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LETTER

Nutrient identity modifies the destabilising effects of eutrophication in grasslands

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Abstract

Nutrient enrichment can simultaneously increase and destabilise plant biomass production, with co-limitation by multiple nutrients potentially intensifying these effects. Here, we test how factorial additions of nitrogen (N), phosphorus (P) and potassium with essential nutrients (K+) affect the stability (mean/standard deviation) of aboveground biomass in 34 grasslands over 7 years. Destabilisation with

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fertilisation was prevalent but was driven by single nutrients, not synergistic nutrient interactions. On average, N-based treatments increased mean biomass production by 21–51% but increased its standard deviation by 40–68% and so consistently reduced stability. Adding P increased interannual variability and reduced stability without altering mean biomass, while K+ had no general effects. Declines in stability were largest in the most nutrient-limited grasslands, or where nutrients reduced species richness or intensified species synchrony. We show that nutrients can differentially impact the stability of biomass production, with N and P in particular disproportionately increasing its interannual variability.

KEYWORDS
biodiversity loss, biomass, co-limitation, ecosystem function, ecosystem stability, nutrient enrichment, nutrient Network (NutNet), synchrony, variability

INTRODUCTION

Biomass production is a critical ecological function that supports many ecosystem services (Cardinale et al., 2012; Gounand et al., 2020; Kremen, 2005), especially in grasslands where it contributes to carbon storage and food production (Borer et al., 2020; Haberl et al., 2007; Song et al., 2019). Biomass may be limited by the availability of single resources like nitrogen (N; LeBauer & Treseder, 2008), phosphorus (P; Hou et al., 2020) or water (Huxman et al., 2004; Morgan et al., 2016), or co-limited by multiple resources that interactively affect biomass production (Elser et al., 2007; Fay et al., 2015; Harpole et al., 2011; Kaspari & Powers, 2016). Accordingly, human-driven increases in nutrient availability, a common disturbance of grasslands (Stevens et al., 2004), can strongly impact biomass production and its associated ecosystem services (Song et al., 2019; Tilman & Lehman, 2001; Tilman, 2001). Over time, chronic nutrient enrichment may impact different aspects of grassland biomass, including mean annual production (Fay et al., 2015; Seabloom et al., 2021), its standard deviation (henceforth 'interannual variability'; Avolio et al., 2020; Koerner et al., 2016), and its temporal stability (here, 'invariability' calculated as $S = mean/standard\ deviation$; Tilman, 1999; Tilman et al., 2006). While previous work has shown that multiple nutrient inputs can exert interactive effects on mean biomass production (Elser et al., 2007; Fay et al., 2015; Harpole et al., 2011), to date, it is not known if different single- or multiple-nutrient inputs exert independent or interactive effects on its interannual variability or overall stability.

Several processes operating among individuals and populations interact to regulate community biomass production (Hautier et al., 2014, 2020; Loreau, 2010) and its potential responses to different nutrients. At the individual level, resource availability limits biomass production by imposing physiological constraints on growth (Droop, 1974). Subsequently, species interactions determine how individual growth contributes to community biomass production (Loreau, 2010). Trait differences between species, such as in their resource acquisition strategies or competitive abilities, enable multiple species to contribute to community function and can generate a positive relationship between species richness and mean community biomass production (Carroll et al., 2011; Tilman, 1999). This dynamic may be impacted by different single- or multiple-nutrient inputs. The number and identity of limiting resources in a system influences which species coexist (Chesson, 2000; Danger et al., 2008; Harpole & Tilman, 2006; Levin, 1970). In grasslands, changing the availability of limiting nutrients can lead to the competitive exclusion of species (Braakhekke & Hooftman, 1999; Tilman, 1982) and a decline in species richness (Bakelaar & Odum, 1978; Harpole et al., 2016, 2017; Harpole & Tilman, 2007). This may drive changes in mean biomass production that depend on the number or identity of enriching nutrients (Fay et al., 2015; Harpole et al., 2011).

Processes operating within communities also contribute to the interannual variability of biomass production, principally by determining the responsiveness of community productivity to interannual fluctuations in the environment (Loreau & de Mazancourt, 2008; Tilman, 1996). Species richness often minimises interannual variability (Hautier et al., 2015) by increasing the likelihood that a community includes species that can produce biomass in a given environmental context (Loreau, 2010; MacDougall et al., 2013). This effect is influenced by species synchrony—a measure of the similarity of species responses to temporal environmental fluctuations (Gilbert et al., 2020; Hector et al., 2010; Loreau & de Mazancourt, 2013; Valencia et al., 2020a). Low synchrony in species-level biomass production produces compensatory dynamics that reduce interannual variability in community biomass production (Brown et al., 2016; Loreau & de Mazancourt, 2013; Tilman, 1996). As above, synchrony also depends on trait differences among species that allow them to respond differently to environmental fluctuations (Loreau, 2010). Where changes in limiting factor availability reduce species or trait diversity (Harpole et al., 2016), synchrony may increase among the remaining species. For example eutrophication was shown to increase species synchrony and, subsequently, increase the interannual variability of grassland biomass production (Hautier et al., 2014).

Global changes impact the temporal stability of biomass production (see metric above) by altering the relationship between its temporal mean and standard deviation (Cardinale et al., 2013; Ives et al., 2000; Kohli et al., 2019). Different nutrient inputs may drive such transitions by affecting the mechanisms that regulate these aspects of biomass production, which could have serious implications for the maintenance of ecosystem function. Temporal stability provides a scaled measure of interannual changes in biomass relative to the mean production of a community (Carnus et al., 2014; Donohue et al., 2013; Ives & Carpenter, 2007). Accordingly, changes in temporal stability indicate deviations from average levels of production, a process that can increase the likelihood of irreversible change in community composition or functioning (Beisner et al., 2003; Carpenter & Brock, 2006; Scheffer et al., 2001). For example large relative changes in primary productivity can alter food web interactions and cause the local extinction of consumers and their predators (Rosenzweig, 1971). Therefore, grasslands are at an increased risk of irreversible change where nutrient enrichment causes interannual variability to change relative to mean production. While this paradox of enrichment dynamic is well described in the theoretical literature (McCann et al., 2021; Rosenzweig, 1971), its interaction with co-limitation in empirical systems remains poorly characterised.

Here, we assessed the effects of individual and combined N, P and Potassium + essential nutrients (K+) enrichment of 34 grassland sites spanning six continents over 7 years. We aimed to test the hypothesis that the effect of chronic nutrient enrichment on the mean, interannual variability and temporal stability of biomass production is influenced by nutrient identity and multiple-nutrient interactions. We also aimed to test potential mechanisms of temporal biomass production responses. We addressed our aims in three stages:

1. We assessed the temporal stability of biomass production within nutrient treatment plots to determine if different individual and combined nutrient inputs had different stability effects.
2. We assessed the temporal mean and interannual variability of biomass production within treatment plots to determine if changes in stability were mean- or variability-driven (Carnus et al., 2014; Kohli et al., 2019) and if this differed among treatments. Variability-driven destabilisation would occur if the mechanisms that control interannual variability show strong responses to nutrient enrichment, causing increases in the standard deviation relative to the mean. Alternatively, multiple nutrient inputs could cause synergistic increases in mean biomass (Harpole et al., 2011) that mitigate against destabilisation.
3. We examined between-site differences in stability responses and tested four potential mechanisms of destabilisation. Specifically, we tested if destabilisation following nutrient addition was stronger at sites where nutrient limitation was stronger. We tested if enrichment had less effect on stability at sites with lower precipitation, where biomass was likely to be more limited by water availability than nutrients, and greater effect at sites with higher precipitation, where nutrient inputs could increase plant responsiveness to precipitation (Morgan et al., 2016; Paruelo et al., 1999; Wang et al., 2017). Finally, we tested if changes in stability were driven by changes in species richness (Hautier et al., 2015) or species synchrony (Valencia et al., 2020a), such that stability decreases where species are lost or synchronised. We predicted that multiple nutrient treatments would be more destabilising than single nutrient treatments because they are likely to cause greater species loss (Harpole et al., 2016) and impose greater constraints on the niche differences that tend to prevent synchrony.

MATERIALS AND METHODS

Experimental design and nutrient additions

We assessed the mean, interannual variability and stability of aboveground biomass production in 34 grassland sites that received standardised annual inputs of N, P and K+ for 7 years (Table S1). These data are from the globally distributed Nutrient Network (NutNet) experiment, described in Borer et al. (2014). We studied a 7-year treatment period to balance duration, thereby allowing temporal dynamics to unfold, with replication of sites. We tested the sensitivity of our analyses to these criteria by comparing our results with all subsets between 3 and 12 years (Table S2).

Most sites contain three blocks (but ranges from 1 to 6; Table S1) comprising 25 m^2 treatment plots that receive one of the possible factorial combinations of N, P and K+ and an unfertilised control plot. Plots are arranged in a randomised block design. Nutrients were applied at a standardised yearly rate, using 10 g N (time-release urea) m^{-2} $year^{-1}$, 10 g P (triple-super phosphate, which also includes Ca) m^{-2} $year^{-1}$, and 10 g K (potassium sulphate, which also includes S) m^{-2} $year^{-1}$. In the first year only, all K plots also received 100 g m^{-2} of an essential nutrient mix, comprising: 15% Fe, 14% S, 1.5% Mg, 2.5% Mn, 1% Cu, 1% Zn, 0.2% B and 0.05% Mo—forming the K+ treatment. All plots included in this analysis were open to herbivory. Site-level mean annual precipitation (MAP) and MAP variability data were obtained from the WorldClim Global Climate database (Version 1.4; Hijmans et al., 2005).

Metrics

We harvested aboveground biomass annually from two 10 × 100 cm strips in each plot at the site-specific time of peak biomass. Live biomass was separated from dead biomass, dried at 60°C and weighed to estimate biomass production in g m^{-2} $year^{-1}$ for each plot (Borer et al., 2014). Harvest strips were relocated within each plot each year to avoid a clipping effect. We calculated the temporal mean (μ) of biomass within plots as the 7-year mean of annual biomass measurements. Data for multiple nutrient effects on mean biomass over 3 years were previously presented (Fay et al., 2015), but did not jointly consider interannual variability. Considering both metrics concurrently is critical to interpreting stability effects (Carnus et al., 2014; Kohli et al., 2019).

Ecosystems responding to chronic nutrient inputs can display directional trends in biomass (Seabloom et al., 2021) that may influence stability metrics (Lepš et al., 2019). To focus our analysis on interannual variability in biomass production, we detrended our data by taking the residuals from a linear regression of biomass over years of treatment in each plot (Tilman et al., 2006). We used model 1 regression to isolate residuals perpendicular to the x axis (Legendre & Legendre, 2012). Subsequently, the standard deviation of residuals in a plot (σ_{detr}) was used as a measure of interannual variability and in calculating a single detrended S value for each plot, as: $S_d = \mu / \sigma_{detr}$.

Plant species richness and percent cover (to the nearest 1%) were surveyed in permanent 1 m^2 quadrats in each plot, based on visual assessment. Surveys were conducted annually or biannually according to the growing season at each site. We used these data to calculate the temporal mean of species richness for each plot. Additionally, we used species' percent cover to calculate detrended species synchrony in each plot, using the calc_sync function (Lepš et al., 2019) in R (v 3.6.3; R Foundation for Statistical Computing). This function detrends the φ synchrony metric (Loreau & de Mazancourt, 2008) by aggregating φ values from a moving 3-year window (φ_{t3}; Lepš et al., 2019). This mitigates against directional trends that can cause correlations in species abundances over time that are separate from the year-to-year fluctuations that drive synchrony (Lepš et al., 2019; Valencia et al., 2020b). Values of φ_{t3} are bounded between 0 (perfect asynchrony) and 1 (perfect synchrony).

We calculated treatment effects using natural-log response ratios, as: $LRR = \ln(treatment/control)$. This effect size highlights the change in the value of a metric in a treatment plot relative to control plots located within the same experimental block. Using LRRs standardised treatment effects across sites, centred values around zero, and improved the normality of our data (Hedges et al., 1999). We back-transformed LRR estimates and converted them to percent change relative to the control for presentation in figures.

Analysis

We used linear mixed effects models to test how different nutrient inputs impacted the S_d, μ and σ_{detr} of grassland biomass. We assessed each metric using the model:

$$y_{ijk} = \beta_j + b_i + \varepsilon_{ijk} \quad (1)$$

This model provides estimates for the k^{th} observation of y in the j^{th} nutrient treatment at the i^{th} site. The parameter β is the fixed effect intercept for the j^{th} level of the nutrient treatment and b is the random intercept for the i^{th} site. The k index accounts for within-site variation that results from observation of multiple blocks at each site. We chose this model structure after trialing models including random slopes for treatment effects within each site, but these models did not converge. We also used model 1 to test for nutrient effects on species richness and species synchrony. For each response, we tested interactions between nutrients by replacing the β_j term in model 1 with all interactions between dummy coded N, P and K+ factors.

We assessed the dependence of stability responses on mean biomass responses using the model:

$$y_{ijk} = \beta_{1j} + b_i + \beta_2 \chi_{ijk} + \varepsilon_{ijk} \quad (2)$$

where β_1 is the fixed effect intercept for the j^{th} nutrient treatment, b is the random intercept for the i^{th} site and β_2 is the fixed effect slope associated with χ (here, mean biomass). We built these models and obtained estimates of model parameters by maximum likelihood estimation using the lme4 package (Bates et al., 2015) in R.

We evaluated both the statistical and biological significance of our effect size estimates (Nakagawa & Cuthill, 2007). We present mean effects with their 95% confidence intervals and provide p-values that indicate whether a treatment effect was significantly different from controls (at $\alpha < 0.05$). We also compare our results with effect sizes observed in previous studies as a benchmark for interpreting nutrient effects on stability (Table S3).

To test mechanisms of nutrient effects, we built a model for each biomass response that included: plot-level LRRs of plant species richness and synchrony, site-level MAP and MAP variability, nutrient treatment and the interaction of nutrient treatment with each predictor. We evaluated the contribution of these factors to changes in the mean, variability and stability of biomass production using a model selection approach. We used the dredge function in the MuMIn package (Bartoń, 2009) to determine which set of predictors and interactions best explained the responses. We selected all predictors included in models within four AIC of the most parsimonious model and obtained their full averages and summary statistics using the model.avg function (Bartoń, 2009).

RESULTS

Do nutrient identity and nutrient interactions impact the temporal stability of grassland biomass production?

At the global scale, 7 years of single nutrient N enrichment decreased S_d by 14% relative to control plots (LRR$_{N}$ = −0.16, $p < 0.001$; Figure 1a, Table S4). Inputs of P were also generally destabilising (LRR$_{P}$ = −0.12, $p = 0.011$). In contrast, K+ did not significantly affect S_d (LRR$_{K+}$ = −0.04, $p = 0.322$).

Multiple nutrient input treatments destabilised biomass (Figure 1a, Table S4) by 13% with NP (LRR$_{NP}$ = −0.14, $p = 0.003$), 15% with NK+ (LRR$_{NK+}$ = −0.17, $p < 0.001$) and 12% with NPK+ (LRR$_{NPK+}$ = −0.13, $p = 0.004$). However, we did not observe destabilising interactions between any nutrients (Table S5). Instead, stability in NP, NK+ and NPK+ plots was equivalent to the stability of single-nutrient N and P input plots. Furthermore, sub-additive interactions between N and P acted to stabilise biomass relative to the potential additive effect of N and P inputs (LRR$_{N*P}$ = 0.14, $p = 0.045$).

Do nutrient identity and nutrient interactions impact the temporal mean and interannual variability of grassland biomass production?

At the global scale, increases in mean biomass following nutrient inputs were accompanied by greater increases in interannual variability (Figure 1b, c), a trend that defines decreases in S_d. Inputs of N increased mean biomass production by 21% (LRR$_{N}$ = 0.19, $p < 0.001$), while P and K+ did not significantly impact mean biomass globally (Figure 1b, Table S6). Concurrently, N additions increased the interannual variability of biomass by 40% (LRR$_{N}$ = 0.36, $p < 0.001$) and P additions by 19% (LRR$_{P}$ = 0.17, $p = 0.007$; Figure 1c, Table S7). K+ inputs had no significant effect on variability.

Multiple nutrient addition effects on the mean and interannual variability of biomass production were larger than single nutrient effects. Inputs of NP, NK+ and PK+ increased mean biomass by 48% (LRR$_{NP}$ = 0.39, $p < 0.001$), 28% (LRR$_{NK+}$ = 0.26, $p < 0.001$) and 16% (LRR$_{PK+}$ = 0.15, $p < 0.001$) respectively (Figure 1b, Table S6). Concurrently, they increased interannual variability by 68% (LRR$_{NP}$ = 0.52, $p < 0.001$), 49% (LRR$_{NK+}$ = 0.42, $p < 0.001$) and 21% (LRR$_{PK+}$ = 0.2, $p = 0.002$) respectively (Figure 1c, Table S7). Simultaneous NPK+ additions increased mean biomass by 51% (LRR$_{NPK+}$ = 0.41, $p < 0.001$), exceeding the effect of all one- or two-nutrient treatments, and increased variability by 68% (LRR$_{NPK+}$ = 0.53, $p < 0.001$).

We observed a general synergistic co-limitation of mean biomass production by N and P (LRR$_{N*P}$ = 0.14, $p = 0.011$, Table S5). There was also a notable interaction between P and K+ (LRR$_{P*K+}$ = 0.1, $p = 0.071$) that increased biomass in PK+ plots relative to controls. In contrast, we did not observe any significant nutrient interactions for interannual variability (Table S5). Instead, multiple nutrient effects on interannual variability were driven by significant effects of N and P that produced additive increases in σ_{detr} (Table S5).

How consistent were effects among the 34 globally distributed grassland sites?

Destabilisation most frequently occurred in response to treatments containing N. Inputs of N alone decreased stability by more than 10% relative to control

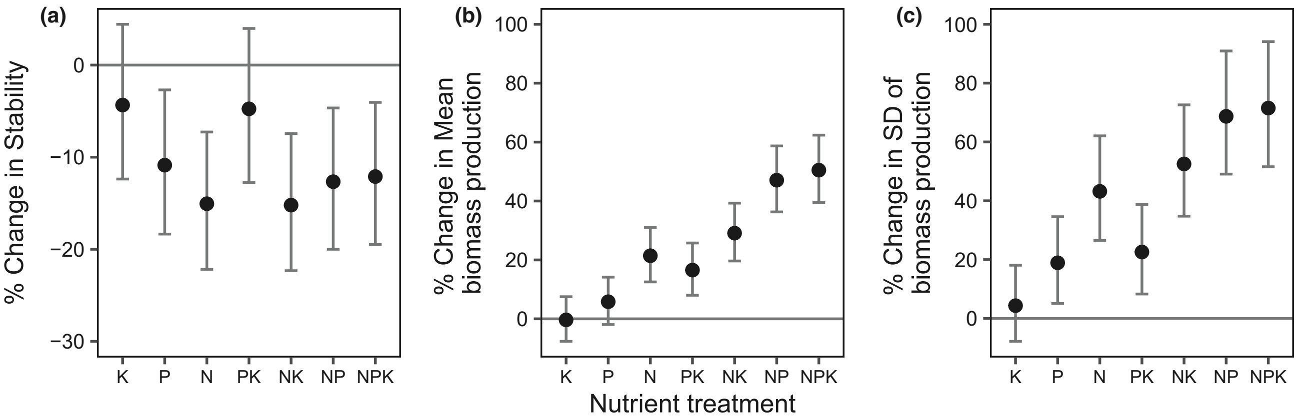

FIGURE 1 Effect of 7 years of single- and multiple-nutrient additions on the detrended stability (inverse CV) (a), temporal mean (b) and detrended standard deviation (SD) (c) of grassland biomass production in 34 sites. Different individual and combined additions of nitrogen (N), phosphorus (P) and potassium with essential nutrients (K) influenced the magnitude of stability, mean and interannual variability responses. The points show percent change relative to unenriched control plots. They represent back-transformed fixed effect estimates (with 95% confidence intervals) from mixed effects models that accounted for site as a random grouping factor. See Supplementary Information for detailed model specification and summary statistics

plots at 23 sites and by more than 20% at eight sites (Table S8). Similarly, large biomass and standard deviation responses were most frequently observed in response to N treatments. Mean biomass increased by over 25% with NPK+ at 31 sites and by over 50% at 18 sites (Table S8). Interannual variability increased by over 25% at 33 sites and by over 50% at 26 sites. Multiple nutrient treatments produced mean biomass and variability responses more frequently than inputs of single nutrients (Table S8).

Does nutrient limitation status impact the destabilisation potential of nutrient enrichment?

Across the study, sites with larger biomass responses, indicative of stronger underlying nutrient limitations, were associated with larger destabilisation responses to nutrient enrichment (Figure 2, Table S9). This relationship held for all nutrient combinations except NP and NPK+ (Table S9).

Does average site precipitation influence the response of temporal stability to nutrient enrichment?

Average site precipitation did not strongly drive stability effects; MAP and MAP variability were retained in the model selection procedure for the stability, mean biomass and interannual variability models but were not significant predictors of these responses (Table S10).

Do nutrient effects on species richness or species synchrony influence the response of temporal stability to nutrient enrichment?

Species richness declined with N addition and all multiple nutrient treatments but was not generally impacted by P or K+ additions (Figure 3a, Table S11). Species loss was highest with simultaneous NPK+ inputs, which reduced species richness by 16% ($LRR_{NPK+} = -0.17$, $p < 0.001$) across the study. Species synchrony did not display a clear directional response to any nutrient treatment at the global scale (Figure 3b, Table S12).

S_d was positively associated with species richness ($p = 0.009$; Figure 4a, Table S10). Specifically, species loss was associated with decreased stability of biomass production whilst species gains were associated with increased stability. In contrast, overall mean biomass responses were negatively associated with species richness such that biomass was most likely to increase where species were lost ($p = 0.001$; Figure 4b, Table S10). Similarly, change in the interannual variability of biomass production was negatively associated with species richness such that plots displayed greater increases in interannual variability where species loss was higher ($p < 0.001$; Figure 4c, Table S10).

Species synchrony and S_d responses displayed a negative relationship ($p = 0.052$; Figure 5, Table S10). Consequently, destabilisation of community biomass was more likely where nutrients caused species synchrony to increase, and stabilisation more likely where nutrients promoted asynchrony (Figure 5). Species synchrony was retained in the model set for the mean and interannual variability of biomass but was not a statistically significant predictor of these responses (Table S10).

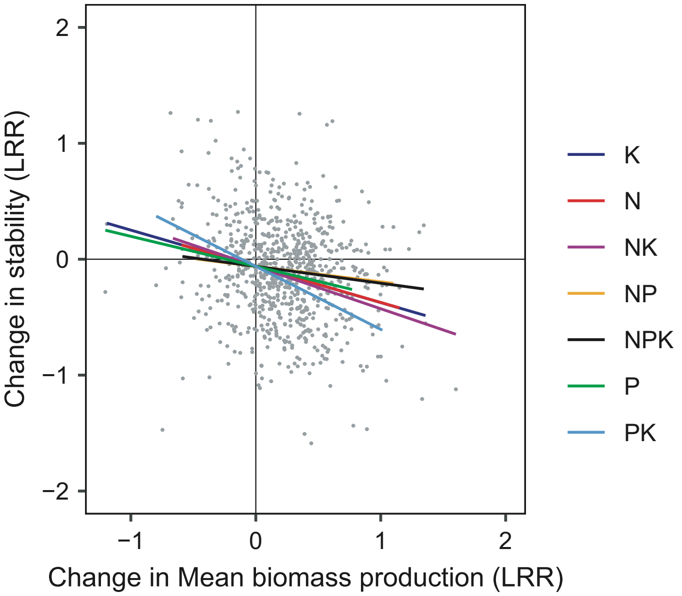

FIGURE 2 Relationship between change in mean biomass production and change in stability under 7 years of different individual and combined additions of nitrogen (N), phosphorus (P) and potassium with essential nutrients (K). Larger biomass responses were associated with larger declines in stability for all treatments except NP and NPK. Points show plots within blocks at 34 grassland sites. Coloured lines are fixed-effect regression slopes for each treatment from mixed effects models. See Supplementary Information for detailed model specification and summary statistics

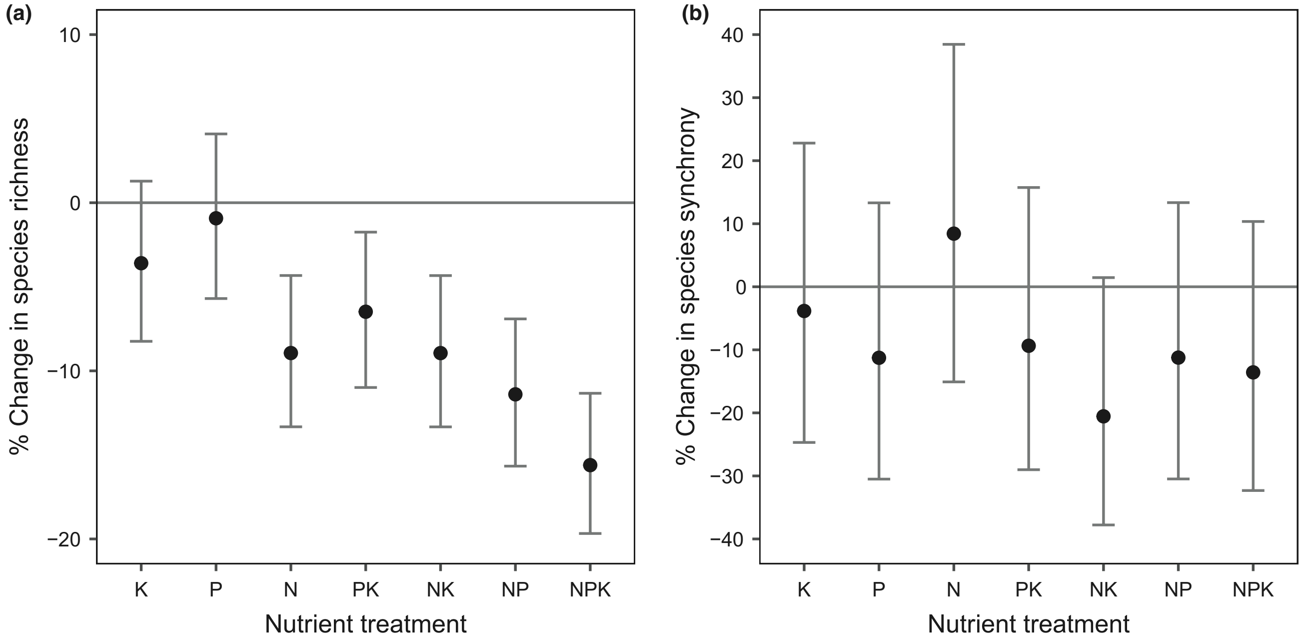

FIGURE 3 Effect of individual and combined additions of nitrogen (N), phosphorus (P), and potassium with essential nutrients (K) on the temporal mean of species richness (a) and detrended species synchrony (b) in 34 grassland sites. Positive responses in species synchrony indicate species were more synchronised, while negative responses indicate increased asynchrony. Points show fixed effect estimates with 95% confidence intervals (see Figure 1 caption and Supplementary Information)

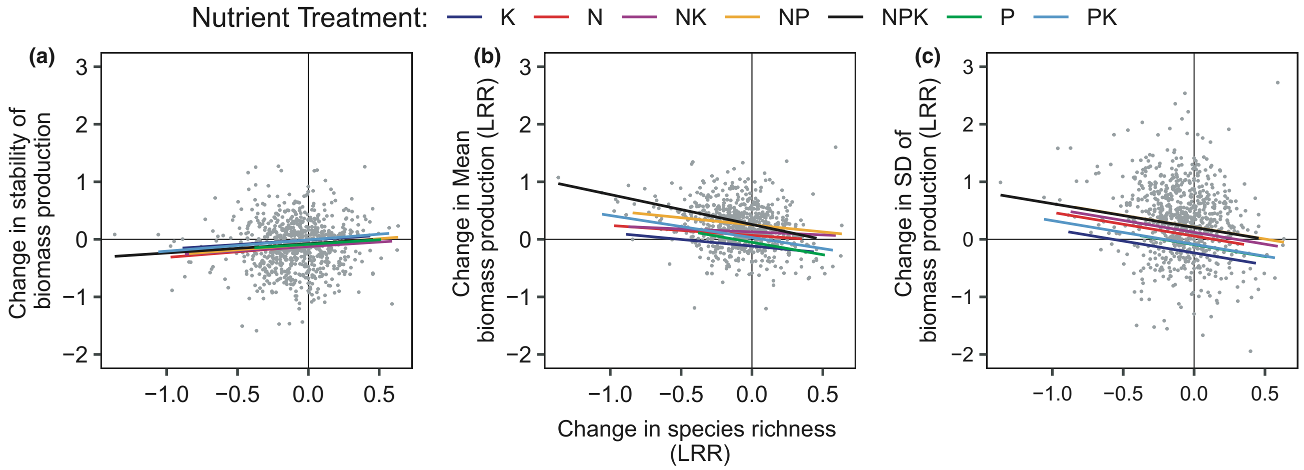

FIGURE 4 Nutrient-driven changes in species richness contribute to nutrient effects on the temporal stability (inverse CV) (a), mean (b) and detrended standard deviation (SD) (c) of grassland biomass production. Points show plots within blocks at 34 globally distributed grassland sites. Coloured lines are fixed-effect regression slopes from mixed effects models for individual and combined nitrogen (N), phosphorus (P) and potassium with essential nutrients (K) addition treatments. Similar trends caused overlapping lines for some treatments in panels (a) (PK overlaps P) and (c) (PK overlaps K). See Supplementary Information for detailed model specification and summary statistics

DISCUSSION

Do nutrient identity and nutrient interactions impact the temporal stability, mean and interannual variability of grassland biomass production?

Grassland biomass production is often limited or co-limited by nutrients (Fay et al., 2015; Harpole et al., 2011). However, understanding of how co-limitation dynamics affect grassland stability is still lacking. Our analyses showed that N and multiple nutrient enrichment generally increased mean biomass production but destabilised it by inducing even greater increases in interannual variability. This indicates that, despite elevated biomass production, N inputs also increased the magnitude of fluctuations among years (McCann et al., 2021). Enrichment of P did not generally increase mean biomass but still increased its interannual variability and therefore had a general destabilising effect. In contrast, K+ enrichment did not change either the mean or

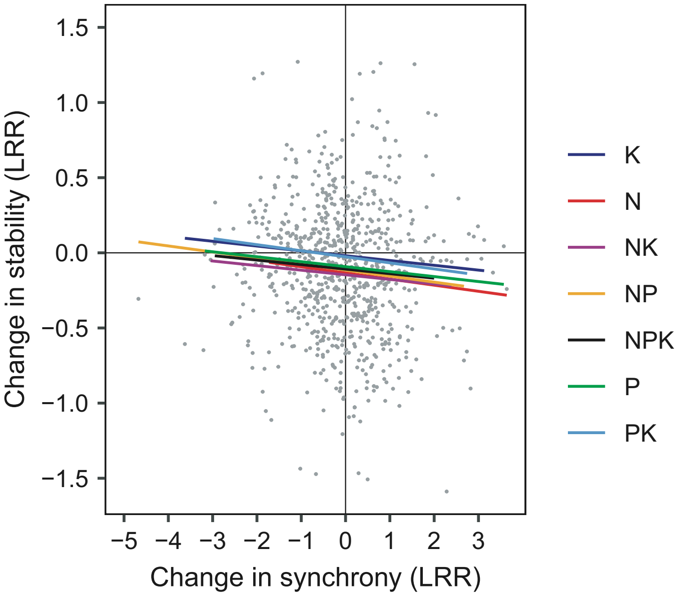

FIGURE 5 Nutrient-driven changes in species synchrony contribute to nutrient effects on the stability of grassland biomass production over 7 years. Positive responses in species synchrony indicate species were more synchronised, while negative responses indicate increased asynchrony. Coloured lines show fixed-effect slopes within different nitrogen (N), phosphorus (P) and potassium with essential nutrients (K) treatments (see Figure 4 caption and Supplementary Information)

variability of biomass, and therefore did not impact stability at the global scale.

Multiple nutrient treatments revealed interactive effects on mean biomass production, including a general synergistic interaction between N and P, consistent with previous observations of co-limitation (Fay et al., 2015; Harpole et al., 2011). However, this did not directly translate to stability responses. Multiple nutrient inputs did not drive transitions in mean-variability scaling beyond the effects of single N or P inputs. Consequently, nutrient interaction effects on stability were generally subadditive (i.e. less than the sum of multiple single-nutrient effects; Harpole et al., 2011). This mitigated against compounding destabilisation effects that could occur if all added nutrients exerted additive or synergistic effects (Harpole et al., 2011).

Accordingly, multiple-nutrient enrichment was not more destabilising than single-nutrient enrichment at the global scale. Declining stability may indicate an increased risk of reaching a minimum acceptable value of an ecosystem function (Carnus et al., 2014) where, for example substantial changes to community composition become likely (Beisner et al., 2003; McCann et al., 2021) or a food production system fails to reach a profit. Our study suggests that single N inputs generally increased mean biomass production (more reward) but decreased stability (more risk). In contrast, relative to N, multiple-nutrient NP and NPK+ inputs generally increased mean biomass but maintained an equivalent stability.

All inputs containing N generally increased interannual variability in biomass, consistent with previous work (Hautier et al., 2014; Rosenzweig, 1971). However, while NP and NPK+ produced the same risk as N-only inputs, they offered greater biomass production, potentially increasing ecosystem services such as food production and soil carbon sequestration (Gounand et al., 2020). Nonetheless, situations where stability is equivalent but the means are different indicate that total interannual variability is greater in the high means group. Variability can be of interest itself as it determines the absolute size of fluctuations in ecosystem services (Kohli et al., 2019). In this study, the standard deviation was higher in NP and NPK+ treatments than with N only, despite equivalent stability, a result that could still translate to altered nutrient cycling or secondary production (Kohli et al., 2019). Accordingly, it is important to be clear about the aspects of variability and stability that are of concern in a given context (Carnus et al., 2014; Kohli et al., 2019).

Here, explicit consideration of nutrient effects on both the mean and variability of biomass indicated a general effect in which adding limiting nutrients increased mean biomass but drove disproportionate increases in the standard deviation, resulting in variability-driven destabilisation. It also revealed that the type of multiple nutrient limitation of the mean (synergistic vs additive; Harpole et al., 2011) was not the same as multiple limitation of interannual variability. While joint consideration of the mean and variability remains uncommon (Avolio et al., 2020; Hautier et al., 2015; Kohli et al., 2019), global change drivers do not always appear to alter mean-variability proportionality. For example, Kohli et al. (2019) observed that disturbance of consumer food webs had no effect on the stability of grassland biomass production because the mean and variability responded proportionately. These results show that future work should routinely consider how both the mean and variability of ecosystem processes respond to global changes (Avolio et al., 2020).

How consistent was nutrient-driven destabilisation among 34 globally distributed grassland sites?

The magnitude of nutrient-driven changes in stability varied among sites. Twenty sites displayed 10% declines in stability following NPK+ enrichment and eight displayed reductions in stability of more than 20%. This effect size has a similar magnitude to previously reported stability responses. For example, declining species richness is a widely acknowledged driver of significant destabilisation (Tilman et al., 2006) and, in a recent meta-analysis, experimentally reducing richness from 16 to 2 was also shown to destabilise biomass production by 20% (Hautier et al., 2015). This suggests that the effects of nutrient enrichment on stability can match other key global change drivers. Overall, our study suggests that there is a wide range in the magnitude of grassland stability responses to elevated nutrient supply, but that increasing eutrophication will likely drive more grasslands towards critical thresholds of functioning.

Nutrient effects on mean biomass production were more prevalent. At 31 sites, NPK+ enrichment increased mean biomass production by at least 25%. Nutrient limitation has not appeared this prevalent in previous, shorter assessments (Fay et al., 2015). This is consistent with increasing nutrient effects observed over 10 years (Seabloom et al., 2021) and might be explained by a progressive shift in community composition, as opposed to immediate and possibly transient changes in relative abundance and individual biomass production. Nutrient effects on interannual variability were even more prevalent, with 33 sites increasing variability by 25% and 26 sites increasing variability by 50% following NPK+ enrichment.

Was there evidence for mechanisms associated with destabilisation following nutrient enrichment?

Understanding the mechanisms that determine the potential for different nutrients to destabilise biomass production is crucial to maintaining grassland function over the long term. One possible cause of increased interannual variability following nutrient enrichment is the amplified responsiveness of plant growth to precipitation events (Wang et al., 2017) due to increased rain use efficiency (Huxman et al., 2004). In our analysis, there was no clear association of nutrient-driven destabilisation with MAP or the variability of MAP. This is consistent with broader observations that nutrient enrichment can destabilise biomass production in both wet (Tilman et al., 2006) and dry (Wang et al., 2017) grassland systems, where different mechanisms mediate the relationship between moisture availability and stability, but each still promote destabilisation (Wang et al., 2017). Studies that assess wet and dry grasslands separately have provided better insight into the role of precipitation and moisture availability in mediating nutrient effects on the stability of grassland biomass production (Bharath et al., 2020).

Our study suggests that destabilisation following nutrient enrichment is partly driven by the extent of underlying nutrient limitation, suggesting destabilisation with enrichment is stronger where nutrient limitation is stronger. One explanation for this is that nutrient limitations can impose constraints on community composition by mediating competition among species (Braakhekke & Hooftman, 1999; Tilman, 1982). Enrichment of nutrient-limited communities may then cause changes in community composition that impact community biomass production. Despite the overall relationship between mean and stability effects, the response of mean biomass was not a significant predictor of stability within the NP and NPK+ treatments, suggesting these inputs also reduced stability where they did not limit biomass. This may be because NP and NPK+ enrichment can drive species loss even where they are not limiting factors (Harpole et al., 2016), causing destabilisation through lost diversity-stability effects.

Our results also showed that nutrient effects on species richness contributed to changes in mean biomass production and its stability (Hautier et al., 2015). Plots that lost more species typically became more productive but less stable due to proportionally larger increases in the temporal standard deviation of biomass production. This has not been observed in previous analyses of NutNet data (Hautier et al., 2014, 2020). Our ability to detect this here is likely due to the increased power afforded by including observations from all treatment plots (not just NPK+) and the accumulation of more sites with longer-term data. In addition to species richness effects, we also found that changes in species synchrony following enrichment contributed to changes in stability. Overall, stability was reduced where synchrony increased (Hautier et al., 2014, 2020; Muraina et al., 2021). However, in contrast to richness, there were no general effects of nutrient treatments on synchrony, nor differences between treatments.

In addition to the decreased stability observed here, our results also suggest a heightened destabilisation risk over longer periods of nutrient enrichment. Coupled with evidence that species loss can continue for more than a decade with simultaneous NPK+ enrichment (Seabloom et al., 2021), our observation that species loss contributed to nutrient-driven destabilisation suggests that increased variability could be exacerbated over longer periods. Furthermore, our observation of increased overall mean biomass with species loss was characteristic of a shift in community composition towards highly productive species (Tilman, 1982). Productive species can mitigate against destabilisation by maintaining a high temporal mean. However, with higher species loss and increased sensitivity to other environmental fluctuations (MacDougall et al., 2013), mean-driven stabilisation effects may be lost, exacerbating destabilisation and the risk of total collapse over longer timeframes (Isbell et al., 2013). Our findings suggest this risk is particularly enhanced with N and the NP interaction that drove the greatest species loss.

CONCLUSIONS

Despite widespread multiple nutrient effects on mean biomass production (Fay et al., 2015; Harpole et al., 2011), we are lacking studies investigating independent or interactive effects of multiple nutrients on the interannual variability or temporal stability of biomass production. Here, we demonstrated that changes in the mean, interannual variability and stability of biomass production with fertilisation were prevalent across 34 grasslands. We demonstrated that changes in stability were largely driven by single nutrient effects, rather than synergistic nutrient interactions. N- and P-based treatments caused the largest destabilisation effects. Ongoing disruptions of multiple nutrient availability are likely to reduce the reliability of grassland functioning and increase the chance of irreversible change in species composition. This risk is greatest when the most limiting nutrient for production is added, or where nutrients reduce species richness or increase species synchrony.

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AUTHORSHIP

O.C. and A.S.M. developed and framed the research questions. O.C. analysed the data with contributions to analysis from E. B., S.B., E.H.E., Y.H., T.O., E.W.S. and K.S.M. O.C. wrote the paper and all other authors (E.B., S.B., E.T.B., S.C., E.H.E., Y.H., T.O., E.W.S., P.B.A., J.D.B., L.B., M.N.B., M.C., Q.C., K.F.D., P.A.F., J.M.H.K., K.K., J.P.M., K.S.M., J.L.M., J.W.M., T.O.M., B.O., A.C.R., C.S., P.A.W., L.Y., A.S.M.) contributed to paper writing. E.T.B., Y.H., T.O., E.W.S., P.B.A., J.D.B., L.B., M.N.B., M.C., K.F.D., P.A.F., J.M.H.K., K.K., J.P.M., J.L.M., J.W.M., A.C.R., C.S. and A.S.M contributed data. Details of author contributions are provided in Table S13 and Table S14.

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REFERENCES

Avolio, M.L., Wilcox, K.R., Komatsu, K.J., Lemoine, N., Bowman, W.D., Collins, S.L. et al. (2020) Temporal variability in production is not consistently affected by global change drivers across herbaceous-dominated ecosystems. *Oecologia*, 194, 735–744.

Bakelaar, R.G. & Odum, E.P. (1978) Community and population level responses to fertilization in an old-field ecosystem. *Ecology*, 59, 660–665.

Bartoń, K. (2009). MuMIn : multi-model inference.

Bates, D., Mächler, M., Bolker, B. & Walker, S. (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, 1–48.

Beisner, B.E., Haydon, D.T. & Cuddington, K. (2003) Alternative stable states in ecology. *Frontiers in Ecology and the Environment*, 1, 376–382.

Bharath, S., Borer, E.T., Biederman, L.A., Blumenthal, D.M., Fay, P.A., Gherardi, L.A. et al. (2020) Nutrient addition increases grassland sensitivity to droughts. *Ecology*, 101, e02981.

Borer, E.T., Harpole, W.S., Adler, P.B., Arnillas, C.A., Bugalho, M.N., Cadotte, M.W. et al. (2020) Nutrients cause grassland biomass to outpace herbivory. *Nature Communications*, 11, 6036.

Borer, E.T., Harpole, W.S., Adler, P.B., Lind, E.M., Orrock, J.L., Seabloom, E.W. et al. (2014) Finding generality in ecology: a model for globally distributed experiments. *Methods in Ecology and Evolution*, 5, 65–73.

Braakhekke, W.G. & Hooftman, D.A.P. (1999) The resource balance hypothesis of plant species diversity in grassland. *Journal of Vegetation Science*, 10, 187–200.

Brown, B.L., Downing, A.L. & Leibold, M.A. (2016) Compensatory dynamics stabilize aggregate community properties in response to multiple types of perturbations. *Ecology*, 97, 2021–2033.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P. et al. (2012) Biodiversity loss and its impact on humanity. *Nature*, 486, 59–67.

Cardinale, B.J., Gross, K., Fritschie, K., Flombaum, P., Fox, J.W., Rixen, C. et al. (2013) Biodiversity simultaneously enhances the production and stability of community biomass, but the effects are independent. *Ecology*, 94, 1697–1707.

Carnus, T., Finn, J.A., Kirwan, L. & Connolly, J. (2014) Assessing the relationship between biodiversity and stability of ecosystem function – is the coefficient of variation always the best metric? *Ideas in Ecology and Evolution*, 7, 89–96.

Carpenter, S.R. & Brock, W.A. (2006) Rising variance: a leading indicator of ecological transition. *Ecology Letters*, 9, 311–318.

Carroll, I.T., Cardinale, B.J. & Nisbet, R.M. (2011) Niche and fitness differences relate the maintenance of diversity to ecosystem function. *Ecology*, 92, 1157–1165.

Chesson, P. (2000) Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, 31, 343–366.

Danger, M., Daufresne, T., Lucas, F., Pissard, S. & Lacroix, G. (2008) Does Liebig's Law of the Minimum scale up from species to communities? *Oikos*, 117, 1741–1751.

Donohue, I., Petchey, O.L., Montoya, J.M., Jackson, A.L., McNally, L., Viana, M. et al. (2013) On the dimensionality of ecological stability. *Ecology Letters*, 16, 421–429.

Droop, M.R. (1974) The nutrient status of algal cells in continuous culture. *Journal of the Marine Biological Association of the UK*, 54, 825–855.

Elser, J.J., Bracken, M.E.S., Cleland, E.E., Gruner, D.S., Harpole, W.S., Hillebrand, H. et al. (2007) Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecology Letters*, 10, 1135–1142.

Fay, P.A., Prober, S.M., Harpole, W.S., Knops, J.M.H., Bakker, J.D., Borer, E.T. et al. (2015) Grassland productivity limited by multiple nutrients. *Nature Plants*, 1, 15080.

Gilbert, B., MacDougall, A.S., Kadoya, T., Akasaka, M., Bennett, J.R., Lind, E.M. et al. (2020) Climate and local environment structure asynchrony and the stability of primary production in grasslands. *Global Ecology and Biogeography*, 29, 1177–1188.

Gounand, I., Little, C.J., Harvey, E. & Altermatt, F. (2020) Global quantitative synthesis of ecosystem functioning across climatic zones and ecosystem types. *Global Ecology and Biogeography*, 29, 1139–1176.

Haberl, H., Erb, K.H., Krausmann, F., Gaube, V., Bondeau, A., Plutzar, C. et al. (2007) Quantifying and mapping the human appropriation of net primary production in earth's terrestrial ecosystems. *Proceedings of the National Academy of Sciences*, 104, 12942–12947.

Harpole, W.S., Ngai, J.T., Cleland, E.E., Seabloom, E.W., Borer, E.T., Bracken, M.E.S. et al. (2011) Nutrient co-limitation of primary producer communities. *Ecology Letters*, 14, 852–862.

Harpole, W.S., Sullivan, L.L., Lind, E.M., Firn, J., Adler, P.B., Borer, E.T. et al. (2016) Addition of multiple limiting resources reduces grassland diversity. *Nature*, 537, 93–96.

Harpole, W.S., Sullivan, L.L., Lind, E.M., Firn, J., Adler, P.B., Borer, E.T. et al. (2017) Out of the shadows: multiple nutrient limitations drive relationships among biomass, light and plant diversity. *Functional Ecology*, 31, 1839–1846.

Harpole, W.S. & Tilman, D. (2006) Non-neutral patterns of species abundance in grassland communities. *Ecology Letters*, 9, 15–23.

Harpole, W.S. & Tilman, D. (2007) Grassland species loss resulting from reduced niche dimension. *Nature*, 446, 791–793.

Hautier, Y., Seabloom, E.W., Borer, E.T., Adler, P.B., Harpole, W.S., Hillebrand, H. et al. (2014) Eutrophication weakens stabilizing effects of diversity in natural grasslands. *Nature*, 508, 521–525.

Hautier, Y., Tilman, D., Isbell, F., Seabloom, E.W., Borer, E.T. & Reich, P.B. (2015) Anthropogenic environmental changes affect ecosystem stability via biodiversity. *Science*, 348, 336–340.

Hautier, Y., Zhang, P., Loreau, M., Wilcox, K.R., Seabloom, E.W., Borer, E.T. et al. (2020) General destabilizing effects of eutrophication on grassland productivity at multiple spatial scales. *Nature Communications*, 11, 5375.

Hector, A., Hautier, Y., Saner, P., Wacker, L., Bagchi, R., Joshi, J. et al. (2010) General stabilizing effects of plant diversity on grassland productivity through population asynchrony and overyielding. *Ecology*, 91, 2213–2220.

Hedges, L.V., Gurevitch, J. & Curtis, P.S. (1999) The meta-analysis of response ratios in experimental ecology. *Ecology*, 80, 1150–1156.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, 25, 1965–1978.

Hou, E., Luo, Y., Kuang, Y., Chen, C., Lu, X., Jiang, L. et al. (2020) Global meta-analysis shows pervasive phosphorus limitation of aboveground plant production in natural terrestrial ecosystems. *Nature Communications*, 11, 637.

Huxman, T.E., Smith, M.D., Fay, P.A., Knapp, A.K., Shaw, M.R., Loik, M.E. et al. (2004) Convergence across biomes to a common rain-use efficiency. *Nature*, 429, 651–654.

Isbell, F., Reich, P.B., Tilman, D., Hobbie, S.E., Polasky, S. & Binder, S. (2013) Nutrient enrichment, biodiversity loss, and consequent declines in ecosystem productivity. *Proceedings of the National Academy of Sciences*, 110, 11911–11916.

Ives, A.R. & Carpenter, S.R. (2007) Stability and diversity of ecosystems. *Science*, 317, 58–62.

Ives, A.R., Klug, J.L. & Gross, K. (2000) Stability and species richness in complex communities. *Ecology Letters*, 3, 399–411.

Kaspari, M. & Powers, J.S. (2016) Biogeochemistry and geographical ecology: embracing all twenty-five elements required to build organisms. *American Naturalist*, 188, S62–S73.

Koerner, S.E., Avolio, M.L., Pierre, K.J.L., Wilcox, K.R., Smith, M.D. & Collins, S.L. (2016) Nutrient additions cause divergence of tallgrass prairie plant communities resulting in loss of ecosystem stability. *Journal of Ecology*, 104, 1478–1487.

Kohli, M., Borer, E.T., Kinkel, L. & Seabloom, E.W. (2019) Stability of grassland production is robust to changes in the consumer food web. *Ecology Letters*, 22, 707–716.

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

LeBauer, D.S. & Treseder, K.K. (2008) Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed. *Ecology*, 89, 371–379.

Legendre, P. & Legendre, L. (2012) *Numerical ecology*. Elsevier, Amsterdam: Developments in environmental modelling. Third English edition.

Lepš, J., Götzenberger, L., Valencia, E. & de Bello, F. (2019) Accounting for long-term directional trends on year-to-year synchrony in species fluctuations. *Ecography*, 42, 1728–1741.

Levin, S.A. (1970) Community equilibria and stability, and an extension of the competitive exclusion principle. *American Naturalist*, 104, 413–423.

Loreau, M. (2010) *From populations to ecosystems: theoretical foundations for a new ecological synthesis (MPB-46)*. Princeton: Princeton University Press.

Loreau, M. & de Mazancourt, C. (2008) Species synchrony and its drivers: neutral and nonneutral community dynamics in fluctuating environments. *American Naturalist*, 172, E48–E66.

Loreau, M. & de Mazancourt, C. (2013) Biodiversity and ecosystem stability: a synthesis of underlying mechanisms. *Ecology Letters*, 16, 106–115.

MacDougall, A.S., McCann, K.S., Gellner, G. & Turkington, R. (2013) Diversity loss with persistent human disturbance increases vulnerability to ecosystem collapse. *Nature*, 494, 86–89.

McCann, K.S., Cazelles, K., MacDougall, A.S., Fussmann, G.F., Bieg, C., Cristescu, M. et al. (2021) Landscape modification and nutrient-driven instability at a distance. *Ecology Letters*, 24, 398–414.

Morgan, J.W., Dwyer, J.M., Price, J.N., Prober, S.M., Power, S.A., Firn, J. et al. (2016) Species origin affects the rate of response to inter-annual growing season precipitation and nutrient addition in four Australian native grasslands. *Journal of Vegetation Science*, 27, 1164–1176.

Muraina, T.O., Xu, C., Yu, Q., Yang, Y., Jing, M., Jia, X. et al. (2021) Species asynchrony stabilises productivity under extreme drought across Northern China grasslands. *Journal of Ecology*, 109, 1665–1675.

Nakagawa, S. & Cuthill, I.C. (2007) Effect size, confidence interval and statistical significance: a practical guide for biologists. *Biological Reviews*, 82, 591–605.

Paruelo, J.M., Lauenroth, W.K., Burke, I.C. & Sala, O.E. (1999) Grassland precipitation-use efficiency varies across a resource gradient. *Ecosystems*, 2, 64–68.

R Foundation for Statistical Computing. (n.d.). R: The R Project for Statistical Computing. Vienna, Austria.

Rosenzweig, M.L. (1971) Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. *Science*, 171, 385–387.

Scheffer, M., Carpenter, S., Foley, J.A., Folke, C. & Walker, B. (2001) Catastrophic shifts in ecosystems. *Nature*, 413, 591–596.

Seabloom, E.W., Adler, P.B., Alberti, J., Biederman, L., Buckley, Y.M., Cadotte, M.W. et al. (2021) Increasing effects of chronic nutrient enrichment on plant diversity loss and ecosystem productivity over time. *Ecology*, 102, e03218.

Song, J., Wan, S., Piao, S., Knapp, A.K., Classen, A.T., Vicca, S. et al. (2019) A meta-analysis of 1,119 manipulative experiments on terrestrial carbon-cycling responses to global change. *Nature Ecology & Evolution*, 3, 1309–1320.

Stevens, C.J., Dise, N.B., Mountford, J.O. & Gowing, D.J. (2004) Impact of nitrogen deposition on the species richness of grasslands. *Science*, 303, 1876–1879.

Tilman, D. (1982) *Resource competition and community structure. Monographs in population biology*. Princeton, N.J: Princeton University Press.

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

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

Tilman, D. & Lehman, C. (2001) Human-caused environmental change: impacts on plant diversity and evolution. *Proceedings of the National Academy of Sciences*, 98, 5433–5440.

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

Tilman, D., Reich, P.B., Knops, J., Wedin, D., Mielke, T. & Lehman, C. (2001) Diversity and productivity in a long-term grassland experiment. *Science*, 294, 843–845.

Valencia, E., de Bello, F., Galland, T., Adler, P.B., Lepš, J., E-Vojtkó, A. et al. (2020a) Synchrony matters more than species richness in plant community stability at a global scale. *Proceedings of the National Academy of Sciences*, 117, 24345–24351.

Valencia, E., de Bello, F., Lepš, J., Galland, T., E-Vojtkó, A., Conti, L. et al. (2020b) Directional trends in species composition over time can lead to a widespread overemphasis of year-to-year asynchrony. *Journal of Vegetation Science*, 31, 792–802.

Wang, J., Knops, J.M.H., Brassil, C.E. & Mu, C. (2017) Increased productivity in wet years drives a decline in ecosystem stability with nitrogen additions in arid grasslands. *Ecology*, 98, 1779–1786.

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