analyses revealed links between means and variability in weighted SLA and both patch- and aggregate-scale temporal variability in ANPP of grassland communities. The ANPP of aggregate communities varied among years because patch-scale ANPP varied, as predicted. Increased SLA increased the mean of aggregate ANPP, as also predicted. By contrast, heightened interannual variance in patch SLA (SLA response to precipitation) reduced variance in aggregate ANPP. Interannual increases in precipitation increased SLA in some patches but reduced SLA in other patches. This difference in the sign of the SLA response to precipitation among patches reduced precipitation effects on ANPP by lessening the influence of precipitation-caused change in ANPP-SLA slopes on productivity. The net effect of increased mean SLA was to stabilize aggregate ANPP largely by increasing average productivity. Conversely, increasing species diversity over the narrow range measured destabilized productivity by reducing mean ANPP. Stability was greater at low than high diversity because productivity of the exotic C_4 grasses that dominated low-diversity patches varied relatively little among years (Wilsey et al., 2014). Our results demonstrate that community SLA mediated the response of grassland ANPP to interannual variation in precipitation via patch differences in the SLA response to precipitation and temporally variable SLA effects on the ANPP. Variability in aggregate ANPP was reduced by both high values of SLA at the aggregate community scale and large interannual variation in the SLA at the patch scale. More generally, our results implicate SLA means and the SLA response to precipitation as indicators of differences in ANPP variability among grassland communities.

Variability at aggregate spatial scales depends on both patch-scale variability and synchrony in dynamics among patches (McGranahan et al., 2016; Wang & Loreau, 2014). The ANPP of the aggregate communities we studied varied among years mainly because patch-scale ANPP varied. Wilcox et al. (2017) reached a similar conclusion in a study of species abundance data from 62 grasslands, finding that local-scale stability explained almost two-thirds of variance in aggregate-scale stability. Synchrony equals the proportion by which a unit increase in patch variability increases aggregate variability. Synchrony averaged 0.8 among patches across the 42 aggregate communities analysed. Temporal variability in ANPP decreases in scaling from local to larger areas (Wang & Loreau, 2014), in this analysis by 20%.

Increasing SLA reduced temporal variability in both patches and aggregate communities by increasing mean productivity. SLA was positively correlated to the average maximum value of gross primary productivity of the exotic and native communities studied (Polley et al., 2016). ANPP and SLA usually are positively correlated, as high values of SLA are associated with rapid growth of plants and plant communities (Garnier et al., 2004; Reich, Walters, & Ellsworth, 1997).

Patch differences in the SLA response to precipitation (response diversity) reduced the impact of interannual shifts in ANPP-SLA slopes on ANPP, an insurance effect (Yachi & Loreau, 1999). As a result, precipitation fluctuations did not consistently increase abundances of species with either high or low SLA values and, therefore, with either a strong negative or positive effect on ANPP.

Community SLA varied among years in this experiment because species relative abundances varied. The presence of strong dominants in some patches limited interannual variation in species abundances and may explain inconsistency in the relationship between precipitation and patch SLA. Fifteen of 22 patches with negative covariance between SLA and precipitation were dominated by pairs of exotic grasses (*P. coloratum* and *S. halepense*, 52–89% of total ANPP; *P. coloratum* and *E. curvula*, 37–77% of total ANPP) or by the native forb, *Ratibida columnifera* (Nutt.) Wooton & Standl. (35–50% of total ANPP), for example. Alternately, growth responses of some species to precipitation may have depended on traits other than SLA. The trend in SLA of individual species across a gradient in incident solar radiation was weaker than that for community SLA (Ackerly, Knight, Weiss, Barton, & Starmer, 2002), for example. If precipitation had consistently increased SLA, we likely would have observed a greater precipitation enhancement of ANPP and a positive correlation between statistical variances in ANPP and SLA.

Increasing species diversity increased temporal variability in patch and aggregate ANPP, opposite trends expected from numerous experiments on small spatial scales (e.g. Craven et al., 2016; de Mazancourt et al., 2013; Gross et al., 2014; Hector et al., 2010; Isbell et al., 2009; Tilman et al., 2006). Increasing diversity increased variability in and thereby destabilized productivity in our experiment partly by reducing mean ANPP. The exotic C_4 grasses that dominated low-diversity patches were both highly productive and relatively insensitive to interannual variation in weather (Wilsey et al., 2014), contributing to the reduction in temporal variability in ANPP at low diversity. Greater diversity may have reduced ANPP variability, as expected from most experiments and a recent modelling study (Wang & Loreau, 2016), had a greater range in species diversity been considered. On the other hand, Wilcox et al. (2017) found no correlation between the mean of species diversity of patches and temporal variability at either the patch or aggregate scales in an analysis of data from 62 plant communities. Pfestorf et al. (2013) and Debouk, de Bello, and Sebastià (2015) both reported finding a more direct coupling between environmental drivers and plant functional traits than diversity. Aggregate ANPP in our study was stabilized through time by attributes linked to species identity and dominance rather than by species richness.

Specifics of applying the response–effect framework to link vegetation attributes to ANPP variability will depend on the primary driver of interannual variability in ANPP and the community attribute or attributes considered. In general, we expect a stronger coupling of ANPP to driver variation when both the attribute and ANPP-attribute relationships respond to interannual change in drivers. A strong coupling of attribute effect and response often is observed when canopy-based traits are considered and resources drive ANPP variation (Lavorel & Garnier, 2002). The effect and response were positive, on average, for SLA and ANPP-SLA relationships in the face of precipitation fluctuation, but drivers may influence attribute effects and responses negatively or differentially. For example, evidence implies that both the mean effect of weighted leaf dry matter content (LDMC) on ANPP (Ansquer, Duru, Theau, & Cruz, 2009) and response of LDMC to grazing disturbance are negative (Pfestorf et al., 2013).

In our study, and as may be common at spatial scales over which soils, vegetation and the environment (weather) are similar among local communities, patch dynamics were highly synchronous and aggregate variability in ANPP was determined mainly by patch variability in productivity. Similar environmental conditions among patches should lead to strong synchrony in vegetation dynamics (the Moran effect; Hudson & Cattadori, 1999) and to near-maximal expression of attribute effects on ANPP. The small size of the patches we studied likely reduced capacity for temporal shifts in species abundance and weighted SLA. Whether the ANPP-SLA correlations observed remain consistent over temporal and spatial scales that present greater variation in SLA remains to be determined. Nevertheless, spatial and temporal variability of ANPP and SLA were highly correlated in the communities we studied, implicating patterns and dynamics in weighted SLA as indicative of variability in primary productivity of grassland communities.

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AUTHORS' CONTRIBUTIONS

B.J.W. conceived BEF experiments. H.W.P. conceived this analysis and wrote the initial draft. Both authors contributed to data collection and processing and the final version of the manuscript.

DATA ACCESSIBILITY

Data deposited in the Dryad Digital Repository https://doi.org/10.5061/dryad.5g1d01v, (Polley & Wilsey, 2018).

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