

Nitrogen enrichment alters multiple dimensions of grassland functional stability via changing compositional stability

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INTRODUCTION

Anthropogenic nitrogen (N) and phosphorus (P) enrichment, due to increased fossil fuel use and agricultural fertiliser applications, are among the most significant global environmental changes affecting the world's ecosystems (Galloway et al., 2004; Galloway et al., 2008; Smil, 2000; Vitousek et al., 1997; Yuan et al., 2018). Nitrogen is an essential component of proteins, nucleic acids and chlorophyll,

Abstract

Anthropogenic nutrient enrichment is known to alter the composition and functioning of plant communities. However, how nutrient enrichment influences multiple dimensions of community- and ecosystem-level stability remains poorly understood. Using data from a nitrogen (N) and phosphorus (P) addition experiment in a temperate semi-arid grassland that experienced a natural drought, we show that N enrichment, not P enrichment, decreased grassland functional and compositional temporal stability, resistance and recovery but increased functional and compositional resilience. Compositional stability and species asynchrony, rather than species diversity, were identified as key determinants of all dimensions of grassland functional stability, except for recovery. Whereas grassland functional recovery was decoupled from compositional recovery, N enrichment altered other dimensions of functional stability primarily through changing their corresponding compositional stability dimensions. Our findings highlight the need to examine ecological stability at the community level for a more mechanistic understanding of ecosystem dynamics in the face of environmental change.

KEY WORDS

asynchrony, compositional stability, disturbance, drought, functional stability, grassland, nutrient addition

and thus critical for many cellular and physiological processes (Chapin, 1980; Field & Mooney, 1986). Phosphorus constitutes a major ingredient of cellular membranes and nucleic acids (DNA and RNA; Schachtman et al., 1998). Grasslands, which cover approximately 40% of the Earth's ice-free land area (White et al., 2000), are often limited by the availability of reactive N and P (Elser et al., 2007; Fay et al., 2015; Harpole et al., 2011; Vitousek & Howarth, 1991; Walker & Syers, 1976). Increased N and

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P input into grasslands, either individually or in combination, has often resulted in increased primary productivity (Elser et al., 2007; Fay et al., 2015; Harpole et al., 2011; Hou et al., 2020; Li et al., 2016). There is also mounting evidence that N enrichment often reduces grassland plant diversity (Bobbink et al., 1998; Midolo et al., 2019; Payne et al., 2017; Stevens et al., 2004), although the effects of P enrichment on grassland diversity are mixed (DeMalach, 2018; Soons et al., 2017). N and P enrichment are also known to alter other compositional (e.g. Yang, Li, et al., 2011; Zhao et al., 2019) and functional (Song et al., 2019) properties of grasslands. However, how N and P enrichment influences various aspects of grassland stability remains poorly understood.

Ecological stability encompasses multiple dimensions, such as temporal stability, resistance, resilience and recovery, each of which captures the dynamics of ecological systems and their responses to environmental changes in different ways (Figure 1; Pimm, 1984; Ives & Carpenter, 2007; Donohue et al., 2013, 2016). Efforts to understand the dimensionality of ecological stability have revealed various relationships between different stability components (Donohue et al., 2013; Donohue et al., 2016; Hillebrand et al., 2018; Polazzo & Rico, 2021; Radchuk et al., 2019), indicating that one stability component may not necessarily substitute for another. Thus, adopting the multidimensional framework in stability research is becoming increasingly important for gaining a comprehensive understanding of ecological stability (Donohue et al., 2013; Kéfi et al., 2019; Pennekamp et al., 2018; Yang et al., 2019), and for fully characterising ecosystem dynamics in response to global environmental

changes. However, most studies of ecological stability have focused on a single dimension of stability (Donohue et al., 2016), risking a potentially biased understanding of the overall stability of ecological systems.

Recent stability research has primarily focused on the stability of ecosystem processes and functions (i.e. functional stability; Xu et al., 2021), coinciding with ecologists' interest in understanding the consequences of biodiversity loss for ecosystem functioning over the last three decades (Loreau et al., 2022). Previous studies have reported positive effects of species diversity on the temporal stability (Hector et al., 2010; Tilman et al., 2006), resistance (Baert et al., 2016; Isbell et al., 2015), resilience (Van Ruijven & Berendse, 2010) and recovery (Kreyling et al., 2017) of ecosystem functions. These positive biodiversity-functional stability relationships may be attributed to two primary mechanisms: increased asynchronous population dynamics among species (i.e. the insurance effect; Ives et al., 1999; Yachi & Loreau, 1999; Loreau & de Mazancourt, 2008, 2013), and the increased presence of dominant, stable species in more diverse communities (i.e. the selection effect; Loreau & Hector, 2001). On the other hand, as predicted by the mass ratio hypothesis (Grime, 1998), ecosystem-level stability may be largely driven by the stability of dominant species, rather than species diversity, if one or a few species contribute predominantly to ecosystem functioning (Doak et al., 1998; Hillebrand et al., 2008; Steiner et al., 2005). Nutrient enrichment is known to affect species richness (DeMalach, 2018; Suding et al., 2005), asynchronous dynamics among species (hereafter species asynchrony; Hautier et al., 2014; Zhang et al., 2016) and the stability of dominant species (Liu et al., 2019), with consequences for ecosystem temporal stability (Hautier et al., 2014; Zhang et al., 2016). By comparison, few studies have examined nutrient enrichment effects on ecosystem resistance to disturbance (Hofer et al., 2017; Xu et al., 2014), resilience after disturbance (Kinugasa et al., 2012; Xu et al., 2014) or recovery to the pre-disturbance state (Xu et al., 2014). Overall, the effects of nutrient enrichment on multiple dimensions of functional stability have rarely been explored, leaving a significant gap in our knowledge.

Compared with functional stability, community compositional stability, which considers changes in community membership and species relative abundance (Micheli et al., 1999; Sankaran & McNaughton, 1999), has received considerably less attention. Several earlier studies have examined compositional stability in relation to species diversity and documented various relationships between the two (Foster et al., 2002; Frank & McNaughton, 1991; Sankaran & McNaughton, 1999; Shurin et al., 2007; Wang et al., 2010). These results suggest varied importance of species diversity for regulating community compositional stability. More recent investigations have explored the relationship between functional and compositional stability, echoing calls for the need to investigate both types of stability concurrently (Lamy et al., 2021;

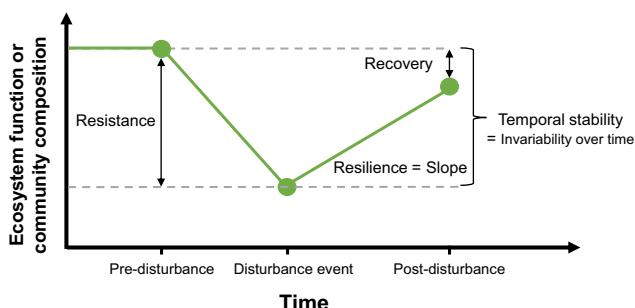


FIGURE 1 A conceptual diagram of the four dimensions of ecological stability examined in this study. Resistance is defined as the ability to withstand disturbance and quantified as the difference in ecosystem function or community composition between the disturbance year and pre-disturbance year. Resilience is defined as the rate of return of ecosystem function or community composition to the pre-disturbance state, and quantified as the slope of change following disturbance. Recovery is defined as the extent to which ecosystem function or community composition, following disturbance, returns to its pre-disturbance state and quantified as the difference between the post-disturbance year and the pre-disturbance year. Temporal stability is defined as the degree of constancy of ecosystem function or community composition over time. Table 2 Provides more details on the calculations of these stability dimensions.

Micheli et al., 1999). These investigations have also produced mixed results. On the one hand, some studies have reported that compositional and functional stability are positively associated (Baert et al., 2016; Guelzow et al., 2017; Hillebrand et al., 2018). On the other hand, functional stability has been found to be decoupled from compositional stability. This could happen, for instance, when dominant species largely determine ecosystem functioning despite appreciable changes in community composition (e.g. Hoover et al., 2014), or when species asynchrony maintains the stability of aggregated ecosystem properties (Xu et al., 2021; Yachi & Loreau, 1999). However, how nutrient enrichment influences multiple dimensions of compositional stability and functional-compositional stability relationships remains a largely open question.

By taking advantage of a resource addition experiment in a temperate semiarid grassland that experienced a severe, natural drought, we investigated how N and P enrichment affected multiple dimensions of ecological stability, including resistance, resilience, recovery and temporal stability, at both ecosystem and community levels. The temperate semi-arid grassland, located in Inner Mongolia, China, is a part of the Eurasian grassland biome. It has been subjected to intensifying environmental changes, including increased N and P input (Niu et al., 2010; Yang, Li, et al., 2011), and more frequent and intense droughts (Angerer et al., 2008; Yu et al., 2014). In 2007, our study site experienced the worst drought in nearly 60 years, offering a unique opportunity to explore how nutrient enrichment influences grassland stability properties. Our study aimed at addressing three main questions. First, how does N and P enrichment influence multiple dimensions of grassland functional and compositional stability? Second, what are the relative contributions of species richness, species asynchrony and the stability of dominant species in stabilising ecosystem function and community composition? Third, what are the relationships between functional and compositional stability? Table 1 summarises our hypotheses corresponding to these questions.

MATERIAL AND METHODS

Study site

Our study was conducted at the Duolun Restoration Ecology Research Station ($42^{\circ}02'N$, $116^{\circ}17'E$, 1324 m. a. s. l.) of the Institute of Botany, Chinese Academy of Sciences, located in Inner Mongolia, China. The study site has a semi-arid, continental monsoon climate with a relatively short growing season (from May to September). The mean annual precipitation is 378 mm; the mean annual temperature is $2.1^{\circ}C$. The year 2007 was the driest on record in our study area since 1953 (Figure S1), with a growing season precipitation of 185.0 mm, compared

TABLE 1 Our hypotheses corresponding to the three research questions

Hypotheses	Relevant literature
H1: Nutrient enrichment would decrease functional and compositional temporal stability, resistance and recovery but may increase resilience (i.e. increased rate of return to the pre-disturbance state, due to nutrient-induced increases in growth rate). We expect that lower resistance under nutrient enrichment contributes to lower recovery and temporal stability but allows more room for higher resilience.	Hautier et al., 2014; Isbell et al., 2015; Xu et al., 2014
H2: Nutrient enrichment reduces species richness, species asynchrony and the stability of dominant species, with ensuing consequences for grassland functional and compositional stability.	Hautier et al., 2014; Liu et al., 2019; Zhang et al., 2016
H3: Across stability dimensions, functional and compositional stability would exhibit positive relationships as lesser changes in community composition favour lesser changes in ecosystem functions.	Hillebrand et al., 2018

with the long-term growing season average of 328.3 mm. The vegetation is dominated by perennial plant species, such as *Agropyron cristatum*, *Artemesia frigida*, *Medicago ruthenica* and *Stipa krylovii*. Large herbivores have been excluded from our study site by fencing since 2001.

Experimental design and sampling

Our experiment was established in 2005, using a randomised complete block design. Four 92×60 m blocks were established with a 5-meter-wide buffer zone between adjacent blocks. Each block was divided into four 44×28 m plots, with each plot randomly assigned to one of the four nutrient addition treatments: control (i.e. ambient condition with no nutrient addition), N enrichment (10 g N/m^2 per year in the form of ammonium nitrate), P enrichment (5 g P/m^2 per year in the form of triple superphosphate) and the combined enrichment of N and P ($10 \text{ g N/m}^2 + 5 \text{ g P/m}^2$ per year). Pelletised fertiliser was evenly distributed by hand into designated plots in July each year. The background rate of N deposition in the study area is approximately 1.47 g N/m^2 per year (Zhang et al., 2017); the amount of N applied in our experiment is comparable with the rate of atmospheric N deposition in the North China Plain (about 8.33 g N/m^2 per year; He et al., 2007). The amount of P fertiliser applied is comparable with those in several other grassland experiments that manipulated P availability (e.g. Harpole & Tilman, 2007).

Plant communities in the experimental plots were surveyed in August, when our study grassland attained its

peak biomass, annually from 2006 to 2008. We estimated plant cover, rather than biomass, as a proxy of primary production. The non-destructive plant cover survey avoids disturbances associated with biomass estimation; our prior work also indicates strong positive relationships between plant species cover and biomass at our experimental site (Figure S2; Xia et al., 2009). Plant cover was measured by placing a 1×1 m frame with 100 10×10 cm grids above a 1×1 m permanent quadrat. We identified all species in each grid and estimated the percent cover of each species based on their occurrence within the 100 grids. Percent coverage was summed across species to obtain total community cover. Species richness was quantified as the number of species recorded within each quadrat; evenness was quantified using the Simpson index: $E = 1 - \sum_{i=1}^S P_i^2$, where P_i is the relative abundance of species i . We classified all species into dominant (relative abundance $>5\%$), subordinate (relative abundance between 1% to 5%), and rare (relative abundance $<1\%$) species.

Stability calculations

We quantified four stability dimensions (temporal stability, resistance, resilience and recovery) for both total plant cover and community composition as measures of functional and compositional stability, respectively. We define resistance as the grassland's ability to withstand disturbance (Ives & Carpenter, 2007; Pimm, 1984), resilience as the rate of return to the pre-disturbance state after disturbance (i.e. engineering resilience; Holling, 1973; Pimm, 1984; Pimm et al., 2019), recovery as the extent to which ecosystem function or community composition, following disturbance, returns to its pre-disturbance state (Hillebrand et al., 2018) and temporal stability as the degree of constancy of community or ecosystem properties over time (Pimm, 1984; Tilman et al., 2006). We illustrated how these stability dimensions are measured in Figure 1 and provided details on their calculation in Table 2. All the stability metrics were also calculated for each of species abundance groups. Species asynchrony was quantified as the community-wide asynchrony index, following Loreau and de Mazancourt (2008). Species asynchrony was calculated separately for each dimension of stability, using the data from the years relevant to the stability component (i.e. data from 2006 and 2007 for resistance, data from 2007 and 2008 for resilience, data from 2006 and 2008 for recovery and data from 2006, 2017 and 2008 for temporal stability).

Statistical analysis

Linear mixed-effects models were used to assess the effects of N enrichment, P enrichment and year on plant cover and richness, in which N enrichment, P enrichment and year were treated as fixed factors, and block was treated as a random factor. Likewise, permutational multivariate analysis

of variance (PERMANOVA) was used to assess treatment effects on community composition, with among-plot Bray–Curtis dissimilarity as the dependent variable. We also used linear mixed-effects models to assess the effects of N and P enrichment on different dimensions of stability at the ecosystem level (functional stability) and the community level (compositional stability), species asynchrony and the stability of dominant species. We also assessed the treatment effects on subordinate and rare species stability (see Figure S3) but focused on dominant species stability in subsequent analyses given their greater contributions to community and ecosystem stability (see Results).

Simple linear regressions were used to assess how species asynchrony, species richness, and the stability of dominant species relate to each dimension of grassland functional and compositional stability. Linear regressions were also used to assess the relationships between functional and compositional temporal stability, resistance, resilience and recovery. We further performed piecewise structural equation modelling (SEMs) to examine the pathways through which nutrient enrichment affected grassland functional and compositional stability. A separate SEM was constructed for each dimension of stability. We first constructed a priori models that included all plausible pathways (Figure S4) and then obtained the final SEMs by eliminating non-significant pathways. For species richness, we considered either initial richness (species richness in 2006 for resistance, recovery and temporal stability, and species richness in 2007 for resilience) or species richness averaged across 3 years. As the SEMs based on initial and average species richness were similar, we focus on results based on average species richness here (see Figure S5 for SEMs based on initial species richness). We also considered evenness but found that it was a non-significant factor in the SEMs (see Figure S6). Model adequacy was evaluated using Shipley's test of directed separation on Fisher's C statistic (Shipley, 2013) and Akaike information criteria corrected for sample size (AICc).

All statistical analyses were conducted in R version 4.1.2 (R Core Team, 2021). The 'nlme' package was used for conducting linear mixed-effects models, the 'vegan' package for calculating Bray–Curtis dissimilarity and conducting PERMANOVA, and the 'piecewiseSEM' package for constructing SEMs (Lefcheck, 2016).

RESULTS

Effects of nutrient enrichment on functional and compositional stability

N enrichment increased total plant cover and dominant species cover (linear mixed-effects model: $p < 0.001$ and $p = 0.012$, respectively; Figure S7a,b; Table S1) but decreased species richness ($p = 0.017$, Figure S7c, Table S1), whereas P enrichment had little effect ($p = 0.159$, $p = 0.810$ and $p = 0.991$ for total plant cover, dominant species cover

TABLE 2 The four stability dimensions investigated in this study, as well as how each stability dimension was quantified and its interpretation at the ecosystem (i.e. functional stability) and community (i.e. compositional stability) levels

Stability dimension	Function		Composition	
	Method of quantification	Interpretation	Method of quantification	Interpretation
<i>a</i> : Temporal stability	The inverse of coefficient of variation (1/CV) of total plant cover in each experimental plot over time (2006–2008).	Larger values indicate greater temporal stability over time.	One minus the mean Euclidean distance from each plot to its three-year (2006–2008) plot centroid, with distance calculated based on cross-year Bray–Curtis dissimilarity among communities of the same plot.	Larger values indicate greater temporal stability over time.
<i>b</i> : Resistance	Log response ratio (i.e. log-transformed proportional changes) of total plant cover between drought (2007) and pre-drought (2006) years. $b = \ln(F_{07}/F_{06})$	More negative values indicate lower resistance. 0 = max resistance	Bray–Curtis similarity between pre-drought and drought communities.	Range: 0–1. Larger values correspond to greater resistance.
<i>c</i> : Resilience	Slope of change in total plant cover between post-drought (2008) and drought (2007) years (equivalent as the difference between 2008 and 2007). $c = \ln(F_{08}/F_{07})$	More positive values indicate greater resilience. 0 = no resilience	Bray–Curtis dissimilarity between drought and post-drought communities.	Range: 0–1. Larger values correspond to greater resilience.
<i>d</i> : Recovery	Log response ratio between post-drought (2008) and pre-drought (2006) years. $d = \ln(F_{08}/F_{06})$	More negative values indicate lower recovery. 0 = max recovery	Bray–Curtis similarity between pre-drought and post-drought communities.	Range: 0–1. Larger values correspond to greater recovery.

Note: F = ecosystem function of interest.

and species richness, respectively; Figure S7, Table S1). However, the effects of N enrichment on total plant cover and dominant species cover were stronger under P enrichment, resulting in a significant N × P term in the linear mixed-effects models ($p = 0.012$ and $p = 0.011$, respectively; Figure S7a,b; Table S1). Likewise, PERMANOVA revealed a significant N × P effect on community composition (Table S2).

N enrichment significantly reduced functional temporal stability (linear mixed-effects model: $p < 0.001$; Figure 2a; Table S3), functional resistance ($p < 0.001$; Figure 2c; Table S3) and functional recovery ($p = 0.018$; Figure 2g; Table S3) but increased functional resilience ($p < 0.001$; Figure 2e; Table S3). The effects of N enrichment on different dimensions of compositional stability largely mirrored those on functional stability (Figure 2b,d,f,h; Table S3). By contrast, P enrichment had no discernable effect on functional or compositional stability ($p > 0.05$; Figure 2, Table S3). Similar trends were found for dominant species (Table S4; Figure S8). No significant N × P term was detected for any stability metrics (Tables S3, S4).

Pathways through which nutrient enrichment affected stability

SEM confirmed that both functional and compositional temporal stability, resistance, and recovery decreased

with N enrichment, while functional and compositional resilience increased with N enrichment (Figure 3). P enrichment had similar, albeit considerably weaker, effects on temporal stability and resistance, and did not affect resilience or recovery (Figure 3). SEM also confirmed that N enrichment reduced species richness; however, species richness did not affect temporal stability, resilience or recovery, except for a small effect on resistance (Figure 3). We also found that species asynchrony, which was unaffected by nutrient enrichment (Figure S9), contributed positively to functional temporal stability and resistance, but negatively to functional resilience; species asynchrony had no discernable effect on functional recovery (Figure 3). Importantly, with the exception of recovery, the effects of N enrichment on functional stability were largely modulated by its effects on corresponding compositional stability (Figure 3).

Relationships between compositional and functional stability and between stability dimensions

Consistent with SEM results, linear regressions showed that across all treatments, strong positive relationships existed between compositional and functional temporal stability, resistance and resilience, but not recovery (Figure 4). Different stability dimensions also tended to show strong relationships with each other (Figure S10).

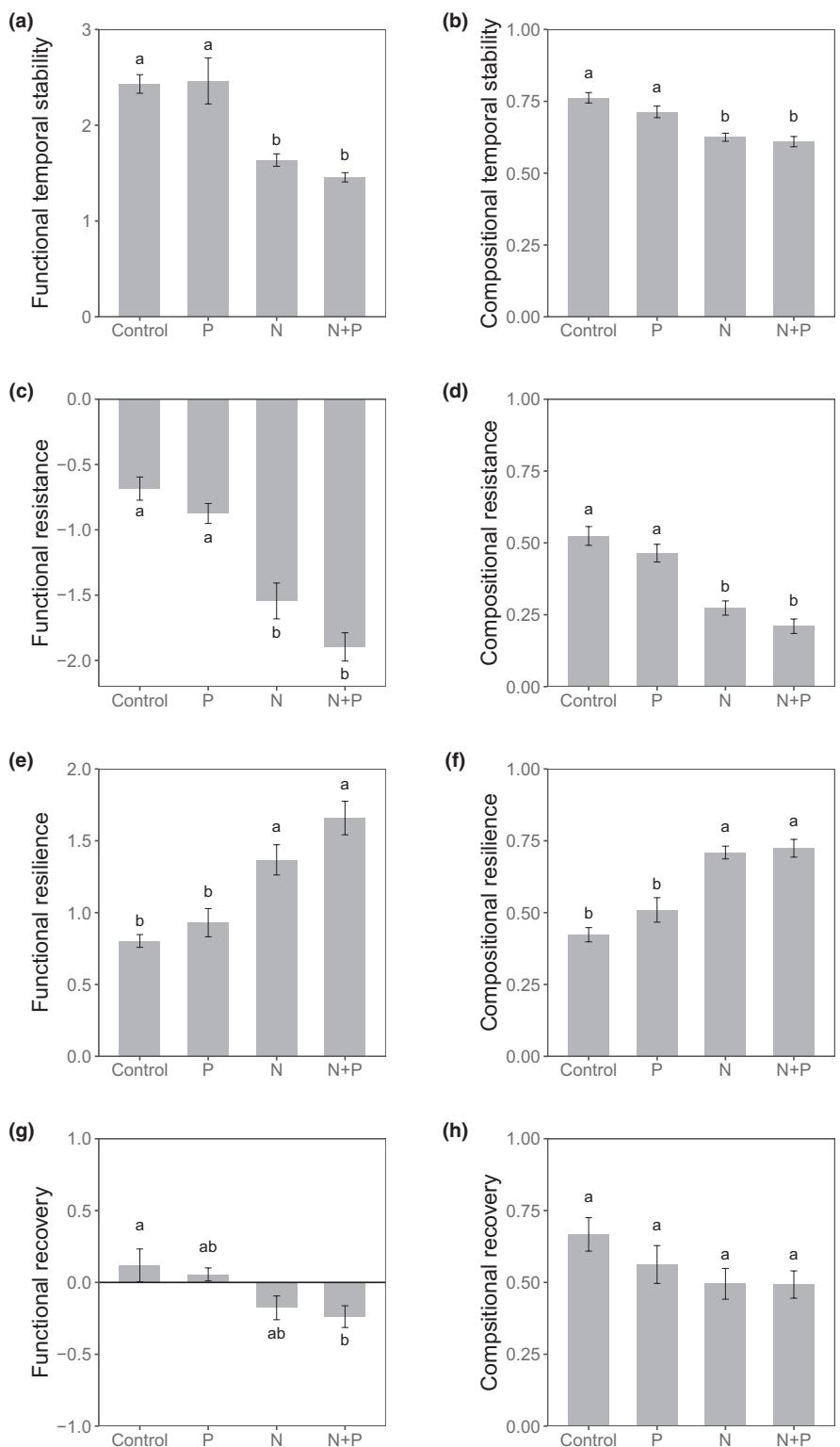


FIGURE 2 Effects of nitrogen and phosphorus enrichment on multiple stability dimensions of grassland functional (a, c, e, g) and compositional (b, d, f, h) stability. Control: no nutrient enrichment; P: Phosphorous enrichment; N: Nitrogen enrichment; N+P: Nitrogen and phosphorous enrichment. Bars indicate means (± 1 SE). treatments sharing the same letter are not statistically different from each other in a post hoc Tukey's HSD test at the level of $p = 0.05$.

For example, resistance was positively associated with temporal stability and recovery, but negatively associated with resilience, at both ecosystem (Figure S10a) and community (Figure S10b) levels.

DISCUSSION

Ecologists have long recognised the significance of disturbances in shaping ecological communities and

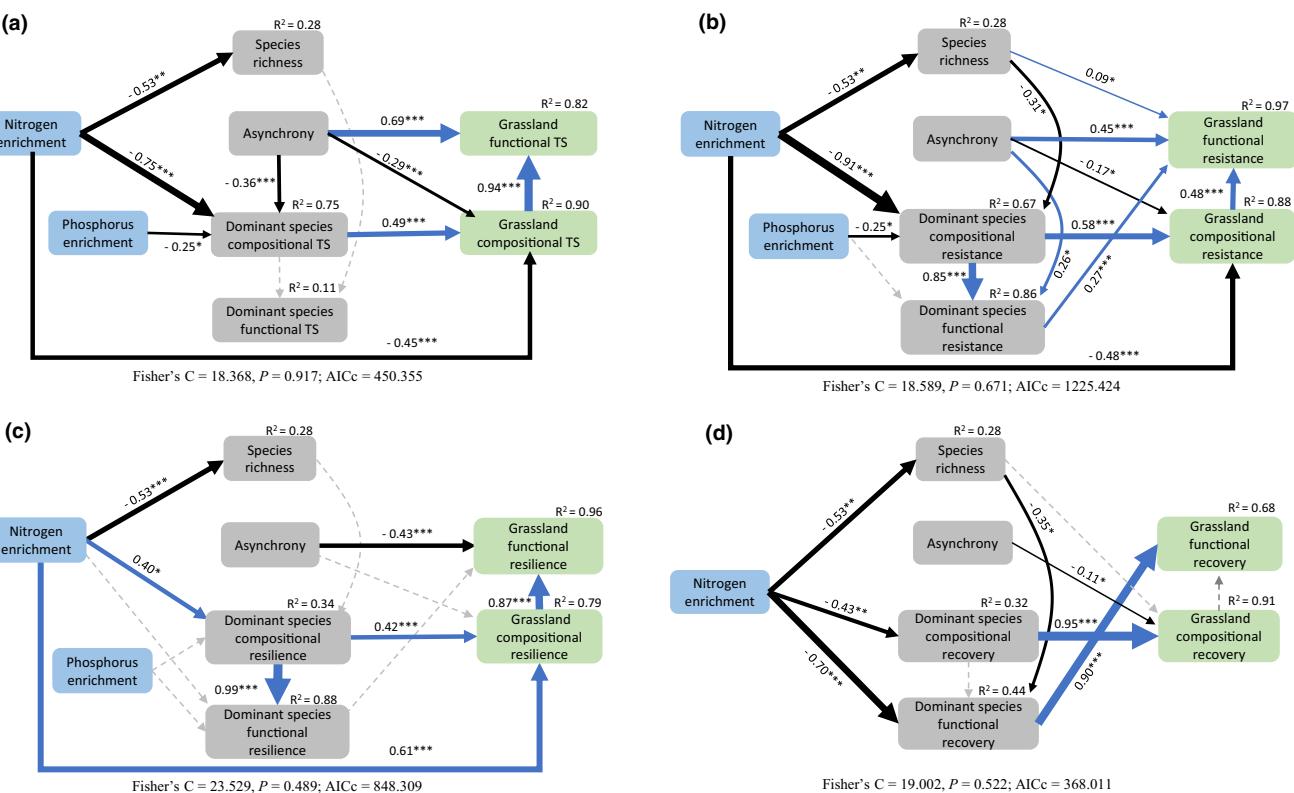


FIGURE 3 The final structural equation models showing the direct and indirect effects of nutrient enrichment on grassland functional and compositional (a) temporal stability (TS), (b) resistance, (c) resilience, and (d) recovery. Blue and black arrows indicate positive and negative pathways, respectively (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). Numbers along the arrows indicate standardised path coefficients. Arrow width is proportional to the strength of the relationship. The proportion of variance explained (R^2) appears alongside response variables in the models.

ecosystems (Sousa, 1984; White & Pickett, 1985). However, a general understanding of the mechanisms underlying community and ecosystem stability remains elusive, which is, at least in part, due to the multidimensional nature of ecological stability. Our study explored the effects of N and P enrichment on the multiple dimensions of functional and compositional stability of a temperate grassland that had experienced a severe drought and yielded three notable findings. First, N enrichment negatively affected grassland functional and compositional resistance, recovery and temporal stability but positively affected resilience. The effects of P enrichment were either considerably weaker or non-significant compared with those of N. Second, most dimensions of grassland functional stability were largely independent of species richness, but were influenced by species asynchrony, and to a greater extent, by the corresponding grassland compositional stability (Figure 3). Third, the effects of N enrichment on grassland functional stability, except for recovery, were largely modulated by its effects on compositional stability (Figure 3). Correspondingly, we found a positive relationship between functional and compositional resistance, resilience, and temporal stability (Figures 3 and 4). These results provide novel insights into grassland stability in the face of ongoing global environmental change.

Effects of nutrient enrichment on grassland functional and compositional stability

Consistent with previous studies conducted at our study site (Xu, Wan, Ren, Han, & Jiang, 2012; Xu, Wan, Ren, Han, Li, et al., 2012), we found that N enrichment resulted in increased total plant cover. Although we observed a lack of grassland cover response to P enrichment alone, P enrichment significantly increased plant cover in combination with N enrichment (Figure S7a). This finding indicates serial co-limitation (Harpole et al., 2011), implying that N is the more limiting resource in our study grassland than P. This result supports the idea that N and P co-limitation is common throughout the world's ecosystems (Bracken et al., 2015; Elser et al., 2007; Fay et al., 2015; Li et al., 2016).

In support of our first hypothesis (Table 1), we found that N enrichment alone and in combination with P significantly altered different dimensions of functional stability. Specifically, N and N+P enrichment reduced functional temporal stability, resistance, and recovery, but increased resilience (Figure 2). By comparison, P enrichment alone had a much weaker or non-significant effect on the four dimensions of functional stability (Figures 2 and 3). Our findings are consistent with several empirical studies reporting that N enrichment can reduce grassland functional temporal stability (e.g. Hautier

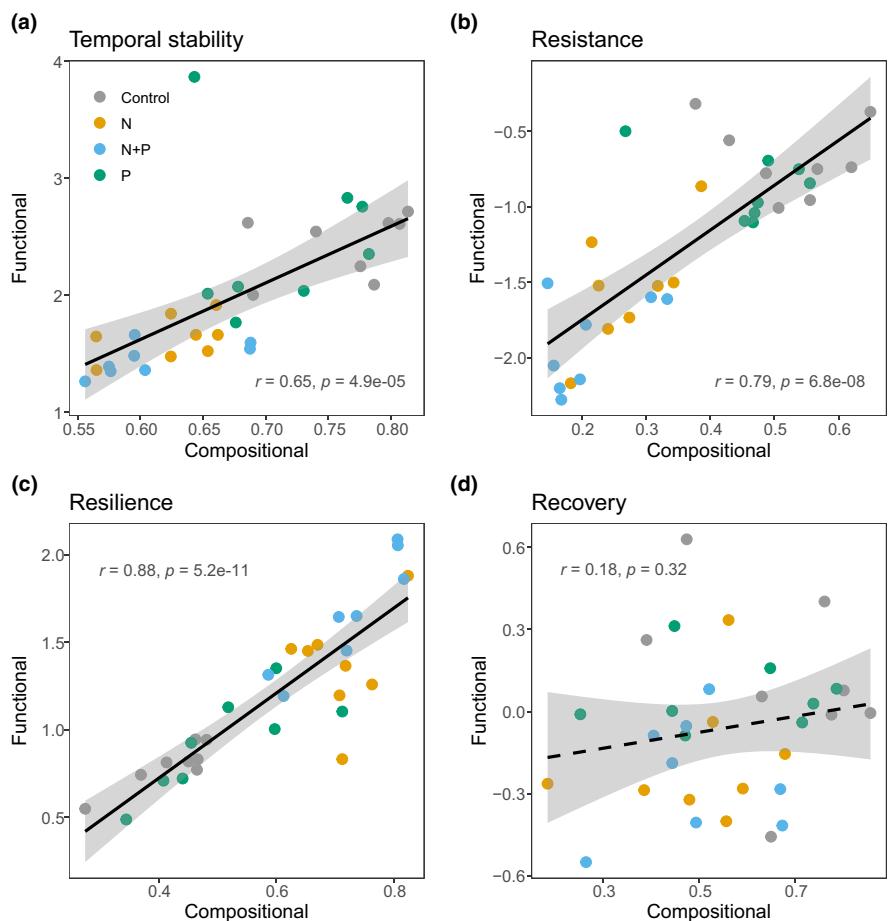


FIGURE 4 Bivariate relationships between grassland functional and compositional stability for the four stability dimensions: (a) temporal stability, (b) resistance, (c) resilience and (d) recovery. Each dot represents an individual plot from the experiment. Significant relationships are denoted as solid regression lines. The shaded areas represent 95% confidence intervals.

et al., 2014; Yang et al., 2012; Zhang et al., 2016; but see Grman et al., 2010) and resistance (Bharath et al., 2020; Xu et al., 2014). However, our finding that N enrichment increased functional resilience but decreased functional recovery contrasts with that of Xu et al. (2014), who reported no effect of N addition on grassland functional resilience and recovery. This discrepancy may have been caused by the differences in N application regime between the two studies. First, while our experiment used ammonium nitrate as the N fertiliser, Xu et al. (2014) used urea, where nitrogen availability for plants could have been reduced by ammonium volatilisation (Soares et al., 2012). Second, while N fertiliser was applied once in July in our experiment, the same total amount of N fertiliser was divided to two equal amounts and applied in early May and late June in Xu et al. (2014). Prior work has shown that less frequent application of the same amount of N fertilisers had stronger impact on grassland communities (Zhang et al., 2014).

Our study provides, to our knowledge, the first empirical evidence of nutrient enrichment influencing multiple dimensions of community compositional stability. The effects of nutrient enrichment on compositional stability largely mirror those on functional stability. Specifically,

we found that N enrichment negatively affected grassland compositional temporal stability, resistance and recovery, but positively affected compositional resilience (Figures 2 and 3), both directly and indirectly via influencing dominant species compositional stability (Figure 3). By comparison, P enrichment had a much lesser negative effect on compositional temporal stability and resistance through reducing dominant species compositional stability and did not affect compositional resilience or recovery (Figures 2 and 3). Furthermore, in line with the mass ratio hypothesis (Grime, 1998), we found that the dominant species compositional stability, not species richness, was the most important determinant of grassland compositional stability for all four stability dimensions (Figure 3). These patterns emerged as the three most dominant species in our experiment increased in abundance following N and N+P enrichment in 2006, lost proportionally more biomass in the N and N+P enrichment plots when experiencing drought in 2017 and recovered their biomass more quickly in these plots in 2008 (Figure S11). These changes in the abundance of dominant species under N enrichment thus translated into reduced compositional resistance and temporal stability, but increased compositional

resilience. Our study extended the mass ratio hypothesis, which has been previously applied to functional stability at the ecosystem level (Grman et al., 2010; Lepš, 2004; Polley et al., 2007; Sasaki & Lauenroth, 2011; Yang, van Ruijven, & Du, 2011), to compositional stability at the community level.

Species diversity and asynchrony as potential drivers of stability

N enrichment can reduce grassland functional temporal stability via diversity-mediated effects on the temporal variation of primary production (Hautier et al., 2015, 2020; Yang et al., 2012). Our study showed that species richness decreased with N enrichment but not P enrichment (Figure 3 and Figure S7a), which is consistent with the frequently reported negative effects of N enrichment on plant diversity (Midolo et al., 2019; Stevens et al., 2004; Suding et al., 2005; Tognetti et al., 2021), while also providing empirical evidence for a lack of P effect on plant diversity (DeMalach, 2018; Soons et al., 2017). In partial contrast to our second hypothesis (Table 1), SEMs revealed that the negative effect of N enrichment on functional temporal stability and recovery, and the positive effect of N enrichment on resilience were not modulated by species richness, whereas the negative effect of N enrichment on functional resistance through species richness was quite small (Figure 3). The lack of diversity effect on multiple stability dimensions in our study could be partly attributed to the modest gradient (9–18 species) of species richness observed in our experiment, compared with studies that experimentally established large diversity gradients (e.g. 1–16 species in Tilman et al., 2006 and Roscher et al., 2011; 1–32 species in Hector et al., 2010). On the other hand, the nonsignificant diversity effect may not negate the contribution of other factors, such as species asynchrony, to ecosystem stability.

Species asynchrony has been recognised as an important mechanism promoting temporal stability of ecosystem functions (Loreau & de Mazancourt, 2008; Xu et al., 2021), but its role for other stability dimensions has been much less appreciated. In our experiment, species asynchrony, which was unaffected by nutrient enrichment or species richness (Figures 3 and Figure S9), was a significant predictor of all but one dimensions of grassland functional stability (Figure 3). For example, we found a positive relationship between species asynchrony and functional temporal stability, supporting species asynchrony as an important stabilising mechanism in plant communities (e.g. Hector et al., 2010; Ma et al., 2017; Roscher et al., 2011). We also found that species asynchrony increased functional resistance to drought but decreased functional resilience after drought. Drought reduced the abundance of dominant species in our experiment, allowing a few less abundant but more drought-tolerant species (e.g. *Potentilla bifurca*,

Allium ramosum, *Phlomis umbrosa*; Yi et al., 2019), to increase in abundance and compensate for the reduced abundance of dominant species. The asynchronous responses of different species to drought thus contributed to high functional resistance and stable ecosystem dynamics over time. Note that increasing species asynchrony is expected to translate into decreased compositional stability, as observed for three of four stability dimensions (temporal stability, resistance and recovery; Figure 3). However, for temporal stability and resistance, the direct positive effect of species asynchrony on functional stability overwhelmed its indirect, negative effect through compositional stability (Figure 3). On the other hand, high species asynchrony for resilience indicates large difference in the degree of growth among species in the year following drought. This means that the growth of dominant species may have been slowed down by the increased abundances of the previously less abundant species, resulting in the slow resilience of community biomass. Overall, our results highlight the role of species asynchrony as an important determinant of multiple dimensions of functional stability.

Relationships between compositional and functional stability and between stability dimensions

Among our most important findings is that the effects of nutrient enrichment on functional stability were largely mediated by changes in compositional stability, where functional stability was positively related to the corresponding compositional stability for all but one of stability dimensions (Figures 3 and 4). These findings, which lend support to our third hypothesis (Table 1), suggest that preserving and restoring the pre-drought community composition is important for maintaining functional stability of our study grassland. These findings echo those of several experimental studies conducted in aquatic systems (Baert et al., 2016; Guelzow et al., 2017; Hillebrand et al., 2018; Polazzo & Rico, 2021) as well as a recent meta-analysis (Hillebrand & Kunze, 2020) reporting that the maintenance of pre-disturbance community composition favours ecosystem functional stability. Our study differs, however, from previous work by examining the consequences of nutrient enrichment for multiple dimensions of both functional and compositional stability of a natural grassland. It should be noted that functional stability may not be necessarily associated with compositional stability (Hillebrand & Kunze, 2020), which could occur when functional redundancy among species helps maintain ecosystem functioning despite changes in community composition (Allison & Martiny, 2008; Yachi & Loreau, 1999). For example, Hoover et al. (2014) subjected a tallgrass prairie to simulated drought and found that full recovery of plant community biomass was achieved despite drought-induced shifts in community

composition, as the increased biomass of one dominant grass species compensated for the loss in the biomass of a dominant forb species. This is also the case for recovery in our experiment, where functional and compositional recovery were decoupled as total plant cover have fully recovered or were close to pre-drought values, but community composition recovery was incomplete (Figure 2).

In our study, the generally strong relationships between stability dimensions suggest a lower stability dimensionality than the number of actual stability components considered (Donohue et al., 2013), offering hope for reduced effort to obtain a comprehensive understanding of the stability of a particular ecological system. For example, resistance exhibited significant relationships with all other stability dimensions at both community and ecosystem levels (Figure S10), pointing to the intriguing possibility of using resistance to project community and ecosystem post-disturbance dynamics. Indeed, it has been reported that grassland resistance to climate events strongly influences their functional temporal stability (Isbell et al., 2015). However, this hope is complicated by the fact that stability dimensionality can vary considerably across environmental context (Donohue et al., 2013; Polazzo & Rico, 2021). Overall, our understanding of relationships between different stability dimensions and their context dependency is still in its infancy and deserves further attention from ecologists.

Caveats

One caveat of note is that several studies of drought effects on ecological stability have compared stability under control and drought conditions, where drought was experimentally manipulated by implementing rain shelters in the field to reduce precipitation (Fay et al., 2000). Our study, on the other hand, took advantage of a severe natural drought to investigate the effects of nutrient enrichment on multiple dimensions of stability, by comparing grassland community composition and cover across the pre-drought, mid-drought and post-drought years. While drought manipulation experiments allow for explicit tests of the role of drought characteristics such as intensity and duration, our study, together with a number of other studies (Isbell et al., 2015; Mariotte et al., 2013; Tilman & Downing, 1994; Van Ruijven & Berendse, 2010; Xu et al., 2014), provide assessment of how natural drought events influence the study ecosystems. Another caveat is that our experiment was conducted at small spatial scales. An interesting question to ask next is whether our findings can be generalised to larger spatial scales where spatial variability among local communities may contribute to regional stability (Hautier et al., 2020; Wang & Loreau, 2016; Zhang et al., 2019). Also note that our examination of stability was based on data from 3 years (2006–2008). Data beyond 2008 were not considered because 2009 was another drought year;

including 2009 data may potentially complicate the analysis of resilience and recovery. Nevertheless, the negative nitrogen enrichment effect on functional temporal stability, observed in our study, is consistent with the finding of a 7-year (2005–2011) study conducted at the same experimental site (Yang et al., 2012).

CONCLUSION

Our study is the first, to our knowledge, to link nutrient enrichment effects on the multiple dimensions of functional stability to its effects on the respective dimensions of compositional stability. By so doing, we show that nitrogen enrichment altered grassland functional stability primarily via its effect on the corresponding compositional stability, for three important stability dimensions (resistance, resilience, and temporal stability). While highlighting the importance of nutrient enrichment in influencing grassland ecosystem dynamics, our study points to the need to incorporate compositional stability into future stability research to obtain a more mechanistic understanding of ecosystem dynamics under ongoing global environment change.

AUTHOR CONTRIBUTIONS

Lin Jiang and Shiqiang Wan conceived the study. Jian Song, Jingyi Ru and Jianyang Xia carried out the field experiment and collected data. Qianna Xu and Xian Yang analysed the data. Qianna Xu, Xian Yang and Lin Jiang wrote the manuscript. All authors contributed substantially to revisions. Qianna Xu and Xian Yang contributed equally to this work.

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CONFLICT OF INTEREST

The authors do not have any competing financial or non-financial interests to declare.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

All data and code that support the findings of this study have been deposited to the Dryad Digital Repository (<https://doi.org/10.5061/dryad.2280gb5wd>).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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