RESEARCH PAPER

Climate and local environment structure asynchrony and the stability of primary production in grasslands

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Abstract

Aim: Climate variability threatens to destabilize production in many ecosystems. Asynchronous species dynamics may buffer against such variability when a decrease in performance by some species is offset by an increase in performance of others. However, high climatic variability can eliminate species through stochastic extinctions or cause similar stress responses among species that reduce buffering. Local conditions, such as soil nutrients, can also alter production stability directly or by influencing asynchrony. We test these hypotheses using a globally distributed sampling experiment.

Location: Grasslands in North America, Europe and Australia.

Time period: Annual surveys over 5 year intervals occurring between 2007 and 2014.

Major taxa studied: Herbaceous plants.

Methods: We sampled annually the per species cover and aboveground community biomass [net primary productivity (NPP)], plus soil chemical properties, in 29 grasslands. We tested how soil conditions, combined with variability in precipitation and temperature, affect species richness, asynchrony and temporal stability of primary productivity. We used bivariate relationships and structural equation modelling to examine proximate and ultimate relationships.

Results: Climate variability strongly predicted asynchrony, whereas NPP stability was more related to soil conditions. Species richness was structured by both climate variability and soils and, in turn, increased asynchrony. Variability in temperature and precipitation caused a unimodal asynchrony response, with asynchrony being lowest at low and high climate variability. Climate impacted stability indirectly, through its effect on asynchrony, with stability increasing at higher asynchrony owing to lower inter-annual variability in NPP. Soil conditions had no detectable effect on asynchrony but increased stability by increasing the mean NPP, especially when soil organic matter was high.

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Main conclusions: We found globally consistent evidence that climate modulates species asynchrony but that the direct effect on stability is low relative to local soil conditions. Nonetheless, our observed unimodal responses to variability in temperature and precipitation suggest asynchrony thresholds, beyond which there are detectable destabilizing impacts of climate on primary productivity.

1 | INTRODUCTION

Annual precipitation and temperature fluctuate considerably in many parts of the world (IPCC, 2012, 2013), and this variability has large impacts on the diversity and function of communities (Angert, Huxman, Chesson, & Venable, 2009; Harrison, Gornish, & Copeland, 2015). These impacts can drive the evolution of asynchronous dynamics among species, reflecting niche-based differences in the response to climate (Abrams, Tucker, & Gilbert, 2013). Asynchronous dynamics cause aggregate community-level responses to be more stable than would occur if species responded in unison (Gross et al., 2014; Loreau & de Mazancourt, 2008; Yachi & Loreau, 1999). A growing body of literature has described the pervasiveness of species asynchrony in nature and its importance for stabilizing ecosystem functions (Craven et al., 2018; Hautier et al., 2014; Wang, Knops, Brassil, & Mu, 2017; Wilcox et al., 2017). This research has also found that the apparent effects of species asynchrony on stability depend on local conditions that influence each of these properties of ecosystems directly, such as soil nutrients and species diversity (Hautier et al., 2014; Wang et al., 2017). Despite a growing recognition of the interdependence of species asynchrony and stability on shared drivers of ecosystem processes, there is yet to be a global test of how climate variability and local conditions affect species asynchrony and stability.

Climate variability may have particularly strong impacts on species asynchrony and, ultimately, primary production. Climate variability can increase temporal partitioning among species, allowing more species to coexist and more effectively stabilize function (e.g., Adler & Drake, 2008; Hautier et al., 2014). However, climate fluctuations may also cause temporal dynamics of species to converge (i.e., synchronize), as occurs when fluctuations result in extreme events, such as drought, summer frost or heat waves, that cause correlated mortality among species (e.g., Harrison et al., 2015). It is currently unknown when species responses converge (become more synchronous) as precipitation or temperature becomes highly variable (Ma et al., 2017). Precipitation is a key determinant of water availability to plants, which underpins photosynthesis, cell structure, the transport of nutrients and, ultimately, carbon balance (Raven, Evert, & Eichorn 2005). Temperature regulates plant production by controlling reaction rates of photosynthesis and respiration and, in extreme cases, by damaging plants at the cellular level through freezing or protein denaturing (Berry & Bjorkman, 1980). Although direct effects of precipitation and temperature cause shared responses among plant species in extreme temperatures or drought (Harrison et al., 2015), species responses may differ with less extreme variability both directly (Angert et al., 2009; Kardol et al., 2010) and through indirect effects mediated by competitors and consumers (Gilbert et al., 2014; Kardol et al., 2010). As a result, it is unclear when the net effect of climate variability will promote or inhibit asynchronous dynamics, representing a key uncertainty in predicting the impacts of climate change.

Uncertainties about asynchrony and climate are compounded further by the potential influence of local factors, including past legacies of local climate variability and adaptation (Seddon, Macias-Fauria, Long, Benz, & Willis, 2016; Wang et al., 2017) and more static environmental conditions, such as soils (Hautier et al., 2014; Xu et al., 2015). These local factors can cause relationships among species asynchrony, climate and stability to vary (Hallett et al., 2014; Zhang et al., 2018), in turn hampering our understanding of how and in what conditions biological systems are likely to buffer climate fluctuations. Grasslands, for example, vary globally in climate mean and variability, the identity of limiting factors (e.g., precipitation versus temperature), and species traits and composition (Fay et al., 2015). As a result, inter-annual variability in precipitation may reduce the stability of grassland primary production in some parts of the world but not others (Fang, Piao, Tang, Peng, & Ji, 2001; Knapp & Smith, 2001; Yang, Fang, Ma, & Wang, 2008). Experimental tests of the effects of local environmental conditions have shown that fertilized communities can become less stable through a loss of asynchrony (Hautier et al., 2014; Xu et al., 2015), while being more susceptible to drought via increased demand for water (Chapin, Bloom, Field, & Waring, 1987). Likewise, natural gradients in soil conditions may influence species asynchrony directly or through shifts in plant diversity and functional trait variation, although current support for these hypotheses is limited (Craven et al., 2018). In total, the potential for regional differences between climate variability and asynchronous species dynamics means that generalization requires data on long-term, species-specific responses to climate variation in different regions globally.

In lieu of global empirical studies, researchers have turned to theory to predict how increased climate variability should influence asynchronous dynamics and stability. Predictions from theory are, however, conflicting. Increased variability is necessary for greater species asynchrony but also for supporting a greater diversity of species that specialize on conditions specific to some years (Chesson & Huntly, 1989). Nonetheless, climate variability is a "double-edged sword", whereby overly high variability leads to the loss of species diversity (Adler & Drake, 2008; Shurin et al., 2010). Species diversity may have important impacts on stability directly and through its effects on species asynchrony, such that a loss of diversity at high variability is, in turn, expected to cause a loss of stability (Loreau & de Mazancourt, 2013; Tredennick, Adler, & Adler, 2017). Together, these theoretical studies suggest that moderate levels of climate variability should increase species asynchrony but that the net effects on stability are unclear because they depend on changes in both average fluctuations across species and their asynchronous responses to climate. High levels of variability, in contrast, are likely to cause a decline in species asynchrony and stability, both directly and through the loss of species. These qualitative predictions have yet to be tested globally, and it is unclear how they map onto levels of climate variability observed in extant ecosystems.

Here, we analyse data on climate, asynchrony, the stability of aboveground production, and local soil conditions from a multi-year grassland study spanning five global climate regions. We use grasslands that cover a wide range of climate conditions to address three issues: (a) whether species asynchrony is associated with community-level temporal stability of aboveground annual net primary production (NPP) or whether direct effects of climate variability and local soil conditions predominate; (b) the degree to which local soil conditions and climate variability affect species asynchrony and NPP stability directly versus indirectly through their impacts on species richness; and (c) if, and where, climate variability is sufficiently large that species asynchrony weakens. We address these questions by first establishing pairwise relationships amongst species richness, species asynchrony, local soil conditions, climate variability and stability of NPP, and then incorporating these relationships into a structural equation model to test for direct and indirect effects of climate variability and species richness on species asynchrony and stability of NPP. We show that impacts of climate variability and species richness on stability are indirect and mediated by their influences on species asynchrony, with maximum species asynchrony and richness occurring at intermediate levels of climate variability. Local soil conditions, in contrast, mainly influence stability directly, underlying much of the variation in stability among grasslands.

2 | METHODS

2.1 | Study sites and variability metrics

The sites used (Supporting Information Figure S1) are part of the Nutrient Network Global Research Cooperative. All sites have identical methods for gathering of field data on plant richness, species cover per plot, soil properties and community-level biomass (described by Borer et al., 2014). The data for this study spanned 2007–2014 and yielded 350 observations, where each observation included 5 years of plant cover and aboveground biomass data obtained continuously within a single plot. Given that climate and soil data were not available for all sites in all years, the final number of observations used was 180, distributed among 29 field sites. We used 1 m^2 control plots, which varied from one to six plots per site, in conjunction with mixed models to account for non-independence of observations. Some sites had data for >5 years, in which case plots within these sites provided more than one data point (mean and median of two data points per plot). Owing to errors associated with averaging across plots with spatially clustered species distributions (Bennett & Gilbert, 2016), we did not average plots. Instead, to treat the lack of independence among data points within plots and sites, we used mixed models to account for the nested structure of the data (detailed in Statistical Methods below) and provide the estimated degrees of freedom using the Satterthwaite approximation (Kuznetsova, Brockhoff, & Christensen, 2017) for each test. We note that using 5 year windows was necessary to avoid having maximum community variation (denominator in our metric, below) increase with length of time sampled (examined in exploratory analysis).

We quantified community-level NPP (in grams per square metre per year), using two 10 cm × 100 cm biomass samples per plot per year at each site. Species-level variation in performance among years was based on percentage cover (visually estimated to 1% per plot annually at each site), and aggregate community-level performance was the sum of species-level percentage cover each year. Soil properties (percentage C, percentage N, extractable soil P, K, micronutrients, soil pH and soil organic matter) were attained from two litter-free cores per plot, 2.5 cm in diameter × 10 cm depth. All soil cores from within a plot were combined, air dried and analysed at a single laboratory (Borer et al., 2014). We performed a principal components analysis (PCA) on $\log_{10}$-transformed soil variables, because high collinearity among some soil variables caused analyses with raw variables to be unstable Supporting Information (Supplementary Methods). We used the first eight axes, representing >90% of the total variation, in subsequent analyses. The loadings of the soil variables on the PCA axes and a more detailed rationale for using a PCA are given in the Supporting Information (Supplementary Methods; Table S1).

The temporal stability of NPP was defined for each plot as μ/σ (i.e., inverse of CV), where μ is the temporal mean of community-level NPP from the control plots at each site over a 5 year period and σ is the temporal standard deviation over the same period. Temporal stability is unitless (it is measured in grams per square metre divided by grams per square metre).

The species asynchrony was measured for each plot as $1 - \varphi$, where φ is species synchrony and is calculated as $1 - \varphi = 1 - \dfrac{\sigma_T^2}{\left(\sum_{i=1}^{S} \sigma_i\right)^2}$,

where σ_i is the temporal standard deviation of the percentage cover of species i in a plot with S species over the 5 years and σ_T^2 is the variance of the aggregate (summed) percentage cover of all species (Loreau & de Mazancourt, 2008). This metric of species asynchrony integrates annual population-based and community-level fluctuations (Supplementary Methods), thereby capturing the compensatory mechanisms predicted to stabilize function in response to climate fluctuations (Loreau & de Mazancourt, 2008). The metric is correlated with species diversity and other measures of species asynchrony (Gross et al., 2014; Figures S2-S4) but differs in recognizing that numerically dominant species have a greater influence on community dynamics. Note that the standard deviation in the denominator of the synchrony index also occurs in the numerator, and the divergence from unity reflects the degree to which the sum of the off-diagonal elements (covariances) differ from the sum of the diagonal elements. We discuss the choice of the species asynchrony metric further in the Supplementary Methods.

Climate data for each site were derived from a 0.5° gridded time series dataset (Harris, Jones, Osborn, & Lister, 2014), with details on the climate data presented by Flores-Moreno et al. (2016). To estimate inter-annual climate variability, we used two metrics for each climate variable (temperature and precipitation): the coefficient of variation among years and the standard deviation of $\log_{10}$-transformed annual means, with the calculation of annual means explained below. These two metrics are strongly correlated ($r = .98$ for precipitation and $r = .99$

for temperature, both $p < .0001$). We used the standard deviation of $\log_{10}$-transformed data because it was a slightly better predictor of species asynchrony, as measured by the difference in AIC between models (ΔAIC = 10), although the results were qualitatively similar. As is commonly the case with coefficients of variation (and standard deviation of logarithmic data), the estimated variation was correlated with the mean for both variables (Figure S5). We discuss the consequences of these correlations in the Supplementary Methods.

For temperature variability, we first calculated the mean annual temperature at each site (in degrees Celsius), and then calculated the standard deviation of the $\log_{10}$-transformed annual means over the 5 years that corresponded to the years of cover and biomass sampling. One observation was removed because the coefficient of variation was negative, given that the mean annual temperature was <0°C, and the standard deviation of the $\log_{10}$-transformed mean could not be calculated. Nonetheless, we chose to use the Celsius scale (rather than the Kelvin scale) because the freezing point of water closely matches the absolute limit of photosynthesis in plants. A second temperature observation was removed because it was an extreme outlier with very high leverage; removal of this observation did not change our results qualitatively but did have a large influence on the slopes reported.

To estimate mean annual precipitation, we calculated the geometric mean for each year by first $\log_{10}$-transforming monthly precipitation (measured in millimetres) and calculating the mean monthly precipitation for each year. This use of the geometric mean for annual precipitation down-weights extreme one-time events (a month with extremely high precipitation, for example) and gives more weight to months low with rainfall, which is likely to be important for grasslands. Biologically, this is important when single large precipitation events cannot be assimilated biologically. We chose this approach to reduce the impact of intra-annual variation on our calculation of annual means, because our plant data were collected annually and we were therefore unable to test the effects of within-year dynamics (see Discussion). As with temperature, we explore an alternative transformation of precipitation in the Supporting Information (Figures S6 and S7).

Data compiled for our analyses are available through Dryad (Gilbert et al., 2020), and raw data are available through the Nutrient Network (https://nutnet.org/).

2.2 | Statistical methods

For all analyses, we used hierarchical (mixed) models, in which region, and plot nested within site, were included as random effects using the lme4 and lmerTest packages (Bates, Machler, Bolker, & Walker, 2015; Kuznetsova et al., 2017). The effect of region was tested by comparing model AIC and removed when it did not improve model fit, whereas plot nested within site was maintained in all analyses to account for the lack of independence of observations at different scales. Our specific tests were: (a) stability (response) was predicted by species richness, species asynchrony, climate variability and soils;

(b) species asynchrony (response) was predicted by species richness, climate variability and soils; and (c) species richness (response) was predicted by climate variability and soils. We also explored the roles of significant predictors of asynchrony and stability on the components of stability (mean and standard deviation of primary productivity Supplementary Information Figure S8).

Species asynchrony was logit transformed and stability was $\log_{10}$-transformed to match model assumptions better. Climate variability included both linear and quadratic terms for temperature and precipitation variability to account for the predicted increase in species asynchrony and richness with variability at low levels of climate variability, but the opposite trends at high levels of variability. Species richness was transformed using an $(S − 1)/S$ transformation, where S was the number of species (Loreau & de Mazancourt, 2008), with this transformation causing the richness–species asynchrony relationship to be linear (relationship shown in Figure S2). All tests, including bivariate tests, had species richness included as a covariate to avoid non-causal relationships between species asynchrony and its other predictors (Supplementary Methods).

We used structural modelling to identify the overall response of stability to climate variability, species richness and soils, both directly and indirectly, via species asynchrony. Structural equation modelling was performed using the PIECEWISESEM package designed for mixed effect models (Lefcheck, 2016), and all tests were run in the R language (R Core Team, 2018).

3 | RESULTS

Our data showed distinct impacts of climate variability and local soil conditions on species asynchrony and NPP stability. Climate had a large impact on species asynchrony, but influenced stability only indirectly, through asynchrony. Local soil conditions, in contrast, had no direct effect on species asynchrony but instead had a direct influence on stability. Below, we outline the results that led to these conclusions. We note that we report traditional tests of significance below, but complement these with model selection and variation explained (approximate R^2 values) in the Supporting Information (Table S2).

We detected high levels of species asynchrony globally, with aggregate vegetative cover of communities fluctuating far less than would occur if all species converged to respond in an identical manner to climate conditions (Supporting Information Figure S3; numerator and denominator of the synchrony index, respectively). The global relationship between species asynchrony and climate variability was characterized by unimodal responses, in which species asynchrony peaked at moderate levels of variation (Figure 1a,b). With both more uniform or more highly variable climate, there were smaller asynchronous fluctuations in plant cover among species (quadratic term $F_{1,118} = 13.6$, $p < .001$ for precipitation, $F_{1,100} = 8.7$, $p < .004$ for temperature; Supporting Information Table S2). These general trends were consistent across the five regions; models that

included region as a random effect had consistently higher AIC than those with the region effect removed, despite regional differences in average climate variation (Figure 1).

Species richness was also a significant predictor of species asynchrony (Figure 1c; Supporting Information Figure S2; $F_{1,149} = 9.2$, $p < .001$) and, in turn, showed a unimodal response to precipitation variability (Figure 1d; negative quadratic term, $F_{1,103} = 20.1$, $p < .001$) but no response to temperature (both linear and quadratic $p > .4$). Soil conditions (Supporting Information Table S1 and Figure S9) did not influence asynchrony directly (all $p > .05$), but did structure species richness, which decreased with soil P [principal component (PC) 4; $F_{1,60} = 5.0$, $p < .03$; Figure 1e] and also responded positively to soil micronutrients (PC8; $F_{1,81} = 4.41$, $p < .04$; Figure 1f).

There was no evidence of a direct relationship between climate variability and stability (Figure 2c,d; both $p > .18$), nor between species richness and stability ($p > .8$, not shown). Species asynchrony, in contrast, significantly predicted stability (Figure 2a; $F_{1,178} = 9.2$, $p < .003$), suggesting that the influences of climate and species richness on stability were indirect. Soil conditions and, in particular, soil organic matter (PC2) had the strongest direct effect on the stabilization of NPP across years (Figure 2b; Supporting Information Table S3; $F_{1,38} = 12.7$, $p < .002$).

We used the inverse coefficient of variation (i.e., μ/σ) as our measure of stability, which allowed us also to investigate whether variables altered stability by changing mean biomass production or its temporal variation (e.g., Craven et al., 2018; Jucker, Bouriaud, Avacaritei, & Coomes, 2014). Higher levels of soil organic matter caused a more rapid increase in mean production than temporal variation ($F_{1,267} = 65.0$, $p < .001$; Supporting Information Figure S8), resulting in increased stability. Asynchrony had no detectable effect on mean production ($p = .47$) but reduced its variation ($F_{1,267} = 11.9$, $p < .001$), causing an increase in stability with asynchrony (Supporting Information Table S3; Figure S8). Climate variation had no consistent direct effect on either component of stability (all $p > .2$). Species richness caused a marginally greater reduction in the temporal variation of production ($F_{1,268} = 4.1$, $p = .044$), although this difference was not sufficiently large to detect an effect on stability ($F_{1,140} = 0.06$, $p = .8$; Supporting Information Figure S8).

We used structural equation modelling to test the hypothesis that high climate variability and soil conditions directly and indirectly alter species asynchrony and stability (Figure 3). This analysis confirmed that asynchrony was largely driven by climate variability, which affected species asynchrony directly and, to a lesser extent, indirectly, through its impact on species richness (Fisher's C = 18.458, $p = .86$, indicating strong global goodness-of-fit of path model). Soil properties had a minimal impact on asynchrony, acting solely through their influence on species richness. However, soil properties had a large impact on stability, albeit owing to distinct soil properties from those that influenced species richness (Figure 3). Asynchrony had a smaller, but nonetheless significant, impact on stability. The relative importance of variables influencing asynchrony and stability was largely consistent between the SEM approach and simpler linear models with components, with some differences emerging
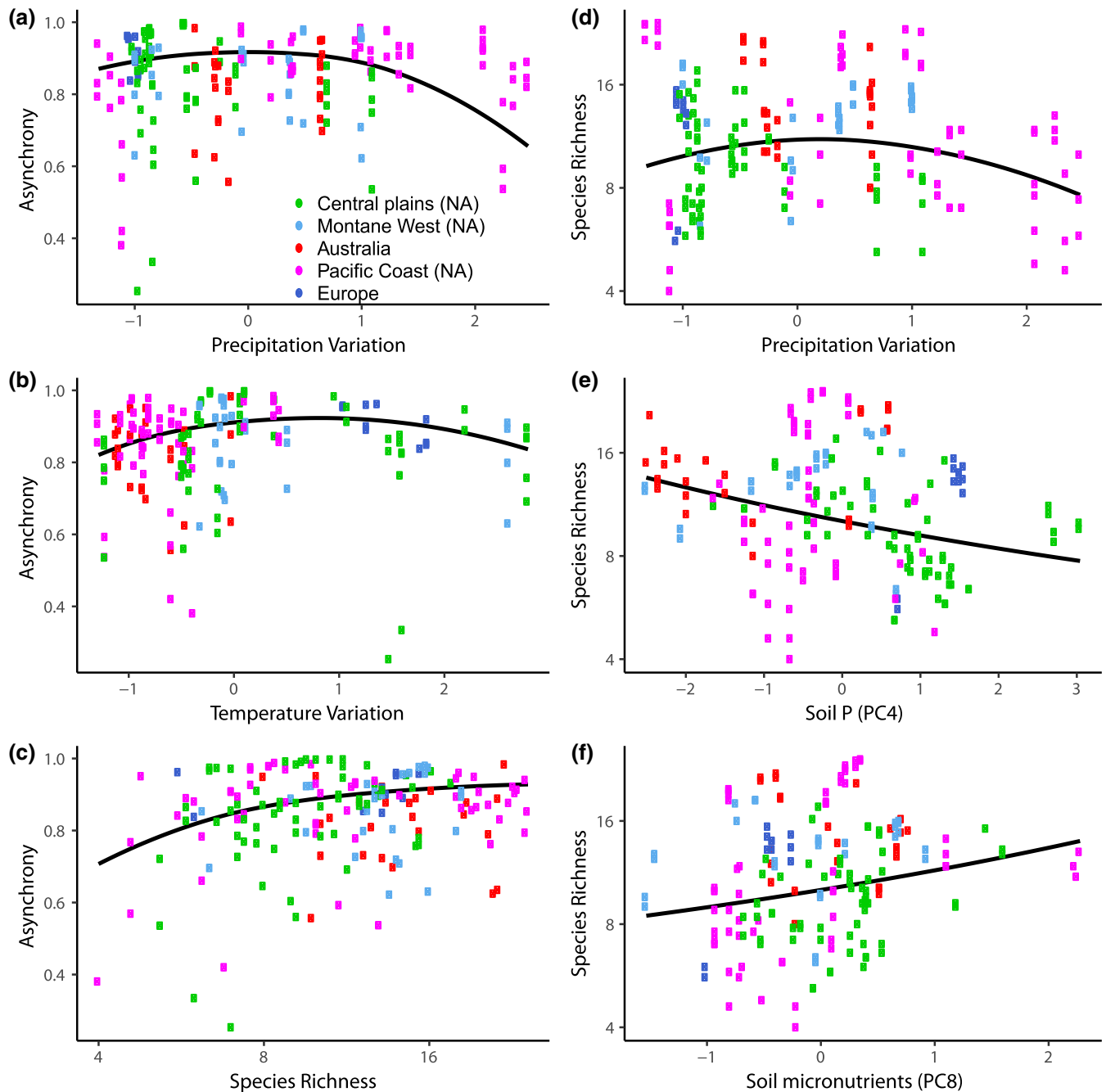
FIGURE 1 Bivariate relationships between predictor variables and species asynchrony (a–c) and species richness (d–f). Asynchrony was significantly explained by variation in precipitation (a), variation in temperature (b) and species richness (c). Species richness, in turn, was explained by variation in precipitation (d), soil phosphorus (e) and soil micronutrients (f). Colours correspond to bioclimatic region, as shown in panel (a), with NA indicating regions in North America. Response variables are shown on their natural scales. Transformed response variables (as used in our analyses) are shown in the Supporting Information (Figure S10) [Colour figure can be viewed at wileyonlinelibrary. com]

as a result of relationships among predictor variables (Supporting Information Table S3).

We examined the relationship between temperature and precipitation variability at our sites versus patterns seen in grasslands globally, to determine the potential generality of our results (Figure 4). Our grasslands tended to have high variation in precipitation or temperature but never both, a trend that was also seen globally. The variation in precipitation in our study was broadly representative of global patterns,

whereas our sites did not contain some of the more extreme temperature fluctuations observed elsewhere on the planet (Figure 4b).

4 | DISCUSSION

Ecologists are increasingly recognizing the need to quantify drivers that impact both species richness and the emergent properties
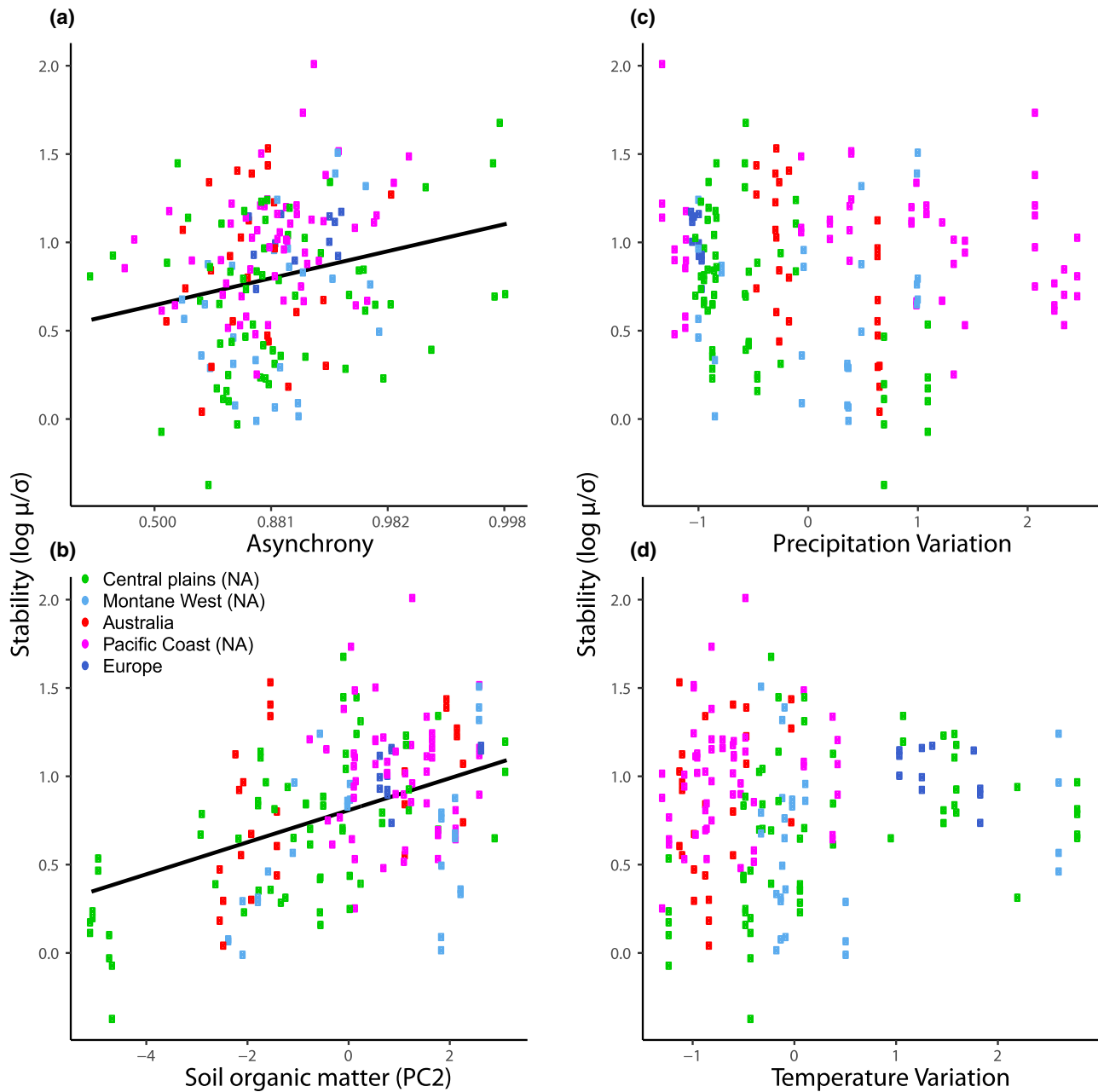
FIGURE 2 Bivariate relationship between the temporal stability of annual aboveground net primary productivity (NPP) and predictor variables. Asynchrony and soil organic matter were significant predictors of stability (a,b), whereas climate variation was not (c,d). The fitted lines show statistically significant relationships. There were no significant linear effects of climate variation or species richness (not shown; all $p > .18$). The stability of primary production is the inverse of the temporal coefficient of variation and is log_{10}-transformed to meet model assumptions. Note the scaling of asynchrony (x axis, panel a), which matches the logit transformation used in analysis [Colour figure can be viewed at wileyonlinelibrary.com]

of ecosystems (Ives & Carpenter, 2007). Climate variability and soil properties are two drivers that impact species richness, asynchronous dynamics, population stability and ecosystem properties (Angert et al., 2009; Yang et al., 2008; Zhang et al., 2018). Our analysis reveals that climate variability has a pervasive impact on species asynchrony, generating unimodal responses both directly and indirectly, through its influence on species richness. Surprisingly, soil properties had a weak influence on asynchrony, detectable only through their influence on species richness. The relative importance of soils and

climate were reversed for the stability of NPP in our grasslands, with soils having a large direct effect on stability and species asynchrony mediating the weaker influence of climate variability. These results suggest that the processes governing temporal community dynamics might be decoupled, in part, from those that determine stability of primary productivity across large spatial scales. Nonetheless, the globally consistent effects of the variability in precipitation and temperature on ecosystem properties reflect how grasslands are likely to respond to ongoing changes to climate (IPCC, 2012).
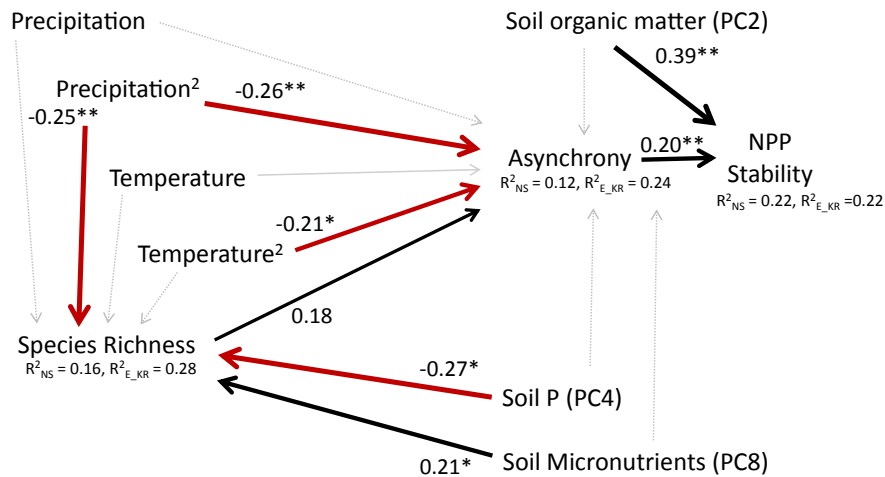
FIGURE 3 Structural equation model illustrating the hypothesized causal relationships among climate variability ("Precipitation" and "Temperature"), soil, species richness, asynchrony and stability of aboveground net primary productivity (NPP). Arrow colour indicates a positive (black) or negative (red) relationship, with negative quadratic terms indicating a unimodal trend (as in Figure 1). Arrow widths scale with standardized regression coefficients, given for each path. Grey arrows show tested but statistically non-significant relationships ($p > .1$); no asterisk indicates marginal significance $p < .1$, and asterisks denote $p < .05$ (*) and $p < .005$ (**). Variables that were not significant in any analysis [several soil principal component (PC) axes] are not included, and non-significant relationships with NPP stability (all variables except asynchrony and soil organic matter) are not shown, for clarity. Variables are transformed as in Figures 1 and 2. Estimates of variation explained (R^2 values) are for the fixed effects only, based on the Nakagawa–Schielzeth (NS) method and the Edwards method using Kenward–Roger degrees of freedom (E_KR), as explained in the Methods [Colour figure can be viewed at wileyonlinelibrary.com]
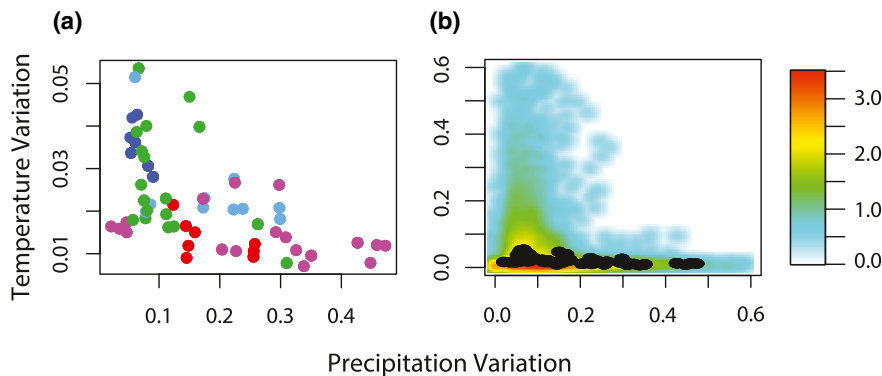

FIGURE 4 Relationship between variation in temperature and variation in precipitation, measured as the standard deviation of the $\log_{10}$-transformed mean annual values, in: (a) our 29 study sites; and (b) globally. The values in (b) represent the relative density of grasslands with the level of variation shown, with data calculated for grasslands globally as defined by the World Wide Fund for Nature, using 0.5 arc degree grids and calculated from 2009 to 2013 (for details, see Supporting Information Figure S1). Our grassland sites (black dots) represent the levels of variation most commonly observed globally, but not the extreme variation in temperature seen in relatively few locations [Colour figure can be viewed at wileyonlinelibrary.com]

Several recent studies have suggested that the sensitivity of species asynchrony and stability to climate varies widely by region, possibly owing to the adaptive familiarity of species to climate fluctuations (Seddon et al., 2016). Regional differences emerge in our data but, contrary to this explanation, they are driven by globally consistent, nonlinear responses to climate variability, coupled with differences in climate variation among regions (Figure 1; Supporting Information Figure S5). In Europe, for example, greater temperature variation is associated with a decrease in species asynchrony because European sites are to the right of the peak unimodal response (blue points in Figure 2b). The Pacific Coast of North America,

characterized by a mediterranean climate, shows the opposite trend owing to lower average temperature variation encountered in this region (pink points lie to the left of the peak in Figure 2b). Indeed, these regional differences might explain why observational studies from different regions show opposite effects of climate variability on species asynchrony (Hallett et al., 2014; Zhang et al., 2018), even if they share a common underlying response. In other words, differences among regions in past and current levels of climate variation could have important consequences for future shifts in species asynchrony; the nonlinear response of species asynchrony to climate variability might mean that the current climatic variability of a region

will determine the strength and direction of change in species asynchrony as this variability increases.

The unimodal response of species asynchrony to climate variability supports theory predicting that low or extreme inter-annual climate variation will limit asynchronous dynamics by reducing the potential for temporal niche partitioning (Adler & Drake, 2008). When a site is characterized by slight climate variability, plant species either have little opportunity to differentiate in their responses to temporal fluctuations (Shurin et al., 2010) or the fluctuations are so infrequent that species cannot persist through prolonged suboptimal conditions (Abrams et al., 2013). For sites characterized by high inter-annual variability, physiological constraints may cause species to respond in a more similar manner to extreme events that drive variability, such as freezing events, drought or heatwaves (Angert et al., 2009; Harrison et al., 2015; Raven et al., 2005). High climate variability may also reduce the persistence of species that would otherwise specialize on some conditions by increasing their susceptibility to extinction (Adler & Drake, 2008; Shurin et al., 2010). Our analyses suggest that both hypotheses for the negative effects of high climate variability might be correct. Species richness showed a unimodal response to variability in precipitation, supporting empirical research that has shown a negative effect of high variability on richness over time (Zhang et al., 2018). Likewise, examination of the relationships among species asynchrony, climate means and climate variability suggests that the negative effect of high variability on species asynchrony might be contingent on variation resulting in extreme conditions (Supporting Information Figures S5–S7). Ultimately, these processes dampen asynchronous dynamics when species encounter low or high climate variability.

The different drivers of species asynchrony and stability in grasslands highlight how climate fluctuations and soil properties influence ecosystem properties through distinct pathways. The most obvious difference arises from the temporal scale of variability, with the soil properties we measured tending to be relatively constant over the time-scale considered (for review and exceptions, see Ehrenfeld, Ravit, & Elgersma, 2005). Nonetheless, previous research has found that eutrophication can reduce asynchrony by altering species richness or its influence on temporal dynamics (Hautier et al., 2014; Xu et al., 2015), effects that emerge, in part, from the impact of eutrophication on species composition and abundances (Seabloom et al., 2015). In this previous work, it was possible to examine impacts of eutrophication by maintaining controls and fertilized plots at the same site, whereas in our study we considered unmanipulated plots within and across sites and failed to find strong effects of soil nutrient levels on asynchrony. In other words, the different results from our study and previous research could arise from differences between fertilization treatments and differences in natural soil resources or because any effects of differences in soil resources on asynchrony are overwhelmed by other among-plot and among-site differences.

The second distinct influence of climate and soils on ecosystems is evident from their influence on the stability of NPP. Previous studies have provided conflicting support for the prediction that grassland stability should respond to variability in precipitation,

with some research showing no relationship (Hallett et al., 2014; Ma et al., 2017) and other research showing a negative impact on stability (Craven et al., 2018; Zhang et al., 2018). Our globally distributed study was consistent with work by Hallett et al. (2014) and also supported their finding that climate variability indirectly influences stability through asynchronous responses. Moreover, our analyses reveal that the influence of species asynchrony on stability arises through a reduction in the temporal variability of NPP (Supporting Information Figure S8). Our study also differs from previous observational studies in that it accounts for the combined influence of climate and soils and, in doing so, reveals that soils have a larger influence on stability. As a result, differences in soil properties among grasslands are likely to obscure the influence of climate on stability when space-for-time substitutions are used, as in our study.

The strong influence of soil properties on stability reinforces results from experimental manipulations (Hautier et al., 2014; Xu et al., 2015), yet the underlying mechanism by which these differences emerge appears different. Experimental manipulations of soil nutrients have altered stability through their direct effects on species asynchrony (Xu et al., 2015) or the species diversity–asynchrony relationship (Hautier et al., 2014), indirect pathways that have also been important for experimental warming and grazing (Ma et al., 2017; Ren et al., 2018). In contrast, our results indicated that soil properties influence stability directly by increasing mean NPP more quickly than its temporal variability, unlike species asynchrony, which stabilizes by altering temporal variability alone (Supporting Information Figure S8). Interestingly, the soil properties that directly influence stability (organic matter, percentage soil C and N) are distinct from those that influence the species richness–asynchrony pathway, meaning that soil properties have both direct and indirect influences on stability.

A recent synthesis concluded that species richness indirectly impacts stability by altering species asynchrony, rather than through a direct influence (Craven et al., 2018). This synthesis, which collated experimentally manipulated biodiversity plots, showed an overwhelming influence of species richness and relatively little impact of climate variability. Our results build on this work by identifying climate variability and soils as drivers of species richness and by revealing the direct role of climate variability on species asynchrony. Our analysis further suggests that soil conditions and climate variability have a larger impact on stability and species asynchrony than current variation in species richness in unmanipulated grasslands. Although soil properties and their effects are unlikely to change dramatically over the short term, the relative impact of climate and species richness will be likely to depend on their relative changes and the proximate drivers of changes in species richness. Although both climate variability and changes in species richness are the focus of active research, data suggest that large changes in climate variability are more likely, at least in the near future (Gonzalez et al., 2016; IPCC, 2013; Vellend et al., 2017).

The generality of our results on the biotic consequences of climate variability and soil properties must be tempered with a few important caveats. First, our experiment documents differences among

sites, and a significant portion of stability and species asynchrony are unexplained by climate and soils alone. Although the explanatory power of our variables is comparable to other studies on temporal stability (e.g., Craven et al., 2018) and typifies climate and environmental uncertainties that face decision-makers (IPCC, 2012; Polasky, Carpenter, Folke, & Keeler, 2011), we suspect that other factors explain the site-level differences observed. These differences might reflect evolutionary or historical processes, such as differences in species composition that arise from historical climate conditions (Liu et al., 2018). Alternatively, they might reflect more nuanced climate variability that cannot be captured in global comparisons. For example, variation in growing degree days might be important in high-latitude and high-elevation grasslands, whereas the timing of first rain might be important in low-precipitation grasslands (Levine, McEachern, & Cowan, 2008). Our approach avoided spurious correlations that can arise from including the huge number of climate variability metrics; site-specific analyses might be better suited to other metrics, because researchers can test locally relevant variability (Zhang et al., 2018). Nonetheless, our results and their sensitivity to different measures of climate variability (Supporting Information Supplementary Methods; Figures S5–S7) suggest that the correct modelling of climate variability is a non-trivial task. In other words, the global patterns reported here form a basis for understanding globally consistent climatic drivers of species asynchrony, while providing a starting point for detailed site-level analyses.

Second, fluctuating climate might select for species with distinct water-use strategies and distinct temperature response curves, potentially creating larger species asynchrony over the long term with increased climate variability (Abrams et al., 2013). However, the emergent effects of evolution on limits to community-level species asynchrony are only beginning to be understood (Abrams et al., 2013; De Mazancourt, Johnson, & Barraclough, 2008) and do not yet incorporate limits to evolution when fluctuations increasingly cause extreme climate conditions. Understanding the importance of evolutionary shifts to species asynchrony, and associated lags in these shifts, is necessary for long-term predictions about grassland stability.

Third, the temporal scale at which climate variability is considered might also play a role in detecting its importance. Recent research by Usinowicz et al. (2017) has highlighted how within-season asynchrony reduces among-year asynchrony and average competitive interactions, because extreme climatic conditions are unlikely to occur at exactly the same time each year. Temperature often fluctuates widely during the growing season, and species that are highly sensitive pay a large fitness cost (Vasseur et al., 2014). In contrast, within-season rainfall variability may frequently be overcome by several mechanisms, including shortened phenology and other plastic responses (Valladares, Gialoni, & Gómez, 2007), but these mechanisms fail when rainfall is low throughout a season (Craine et al., 2013; Harrison et al., 2015). In sum, the different responses of plants to fluctuating temperature and precipitation might be important for structuring diversity and species asynchrony, and this is an important emerging area of study.

A final caveat for global experiments is that they are reliable only if they represent the range of conditions that occur globally (Gonzalez et al., 2016). Our study sites frequently showed high inter-annual variation in temperature or precipitation, but never both together (Figure 4a). This pattern is surprisingly consistent with global patterns of climate variability in grasslands, where extremes of temperature and precipitation rarely act in concert (Figure 4b; Supporting Information Figure S1). Our data thus broadly represent present-day conditions around the globe but do not fully capture the most extreme levels of temperature variability in grasslands (Figure 4b), nor can they capture any lagged dynamics that might emerge over periods >5 years. Models and data generally predict that differences in temperature and rainfall variation will persist into the future, although scientists lack confidence in long-term predictions of precipitation variability, in particular (IPCC, 2012). In other words, our study sites are representative of most current patterns of climate variation, but might not represent future climates that experience simultaneous shifts in mean conditions and increased variability (Williams & Jackson, 2007).

Climate change is predicted to intensify the variation in precipitation and the frequency of extreme temperature events (IPCC, 2012, 2013). We have shown that asynchronous dynamics in the grasslands of the world might act to buffer these changes somewhat, by stabilizing primary productivity. However, we have also demonstrated substantial sensitivity of species asynchrony to high climate variability; we see strong evidence of biotic thresholds in response to climate variability. These thresholds imply that regions currently experiencing high variability are particularly sensitive to changing climate and are expected to show losses in species richness, species asynchrony and stability as climate variability increases.

AUTHOR CONTRIBUTIONS

E.W.S., E.T.B., W.S.H. and E.M.L. are Nutrient Network coordinators. B.G., A.S.M., T.K., M.A. and J.R.B. developed and framed research questions, designed analyses, wrote the initial draft and provided editing. A.S.M., E.M.L., H.F.-M., J.F., Y.H., E.T.B., E.W.S., P.B.A., E.E.C., J.B.G., W.S.H., E.H.E., J.L.M., J.K., R.M. and B.M. contributed data and provided editing.

DATA ACCESSIBILITY

The data used in these analyses is available through dryad (Gilbert et al., 2020; https://doi.org/10.5061/dryad.vx0k6djnb)

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.