Title: Nutrient addition increases grassland resistance during dry and wet climate extremes despite functional diversity loss

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Summary

Eutrophication impacts plant diversity such as species richness, functional trait diversity and composition of grassland communities globally, but whether and how these changes affect the functional stability of grasslands under increasing climate extremes is unknown.

We quantify the direct and diversity-mediated effects of nutrient addition on functional stability as measured by resistance during and resilience after dry and wet growing seasons, and temporal invariability of community productivity across 19 grasslands spanning four continents.

We found that nutrient addition increased resistance during dry and wet growing seasons, although the increased resistance during wet growing seasons was partly offset by the indirect negative effects of nutrient addition promoting fast-growing communities and reducing 'slow-fast' functional diversity. Nutrient addition had, however, weak net effects on resilience and invariability.

Thus, eutrophication strongly impacts plant diversity, but diversity-mediated indirect effects may be weaker on stability.

Keywords

Eutrophication; climate extremes; grasslands; biodiversity; Nutrient Network (NutNet)

Introduction

Earth is undergoing multiple global environmental changes including eutrophication and increased climatic variability, which threaten both the diversity and stability of ecosystems (IPCC, 2019). Mounting evidence shows that declines in diversity reduce the stable provisioning of essential ecosystem functions and services to humanity. Understanding the links between global environmental changes, diversity, and ecosystem stability has thus become a central goal in ecology. However, this understanding is limited because diversity and stability are 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 resilience after perturbations and temporal invariability (Pimm, 1984). Resistance is the ability of a function to remain close to normal levels during a pulse perturbation (e.g. a climate extreme), and resilience is the rate of recovery towards normal levels after a pulse perturbation (Pimm, 1984). Invariability is often quantified as the ratio of the temporal mean of a function to its standard deviation (Pimm, 1984; Tilman, 1996). Because both higher resistance and resilience indicate the proximity of a function to normal levels, higher resistance, higher resilience, or both are expected to increase invariability ((Ives & Carpenter, 2007; Arnoldi *et al.*, 2016). Yet, this intuitive hypothesis has not been rigorously tested. Investigating multiple facets of stability simultaneously is critical to improve our mechanistic understanding and prediction for ecosystem stability.

In grasslands, nutrient addition has been shown to decrease resistance in aboveground primary productivity during dry climate extremes as well as temporal invariability, while its effects on resilience after dry climate extremes are mixed (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, to date, few empirical studies have investigated the impact of nutrient addition on resistance during and resilience after wet climate extremes, which are becoming increasingly frequent just as dry climate extremes globally (IPCC, 2019). Nutrient addition may decrease resistance during dry climate extremes through increasing nutrients-to-water imbalance for plants, which reduces productivity and increases its deviation from normal levels (Meng *et al.*, 2021). Additionally, increased nutrients-to-water imbalance increase plant mortality, thus nutrient addition may decrease resilience after dry climate extremes (Southon *et al.*, 2012; Meng *et al.*, 2021). In contrast, nutrient addition may decrease resistance during wet climate extremes because

increased nutrients and water availability increase plant growth and productivity, which also increase the magnitude of its deviation from normal levels (Wright *et al.*, 2015; Wang *et al.*, 2017; Eskelinen *et al.*, 2020). Additionally, 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), thus nutrient addition may decrease resilience after wet climate extremes (Fig. 1; Table S1).

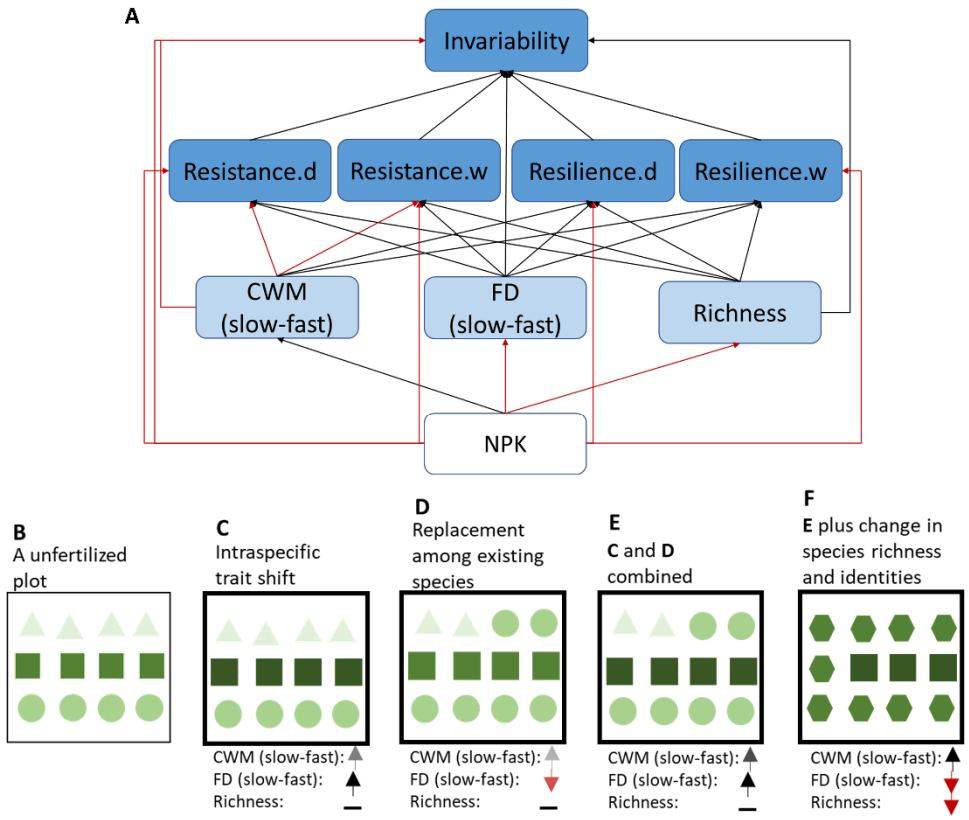

Fig. 1. Conceptual framework illustrating how nutrient addition impacts facets of stability through its direct and diversity-mediated indirect effects (A) and how nutrient addition alters facets of plant diversity (B-F). Shapes represent different species, darker color represents faster-growing species. Thick boxes represent nutrient addition conditions. Black and red arrows represent increase and decrease (darker color represents a larger change). Resistance.d/resistance.w: resistance during dry/wet growing seasons; resilience.d/ resilience.w: resilience after dry/wet growing seasons. 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 facets of stability indirectly by altering different facets of plant diversity including functional trait composition and diversity, and species richness. Nutrient addition may decrease resistance during dry and wet climate extremes but increase resilience after the extremes by promoting fast communities (communities dominated by fast-growing species; Fig.1). Its impact on invariability may, however, be low due to contrasting effects of fast communities on resistance and resilience (Craven *et al.*, 2018). Fast-growing (acquisitive) species are typically associated with high leaf nutrients and specific leaf area, which can make better use of resources by taking up nutrients faster and growing faster, thus these species have higher resilience after climate extremes. In contrast, slow-growing (conservative) species invest more in cell walls and secondary metabolites that may help them endure unfavorable environments, thus they have higher resistance during climate extremes. Nutrient addition may promote fast communities through shifting intraspecific traits related to fast growth, promoting 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 that represents leaf economic spectrum 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 trait or species richness are more likely to include species that are better adapted to perturbations, thus 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 resilience (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 direction and relative importance of its direct and diversity-mediated indirect effects.

Here, we use a globally distributed nutrient addition experiment to investigate whether and how eutrophication impacts resistance during and resilience after climate extremes and temporal invariability directly and indirectly through altering the community composition and diversity of slow-fast trait, and species richness.

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 ambient and nutrient-enriched conditions; 4) average across blocks and experimental years, summed cover of species with traits accounted for >50% of the total cover; 5) during experimental years, at least one climate extreme occurred (see “Defining climate extreme” for more details). Nineteen sites met these criteria (Fig. S1; Table S2). These sites are distributed in North America, Australia, Europe, and Africa. Sites include many grassland types such as montane, alpine, semiarid grasslands, prairies, and old fields. See table S2 for geolocation, climate, and experimental durations for these sites. 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, productivity 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 (although 8 most dominant species were measured at one site). 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 estimated in this study with their mathematical definitions and interpretations.

Variables	Methods	Parameters in the methods explained	Interpretations	References
CWM (slow-fast)	$\frac{\sum a_i x_i}{\Sigma a_i}$	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 plots. CWM_{Nut*} is the CWM in the nutrient addition plots recalculated by using slow-fast trait in the control plots.	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)	$\frac{\sum a_i z_i}{\Sigma a_i}$	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)
Invariability	$\frac{u}{\sigma}$	μ is the mean of aboveground primary productivity, σ is the standard deviation after detrending productivity over time.	A higher value indicates that a plant community varies less in productivity over time.	(Pimm 1984)
Resistance.d/resistance.w	$\frac{\bar{Y}_n}{\lvert Y_e - \bar{Y}_n \rvert}$	$\bar{Y}_n$, Y_e, and Y_{e+1} are aboveground productivity during normal growing seasons (average over all non-extreme growing seasons), during a dry or wet growing season, and one year after a dry or wet growing season, respectively.	A higher value of resistance.d or resistance.w indicates that productivity deviates less under a dry or wet growing season to that of normal growing seasons.	(Isbell *et al*. 2015)
Resilience.d/resilience.w	$\frac{\lvert Y_e - \bar{Y}_n \rvert}{\lvert Y_{e+1} - \bar{Y}_n \rvert}$		A higher value of resilience.d or resilience.w indicates that productivity deviates less one year after a dry or wet growing season relative to that under 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 plots) 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

Following (Isbell *et al.*, 2015), 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. 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). We initially 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 (around 10 % and 25% quantile). Extreme dry: SPEI ≤ -1.28 sd; moderate dry: -1.28 sd < SPEI ≤ -0.67 sd; normal growing season: -0.67 sd < SPEI < 0.67 sd; moderate wet: 0.67 sd ≤ SPEI < 1.28 sd; and extreme wet: SPEI ≥ 1.28 sd. For some years at some sites, dry and wet growing seasons occurred consecutively, limiting our ability to disentangle their separate impact on diversity and stability; these years were therefore removed. For instance, at comp.pt, year 1 was eliminated because year 0 had a dry growing season, which may bias resistance during wet growing season in year 1. Sites and experimental years included in analyses can be found in Fig. S1 and Table S1. In total, 18, 22, 70, 14, and 18 extreme dry, moderate dry, normal, moderate wet, and extreme wet growing seasons across 19

sites were used in our analyses. We compared productivity under the moderate and extreme growing seasons relative to that of normal growing seasons. Productivity under moderate growing seasons was generally more similar to that under extreme growing seasons than normal growing seasons (Fig. S4). Thus, we focus on the cutoff of 0.67 in the following analyses. That is, we included moderate and extreme dry growing seasons as dry growing seasons, while moderate and extreme wet growing seasons as wet growing seasons.

We quantified invariability as the ratio of the temporal mean to the standard deviation of productivity (Pimm, 1984; Tilman *et al.*, 2006). We quantified resistance as the inverse of the proportional displacement of productivity from normal levels during a dry or wet growing season, a measure of the ability of a community to maintain a similar amount of productivity under perturbations, following (Isbell *et al.*, 2015). Also, we quantified resilience 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). There are many ways to quantify resistance and resilience, here we chose this measure to facilitate comparison among sites with different levels of productivity (Ingrisch & Bahn, 2018). We calculated resistance during and resilience after dry and wet growing seasons separately. See Table 1 for mathematical formulas for calculating stability metrics and their interpretations.

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. To facilitate among-site comparison, we present raw data of productivity under different climate extremes over the experimental years at each site in Fig. S5. Next, we aggregated productivity difference to normal levels in control and nutrient addition treatments during and one year after dry and wet growing seasons at each site in Fig. S6. We then aggregated average productivity and the magnitude of productivity deviation to normal levels during and one year after dry and wet growing seasons in control and nutrient addition treatments across sites in Fig. S7. Furthermore, we present the effects of nutrient addition on each stability facet at each site in Fig. S8. 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 make sure that multi-collinearity did not affect parameter estimates (variance inflation < 4). We used 12 sites at which both dry and wet growing seasons occurred. Sites with only one dry or wet growing season in the last year of the experiment were excluded because resilience could not be calculated in this case. See Table S1 for 12 sites and experimental years included. To check whether our results held 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. The link between each plant diversity facet and each stability facet in the SEM was evaluated across the control and nutrient addition treatments, to check whether these relationships differ under these two treatments, we ran bivariate analyses using function “lme” from the R package “nlme” (Pinheiro *et al.*, 2017). In each model, a stability facet was the response variable, a plant diversity facet and its interaction with treatment were fixed variables, and site was included as a random variable.

Results

Although adding nutrient did not change productivity in a consistent manner under different growing seasons across sites (Fig. S5-S6), on average, nutrient addition increased productivity by 54% during normal growing seasons (control: 320.93; nutrient addition: 496.44; $g.m^{-2}$; Fig. S7). During dry growing seasons, nutrient addition decreased productivity more from their normal levels by 45% (control: -79; nutrient addition: -114; $g.m^{-2}$). Thus, nutrient addition also increased the magnitude of productivity deviation by 18% (control: 185.90; nutrient addition: 248.61; $g.m^{-2}$). During wet growing seasons, nutrient addition slightly increased productivity from their normal levels (control: -2.8; nutrient addition: 14.1; $g.m^{-2}$) and it increased the magnitude of productivity deviation by 38% (control: 180.20; nutrient addition: 248.61; $g.m^{-2}$). Because the increased deviations were relatively small compared with the increased productivity during normal growing seasons under nutrient addition, nutrient addition increased resistance during dry

and wet growing seasons (dry: df = 53, t-value = 2.43, p = 0.02; wet: df = 41, t-value = 1.68, p = 0.1; Fig. 2; Table S4). One year after dry growing seasons, nutrient addition increased productivity from their normal levels (control: 4.3; nutrient addition: 46.1; $g.m^{-2}$; Fig. S7), and it increased the magnitude of productivity deviation by 42% (control: 149; nutrient addition: 105; $g.m^{-2}$). Similarly, one year after wet growing seasons, nutrient addition also increased productivity from their normal levels (control: -9.8; nutrient addition: 31.4; $g.m^{-2}$), and increased the magnitude of productivity deviation by 79% (control: 213; nutrient addition: 119; $g.m^{-2}$). However, nutrient addition did not impact resilience after dry and wet growing seasons, nor did it impact invariability (Fig. 2; Table S4; also see stability facets at individual sites in Fig. S8).

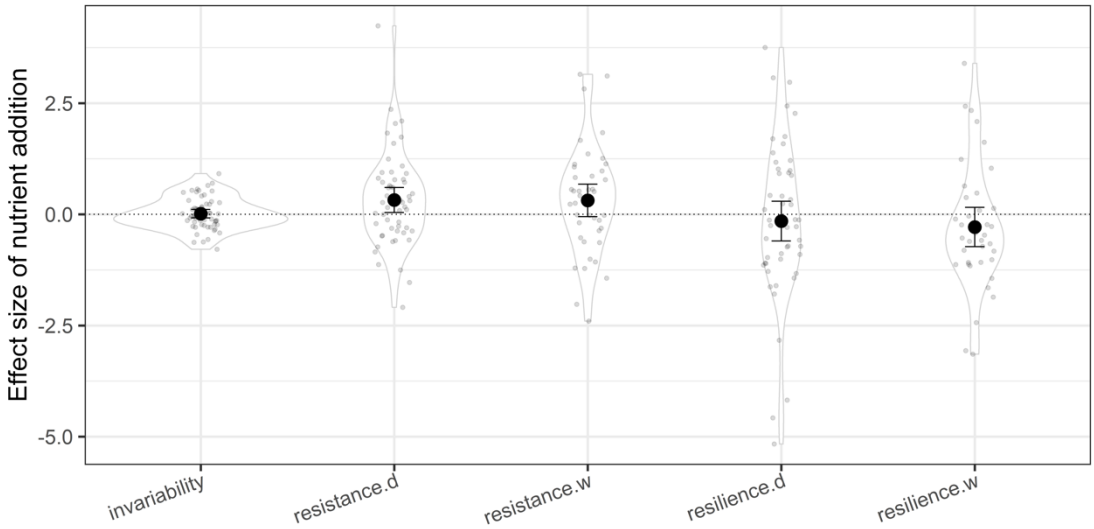

Fig. 2. Effects of nutrient addition on facets of stability. Small dots are raw values from each site. Large black dots are mean over experimental years and over 19 sites estimated from linear mixed effect models, error bars are 95% confidence intervals. See Table S4 for test statistics. All stability facets are on the log scale. Resistance.d/resistance.w: resistance during dry/wet growing seasons; resilience.d/ resilience.w: resilience after dry/wet growing seasons.

Nutrient addition decreased species richness (t-value = -4.98, df = 56, $p < 0.001$). Using all species with traits, nutrient addition decreased the slow-fast FD (t-value = -3.55, df = 56, p = 0.001) but increased the slow-fast CWM (t-value = 7.51, df = 56, $p < 0.001$). Using shared species (species occurring in both control and nutrient addition treatment), the effects of nutrient addition were similar for the slow-fast FD (paired t-test: t = 0.67, df = 56, p = 0.51), but the effects were weaker on the slow-fast CWM compared with that using all species with traits

(paired t-test: t = 1.83, df = 18, p = 0.08). Using the shared species, we further found that increased slow-fast CWM under nutrient addition was largely driven by intraspecific trait variation but not by replacement among existing species (Fig. 3; Table S5).

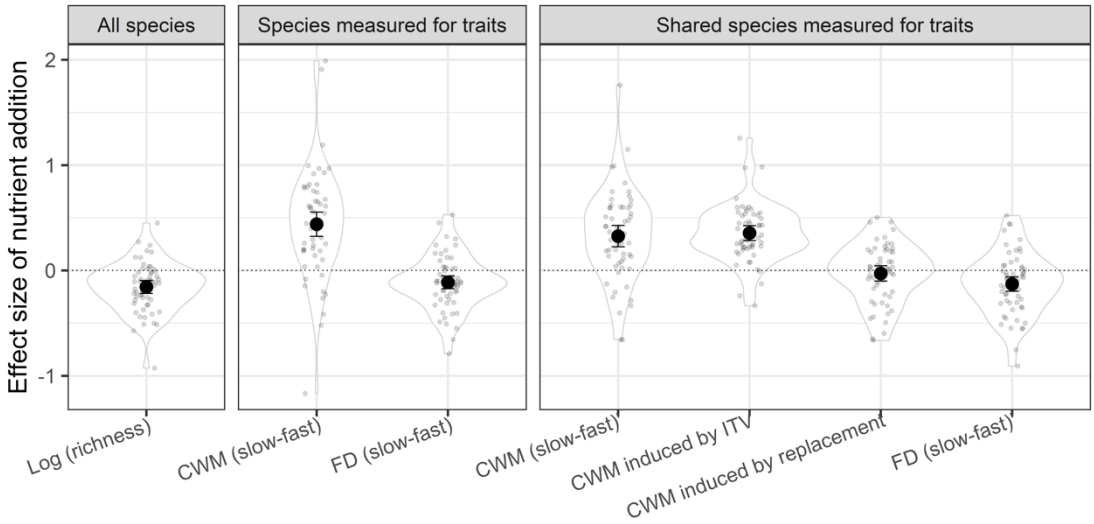

Fig. 3. Effects of nutrient addition on species richness, slow-fast CWM and FD. For shared species (i.e. species encountered in both control and nutrient addition treatments), change in slow-fast CWM was further attributable to species replacement among existing species and intraspecific trait variation (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 S5 for test statistics.

The SEM revealed that nutrient addition impacted facets of stability directly and indirectly by affecting different facets of plant diversity (Fig. 4). Nutrient addition directly increased resistance during dry and wet growing seasons (path coefficient: 0.21 and 0.31). However, the direct effects of nutrient addition on resistance during wet growing seasons were partly offset by its indirect effects through promoting fast communities and reducing slow-fast FD (compound path coefficient: -0.18). As a result, nutrient addition increased invariability due to increased resistance (compound path coefficient: 0.13). Nutrient addition directly decreased resilience after wet growing seasons (path coefficient: -0.18) but had no detectible impact on resilience after dry growing seasons. However, the direct effects of nutrient addition on resilience after wet growing seasons were partly offset by indirect effects through reducing species richness and slow-fast FD (compound path coefficient: 0.09). As a result, nutrient addition decreased invariability due to

decreased resilience (compound path coefficient: -0.02). Moreover, nutrient addition decreased invariability through decreasing species richness (compound path coefficient: -0.04). Summing up the pathways through resistance, resilience, and species richness, nutrient addition weakly increased invariability (net effects: 0.07). These results were generally similar when using shared species to calculate the slow-fast CWM and FD, except that the link between the slow-fast CWM and resistance during wet growing seasons and the link between the slow-fast FD and resilience after wet growing seasons became non-significant (Fig. S9). The relationships between diversity and stability in the SEM were generally consistent with the results from bivariate analyses (Fig. S10).

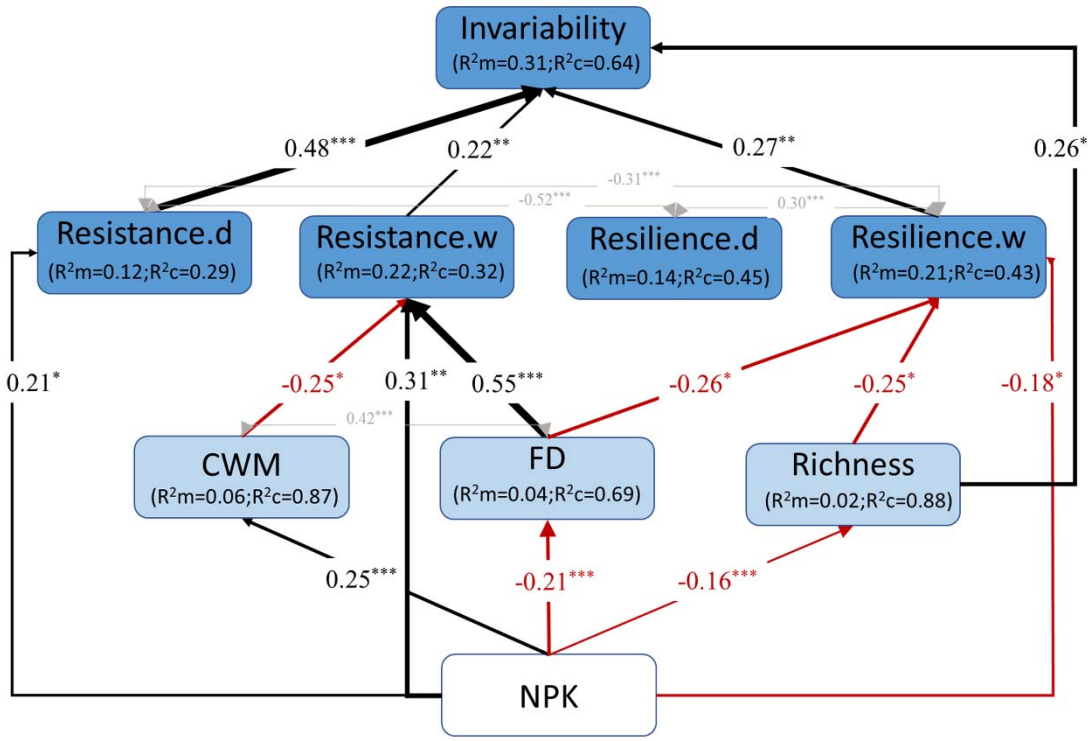

Fig. 4. Direct and indirect effects of nutrient addition on facets of stability. The model described the data well (F = 9.217, p = 0.512, df = 10). Results are based on 12 sites where both dry and wet growing seasons occurred. See Fig. S1 and Table S2 for sites and experimental years included. White 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. Grey lines and text show correlated errors. Non-significant paths are not shown. 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.

Discussion

Our analyses revealed idiosyncratic responses of different facets of stability to nutrient addition: whereas nutrient addition only impacted resistance during dry and wet growing seasons, it did not affect resilience and invariability. Additionally, nutrient addition increased resistance mainly through its direct effects. Although nutrient addition also impacted facets of stability indirectly through different facets of plant diversity, these diversity-mediated indirect effects were relatively weak and were overwhelmed by the direct effects. Our results highlight the necessity of considering multiple facets of stability and the importance of disentangling the direct and diversity-mediated indirect effects to improve our prediction for ecosystem stability in the face of global change.

Effects of nutrient addition on stability facets

To enable comparison among sites with varying productivity and to link resistance and with other stability facets such as temporal invariability, we used the proportional change of productivity from normal levels to quantify resistance. Relative to normal levels, nutrient addition strongly decreased productivity compared with ambient conditions during dry growing seasons (Fig. S7), consistent with previous studies that used change in productivity to quantify resistance (Bharath *et al.*, 2020; Meng *et al.*, 2021; Van Sundert *et al.*, 2021). In contrast, nutrient addition increased productivity, albeit slightly, during wet growing seasons (Fig. S7), consistent with previous single-site studies showing that increased nutrients and rainfall increase productivity (Xu *et al.*, 2014; Wang *et al.*, 2017). Here we found that nutrient addition increased resistance mainly because it increased productivity during normal growing seasons. This suggests that, on average, grassland sites investigated are nutrient-limited (Fay *et al.*, 2015). We found that diversity-mediated indirect effects were evident for resistance during wet but not dry growing seasons suggesting that effects of diversity may depend on climate. During wet growing seasons, an increase in resources may intensify plant-plant competition and thereby compensatory dynamics (Gonzalez & Loreau, 2009). During dry growing seasons, plant species are often under stress, thus abiotic factors and facilitation, which depend less on plant diversity, may be more important than competition in structuring plant communities (de Bello *et al.*, 2021). Moreover, the indirect effects of nutrient addition on resistance during wet growing seasons through the slow-fast CWM

were weaker than that through the slow-fast FD. This is in contrast with a previous greenhouse experiment showing that nutrient addition impacts resistance during flooding more through functional trait composition rather than species richness (Oram *et al.*, 2020). Our study suggests that compensatory dynamics among species may be more important than dominant species in driving community resistance.

One year after dry or wet growing seasons, productivity often recovered to normal levels. Although productivity generally deviated more under nutrient addition than ambient conditions (Fig. S7), productivity changed in a similar manner during and one year after dry and wet growing seasons in both conditions. Thus, nutrient addition did not impact resilience. Theories on how functional trait composition and diversity would impact resilience are well developed, but empirical tests lag behind (Reich, 2014; Díaz *et al.*, 2016; Craven *et al.*, 2018). To our knowledge, no study has yet examined the relationships between slow-fast FD and resilience after dry and wet growing seasons. Our analysis showed that, similar to resistance, functional trait diversity and species richness were better associated with resilience than functional trait composition. Additionally, both species richness and the slow-fast FD were negatively associated with resilience after wet but not after dry growing seasons. Furthermore, this negative association was mainly present in the nutrient addition but not ambient conditions (Fig. S10). This may be because communities with higher diversity in slow-fast trait and higher species richness enhanced resource use efficiency, resulting in higher productivity one year after wet growing seasons under nutrient addition, which increased productivity deviation from normal levels and decreased resilience (Wright *et al.*, 2015).

Our analyses confirmed the intuitive hypothesis that community invariability is jointly determined by resistance and resilience (Fig. 4). Consistent with previous analyses, we found that nutrient addition may decrease invariability through decreasing species richness (Hautier *et al.*, 2015; Carroll *et al.*, 2021), but this indirect negative effect, together with the negative effects through resilience were offset by the positive effects through resistance. Combined, nutrient addition did not impact invariability.

Effects of nutrient addition on diversity facets and the weak diversity-mediated effects

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. 3). Moreover, these subordinate or rare species may still play a role in mediating nutrient effects on stability facets. For instance, some links between CWM, FD and stability facets weakened 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. Thus, ecological studies using traits measured in situ, in which intraspecific trait variation is well captured, may improve the prediction for community stability. At many NutNet sites, leaf traits were measured after 3 to 4 years of nutrient addition, possibly resulting in higher intraspecific trait variation. Although there is a lack of empirical test, in the longer term, species replacement, which can take years to manifest, may become more important than intraspecific trait variation in determining community traits.

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. 4), it is difficult or even impossible to fully separate the effects of diversity from that of composition under natural settings. Unexpectedly, we found overall weak diversity-mediated indirect effects on stability. A few other studies also show that traits are poor predictors for ecosystem properties including productivity and its stability (van der Plas *et al.*, 2020; Pichon *et al.*, 2022). These weak effects may be due to the following three reasons. First, plants have many traits, 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), we may have missed some traits that can directly and strongly impact stability of productivity such as hydrological traits (Schnabel *et al.*, 2021). Second, we did not measure traits for all plants, and these unmeasured traits may strengthen or alter the results found here. Third 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. Digital cameras or spectrometers may be used to automatically record traits in the field, which will help capture temporal intraspecific trait variation and greatly improve trait-based prediction for 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. However, the diversity-mediated indirect effects on facets of stability were weak and overwhelmed by the direct effects of nutrient addition. This is not to say that diversity is not important because diversity-mediated indirect effects and their relative importance, when multiple diversity facets are considered simultaneously, on ecosystem stability remains unclear, particularly under increased environmental perturbations. Thus, whereas preserving and restoring plant diversity should still be one of the priorities in conservation and restoration, other processes/mechanisms (e.g. changing biotic and abiotic growing environments) that impact stability through pathways other than plant diversity should be carefully taken into account.

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Visualization: QC
Supervision: YH, SW
Writing—original draft: QC, YH, SW
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Supplementary Materials for

Nutrient addition increases grassland resistance during dry and wet climate extremes despite functional diversity loss

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This PDF file includes:

Figs. S1 to S10
Tables S1 to S6

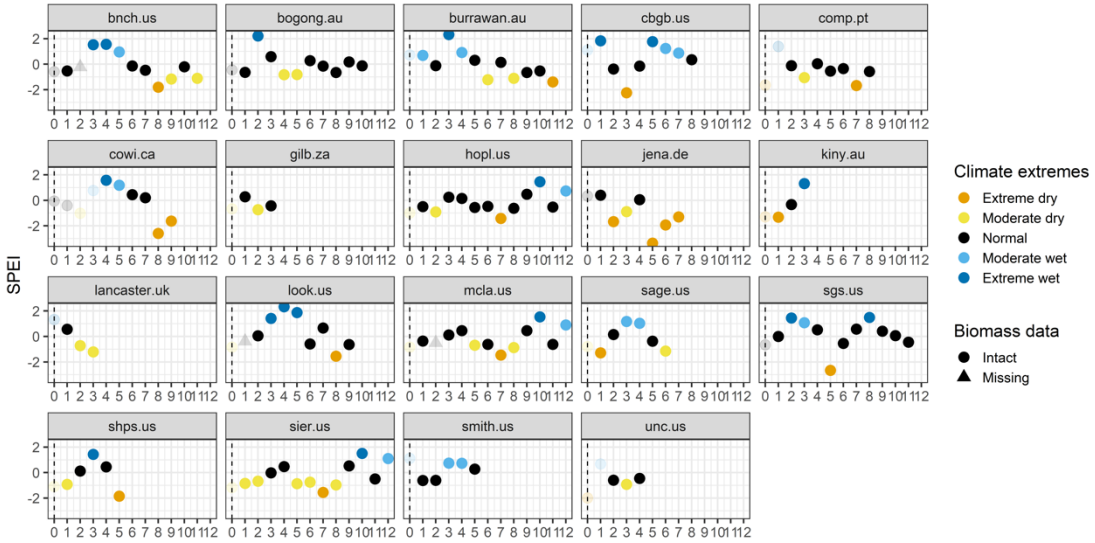

Fig. S1.

Categorize climate extremes at each site during experimental years. To reduce confounding effects of a dry and a wet growing season occurred consecutively, years were eliminated at a few sites. For instance, at comp.pt, year 1 was eliminated because year 0 had a dry growing season, which may bias resistance during a wet growing season in the next year. Grey dots represent years that were not included in analyses.

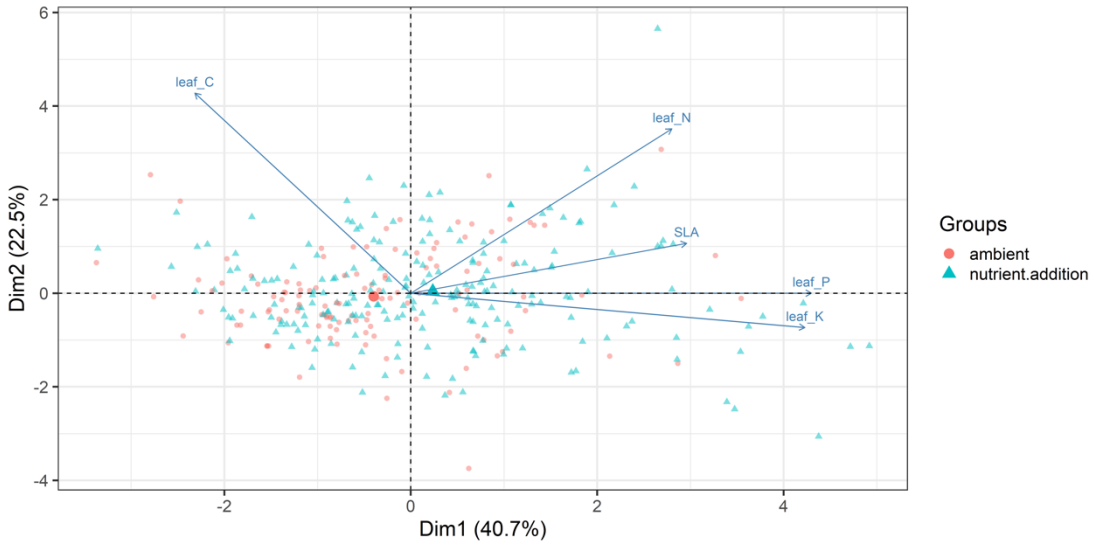

Fig. S2.

PCA using five leaf traits for 179 species from the ambient and nutrient enriched conditions across 19 sites.

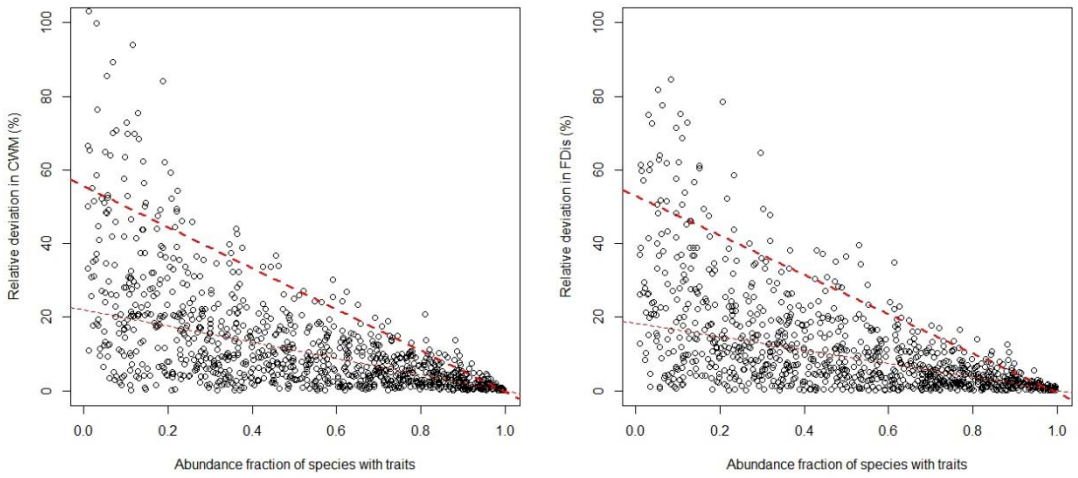

Fig. S3.

Sensitivity test. We first simulated communities with full information (50 species with abundance ranging from 0 to 100 and slow-fast trait ranging from 0 to 8). 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. Linear regressions with Tau 0.9 and 0.5 are shown in thick and thin lines, respectively. Simulation results suggested that the deviation would be smaller than 20 % when species with trait information contributed to > 60% cover.

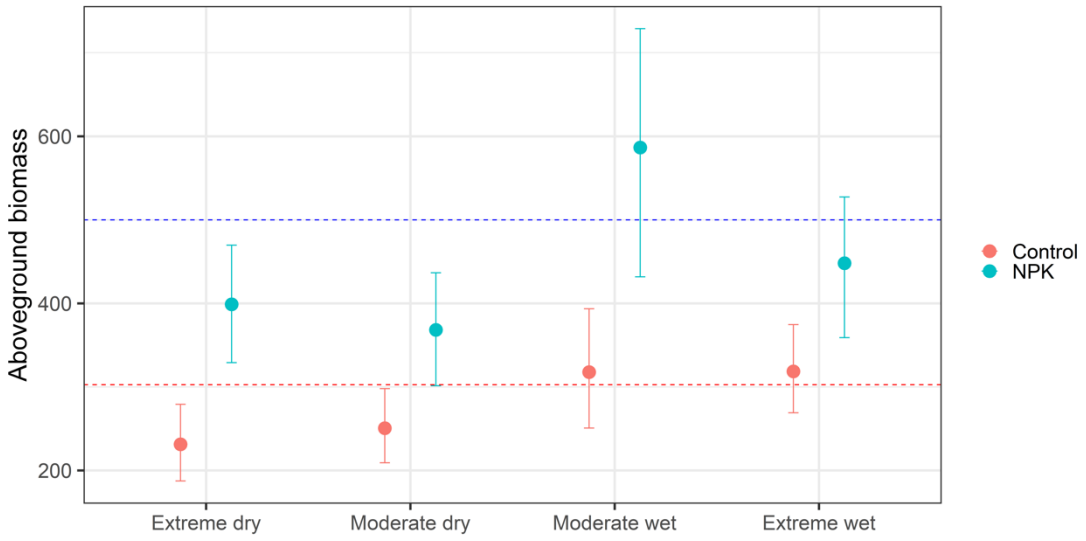

Fig. S4.

Average aboveground biomass (g.m^{-2}) under different growing seasons. Growing seasons correspond to Fig. S1. Dots are means, error bars are 95% bootstrapped confidence intervals. Lines indicate aboveground biomass during normal growing seasons over experimental years over 19 sites. In general, biomass during moderate and extreme dry/wet growing seasons are similar in both treatments, except for that biomass increased during moderate wet growing seasons while decreased during extreme wet growing seasons in nutrient addition treatment.

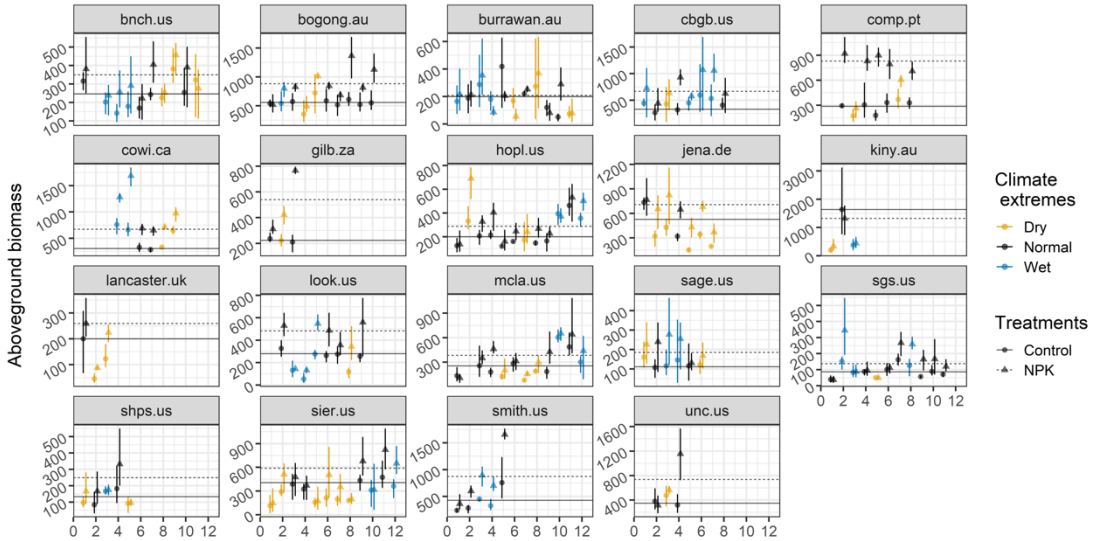

Fig. S5.

Aboveground biomass (g.m^{-2}) over the experimental years in control and nutrient addition plots at each site. Growing seasons correspond to Fig. S1. Dots indicate raw live biomass data averaged over three blocks in each year at each site. Lines indicate average live biomass over normal growing seasons over three blocks at each site. Error bars are 95% bootstrapped confidence interval.

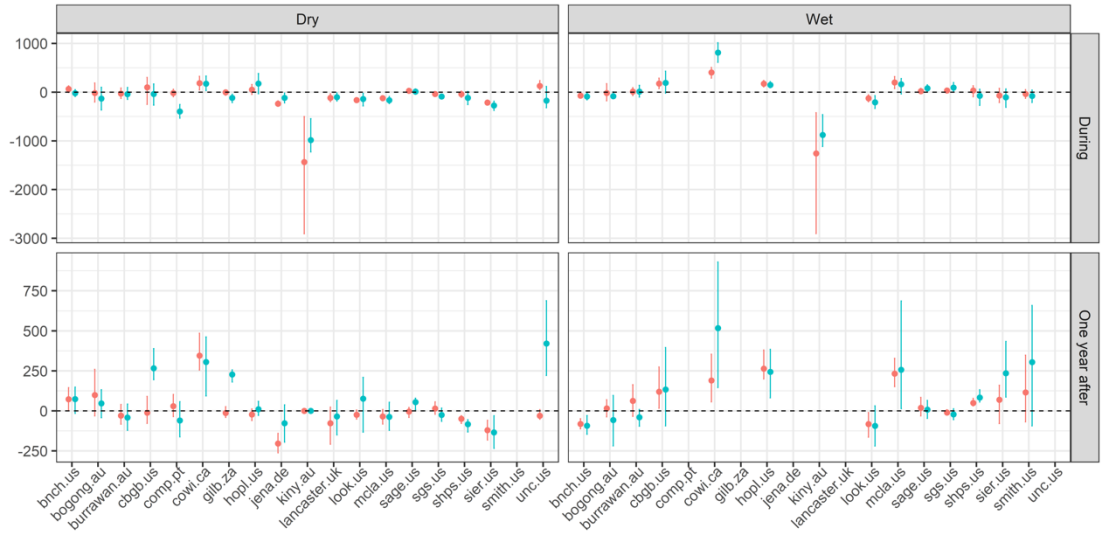

Fig. S6.

Biomass difference (g.m^{-2}) from normal levels in control and nutrient addition treatments at each site. Dots indicate biomass difference (relative from normal level at each block) and then averaged over dry or wet growing season and over three blocks at each site. Error bars are 95% bootstrapped confidence interval.

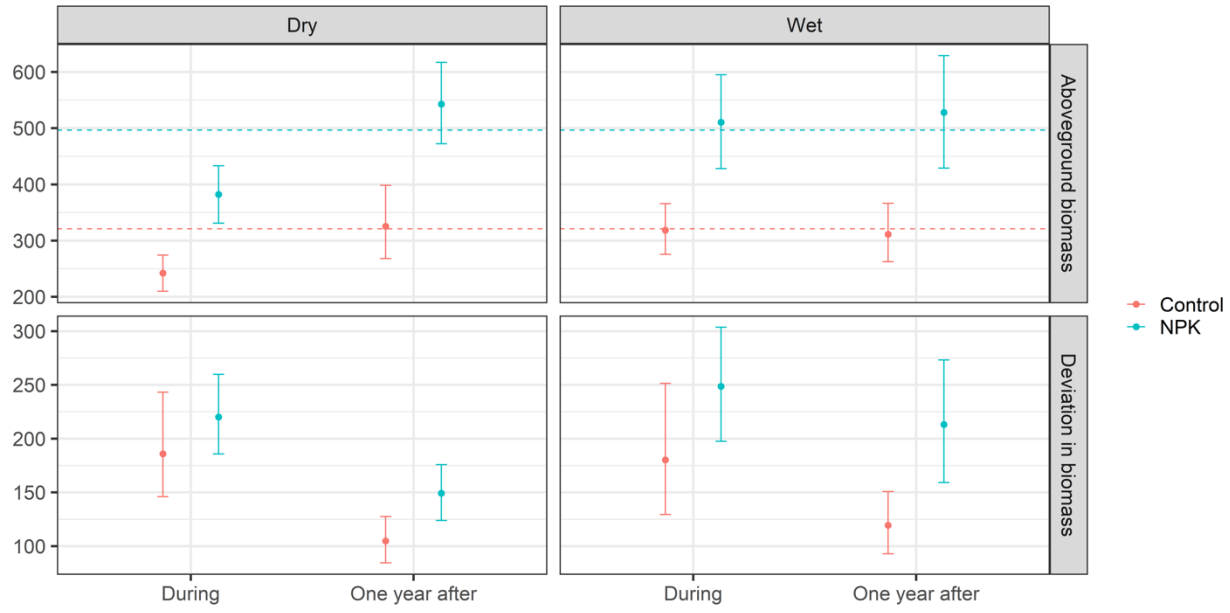

Fig. S7.

Aboveground biomass (g.m^{-2}) and the magnitude of biomass deviation (g.m^{-2}) from normal levels in control (red dots and line) and nutrient addition plots (blue dots and line) under and one year after dry or wet growing seasons. Dots indicate average values over dry or wet growing seasons and over 19 sites. Lines indicate average live biomass under normal growing seasons over 19 sites. Error bars are 95% bootstrapped confidence interval.

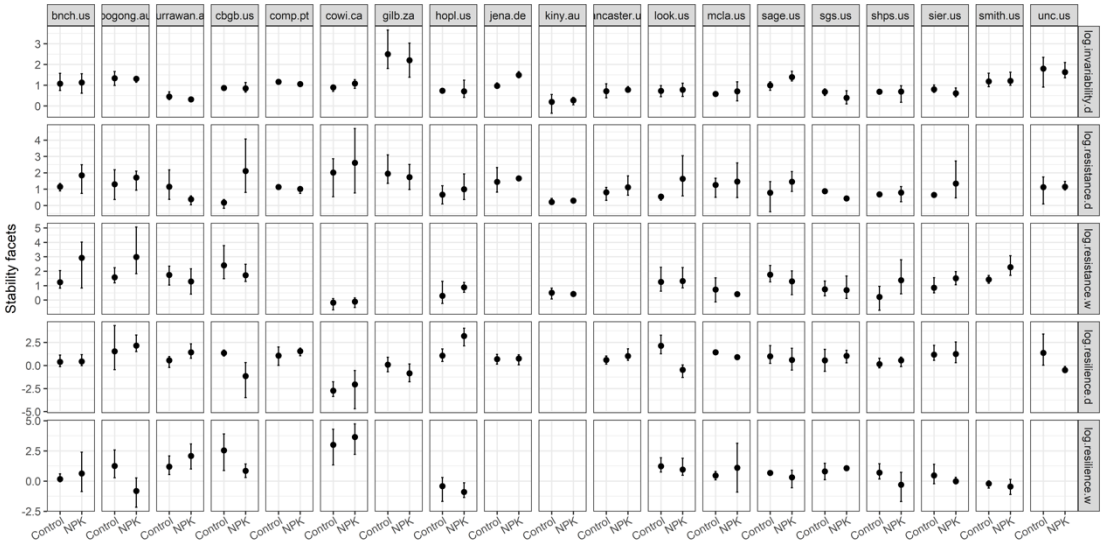

Fig. S8.

Stability facets in control and nutrient addition plots at each site. Growing seasons correspond to Fig. S1. Dots indicate stability facets averaged over blocks and years at each site. Error bars are 95% bootstrapped confidence interval.

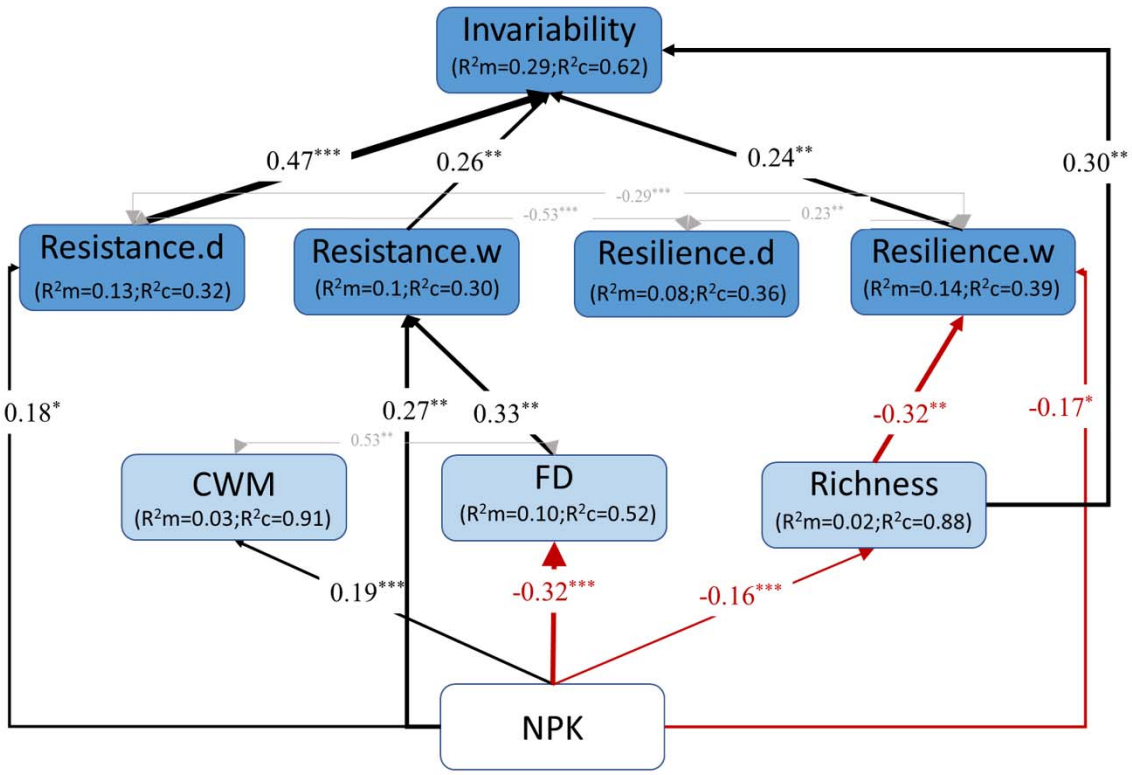

Fig. S9.

Direct and indirect effects of nutrient addition on stability facets. This figure is the same as Fig. 4, but CWM and FD were calculated using the shared species. The model fits the data well (F = 12.182, p = 0.273, df = 10). 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. Grey lines and text show correlated errors. Non-significant paths are not shown. 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.

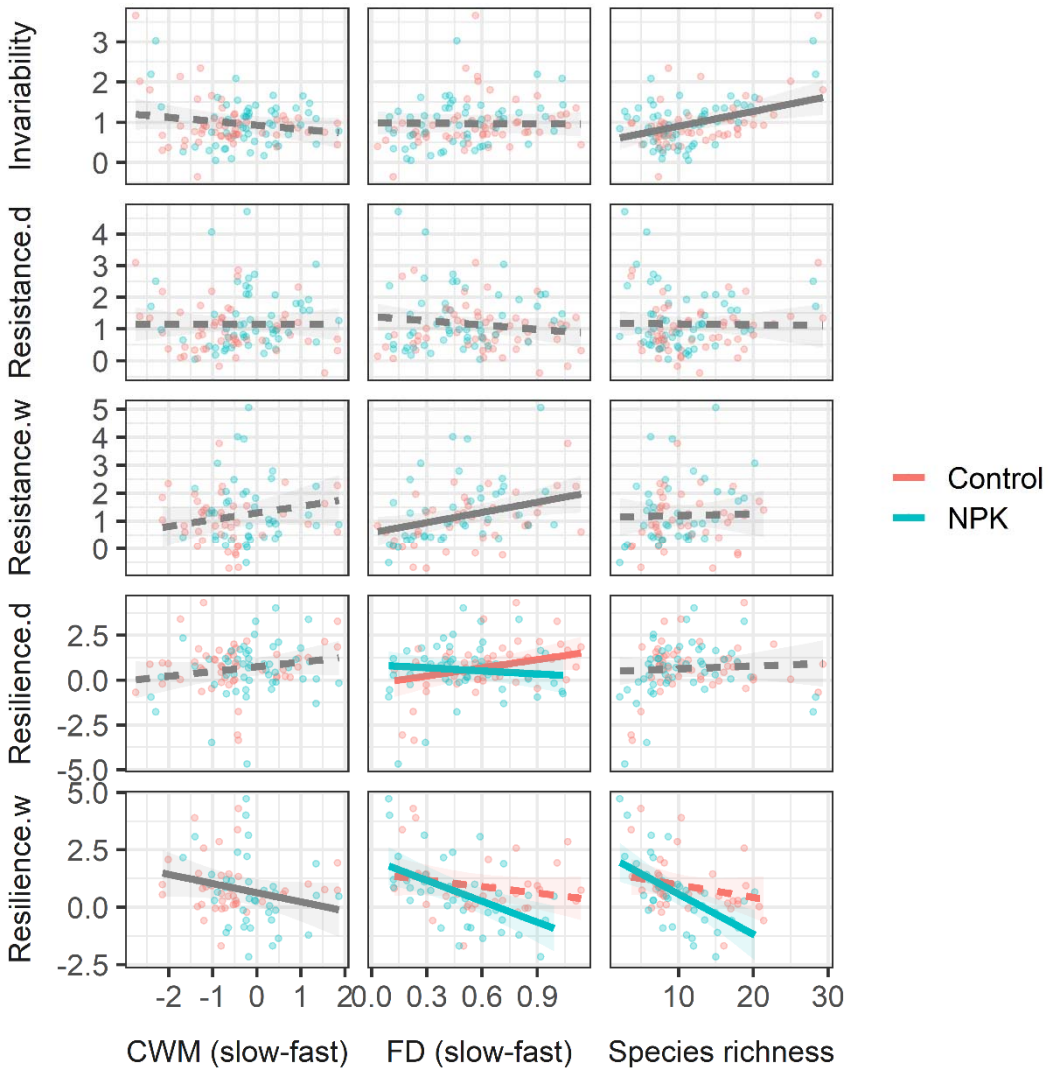

Fig. S10.

Relationships between each facet of plant diversity and stability. black lines indicate relationship over control and nutrient addition treatments as the interaction between plant diversity facet and treatment was not significant, treatment was dropped from the models. Solid lines show significant relationships, dashed lines show non-significant relationships.

Table S1.

Pathways and potential mechanisms for each link in SEM.

Pathways	Potential mechanisms	References
NPK->invariability	Nutrient addition may decrease invariability through decreasing resistance and resilience.	(Hautier *et al*., 2015)
NPK->resistance.d	Nutrient addition may decrease resistance during dry climate extremes through increasing nutrients-to-water imbalance for plants, which reduces productivity and increases its deviation from normal levels.	(Xu *et al*. 2014; Bharath *et al*. 2020; Meng *et al*. 2021)
NPK->resistance.w	Nutrient addition may decrease resistance during wet climate extremes because increased nutrients and water availability increase plant growth and productivity, which also increase the magnitude of its deviation from normal levels.	(Wright *et al*., 2015)
NPK->resilience.d	Nutrient addition may decrease resilience after dry climate extremes because increased nutrients-to-water imbalance increases plant mortality.	(Southon *et al*. 2012; Meng *et al*. 2021)
NPK->resilience.w	Increased productivity due to increased nutrients and water availability may persist or even amplify in later years, thus nutrient addition may decrease resilience after wet climate extremes.	(Sala *et al*. 2012; Wheeler *et al*. 2021)
CWM->ressistance.d, resistance.w, resilience.d, and resilience.w	Plant communities dominated by fast growing species may not respond fast during perturbations but may recovery fast after perturbations. That is, CWM decreases resistance during dry and wet climate extremes, but increases resilience after dry and wet climate extremes.	(Craven *et al*., 2018; Oram *et al*., 2020)
CWM->invariability	Plant communities dominated by fast growing species may vary more under perturbations, thus reducing invariability.	(Craven *et al*., 2018; Lepš *et al*., 1982)
FD->ressistance.d, resistance.w, resilience.d, and resilience.w	Communities with higher functional trait diversity may have a higher chance of harboring more species that are better adapted to these perturbations, thus decreases in some species may be compensated by increases in others. This leads to less productivity deviation from normal levels, which increases resistance and resilience.	NA
FD->invariability	Functional trait diversity increases compensatory dynamics and results in more complete use of resources, thus increasing invariability.	(Craven *et al*., 2018; Polley *et al*., 2013)
Species richness->resistance.d, resistance.w, resilience.d, and resilience.w	Species richness may capture functional trait diversity other than leaf economic spectrum such as root and size-related traits, thus higher species richness may increase resistance and resilience in a similar way to that of a higher FD.	(Craven *et al*. 2018).
Species richness->invariability	Increased number of species increases compensatory dynamics among species, which increases invariability.	(Hector *et al*. 2010)
Ressistance.d, resistance.w, resilience.d, and resilience.w->invariability	Both higher resistance and resilience indicate the proximity of a function from normal levels, higher resistance, higher resilience, or both contribute to higher invariability.	(Ives & Carpenter, 2007)
NPK->CWM	Nutrient addition increases CWM by promoting fast-growing species (with higher leaf nutrients and specific leaf area) and intraspecific trait variation.	(Siefert & Ritchie, 2016; Tatarko & Knops, 2018; Firn *et al*., 2019)
NPK->FD	Nutrient addition decreases functional trait diversity because it increased the dominance of fast-growing species. Also, nutrient addition often decreases species richness, which is often but not always positively correlated with FD.	(De Bello *et al*. 2006; Borer *et al*. 2014)

NPK -> Species richness	Nutrient addition promotes nitrogen-loving plants, increasing dominance, decreasing light availability at the ground level, and thus reducing diversity due to loss of shade-intolerant species.	(Hautier *et al*. 2009)

Table S2.

19 sites selected and their geolocation and experimental years used. Growing season refers to from the start to the end of growing month at each site. Water balance is calculated as the mean over 15 growing seasons (2005-2020) at each site.

Site_code	Habitat	Continent	Latitude	Longitude	Growing season	Water balance	Pre-experiment year	Experimental years used for Fig. 2 - Fig. 3	Experimental years used for Fig. 4
bnch.us	montane grassland	North America	44.28	-121.97	4-8	-385.13	2008	1,3-11	1,3-11
bogong.au	alpine grassland	Australia	-36.87	147.25	10-1	-254.46	2010	1-10	1-10
burrawan.au	semiarid grassland	Australia	-27.73	151.14	10-5	-767.42	2009	1-11	1-11
cbgb.us	tallgrass prairie	North America	41.79	-93.39	5-10	-69.76	2010	1-8	1-8
comp.pt	annual grassland	Europe	38.83	-8.79	10-5	107.07	2013	2-8	
cowi.ca	old field	North America	48.81	-123.63	4-7	-178.57	2008	4-9	4-9
gilb.za	montane grassland	Africa	-29.28	30.29	10-4	-39.97	2011	1-3	
hopl.us	annual grassland	North America	39.01	-123.06	11-4	586.26	2008	1-12	1-12
jena.de	grassland	Europe	50.94	11.53	3-10	-250.06	2014	1-7	
kiny.au	semiarid grassland	Australia	-36.20	143.75	5-10	-176.02	2008	1-3	
lancaster.uk	mesic grassland	Europe	53.99	-2.63	3-8	111.23	2009	1-3	
look.us	montane grassland	North America	44.21	-122.13	3-8	-237.43	2008	2-9	2-9
mcla.us	annual grassland	North America	38.86	-122.41	11-4	355.41	2008	1,3-12	1,3-12
sage.us	montane grassland	North America	39.43	-120.24	4-7	-474.58	2008	1-6	1-6
sgs.us	shortgrass prairie	North America	40.82	-104.77	4-8	-506.28	2008	1-11	1-11
shps.us	shrub steppe	North America	44.24	-112.20	4-9	-628.74	2008	1-5	1-5
sier.us	annual grassland	North America	39.24	-121.28	11-4	501.67	2008	1-12	1-12
smith.us	mesic grassland	North America	48.21	-122.62	10-6	1406.28	2008	1-5	
unc.us	old field	North America	36.01	-79.02	4-9	-114.62	2008	2-4	

Table S3.

Information for leaf traits data at 19 sites used.

site_code	Years in which traits were measured	N(spp) with traits under ambient/nutrient addition	N(spp) occurred under both control and NPK	Proportional cover of species with traits under control/NPK	Proportional cover of shared species under control/NPK	Shift in CWM based on all species with traits	Shift in CWM based on shared species	Shift in CWM due to replacement among existing species	Shift in CWM due to intraspecific variation
bnch.us	4	6/9	6	0.66/0.87	0.66/0.84	0.53	0.50	0.01	0.49
bogong.au	2	6/12	6	0.82/0.81	0.82/0.65	0.86	0.48	0.09	0.40
burrawan.au	3	6/7	5	0.87/0.84	0.87/0.82	0.71	0.74	0.17	0.57
cbgb.us	3	9/17	7	0.77/0.91	0.74/0.71	0.26	0.18	-0.06	0.24
comp.pt	2	11/19	10	0.69/0.47	0.67/0.41	0.20	0.14	-0.15	0.29
cowi.ca	4	5/4	3	0.94/0.99	0.93/0.99	0.19	0.19	-0.03	0.22
gilb.za	2	4/7	4	0.48/0.56	0.48/0.44	0.32	0.28	0.05	0.23
hopl.us	4	9/14	6	0.53/0.86	0.49/0.62	1.31	0.52	0.12	0.40
jena.de	2	10/20	9	0.86/0.92	0.74/0.75	0.17	-0.11	-0.34	0.23
kiny.au	4	3/8	3	0.63/0.72	0.63/0.68	0.25	0.18	-0.09	0.27
lancaster.uk	3	5/7	5	0.8/0.91	0.8/0.84	0.42	0.52	0.04	0.48
look.us	4	6/10	4	0.82/0.88	0.71/0.82	-0.13	-0.41	-0.37	-0.04
mcla.us	4	8/13	8	0.83/0.93	0.83/0.79	0.42	0.42	0.19	0.23
sage.us	4	7/9	6	0.57/0.58	0.49/0.37	-0.55	-0.17	-0.09	-0.08
sgs.us	4	4/6	4	0.72/0.78	0.72/0.77	0.61	0.58	0.02	0.56
shps.us	4	5/10	3	0.59/0.7	0.44/0.53	0.81	0.29	0.02	0.27
sier.us	4	6/13	6	0.61/0.85	0.61/0.51	0.27	0.58	-0.05	0.63
smith.us	4	5/9	5	0.58/0.55	0.53/0.32	0.49	0.12	-0.21	0.33
unc.us	4	8/14	7	0.77/0.93	0.69/0.85	1.29	1.19	0.12	1.07

Table S4.

Model output for the fixed effects for Fig. 2. All stability facets were log-transformed to improve normality and homogeneity of variance.

variable	terms	Value	Std.Error	DF	t-value	p-value	r2m	r2c
invariability	(Intercept)	0.97	0.12	56.00	8.42	0.00	0.00	0.81
invariability	trtNPK	0.02	0.05	56.00	0.31	0.76	0.00	0.81
resistance.d	(Intercept)	0.99	0.13	53.00	7.45	0.00	0.03	0.27
resistance.d	trtNPK	0.32	0.14	53.00	2.24	0.03	0.03	0.27
resistance.w	(Intercept)	1.04	0.22	41.00	4.84	0.00	0.02	0.37
resistance.w	trtNPK	0.31	0.19	41.00	1.68	0.10	0.02	0.37
resilience.d	(Intercept)	0.73	0.26	50.00	2.76	0.01	0.00	0.36
resilience.d	trtNPK	-0.15	0.23	50.00	-0.66	0.51	0.00	0.36
resilience.w	(Intercept)	0.92	0.31	38.00	2.99	0.01	0.01	0.49
resilience.w	trtNPK	-0.29	0.23	38.00	-1.27	0.21	0.01	0.49

Table S5.

Model output for the fixed effects for Fig. 3.

variable	species	terms	Value	Std.Error	DF	t-value	p-value	r2m	r2c
Log (Species richness)	All species	(Intercept)	2.42	0.11	56.00	21.58	0.00	0.02	0.90
Log (Species richness)	All species	trtNPK	-0.16	0.03	56.00	-5.01	0.00	0.02	0.90
FD (slow-fast)	All species with traits	(Intercept)	0.59	0.05	56.00	11.61	0.00	0.05	0.62
FD (slow-fast)	All species with traits	trtNPK	-0.11	0.03	56.00	-3.66	0.00	0.05	0.62
CWM (slow-fast)	All species with traits	(Intercept)	-0.63	0.22	56.00	-2.91	0.01	0.05	0.90
CWM (slow-fast)	All species with traits	trtNPK	0.44	0.06	56.00	7.48	0.00	0.05	0.90
FD (slow-fast)	Shared species	(Intercept)	0.57	0.05	56.00	12.35	0.00	0.06	0.49
FD (slow-fast)	Shared species	trtNPK	-0.13	0.04	56.00	-3.68	0.00	0.06	0.49
CWM (slow-fast)	Shared species	(Intercept)	-0.62	0.22	56.00	-2.84	0.01	0.03	0.92
CWM (slow-fast)	Shared species	trtNPK	0.33	0.05	56.00	6.26	0.00	0.03	0.92
CWM induced by replacement	Shared species	(Intercept)	-0.62	0.23	56.00	-2.71	0.01	0.00	0.96
CWM induced by replacement	Shared species	trtNPK	-0.03	0.04	56.00	-0.80	0.43	0.00	0.96
CWM induced by ITV	Shared species	(Intercept)	-0.65	0.21	56.00	-3.12	0.00	0.04	0.96
CWM induced by ITV	Shared species	trtNPK	0.36	0.04	56.00	9.80	0.00	0.04	0.96

Table S6.
Principal investigators contributing data but are not authors; site names match that in Table S1. Their effort in providing data is critical to this manuscript.

Site_code	Firstname	Lastname
bogong.au	John	Morgan
burrawan.au	Jennifer	Firn
cbgb.us	Lori	Biederman
cbgb.us	W.	Harpole
cbgb.us	Kirsten	Hofmockel
cbgb.us	Lauren	Sullivan
comp.pt	Miguel	Bugalho
gilb.za	Peter	Wragg
hopl.us	W.	Harpole
kiny.au	John	Morgan
mcla.us	W.	Harpole
sage.us	Daniel	Gruner
sage.us	Louie	Yang
sgs.us	Dana	Blumenthal
sgs.us	Cynthia	Brown
sgs.us	Julia	Klein
sgs.us	Alan	Knapp
shps.us	Peter	Adler
sier.us	W.	Harpole
smith.us	Janneke	Hille Ris Lambers
unc.us	Charles	Mitchell
unc.us	Justin	Wright