Title: Nutrient addition impacts grassland productivity responses to dry and wet climate extremes despite functional diversity loss

Authors

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Summary

Eutrophication impacts grassland diversity such as species richness, functional trait diversity and composition, but whether and how these changes affect ecosystem functional stability under increasing climate extremes is unknown. We quantify the direct and diversity-mediated effects of nutrient addition on functional stability of productivity as measured by resistance during and recovery after dry and wet growing seasons, and temporal invariability across 19 grasslands spanning four continents. We use leaf traits measured in the field to construct slow-fast leaf economic spectrum and calculate functional trait composition and diversity of the slow-fast trait. Nutrient addition increased resistance during dry growing seasons mainly through its direct effects. It also increased resistance during wet growing seasons directly, but these positive effects were weakened by indirect negative effects through reducing slow-fast functional diversity. Nutrient addition had weak effects on recovery after dry growing seasons, but it decreased recovery after wet growing seasons mainly through its direct effects. Nutrient addition increased temporal invariability through resistance, but decreased it through recovery and reducing species richness, leading to overall weak net effects. Thus, processes and influencing pathways independent of plant diversity should be carefully taken into account in understanding ecosystem stability in response to increasing global changes.

Keywords

Nutrient enrichment; drought; rainfall, grasslands; biodiversity; functional traits; Nutrient Network (NutNet)

Introduction

Earth is undergoing multiple global environmental changes, which threaten both the diversity and stability of ecosystems (IPCC, 2019). Mounting evidence shows that environmental changes can reduce the stability of ecosystems directly or indirectly via decreasing diversity (Hautier *et al.*, 2015; Zhang *et al.*, 2022). However, our understanding of ecosystem stability is limited because diversity and stability are both multifaceted concepts, yet most studies have analyzed one or a few facets in isolation (Donohue *et al.*, 2013; Hillebrand *et al.*, 2018; Kéfi *et al.*, 2019). Stability characterizes ecosystems' responses to different types of perturbations (Pimm, 1984; Donohue *et al.*, 2013). In ecological studies, stability of an ecosystem function (e.g. productivity) can be defined as resistance during and recovery after perturbations and temporal invariability over time (Pimm, 1984). Resistance is the ability of a function to remain close to normal levels (i.e. small deviation) during a pulse perturbation, and recovery is the rate of return towards normal levels after a pulse perturbation (Pimm, 1984). To enable comparison among sites with varying productivity, resistance can be quantified as the inverse of the proportional deviation of productivity from normal levels during a perturbation (e.g. a climate extreme; Isbell *et al.*, 2015). Temporal invariability is often quantified as the ratio of the temporal mean of a function to its standard deviation (also termed as temporal stability in previous studies; Pimm, 1984; Tilman, 1996). Because both higher resistance and recovery maintain a function around its normal level, increased resistance and/or recovery may enhance temporal invariability (Ives & Carpenter, 2007; Isbell *et al.*, 2015). Yet, this intuitive hypothesis has not been rigorously tested. Similarly, plant diversity can be quantified by functional trait composition and diversity, and species richness, and different facets of diversity have been shown to exhibit different responses to global changes and have different effects on ecosystem stability (Craven *et al.*, 2018; Oram *et al.*, 2020; Chen *et al.*, 2022). Disentangling the direct and the diversity-mediated effects of global changes on multiple facets of stability is essential for improving our mechanistical understanding of the stability.

Eutrophication is a major global change factor that poses threats to ecological systems (Galloway *et al.*, 2021). Numerous studies show that nutrient addition decreases the stability of productivity, particularly its temporal invariability and resistance during dry climate extremes (Tilman & Downing, 1994; Xu *et al.*, 2014; Hautier *et al.*, 2015; Bharath *et al.*, 2020; Meng *et al.*, 2021; Van Sundert *et al.*, 2021; Carroll *et al.*, 2021). However, few empirical studies so far have investigated the impact of nutrient addition on resistance during and recovery after wet climate extremes, which are becoming increasingly frequent just as dry climate extremes globally (IPCC, 2019).

Compared with the ambient conditions, during normal climate, increased nutrient availability may increase productivity. During dry climate extremes, plants are under stress and may not be able to use the increased nutrients. Thus, productivity can deviate (due to drought-induced biomass decrease) from normal levels more strongly under nutrient addition (Fig. 1; Table S1). During wet climate extremes, increased nutrients and water availability increase plant growth and productivity. This also increases the magnitude of productivity deviation from normal levels under nutrient addition (Wright *et al.*, 2015; Wang *et al.*, 2017; Eskelinen *et al.*, 2020). However, too much rain may cause nutrient leaching, leading to a small or no productivity deviation (due to little increases in productivity) from normal levels under nutrient addition. Nutrient addition may decrease (or increase) resistance when it increases the magnitude of productivity deviation more (or less) than it increases mean productivity during normal climate compared with the ambient conditions. Nutrient addition may decrease recovery after dry climate extremes because increased plant mortality may increase litter accumulation which in turn may limit species colonization in the short term (Southon *et al.*, 2012; Meng *et al.*, 2021). Lastly, nutrient addition may decrease recovery after wet climate extremes because increased productivity due to increased nutrients and water availability may persist or even amplify in later years (Sala *et al.*, 2012; Wheeler *et al.*, 2021) .

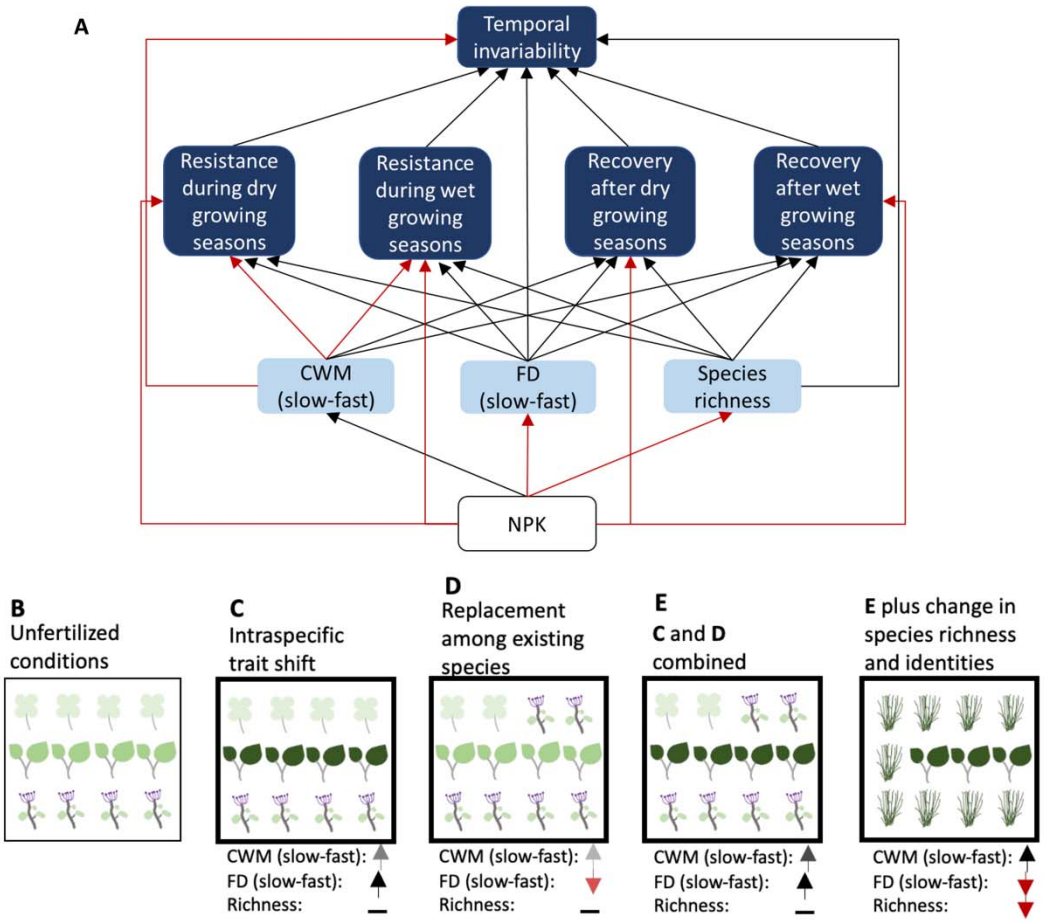

Fig. 1. Conceptual framework illustrating how nutrient addition impacts facets of stability through its direct and diversity-mediated indirect effects (A) and how nutrient addition alters facets of plant diversity (B-F). Line color in A represents positive (black) and negative (red) effects. Darker color in B-F represents faster-growing species. Thick boxes represent nutrient addition conditions. Black and red arrows represent increase and decrease (darker color represents a larger change). CWM (slow-fast): community-weighted mean of the 'slow-fast' leaf economics spectrum; FD (slow-fast): functional diversity of the 'slow-fast' leaf economics spectrum. See Table 1 for the calculation and interpretation of each variable. See Table S1 for detailed potential mechanisms for each link in A.

In addition to these direct effects, nutrient addition may impact different facets of stability indirectly by altering plant diversity such as species richness, and functional trait composition and diversity. While theories on how functional trait composition and diversity in slow-fast trait may impact resistance and recovery are growing, empirical tests of their roles in mediating stability under global changes such as eutrophication is lacking (Reich, 2014; Díaz *et al.*, 2016; Craven *et*

al., 2018; de Bello *et al.*, 2021). This slow-fast trait framework uses integrated life-history traits to locate plant species along a spectrum that ranges from slow (conservative) to fast (acquisitive) strategies. In plant communities, fast-growing species are typically associated with high leaf nutrients and specific leaf area, which facilitate faster up-take and better use of resources. These fast-growing species may recover faster after climate extremes. In contrast, slow-growing species invest more in cell walls and secondary metabolites that may help them endure unfavorable environments, thus they may have higher resistance during climate extremes. Nutrient addition may decrease resistance during dry and wet climate extremes but increase recovery after the extremes by promoting fast communities (communities dominated by fast-growing species; Fig.1; Table S1). Its impact on invariability may, however, be weak due to contrasting effects of the fast strategy on resistance and recovery (Craven *et al.*, 2018). Nutrient addition may promote fast communities through shifting intraspecific traits towards fast growth, promoting a dominance by fast-growing species, or both (Lepš *et al.*, 2011; Siefert & Ritchie, 2016; Tatarko & Knops, 2018; Zhou *et al.*, 2018; Pichon *et al.*, 2022). Additionally, nutrient addition may decrease all stability facets investigated here by decreasing the diversity of slow-fast trait and species richness. Species richness may capture diversity in other traits (e.g. root and size-related traits) that cannot be captured by the leaf economic spectrum. Communities with higher diversity in slow-fast traits or species richness are more likely to include species that are better adapted to perturbations, thus population decreases in some species may be compensated by increases in others during and after climate extremes. This leads to less productivity deviation from normal levels, which increases resistance and recovery (Tilman *et al.*, 2014), as well as invariability (Craven *et al.*, 2018). Together, the net effects of nutrient addition on different facets of stability depend on the directions and relative importance of its direct and diversity-mediated indirect effects.

Here, we use a globally distributed nutrient addition experiment to investigate the effects of eutrophication on five facets of stability of grassland productivity, including resistance during and recovery after dry and wet climate extremes and temporal invariability. In particular, we disentangle the direct and diversity-mediated indirect effects of nutrient addition on these stability facets. We use five leaf traits (leaf C, N, P, K, Specific leaf area) measured in the field to construct slow-fast leaf economic spectrum and calculate functional trait composition and diversity of the slow-fast trait. We hypothesize that nutrient addition decreased all these stability facets mainly through diversity-mediated effects and that functional trait diversity in slow-fast trait is the major mediator.

Materials and Methods

Experimental Design

We used a globally replicated nutrient and herbivore manipulation experiment (NutNet; www.nutnet.org) initiated in 2007 for this analysis (Borer *et al.*, 2014, 2017). At most sites, each of the ten treatments (Control, N, P, K, NP, NK, PK, NPK, Fence, and NPK+Fence) was randomly imposed to a 25 m^2 plot and was replicated in at least three blocks. N was supplied as time-release urea ($(NH_2)_2CO$), P was supplied as triple superphosphate ($Ca(H_2PO_4)_2$), and K as potassium sulfate (K_2SO_4). N, P, K were added annually before the start of the growing season at a rate of 10 g m^{-2} y^{-1}. A micronutrient and macronutrient mix (Fe, S, Mg, Mn, Cu, Zn, B, and Mo in combination) was applied at a rate of 100 g m^{-2} once at the start of the experiment, as part of the K addition. Fencing is designed to exclude large herbivores; fences were around 230 cm tall and the lower 90 cm were covered by 1 cm woven wire mesh. To further exclude digging animals such as voles and rabbits, an additional 30 cm outward-facing flange was stapled to the soil. Four strands of barbless wire were strung at similar vertical distances above the wire mesh. Further details on the design are available in (Borer *et al.*, 2014). We focus on exploring stability in the control and nutrient addition (NPK) treatments, but we used traits measured in all treatments. Specifically, we separated leaf traits measured in ambient (control and Fence) and nutrient-enriched conditions (N, P, K, NP, NK, PK, NPK, NPK+Fence). Additionally, multiple trait measurements for the same species at one site (e.g. from different blocks) were averaged. We did this to maximize the number of species with available trait data and because previous NuNet results found little variation in leaf traits among blocks within the non-fertilized and fertilized conditions at 27 NutNet sites (Firn *et al.*, 2019).

Site selection

We selected sites meeting the following criteria:1) at least 3 years of data for the control and nutrient addition (NPK) treatments; 2) 3 blocks, most sites have 3 blocks, for those with more than 3 blocks, we selected the first 3 blocks following (Hautier *et al.*, 2020); 3) at least 3 common to dominant plant species measured for leaf traits in both non-fertilized and fertilized conditions; 4) average across blocks and experimental years, summed cover of species with traits accounted for >50% of the total cover. Nineteen sites met these criteria (Fig. S1; Table S2). These sites are distributed in North America (12 sites), Australia (3 sites), Europe (3 sites), and Africa (1 sites). Thus, our results may bias towards Northern hemisphere. Sites are dominated by herbaceous plant species, Sites include montane, alpine, semiarid grasslands, prairies, and old fields, which we refer to as grasslands for simplicity. See table S2 for geolocation, climate, and experimental

durations for these sites. Also, see table S3 for the number of species, percent cover of species measured for traits at each site.

Sampling protocol

All sites followed standard NutNet sampling protocols. A 1×1m subplot was permanently marked within a 25 m^2 plot. Number of species, species identity, and their covers were recorded once per year in these 1×1 m subplots at most sites. At a few sites with strong seasonality, cover and biomass were recorded twice per year to include a full list of species and follow typical management procedures. For those sites, the maximum cover for each species and total biomass for a community were used in analyses. The taxonomy was checked and adjusted within sites to ensure consistent naming over time. For instance, when individuals could not be identified as species in all years, they were aggregated at the genus level but referred to as taxa for simplicity. Meanwhile, aboveground biomass was measured adjacent to these permanent subplots within two 1 × 0.1 m strips (in total 0.2 m^2), which were moved from year to year to avoid resampling the same location. All aboveground biomass was clipped within strips. Biomass strips were sorted into dead and live and dried separately at 60 °C to constant mass before weighing to the nearest 0.01 g. Dried biomass was multiplied by 5 to estimate grams per square meter. Following previous analyses, we used dried live aboveground biomass as a measure of primary productivity (Hautier *et al.*, 2020; Seabloom *et al.*, 2021).

Leaf trait measurements

Leaf traits were generally measured after 3 to 4 years of nutrient addition (Table S3). Traits were measured for 3 to 5 of the most dominant species in each subplot. Traits were measured according to standard protocols (Pérez-Harguindeguy *et al.*, 2016). A detailed description of these trait measurements can be found in (Firn *et al.*, 2019). Briefly, for each species measured for leaf traits, five fully grown leaves without clear grazing marks were randomly selected. Leaf area (mm^2) was measured using leaf area meters or scanner. After that, dry weight (g) of leaves was measured after oven-drying at 60 °C for 48 h. Specific leaf area (SLA; mm^2g^{-1}) was calculated as the leaf area divided by the dry weight. Then, leaf nutrient concentrations (%) including C, N, P, and K were determined. Leaf P, K, and C were determined using laser ablation inductively coupled plasma mass spectrometry following (Duodu *et al.*, 2015). Leaf N was determined using a LECO TruMac, based on a combustion technique using thermal conductivity relative to pure gas with an error < 1%.

Table 1. Variables used in this study with their mathematical definitions and interpretations.

Variables	Methods	Parameters in the methods explained	Interpretations	References
CWM (slow-fast)	$\frac{\sum a_i x_i}{\sum a_i}$	a_i is the cover of species i, x_i is the slow-fast trait for species i.	A higher value indicates that a plant community is dominated by fast-growing species.	Garnier et al. 2004)
CWM induced by replacement among existing species	$CWM_{Nut*} - CWM_{control}$	CWM_{Nut} and $CWM_{control}$ are CWM in the nutrient addition and control treatment. CWM_{Nut*} is the CWM in the nutrient addition treatment recalculated by using slow-fast trait in the control treatment.	A higher value of replacement indicates that a change in CWM is more induced by a change in relative cover among existing species while less induced by intraspecific trait shift.	(Jung et al. 2014)
CWM induced by intraspecific trait shift	$CWM_{Nut} - CWM_{Nut*}$			
FD (slow-fast)	$\frac{\sum a_i z_i}{\sum a_i}$	a_i is cover of species i. z_i is the distance of slow-fast trait of species i to community-weighted mean trait (CWM).	A higher value indicates that a plant community has higher dispersion in slow-fast trait.	(Laliberte & Legendre 2010)
Temporal invariability	$\frac{u}{\sigma}$	μ is the mean of aboveground primary productivity, σ is the standard deviation (with or without detrending) over time.	A higher value indicates that a plant community varies less in productivity over time.	(Pimm 1984)
Resistance during dry/wet growing seasons	$\frac{\bar{Y}_n}{\lvert Y_e - \bar{Y}_n \rvert}$	$\bar{Y}_n$, Y_e, and Y_{e+1} are aboveground productivity during normal growing seasons, during a dry or wet growing season, and one year after a dry or wet growing season, respectively.	A higher value indicates that productivity deviates less under a dry or wet growing season from that of normal growing seasons.	(Isbell et al. 2015)
Recovery after dry/wet growing seasons	$\frac{\lvert Y_e - \bar{Y}_n \rvert}{\lvert Y_{e+1} - \bar{Y}_n \rvert}$		A higher value indicates that productivity deviates less one year after a dry or wet growing season relative to that during a dry or wet growing season.	

The slow-fast leaf economic spectrum, community-weighted mean traits, and functional trait diversity

Overall, 179 plant species were measured for leaf traits (leaf C, leaf N, leaf P, leaf K, and SLA). We used these five leaf traits to construct the "slow-fast" leaf economic spectrum using principal component analysis (PCA). We used the function "PCA" from the R package "FactoMineR" (Lê *et al.*, 2008). We extracted the first axis of PCA, which explained around 41% of the variance, to represent the "slow-fast" spectrum (i.e. slow-fast trait). Higher values (i.e. lower leaf C, higher leaf N, leaf P, leaf K, and SLA) indicate faster-growing species (Fig. S2). We used this integrated slow-fast trait to calculate CWM and FD. CWM is the average of the slow-fast trait weighted by the relative cover of that species in a community (Garnier, Eric *et al.*, 2004). FD is cover-weighted dispersion of the slow-fast trait relative to CWM (Laliberte & Legendre, 2010). We calculated the slow-fast CWM and FD using the function "dbFD" from the R package "FD" (Laliberté *et al.*, 2014). See table 1 for mathematical formulas for calculating the slow-fast CWM and FD and their interpretations. These variables were calculated annually for each plot and then

averaged across years. Given that leaf traits were not measured for all plant species that occurred within a subplot, we carried out a sensitivity analysis to evaluate how much slow-fast CWM and FD would be affected by ignoring species with traits. Specifically, we simulated 50 species with abundance ranging from 0 to 100 and slow-fast trait values ranging from 0 to 8 similar to our data. For each simulated community, we calculated the slow-fast CWM and FD using all species. We then randomly (1000 samplings) picked 1~48 species, ignoring their trait values (to simulate lack of trait data) to examine how much slow-fast CWM and FD were influenced by losing these species. Simulation results suggest that the relative deviation is smaller than 20% if species with trait information contribute to > 60% of the total cover (Fig. S3).

Partitioning the slow-fast CWM into intraspecific trait change and species replacement

We first recalculated the slow-fast CWM and FD using shared species (species that were present in both the control and NPK subplots) instead of all species with trait data. We then partitioned the slow-fast CWM based on shared species into intraspecific trait variation and replacement of existing species following (Jung *et al.*, 2014). See Table 1 for mathematical formulas for calculating and interpreting these variables.

Defining climate extreme and stability facets

We used the standardized precipitation–evapotranspiration index (SPEI) to classify climate extremes for each site. SPEI was calculated as the standardized (z-score) water balance (precipitation – evapotranspiration; mm) over the growing season from 1901 to 2020. We used water balance during growing seasons because previous studies show it is better correlated with productivity than the total annual water balance (e.g. Robinson *et al.*, 2013). Precipitation and potential evapotranspiration used to calculate SPEI were downloaded from https://crudata.uea.ac.uk/cru/data/hrg/cru_ts_4.05/ (Harris *et al.*, 2020). Following Isbell *et al.*, (2015), we categorized each growing season into extreme dry, moderate dry, normal, moderate wet, and extreme wet using the cutoff of 1.28 and 0.67 sd (1.28: occurring once per decade; 0.67: once every four years). That is, extreme dry: SPEI $\leq$ -1.28 sd; moderate dry: -1.28 sd < SPEI $\leq$ -0.67 sd; normal growing season: -0.67 sd < SPEI < 0.67 sd; moderate wet: 0.67 sd $\leq$ SPEI < 1.28 sd; and extreme wet: SPEI $\geq$ 1.28 sd. For some years at some sites, dry and wet growing seasons occurred consecutively, limiting our ability to disentangle resistance and recovery; these years were therefore removed from our analysis. For instance, at site comp.pt, year 1 was eliminated because year 0 had an extreme dry growing season, which may bias resistance during the extreme

wet growing season in year 1. Plant communities may not recover if they are under abnormal growing seasons, thus recovery was only calculated for dry or wet growing seasons that are followed by normal growing seasons. For instance, site bnch.us had wet growing seasons from year 3 to 5, followed by a normal growing season, then recovery was only calculated for growing season 5. Sites and experimental years included in analyses can be found in Fig. S1 and Table S2. In total, 18, 22, 71, 15, and 19 extreme dry, moderate dry, normal, moderate wet, and extreme wet growing seasons across 19 sites were detected in our data. By comparing productivity under different growing seasons, we found that productivity under moderate growing seasons was generally similar to that under extreme growing seasons (Fig. S4). In other words, plant communities performed similarly in growing seasons deviating from normal ones by 0.67 sd and 1.28 sd. In addition, a cutoff of 0.67 sd resulted in a much higher number of dry and wet growing seasons occurring at more sites (Table S2), which can increase the power of our statistical analyses. Therefore, we considered both moderate and extreme dry growing seasons as dry growing seasons, and moderate and extreme wet growing seasons as wet growing seasons and we present the corresponding results in the main text. To test the robustness of our results, we also categorized dry and wet growing seasons using more extreme SPEI (e.g., 1.28, 1.5, and 2 sd) and presented corresponding results in the supplementary file.

We quantified temporal invariability as the ratio of the temporal mean to the standard deviation of productivity in each plant community (Pimm, 1984; Tilman *et al.*, 2006). To eliminate potential trends in productivity over time, we also calculated temporal invariability after detrending. That is, we used the same mean but a different sd from the residuals of a linear model (function “lm”) regressing productivity against experimental years (Tilman *et al.*, 2006). We quantified resistance as the inverse of the proportional deviation of productivity from normal levels during a dry or wet growing season. Thus, resistance is a measure of the ability of a community to maintain a similar amount of productivity under perturbations (Isbell *et al.*, 2015). Also, we quantified recovery as the inverse of the proportional lack of recovery in productivity during the year after a dry or wet growing season following (Isbell *et al.*, 2015). See Table 1 for mathematical formulas for calculating stability metrics and their interpretations. To test whether resistance and recovery change as the intensity of SPEI increases, we treated SPEI as a continuous variable. We looked at whether nutrient addition interacted with the direction (dry or wet), and intensity (continuous absolute SPEI) to impact resistance and recovery, respectively. Year was nested into block then into site as a random variable in these models. We found that direction, intensity, and their interaction with nutrient addition had no significant effects on resistance and recovery (See model

specification and output in Table S4). These results were generally similar to that using SPEI as a categorical variable (Table S5). We used the categorical approach of SPEI in the main text because it allows clear definitions of resistance and recovery (which are based on extreme events). We treated resistance during and recovery after dry and wet growing seasons individually, and averaged each over experimental years to match the data structure of temporal invariability.

Statistical analysis

All analyses were performed in R v.4.1.6 (R Core Team., 2022). We used linear mixed-effects models (function "lme") from the R package "nlme" (Pinheiro *et al.*, 2017) for the following analyses. We built models where site and block nested within sites were the random effects, treatments were the fixed effects. First, we tested whether nutrient addition impacted stability facets based on cutoff of 0.67 sd (and other higher cutoffs). We disentangled how nutrient addition impacted resistance and recovery through productivity deviation under abnormal growing seasons from that during normal growing seasons. We aggregated change in productivity (values can be positive or negative) and the magnitude of productivity deviation (values are positive only) from normal levels during and one year after dry and wet growing seasons in control and nutrient addition treatments across sites. To facilitate among-site comparison, we present raw data of productivity under different growing seasons over the experimental years at each site (Fig. S5). Also, we present the effects of nutrient addition on each stability facet at each site (Fig. S6). Since experiment duration differed at different sites, we test whether duration mediated the effects of nutrient addition on each stability facets. We categorized sites with more than 5 years of experiment manipulation as long term (14 sites), otherwise short term (5 sites). We include the duration and its interaction with treatment as fixed effects in the model. We present effects of nutrient addition on stability facets based on cutoff of 1.28, 1.5, and 2 sd in supplementary file (Fig. S7). Second, we tested whether nutrient addition impacted the slow-fast CWM and FD using all species with traits and the shared species. We also tested whether nutrient addition impacted the component parts of the slow-fast CWM based on shared species, that is, intraspecific trait shift and replacement of existing species.

To evaluate whether nutrient addition impacted stability facets through the slow-fast CWM and FD, and species richness, we built a structural equation model (SEM) using the function "psem" from the R package piecewiseSEM (Lefcheck, 2016). An initial model was built based on prior knowledge (Fig. 1A, rationale for each link can be found in Table S1). For each component model

in SEM, we used the function “lme” with site and block nested within sites as the random effects. We estimated variance inflation for each component model to check whether multi-collinearity affects parameter estimates, we found that variance inflation <2 in all component models. We used 11 sites at which both dry and wet growing seasons occurred (based on cutoff of 0.67 sd). We compared our results using invariability with and without detrending. To check whether our results hold using the shared species instead of all species with traits, we ran another SEM using the slow-fast CWM and FD calculated using shared species. Number of sites at which both dry and wet growing seasons occurred decreased to 7, 4, and 0 when using cutoff of 1.28, 1.5, and 2 sd, respectively. We checked whether these results hold under more extreme growing seasons based on cutoff of 1.28 sd but not higher cutoffs (due to too low sample size).

Results

During normal growing seasons, nutrient addition increased productivity by 54% (control: 356.91; nutrient addition: 548.07; $g.m^{-2}$). Productivity decreased in dry growing seasons and such a decrease was more pronounced in fertilized communities (Fig. 2). As a result, nutrient addition increased the magnitude of productivity deviation by 19%. However, increased deviations were smaller compared with the higher productivity during normal growing seasons, so nutrient addition increased resistance during dry growing seasons (df = 53, t-value = 2.20, p = 0.03; Fig. 3; Table S5). In contrast, productivity increased during wet growing seasons under both control and nutrient addition treatments. Again, nutrient addition increased the magnitude of productivity deviation by 44% (Fig. 2). Thus, nutrient addition weakly increased resistance during wet growing seasons (Fig. 3). One year after dry growing seasons, nutrient addition increased the magnitude of productivity deviation by 110% (Fig. 2). During dry growing seasons preceding normal ones, nutrient addition increased biomass deviation by 59% (Fig. 2). One year after wet growing seasons, nutrient addition increased productivity from their normal levels similar to that of control plots, but increased the magnitude of productivity deviation by 73% (Fig. 2). During wet growing seasons preceding normal ones, nutrient addition increased biomass deviation by 44% (Fig. 2). Thus, biomass deviated more one year after than during dry and wet growing seasons under nutrient addition, resulting in decreased recovery, but the effects were only marginally significant for recovery after wet growing seasons (df = 38, t-value = -1.77, p = 0.08; Fig. 3; Table S5). Effects of nutrient addition on resistance and recovery were similar but stronger using cutoff of 1.28 and 1.5 sd, but the effects were weak using cutoff of 2 sd, which may be due to low sample size (Fig. S7; Table S5). Effects of nutrient addition on resistance and recovery were similar at sites with short-term and long-term experiment manipulation. Effects of nutrient

addition on temporal invariability were stronger at sites with short-term experiment manipulation (Table S5). Across 19 sites, nutrient addition had weak effects invariability (Fig. 3; Table S5).

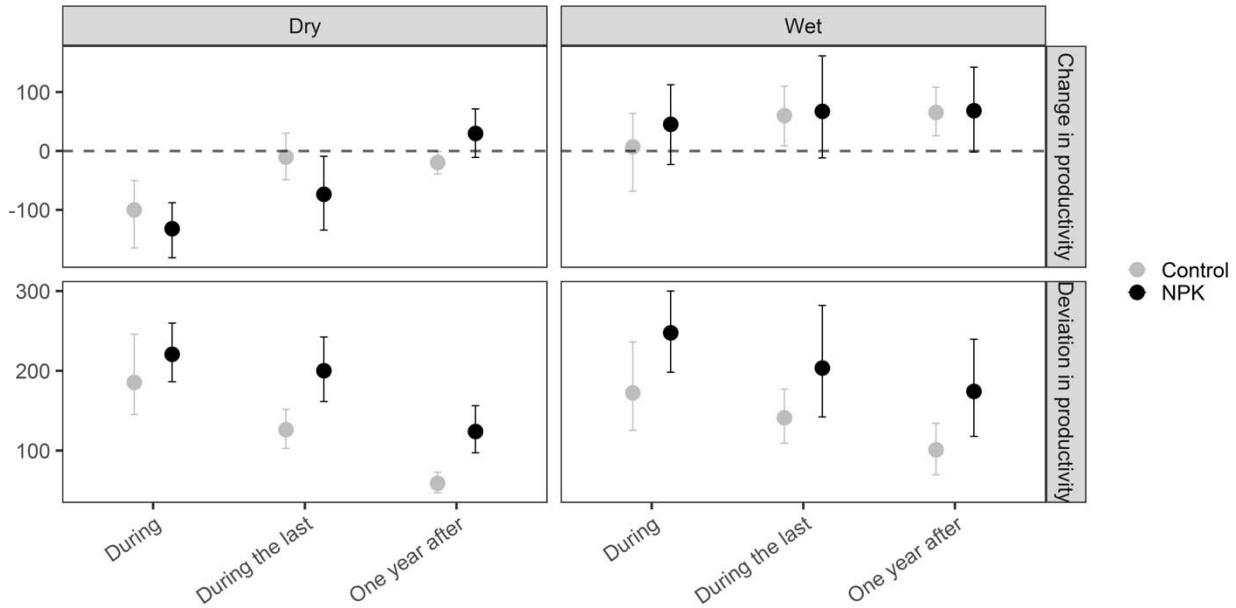

Fig. 2. Change in productivity (g.m^{-2}) and the magnitude of productivity deviation (g.m^{-2}) from normal levels. Change in productivity refers to productivity difference from normal levels, thus values can be positive or negative. Deviation in productivity refers to absolute change in productivity from normal levels, thus values are positive only. The normal levels are the means of productivity over normal growing seasons within treatments in each block at each site. During the last refers to the last dry or wet growing season when more than one dry or wet growing seasons occur consecutively. One year after refers to a normal growing season after a dry or wet growing season. See Fig. S1 for dry and wet growing seasons at 19 sites. Resistance was calculated based on productivity deviation during dry or wet growing seasons and the normal levels. Recovery was calculated based on productivity deviation during the last and one year after dry or wet growing seasons. Dots indicate average values over dry and wet growing seasons and over 19 sites. Dashed lines indicate no change in productivity from normal levels. Error bars are 95% bootstrapped confidence interval.

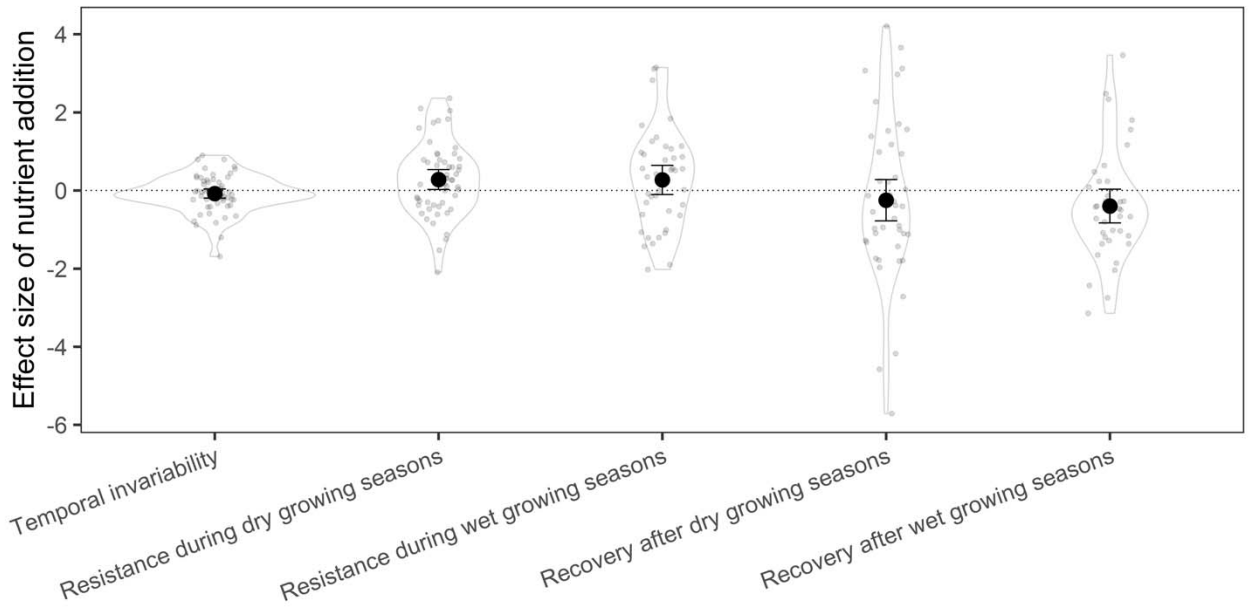

Fig. 3. Effects of nutrient addition on facets of stability. Small dots are raw values from each site. Large black dots are mean over experimental years and over 19 sites estimated from linear mixed effect models, error bars are 95% confidence intervals. All stability facets are on the log scale. See Table S5 for test statistics.

Nutrient addition decreased species richness (t-value = -5.01, df = 56, $p < 0.001$). Using all species with traits, nutrient addition decreased the slow-fast FD (t-value = -3.04, df = 56, $p = 0.001$) but increased the slow-fast CWM (t-value = 7.71, df = 56, $p < 0.001$). Using shared species (species occurring in both control and nutrient addition treatments), the effects of nutrient addition were similar for the slow-fast FD (paired t-test: t = -0.09, df = 56, $p = 0.93$), though their effects were weaker on the slow-fast CWM compared with that using all species with traits (paired t-test: t = -1.91, df = 56, $p = 0.06$). Using the shared species, we further found that increased slow-fast CWM under nutrient addition was largely driven by intraspecific trait shift rather than replacement among existing species (Fig. 4; Table S6).

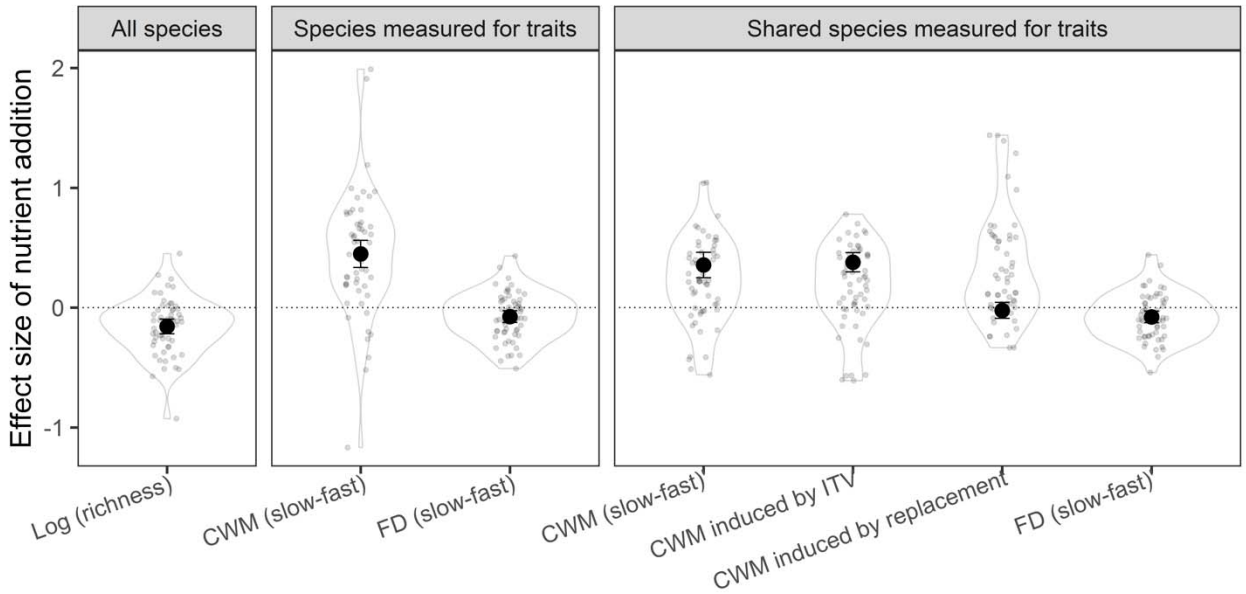

Fig. 4. Effects of nutrient addition on species richness, slow-fast CWM and FD. For shared species (i.e. species encountered in both control and nutrient addition treatments), change in slow-fast CWM was further attributable to species replacement among existing species and intraspecific trait variation (ITV). Small dots are raw values from each site. Large black dots are mean values over experimental years and over 19 sites estimated from linear mixed effect models, error bars are 95% confidence intervals. See Table S6 for test statistics.

The SEM revealed that nutrient addition impacted facets of stability directly and indirectly by affecting different facets of plant diversity (Fig. 5). Nutrient addition increased resistance during dry growing seasons mainly through its direct effects (path coefficient: 0.31). Nutrient addition increased resistance during wet growing seasons both directly (path coefficient: 0.25) and indirectly through reducing species richness (compound path coefficient: 0.05). Such positive effects were partially offset by its negative indirect effects through reducing slow-fast FD (compound path coefficient: -0.13), resulting in a weaker overall effect of nutrient addition on resistance during wet growing seasons (net effect: 0.17). Nutrient addition had no impact on recovery after dry growing seasons but decreased recovery after wet growing seasons (path coefficient: -0.23). Nutrient addition increased invariability through increasing resistance, but decreased it through decreasing recovery after wet growing seasons and species richness. Combined, these pathways mediated a weak positive effect of nutrient addition on invariability (net effect: 0.10). The net effect became slightly negative when including non-significant paths (Table S7). These results were very similar using invariability after detrending (Fig. S8; Table

S8). These results were generally similar when using shared species to calculate the slow-fast CWM and FD, except that the link between FD and resistance during wet growing seasons weakened while the link between FD and resistance during dry growing seasons became stronger (Fig. S9; Table S8). These results were also generally similar for resistance during and recovery after more extreme dry and wet growing seasons (i.e. 1.28 sd), except that the link between slow-fast CWM and recovery after dry growing seasons became positive (Fig. S10; Table S8).

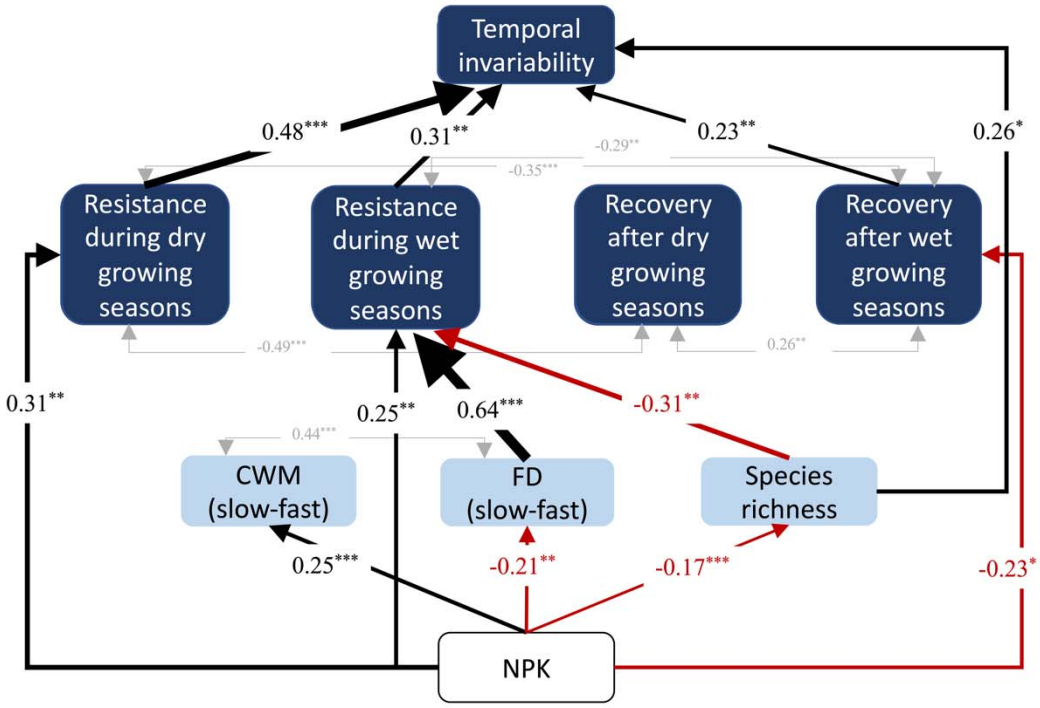

Fig. 5. Direct and diversity-mediated effects of nutrient addition on facets of stability. The structural equation model described the data well (F = 6.67, p = 0.57, df = 8). White box represents nutrient addition by NPK, blue boxes represent measured variables, and arrows represent relationships among variables. The displayed numbers are standardized path coefficients. The width of the arrows indicates the strength of the pathways. Line color represents positive (black) and negative (red) effects. Non-significant paths are not shown. Grey lines and text show correlated errors. Asterisks indicate significant paths: * $p \leq 0.1$; ** $p \leq 0.05$; *** $p \leq 0.001$. All stability facets were on the log scale to improve normality and homogeneity of variance. See Fig. S1 and Table S2 for sites and experimental years included. See Table S7 for a summary of the direct and diversity-mediated indirect effects of nutrient addition on facets of stability. See Table S8 for standardized path coefficients for each path (including non-significant paths) and variance explained (R^2) for each component model.

Discussion

Although many studies have looked at effects of nutrient addition on some facets of stability, the underlying mechanisms or influencing pathways are still unclear. Theories suggested that global changes such as nutrient addition impacts stability through functional traits (de Bello *et al.*, 2021), but direct empirical tests are rare. By developing an integrative conceptual framework, our study explicitly tested the role of slow-fast trait in mediating ecosystem stability under nutrient addition. Our study expanded the scope of stability analyses by including five facets of stability, particularly resistance during and recovery after wet climate extremes, which were largely overlooked by previous studies. Contrary to our hypotheses, our analyses revealed idiosyncratic responses of different facets of stability to nutrient addition: resistance during dry and recovery after wet growing seasons increased and decreased, other stability showed weak responses. Previous studies often use traits compiled from global databases or measured in other conditions to predict stability, ignoring intraspecific trait variation, which may result in weak effects of functional traits on ecosystem functions and stability (Craven *et al.*, 2018; van der Plas *et al.*, 2020). We used five leaf traits directly measured in the field, although a limited sets of plant traits, our analyses include intraspecific trait variation, trait variation in response to nutrient addition, its contribution to community trait change, and the consequence for functional stability. We found that nutrient addition strongly impacted species richness, and community composition and diversity of slow-fast trait through intraspecific trait shift, but the diversity-mediated effects on facets of stability were weak.

Effects of nutrient addition on stability facets

Nutrient addition did not impact recovery after dry growing seasons because productivity deviated at similar level during and one year after dry growing seasons compared with the control. However, during dry growing seasons (proceeding normal growing seasons), increased magnitude of productivity deviation was because nutrient addition decreased productivity more than the control, while one year after, increased magnitude of productivity deviation was because nutrient addition increased productivity more than the control (Fig. 2). In contrast, nutrient addition increased productivity during wet growing seasons although these increases were small relative to the normal level (Fig. 2). Nutrient addition had not effects on resistance during but decreased recovery after wet growing seasons suggests that the effects of increased nutrients and water availability on productivity may amplify (became stronger) in later years (Sala *et al.*, 2012).

Temporal invariability is jointly determined by resistance, recovery, and species richness, but the overall effects were weak (Fig. 5).

Effects of nutrient addition on diversity facets

Nutrient addition promoted fast communities while decreasing the slow-fast FD through intraspecific trait variation, changing species richness and identities (Fig. 1F). Researchers often focus on shared species (that occur both under ambient and nutrient addition conditions) to test the relative importance of inter- and intraspecific trait shifts in shaping community traits (Fig. 1B, C, D, and E). But under natural settings, some species may only be present under ambient or nutrient addition conditions (Fig. 1B and F), and these species have rarely been taken into account. We showed here that these species, though contributing to a small proportion of plant communities (Table S3), can drive community trait change too (Fig. 4). Moreover, these subordinate or rare species may still play a role in mediating nutrient effects on stability facets. For instance, the strength of the path coefficients between slow-fast FD and resistance changed when only considering the shared species (Fig. S9).

When only considering shared species, change in slow-fast CWM was mainly induced by intraspecific trait variation. Other studies partitioning CWM using shared species under other global change factors reported similar results (Jung *et al.*, 2014; Duodu *et al.*, 2015; Niu *et al.*, 2016; Tatarko & Knops, 2018; Oram *et al.*, 2020). These results indicate that plant species can adapt to multiple global change factors including flooding, drought, and nutrient enrichment through a high level of phenotypic plasticity. At many NutNet sites, leaf traits were measured after 3 to 4 years of nutrient addition, possibly resulting in higher intraspecific trait variation. For instance, at site smith.us, species with trait data became less abundant (summed cover with traits <50% of the total cover of a community) after five years of nutrient addition. Although there is a lack of empirical test, in the longer term, species replacement, which take years to manifest, may become more important than intraspecific trait variation in determining community traits.

Diversity-mediated effects on facets of stability

Using SEM, we evaluated the relative importance of species richness, slow-fast FD, and slow-fast CWM in explaining stability under nutrient addition. FD and CWM were strongly confounded (Fig. 5), it is difficult or even impossible to fully separate the effects of diversity from that of composition under natural settings. Consistent with previous analyses, nutrient addition decreases temporal invariability through decreasing species richness (Hautier et al., 2015; Carroll et al.,

2021). Also, we found that slow-fast FD and species richness were better correlated with stability facets than slow-fast CWM, suggesting that compensatory dynamics among species may be more important than dominant species in driving community stability at these sites. Furthermore, the negative link between species richness and resistance during wet growing seasons was much weaker than the positive link between slow-fast FD and resistance during wet growing seasons. This suggests that functional trait diversity may be a better predictor than species richness for resistance. As nutrient addition decreased both slow-fast FD and species richness to a similar degree, the changes in slow-fast FD and richness together mediated a negative indirect effect of nutrient addition on resistance during wet seasons. When using resistance during and recovery after more extreme dry and wet growing seasons (i.e. 1.28 sd in SPEI) in SEM, slow-fast CWM was positively linked with recovery after dry growing seasons (Fig. S10). This suggests that the links between functional traits and facets of stability may be mediated by the intensity of climate extremes and global change factors.

Contrary to our hypotheses, we found overall weak diversity-mediated indirect effects on facets of stability (Fig. 5; Table S7). This may be due to the following four reasons. First, although the slow-fast trait continuum representing the leaf economic spectrum is well established and widely used in predicting community stability (de Bello *et al.*, 2021), the positive link between slow-fast trait and population growth rates is only suggestive, it has not been quantified. Second, plants have many traits, we may miss some traits that can more directly and strongly impact stability of productivity such as root traits which are particularly important for plant species to interact with water and nutrients. Although a greenhouse experiment finds that slow-fast leaf trait can better predict resistance and recovery of community productivity to flooding than slow-fast root trait (Oram *et al.*, 2020). So far, we have too few studies to draw any solid conclusions, future work resolving root traits shall offer new insights to the trait-stability framework. Third, we did not measure traits for all plants, and these unmeasured traits may strengthen or alter the results found here. Fourth and perhaps most important, we did not consider intraspecific trait variation over time, which can be a major source of community trait change and further impact the prediction of community traits on ecosystem stability. This temporal intraspecific trait variation is ignored in many ecological studies using traits to predict ecosystem functions and stability, likely because of the extreme effort required. Future studies incorporating temporal intraspecific trait variation may improve trait-based prediction for community stability.

Our study fills an important knowledge gap by showing that nutrient addition imposed different impacts on different facets of stability, both directly and indirectly through mediating plant diversity. Our results suggest that intraspecific trait shift is a major drive for change in community trait composition and diversity under nutrient addition, thus incorporating intraspecific trait variation is needed for trait-based prediction for ecosystem function and stability. However, the diversity-mediated indirect effects on stability were weak and overwhelmed by the direct effects of nutrient addition. Thus, processes and mechanisms (e.g. changing local biotic and abiotic growing environments) that impact stability through pathways other than plant diversity should be carefully considered for understanding ecosystem stability in response to global changes.

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Visualization: QC

Writing—original draft: QC, YH, SW

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