Received: 10 April 2022 | Accepted: 28 July 2022

DOI: 10.1111/1365-2745.13983

Journal of Ecology BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Multiple global changes drive grassland productivity and stability: A meta-analysis

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Funding information
National Key R&D Program of China, Grant/Award Number: 2017YFA0604702; National Natural Science Foundation of China, Grant/Award Number: 32192464

Handling Editor: Adam Clark

Abstract

1. Temporal stability of primary productivity is the key to stable provisioning of ecosystem services to human beings. Yet, the effects of various global changes on grassland stability remain ambiguous.
2. Here, we conducted a comprehensive meta-analysis based on 1070 multi-year paired observations from 173 studies, to examine the impacts of various global changes on productivity, community stability and plant diversity of grasslands on a global scale. The global change drivers include nitrogen (N) addition, phosphorus (P) addition, N and P addition, precipitation increase, precipitation decrease, elevated CO_2 and warming.
3. Global change drivers generally had stronger impacts on grassland productivity than on temporal stability, except for precipitation changes. Community temporal stability was reduced by N addition, N and P addition and precipitation decrease, but was increased by precipitation increase and remained unchanged under P addition, elevated CO_2 and warming. In addition, species richness decreased under N addition, N and P addition and precipitation decrease. At the plant functional group level, N and P addition reduced grasses' stability and precipitation increase enhanced forbs' stability.
4. Nutrient additions decreased community stability via increasing the inter-annual variation more than the mean of primary productivity, while precipitation changes mainly affected community temporal stability via changing mean productivity. The negative impacts of global change drivers (i.e. N and P addition, warming) on community temporal stability increased with the degree of species loss but decreased with increasing stability of grasses. Moreover, the negative impacts of nutrient addition and precipitation decrease on community stability was lessened while the positive effect of precipitation increase on community stability was enhanced in grasslands with higher historical precipitation variability, greater soil fertility and longer experimental duration.
5. *Synthesis*. Our findings demonstrate that N-based nutrient additions and drought destabilise grassland productivity, while precipitation increase enhances community stability. Impacts of global changes on community productivity and stability are mediated by species richness, plant functional group, site-specific

environmental conditions (i.e. climate, soil) and experimental duration, which deserve more attention in grassland management practices under future global change scenarios.

KEYWORDS
ecosystem stability, environmental conditions, experimental duration, global change ecology, plant functional group composition, primary productivity, species richness

1 | INTRODUCTION

Contemporary global changes are largely attributed to increasing human activities, which have substantially altered ecosystem functions and services in recent decades (IPCC, 2013). Atmospheric nitrogen (N) deposition, phosphorus (P) fertilization, precipitation alterations, elevated CO_2 concentration and climate warming are considered to be some of the most pervasive global change drivers (Yue et al., 2017). Numerous empirical and experimental studies have documented the effects of each of these global change drivers on the functions (e.g. primary productivity, carbon storage) of terrestrial ecosystems, including grasslands (Bai et al., 2010; De Schrijver et al., 2011; Deng et al., 2015; Deng et al., 2017; Li et al., 2016; Soons et al., 2017; Wang et al., 2019; You et al., 2017; Yue et al., 2017; Zhou et al., 2016). However, less attention has been paid to the stability of ecosystem functions, which refers to the ability of a system to maintain its fundamental processes and provide reliable ecosystem services in response to environmental changes (Tilman et al., 2006). A synthetic view of how these global change drivers influence the stability of ecosystem functions, including the temporal stability of primary productivity in grasslands on a global scale, is currently lacking.

For a given ecosystem, temporal stability is often measured as the inverse of the coefficient of variation (CV) for the ecosystem properties (Bai et al., 2004; Hautier et al., 2015; Tilman et al., 2006). Integrative studies have shown that fertilization weakens the stabilizing effect of plant diversity on grassland productivity at multiple spatial scales (Hautier et al., 2014; Hautier et al., 2020). However, these results are derived from a fertilization study with multiple nutrients added at a specific rate, and thus these results may limit our understanding of grassland stability responses to fertilization at various rates (which simulates various nutrient deposition rates occurring in different regions). The effects of nutrient inputs on ecosystem productivity and/or diversity may rely on the intensity of nutrient additions and the experimental duration (Bai et al., 2010; Soons et al., 2017). For instance, several studies demonstrate that species loss intensified with increasing nutrient addition rate in grasslands (Hautier et al., 2015; Isbell, Reich, et al., 2013a; Lan & Bai, 2012). Plant diversity may or may not recover after long term cessation of fertilization, depending on the removal of accumulated nutrient stores, such as haying (Berendse et al., 2021; Isbell, Tilman, et al., 2013b; Tilman & Isbell, 2015). Grassland biodiversity often decreases as the number of limiting resources added increases due to reduced niche dimensionality (Harpole et al., 2016; Harpole & Tilman, 2007). Hence, the effects of fertilization with multiple nutrient elements on grassland functions may differ from those of single nutrient elements, especially for N and P because these essential nutrients are inherently coupled (Li et al., 2016). Additionally, eutrophication effects may vary with nutrient identity (Carroll et al., 2022), calling for a global evaluation of the effects of individual nutrient elements. Additionally, effects of other global change drivers (e.g. elevated CO_2, climatic warming, precipitation increase and precipitation decrease) on grassland stability at the global scale remain unelucidated although their inconclusive effects on grassland stability have been reported in several studies (Grime et al., 2008; Hautier et al., 2015; Ma et al., 2017). Therefore, research efforts should focus on the type, treatment intensity and duration of global change drivers since they could regulate the responses of ecosystem processes to global changes, and these responses are also impacted by vegetation, climate and soil properties (Komatsu et al., 2019; Li et al., 2016; Wang et al., 2019; Yue et al., 2017; Zhou et al., 2016).

The relationship between stability and species diversity has long been debated in biodiversity experiments (Isbell et al., 2015; Tilman et al., 2006; Tilman & Downing, 1994). In agreement with the positive diversity–productivity relationship (Loreau & Hector, 2001), a positive diversity–stability relationship prevails not only in experimental grasslands (Isbell et al., 2015; Tilman et al., 2006) but also in natural grasslands (Hautier et al., 2014). In general, plant diversity promotes the temporal stability of productivity via asynchronous responses among species to environmental fluctuations (Craven et al., 2018; Hector et al., 2010; Valencia et al., 2020); thus, the loss of species diversity may weaken the stabilizing effect of diversity on productivity.

A recent meta-analysis of factorial experiments manipulating both biodiversity and the environment revealed that high-diversity communities are more resistant to environmental change, highlighting the direct role of biodiversity in regulating ecosystem response to global changes (Hong et al., 2022). Given that plant diversity is threatened by many anthropogenic global changes, including global biodiversity loss driven by fertilization (De Schrijver et al., 2011; Soons et al., 2017), changes in plant diversity may substantially alter ecosystem functions and reduce stability. For instance, Hautier et al. (2015) demonstrated that anthropogenic environmental drivers (N deposition, elevated CO_2, fire, herbivory and precipitation change) affected community stability by altering biodiversity regardless of the nature of drivers. More research is necessary for determining whether this 'diversity route' of the global change effect on ecosystem stability within the individual grassland site could be generalised to global grasslands.

Growing evidence shows that the dominant species (Chen et al., 2016; Ma et al., 2017; Yang et al., 2017) or dominant plant functional group (Mackie et al., 2019; Shi et al., 2016), rather than species richness, plays an important role in regulating grassland stability under global changes, especially for communities dominated by only a few species. Large contributions to community primary productivity from dominant species or functional groups may diminish the role of plant diversity in ecosystem functions (Grime, 1998), and variations in community stability may largely depend on the changes in the stability of dominant species or functional groups, irrespective of the changes in species diversity (Chen et al., 2016; Yang et al., 2017). The inconsistency of results from individual studies may arise from inherent differences in plant community structure and/or environmental factors in habitats (Song et al., 2019). Recently, climate and soil conditions have been proposed to have an important role on the plant diversity effect on ecosystem stability (Garcia-Palacios et al., 2018). Temperature and soil nutrients are often stable at an individual site, and the variability in plant productivity is largely determined by the amount of precipitation and precipitation variability (Knapp & Smith, 2001). In addition, the relative importance of the biotic mechanisms of community stability may also vary with the amount of precipitation and precipitation variability (Garcia-Palacios et al., 2018; Hallett et al., 2014). For instance, sites with higher historical rainfall variability are more stable under climatic disturbance (Ciemer et al., 2019), and to determine whether this response pattern is applicable to global grasslands and other global changes requires further investigation. Furthermore, soil fertility may modify community stability responses to global changes by favouring specific plant functional traits and affecting plant productivity via nutrient limitation (Eskelinen & Harrison, 2015). Plant communities on infertile soils often exhibit resource-conservative functional traits, which may limit their responses to climate change (Fernandez-Going et al., 2012). Conversely, they may also be more vulnerable to climate variation once nutrient limitations are relieved under eutrophication (Carroll et al., 2022). At present, the response of the stability of plant communities to various global changes along a soil fertility gradient and the underlying mechanisms remain unelucidated.

Here, we conducted a meta-analysis to assess the effects of multiple global change drivers on grassland productivity and its temporal stability, using the published literature containing multiple years of observations (≥3 years) from globally distributed field manipulated experiments. These global change drivers include N addition, P addition, N and P addition, precipitation increase, precipitation decrease, elevated CO_2 concentration (eCO_2) and warming. Specifically, our study addressed three questions: First, how do primary productivity and community temporal stability respond to seven global change drivers in global grasslands? Second, how do biotic factors (e.g. grassland type, plant species richness and functional group composition) mediate the stability responses to global changes? Third, how do abiotic factors (e.g. climate, soil properties, treatment intensity and duration) affect the responses of grassland stability? To address these questions, we test three interrelated hypotheses: (1) nutrient addition would decrease the temporal stability of grasslands by lessening nutrient limitations (Bai et al., 2010; Carroll et al., 2022); (2) both plant species richness (Hautier et al., 2015) and dominant plant functional group (Mackie et al., 2019; Shi et al., 2016) would play an important role in regulating stability responses to global changes and (3) community stability would be less affected by global changes in grasslands with lower soil fertility (Fernandez-Going et al., 2012), higher climate variability (Ciemer et al., 2019), with low intensity treatments and with treatments that occurred only over short durations.

2 | MATERIALS AND METHODS

2.1 | Data compilation

Peer-reviewed literature were searched on the ISI Web of Science (http://apps.webofknowledge.com/) on 30 November, 2018, by using the following search term combinations: (grassland OR steppe OR prairie OR rangeland OR pasture OR savannah OR meadow) AND (biomass OR productivity OR richness OR diversity OR stability OR temporal variation OR coefficient of variation OR interannual variation) AND (N addition OR nitrogen addition OR nitrogen enrichment OR nitrogen supply OR P addition OR phosphorous addition OR fertili* OR elevated CO_2 OR CO_2 enrichment OR warming OR elevated temperature OR temperature increase OR water addition OR water supply OR precipitation increase OR irrigation OR precipitation decrease OR drought) AND experiment. We aimed to search for literature involving effects of global changes on primary productivity, community stability and plant diversity in global grasslands. Furthermore, we also searched the literature listed in the references of the relevant reviews and meta-analyses. Global change drivers included N addition, P addition, N and P addition, precipitation increase, precipitation decrease, CO_2 enrichment and warming.

To avoid bias in publication selection, each publication was examined based on the following criteria:

1. Focusing on grassland responses to global changes, studies were excluded if herbaceous communities were classified as wetland, tundra or cropland, to avoid potential confounding effects from their intrinsic differences in climatic conditions, plant community characteristics and management practices compared with grasslands.
2. Studies were conducted in the field and contained at least one of the following target variables: above-ground biomass or above-ground net primary productivity (ANPP) at community level or functional group level and plant species richness. When above-ground biomass or ANPP were unavailable, plant coverage, abundance or plant carbon storage were selected as proxies.
3. Studies contained at least three consecutive years of data for subsequent stability calculations.
4. Studies conducted at different sites and with different treatment intensities were treated as independent. Studies conducted at

the same site with the same treatment design but presented in separate papers were combined into one study to obtain multiple years of observations.

In total, these criteria yielded 173 publications which were used for further analysis. A list of the publications is provided in the Data Source section. N addition and N and P addition are the main global change drivers, and a period of 3~5 years is the main duration for the multiple years' data used for the stability calculation (Figure S9). The raw data in the text, tables and figures of the publications were directly extracted. When the data were presented graphically, WebPlotDigitizer 4.1 (https://automeris.io/WebPlotDigitizer/) was used to digitise and extract the data. Additionally, background information of each study was collected, including the mean annual temperature (MAT), mean annual precipitation (MAP), latitude, longitude, treatment intensity (fertilization rate, precipitation percent changes, CO_2 concentration increment, degree of increased temperature) and experimental duration. Notably, MAT and MAP reported in different studies may be derived from different historical climate records and may be missing in some studies. To address this issue, we extracted the uniform long-term climatic characteristics of the same historical period (1970–2000) from the Worldclim dataset (Fick & Hijmans, 2017) (30 × 30 s) at http://www.worldclim.org/ based on the latitude and longitude coordinates for each study site, and we obtained the aridity index, with lower values indicating a drier climate. Inter-annual precipitation variability was calculated as the CV (the ratio of standard deviation [SD] to mean) of annual precipitation and intra-annual precipitation variability, also termed as precipitation seasonality, was calculated as the CV of 12 monthly precipitation totals (Le Bagousse-Pinguet et al., 2017). Among the collected studies, MAT ranged from −2.6°C to 26.5°C, MAP ranged from 129 mm to 2248 mm and aridity index ranged from 0.15 to 2.43. To facilitate our analysis and the interpretation of the results, we also collected a range of soil variables to identify their roles in regulating the response of the grassland community to global changes. Soil variables of 0–20 cm soil depths were obtained from a gridded soil dataset ISRIC-WISE (Batjes, 2016) (30 × 30 s) at https://www.isric.org/ based on the latitude and longitude coordinates for each study site. Soil variables included sand proportion (%), silt proportion (%), clay proportion (%), bulk density (g cm^{-3}), pH, available water content (%), organic carbon content (g kg^{-1}), total nitrogen content (g kg^{-1}), C: N ratio and cation exchange capacity (cmol kg^{-1}).

2.2 | Data analysis

A natural log-transformed response ratio (RR) was used as the effect size to assess the effects of global changes on grassland primary productivity, species richness and stability.

The RR was calculated as follows:

$$\mathrm{RR}(Mean) = \ln\frac{X_t}{X_c}, \tag{1}$$

$$\mathrm{RR}(SD) = \ln\frac{SD_t}{SD_c}, \tag{2}$$

$$\mathrm{RR}(Stability) = \ln\frac{Stability_t}{Stability_c} = \ln\frac{X_t / SD_t}{X_c / SD_c} = \mathrm{RR}(Mean) - \mathrm{RR}(SD). \tag{3}$$

The sampling variance was used to account for the sampling uncertainty for each index. Observations with lower sampling variance were assigned a greater weight in the analysis. As in Hedges et al. (1999) and Nakagawa et al. (2015), we assume that the natural log-transformed mean ($\ln X_t$, $\ln X_c$) and SD ($\ln SD_t$, $\ln SD_c$) are approximately normally distributed and independent from each other; thus, RRs calculated from them are also approximately normally distributed, provided that the mean and variance of each are properly bounded (Marsaglia, 2006). The variances of the RRs for the three indexes described above were calculated as follows:

$$\mathrm{var}(\mathrm{RR}(Mean)) = \mathrm{var}\left(\ln X_t\right) + \mathrm{var}\left(X_c\right) = \frac{SD_t^2}{N_t X_t^2} + \frac{SD_c^2}{N_c X_c^2}, \tag{4}$$

$$\mathrm{var}(\mathrm{RR}(SD)) = \mathrm{var}\ \left(\ln SD_t\right) + \mathrm{var}\ \left(\ln SD_c\right) = \frac{1}{2\left(N_t - 1\right)} + \frac{1}{2\left(N_c - 1\right)}, \tag{5}$$

$$\mathrm{var}(\mathrm{RR}(Stability)) = \mathrm{var}(\mathrm{RR}(Mean)) + \mathrm{var}(\mathrm{RR}(SD)) = \frac{SD_t^2}{N_t X_t^2} + \frac{1}{2\left(N_t - 1\right)} + \frac{SD_c^2}{N_c X_c^2} + \frac{1}{2\left(N_c - 1\right)}. \tag{6}$$

where X and SD represent the temporal mean and temporal SD of the multi-year observations for grassland productivity, respectively; N represents the number of observation years and the subscripts 't' and 'c' refer to the treatment and control groups, respectively.

Stability was calculated as the ratio of the temporal mean to its temporal SD, that is, the inverse of the CV (Tilman et al., 2006). Correlation analysis indicated that the RRs of stability calculated from the multi-year observations of productivity showed no difference with the directly measured ones, indicating that the calculation procedure is reliable (Figures S7 and S8).

For each variable, the weighted mean of the response ratio (RR_{++}) was analysed using the 'rma.mv' function in the R package METAFOR (Viechtbauer, 2010). Because many of the studies contributed more than one RR, the 'study' was treated as a random factor. Based on each individual RR (RR_{ij}) and its corresponding weight W_{ij}. RR_{++} was calculated as follows:

$$RR_{++} = \frac{\sum_{i=1}^{m} \sum_{j=1}^{k} W_{ij} RR_{ij}}{\sum_{i=1}^{m} \sum_{j=1}^{k} W_{ij}}, \tag{7}$$

where m is the number of groups (e.g. grassland types); k is the number of comparisons in the ith group and W_{ij} is the reciprocal of variance for each RR. The effects of global changes were considered significant if the 95% confidence interval did not overlap with zero.

Percent changes of the variables under global changes were calculated as follows:

$$\left(e^{RR_{++}} - 1\right) \times 100\,\%. \tag{8}$$

We examined the relative effects of multiple variables on responses of grassland ANPP and community stability to global changes by using model-selection analysis in the R package GLMULTI (Terrer et al., 2016). The relative importance for each variable was calculated as the sum of the Akaike weights for all the models in which the variable was included, and a cut-off of 0.8 was set to differentiate between important and non-essential predictors (Terrer et al., 2016). In the model-selection analysis for ANPP and stability responses under global changes, MAT, MAP, precipitation variability, aridity and soil fertility of study site, domination and life-form type of grassland, treatment intensity and treatment duration were included. Except for MAT and MAP, the other variables were all treated as categorical moderators to evaluate their relative effects on the responses of grassland ANPP and stability to global changes (see classification details in Table S2). Furthermore, RRs were grouped based on the levels of the moderators, and a Q_M test was conducted to estimate the significance of the differences in the RRs among different levels of moderators (Hedges et al., 1999; Tables S1 and S2). We preformed meta-regressions by using the inverse of the variance as the weight to examine the relationships among the responses of community stability, the responses of functional group stability and site-specific environmental characteristics (e.g. climatic conditions and soil fertility). To examine the temporal trends in the stability responses to global changes, we used the overlapping intervals of three consecutive years to determine short-term stability for the treatment and control groups. In this section, only studies with observations for a minimum of five consecutive years were included. Thus, the stability of years 1–3 after the initiation of the experiment became post treatment period 1, the stability of years 2–4 became post-treatment period 2, and so on (Hautier et al., 2015). Correlation analysis was conducted to test whether the stability responses to global changes depended on the post treatment period.

All the meta-analyses were conducted in R software version 4.0.3 (R Core Team, 2020). To evaluate the possibility of publication bias, we created funnel plots to visualise the distribution asymmetry of observations around the mean effect size (Figures S11 and S12), and Egger's regression was used to statistically assess the publication bias, where $p > 0.05$ indicated the absence of publication bias (Egger et al., 1997).

3 | RESULTS

This meta-analysis focused on the responses of ANPP, community temporal stability and species richness to seven global change drivers in global grasslands. The database used for the analyses was composed of 1070 multi-year comparisons from 173 published studies across 109 study sites, which were mainly located in Asia, Europe and North America (Figure 1). Generally, our results are robust despite the relatively small sample size for the non-N addition global changes, except for ANPP response to P addition, species richness response to N and P addition and grass biomass responses to precipitation decrease and elevated CO_2 (Figures S6, S11 and S12).

3.1 | Productivity, stability and species richness responses

Generally, global change drivers had stronger impacts on grassland productivity than community stability, except for the precipitation changes. On a global scale, ANPP increased on average by 36.9% under N addition, 53.3% under N and P addition, 19.0% under precipitation increase, 12.5% under eCO_2 and 8.1% under warming; whereas it decreased by 13.3% under precipitation decrease and showed no significant response to P addition (Figure 2). The SD of productivity increased on average by 62.8% under N addition, 78.2% under N and P addition, 16.1% under eCO_2; whereas it decreased by 14.1% under precipitation increase and showed no significant response to P addition, precipitation decrease or warming (Figure 2). Community stability and species richness showed similar patterns in their responses to various global changes. Specifically, both stability and richness declined under N addition (−12.7% in stability vs. −11.9% in richness), N and P addition (−17.9% vs. −14.0%) and precipitation decrease (−16.9% vs. −6.7%) (Figure 2). However, the other four global change drivers showed no significant impacts on community stability or species richness on a global scale, except for precipitation increase which enhanced community stability by 40.7% (Figure 2).

At the plant functional group level, the responses of above-ground biomass, SD and temporal stability to global changes differed substantially between grasses and forbs (Figure S1). Specifically, the biomass of grasses was enhanced on average by 48.6% under N addition, 3.8% under N and P addition, 12.2% under precipitation increase, and was not significantly affected by the other global change drivers. The SD of grasses biomass was enhanced by 70.6% and 80.9% under N and N and P additions, respectively. In contrast, the stability of grasses was decreased by 41.2% under N and P addition and exhibited no significant responses to the other global changes. In contrast, both the biomass and stability of forbs were increased by precipitation increase (14.9% in biomass vs. 62.9% in stability). Elevated CO_2 increased the above-ground biomass and SD of forbs by 39.8% and 37.1%, respectively, while having no significant effect on forb stability. The other global changes showed no significant effect on biomass, SD or stability of forbs.

3.2 | Factors regulating productivity and stability responses to global changes

The model-selection analysis showed that soil fertility was the most important predictor for community stability responses to N

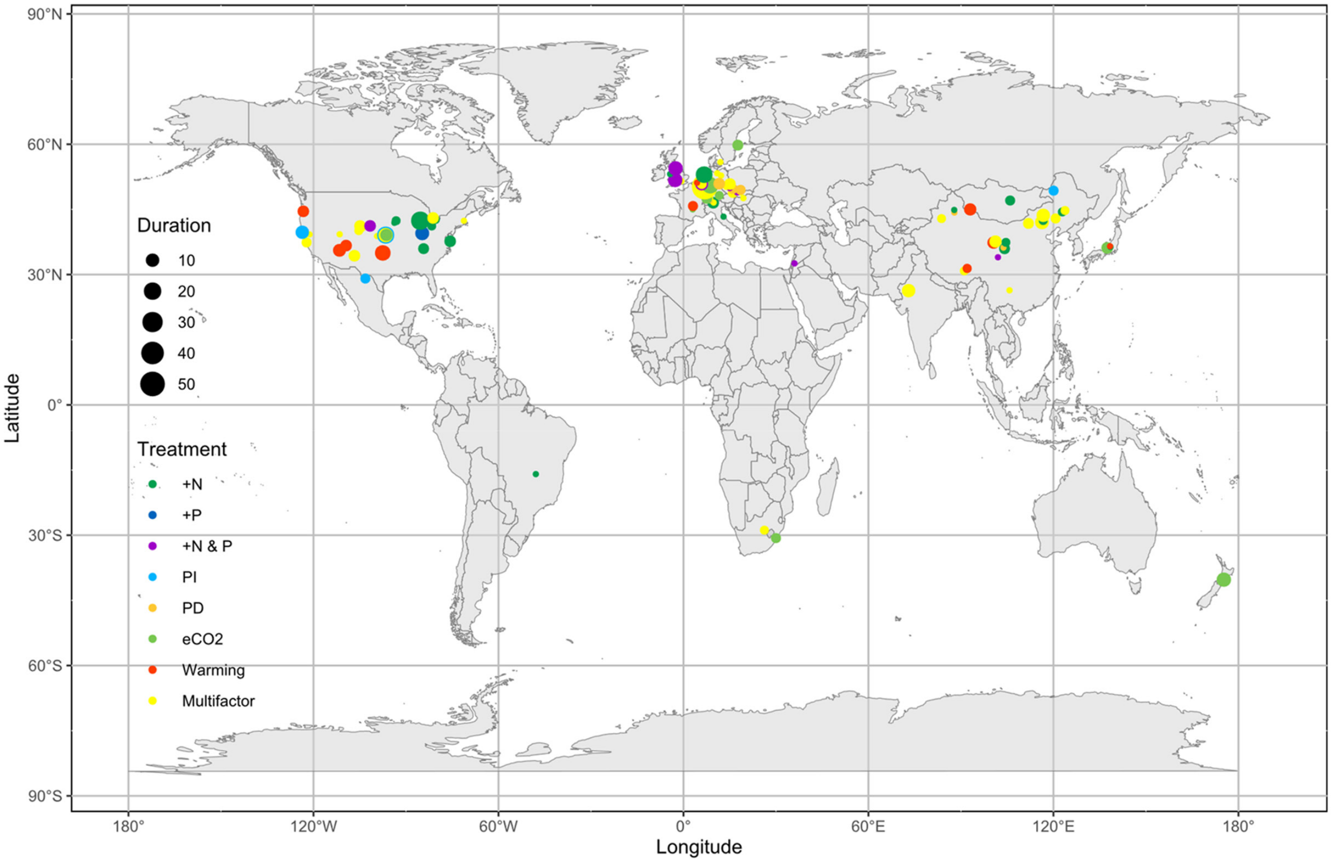

FIGURE 1 Global distribution of the study sites included in the meta-analysis. Different colored dots represent different treatment types, and larger dot sizes denote longer treatment duration (years). +N, N addition; +P, P addition; +N and P, N and P addition; PI, precipitation increase; PD, precipitation decrease; eCO_2, elevated CO_2 concentration; and Multifactor, experimental site with at least two global change drivers.

addition, where N addition decreased the grassland stability in infertile soils, but had no significant impact on grassland stability in fertile soils (Figures 3–5). The response of grassland community stability to N and P addition was best explained by precipitation variability and aridity, and the grassland stability was reduced less by N and P addition in sites with high precipitation amount and precipitation variability (Figures 3–5). Subgroup analysis further implied that community stability responses to global changes might also be impacted by dominant plant functional type (e.g. grasses vs. forbs), life-form (perennials vs. annuals) and the intensity and duration of treatment (Figure 4; Table S1). Specifically, N addition exhibited a significant negative effect on community stability in grasslands dominated by grasses and perennial plants (Figure 4), and the negative effects of N addition on community stability were substantially greater under high N inputs and short-term treatment. The community stability responses to N and P treatment were similar to that of N treatment (Figure 4). Precipitation increase showed a positive effect on community stability in sites with higher precipitation variability and soil fertility and under long-term treatment (Figures 4 and 5), while precipitation decrease reduced the community stability in wetter areas (Figure 4). However, stability responses to P addition, eCO_2 and warming were less affected by climatic conditions, vegetation traits, soil properties and experimental design (Figure 4). Moreover, by analyzing the tendency of stability changes over a 3-year interval, we found that the negative effects of N addition on community stability increased over time, while the magnitude of the positive effects of precipitation increase tended to decrease with increasing experimental duration (Figure S4). The effects of P and N and P additions on community stability shifted from negative to positive over time, and the magnitude of the positive effects of eCO_2 on community stability tended to increase with experimental duration (Figure S4).

In general, the ANPP responses to global changes were largely controlled by climatic condition, dominant plant functional type, life-form, treatment intensity and treatment duration (Figure S2, Figure 3; Table S1). For example, the positive effects of N addition and precipitation increase and negative effects of precipitation decrease on productivity were greater in sites with higher precipitation variability (Figure 5, Figure S3). In addition, the positive effects of N and N and P additions on productivity were greater under high addition rates compared with low addition rates (Figure 5, Figure S3; Table S1). Additionally, the positive effects of N addition and precipitation increase were greater under long-term treatments (Figure 5, Figure S3; Table S1).

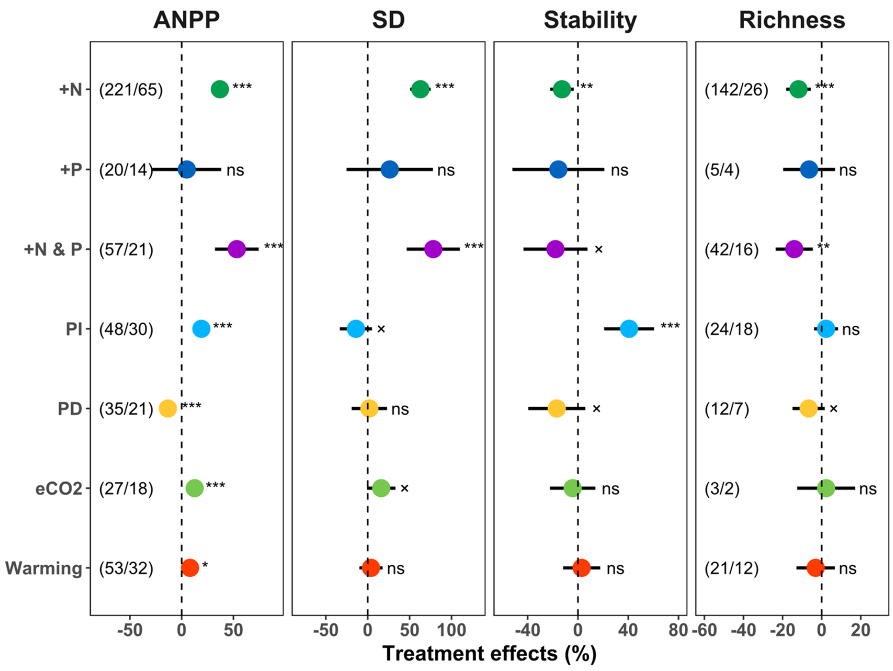

FIGURE 2 Effects of different global change drivers on grassland community above-ground net primary productivity (ANPP), standard deviation (SD), stability and species richness. Error bars depict 95% confidence intervals (CIs). The effects of an individual global change driver are considered significant if the CIs do not overlap with zero. For each global change driver, the numbers of the observations and studies are shown in parentheses, and the numbers of variables 'Stability' and 'SD' are the same as those of the variable 'ANPP'. Significant differences are reported as ***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$; ×, $p < 0.1$ and ns, $p > 0.1$. See Figure 1 for the abbreviations of the global change drivers.

3.3 | Relationships between stability and productivity responses with climate conditions and biotic properties

When data were pooled across all global change drivers, the negative effects of global change drivers on community stability decreased with increasing MAT. Changes in community stability were positively related to those in species richness and stability of grasses and forbs, where the variations in community stability were well explained by the stability of grasses (Figure 6a,d–f). Changes in ANPP were also positively related to biomass changes in both grasses and forbs (Figure 6i,j) but were negatively related to changes in species richness (Figure 6h), and the positive effects of global change drivers on ANPP decreased with increasing MAP (Figure 6g). Additionally, changes in community stability were positively related to those in species asynchrony, but were unrelated to those in the stability of the dominant species (Figure S5).

When data were analyzed for each global change driver, N addition-induced changes in stability and ANPP of community were positively associated with those of grasses (Figure 6d,i), and changes in ANPP were negatively related to those in species richness (Figure 6h). In addition, the enhancement of N addition on ANPP declined with increasing MAP (Figure 6g). The positive effects of P addition on community stability shifted to negative effects as MAP increased (Figure 6b), while P addition-induced changes in community stability were negatively related to changes in species richness but positively related to the stability of grasses (Figure 6c,d). Similarly, P addition-induced changes in ANPP showed positive relationships with changes in grasses and forbs (Figure 6i,j). The negative impacts of N and P addition and warming on community stability decreased with increasing MAT and MAP, while changes in community stability showed positive relationships with changes in species richness and the stability of grasses (Figure 6a,d). Additionally, the enhancement of N and P addition on ANPP increased with MAP and changes in ANPP were negatively associated with changes in species richness (Figure 6b,c). Warming-induced changes in ANPP were positively related to changes in species richness and the biomass of grasses (Figure 6h,i). The positive effects of elevated CO_2 on community stability became negative effects with increasing MAP, while the positive effects of elevated CO_2 on ANPP increased with MAT (Figure 6b,f). The enhancement of precipitation increase on ANPP increased with MAT and MAP, and ANPP changes were negatively related to changes in species richness (Figure 6f–h). In contrast, the impacts of precipitation decrease on community stability and ANPP were little affected by the climatic conditions and biotic properties.

4 | DISCUSSION

This study, to our knowledge, represents the first comprehensive synthesis of the effects of seven global change drivers on primary productivity and community temporal stability in global grasslands. The results demonstrate that variations in ANPP and stability are strongly regulated by the direct effects of global change drivers (i.e. type, intensity and duration of treatment) and the indirect effects mediated by vegetation (i.e. plant diversity, dominant plant functional groups), climate and soil properties.

4.1 | Effects of the type, intensity and duration of global change drivers

Variations in ANPP and stability with global changes were found to depend on the type, intensity and duration of treatments. Our

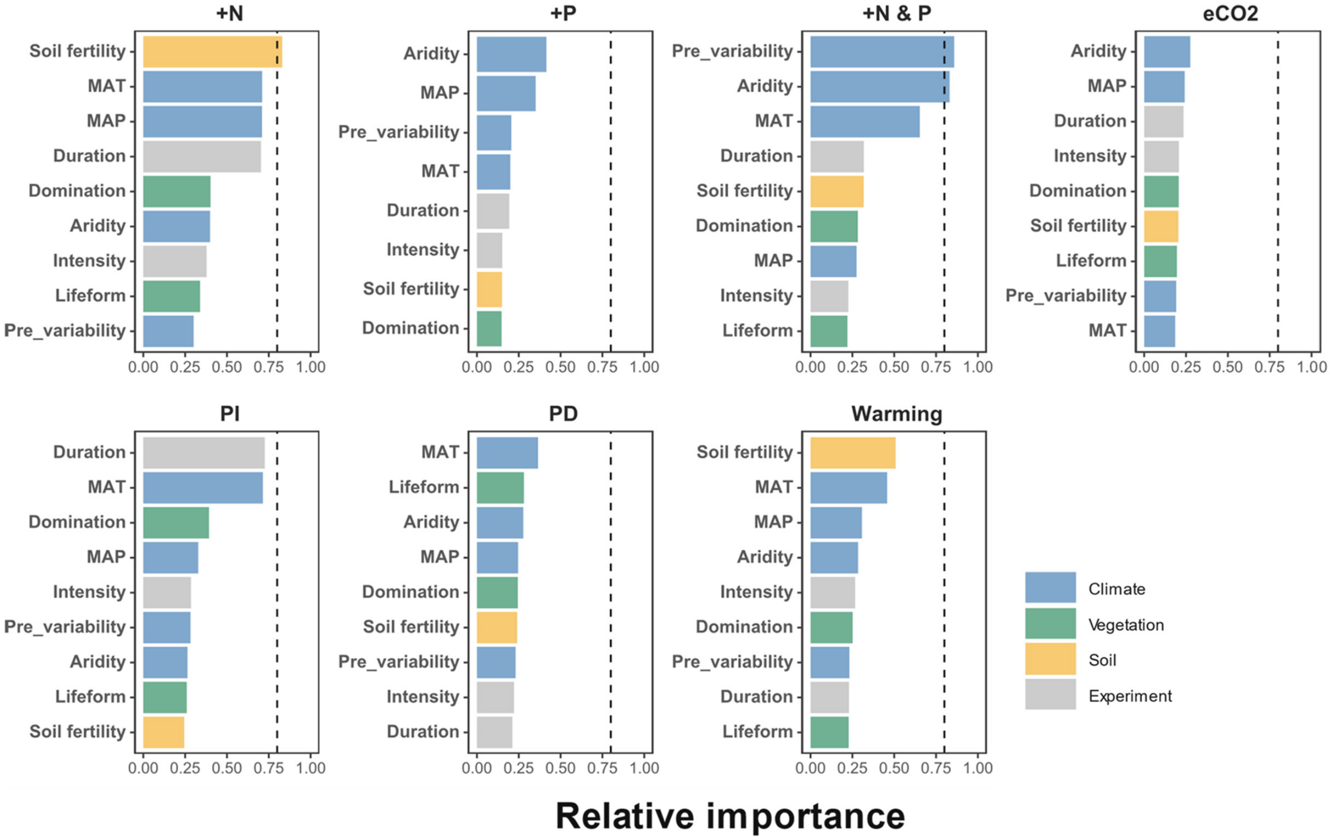

FIGURE 3 Model-averaged importance of the predictors for the effects of different global change divers on grassland stability (a) and above-ground net primary productivity (ANPP) (b). The relative importance value is based on the sum of the Akaike weights derived from the model selection using corrected Akaike's Information Criteria. Cutoff is set at 0.8 to differentiate between essential and nonessential predictors. MAT, mean annual temperature; MAP, mean annual precipitation; Aridity: arid (semi-arid) and humid; Pre_variability, the variability of precipitation, categorised as low and high; Soil fertility: low and high; Life-form: perennial and annual; Domination: grasses and forbs; Intensity: low and high; Duration: short and long term. See Figure 1 for the abbreviations of the global change drivers.

results showed similar ANPP responses to global changes as was reported in previous meta-analyses (De Schrijver et al., 2011; DeMalach et al., 2017; Deng et al., 2015, 2017; Li et al., 2016; Soons et al., 2017; Wang et al., 2019; You et al., 2017; Yue et al., 2017; Zhou et al., 2016). Among the seven global change drivers that we tested, precipitation increase enhanced ANPP and stability, while precipitation decrease reduced ANPP and stability. N and N & P additions increased ANPP but decreased community stability, suggesting that N and N & P additions increased the temporal variability of aggregate ecosystem processes. These findings support our first hypothesis that nutrient additions would destabilise biomass production of grasslands. These results are consistent with general findings from long-term observations and field experiments in which primary productivity of grasslands is primarily limited by water and nutrient availabilities (Bai et al., 2010; Harpole et al., 2011). Precipitation increase and nutrient enrichment (i.e. N addition, N and P addition) reduced water and nutrient limitations, enhanced community photosynthesis and plant growth, and thereby increased ANPP (Bai et al., 2010; Li et al., 2016; Yang et al., 2011). Furthermore, a lower carbon allocation to below-ground tissues under nutrient addition may increase grassland sensitivity to climate changes, which may further destabilise grassland productivity (Bharath et al., 2020; Song et al., 2019). In contrast, precipitation decrease may intensify water and/or nutrient limitations on plant growth, leading to a reduction in ANPP and stability. P addition showed little effect on ANPP and stability, implying that N-limitation rather than P-limitation prevails in grasslands on a global scale.

On a global scale, both eCO_2 and warming showed positive effects on ANPP but had no effect on stability, indicating that eCO_2 and warming did not alter the inter-annual variability of primary productivity. Previous studies suggest that eCO_2 has direct effects on grassland productivity by stimulating plant photosynthesis and growth (Körner, 2006), and eCO_2 has indirect effects by reducing stomatal conductance (Liu et al., 2018). Additionally, warming also enhances grassland productivity by stimulating plant growth and lengthening the growing season (Penuelas et al., 2017).

Our results demonstrated that the intensity and duration of treatments could affect the responses of ANPP and stability to global changes. For example, the increase in ANPP and reduction in stability under N addition were greater under high (>50 kg N ha^{-1} year^{-1}) rather than low N inputs (≤50 kg N ha^{-1} year^{-1}), partly supporting the hypothesis that community stability would be less affected at low treatments intensities. Given that most experiments imposed larger amounts of N than is typically imposed by atmospheric N deposition, the responses of grassland productivity and stability to N inputs may have been

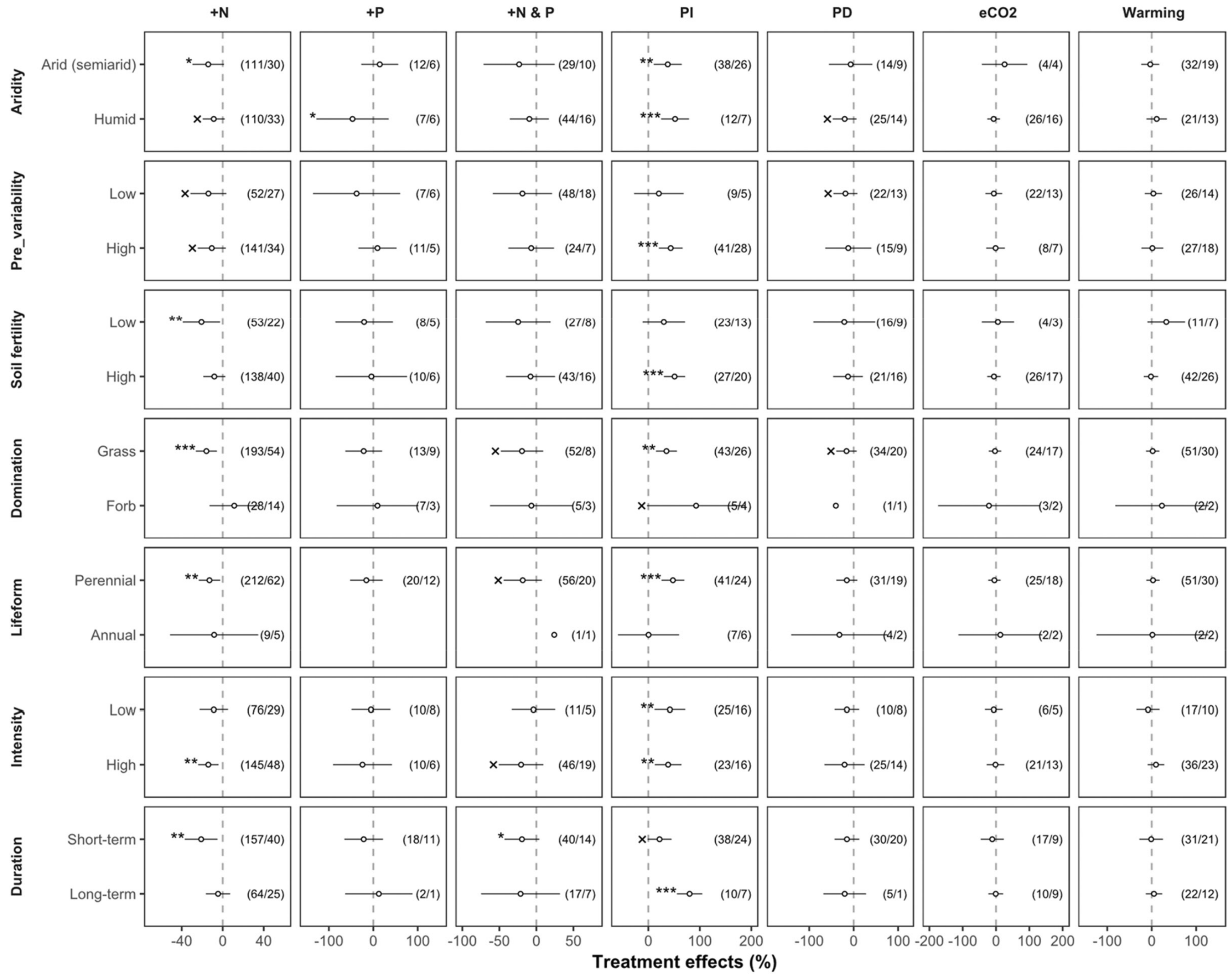

FIGURE 4 Effects of different global change drivers on grassland community stability among different subgroups. Error bars depict 95% confidence intervals (CIs). Significant differences are reported as ***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$; ×, $p < 0.1$. See Figure 1 for the abbreviations of the global change drivers. See Table S2 for details about the categories of aridity, pre_variability, soil fertility, domination, life-form, intensity and duration.

overestimated. Similarly, community stability was decreased less by nutrient additions and increased more by precipitation increase under the long-term treatment duration, suggesting that short-term experiments might also overestimate the negative effects of eutrophication on grassland stability. However, when stability responses were estimated using short-term observations (3 years) for long-term studies, the negative effects of N addition on community stability increased over time, possibly due to the N-induced changes in community composition, indicating that there was a time-scale dependency for stability responses to global changes, especially under N enrichment.

4.2 | Effects of species richness and plant functional groups

Changes in ANPP and stability were found to correlate with those in species richness and plant functional group, providing evidence for the second hypothesis that both plant species richness and dominant plant functional group played an important role in regulating stability responses to global changes. Plant diversity could have direct and indirect effects on the responses of community stability to global change drivers. On one hand, the stabilizing effects of biodiversity on biomass production have been well demonstrated in both biodiversity experiments (Hector et al., 2010; Isbell et al., 2015; Tilman et al., 2006) and observational studies (Hautier et al., 2014; Hautier & Van der Plas, 2022). Plant diversity could directly regulate the effects of global changes on ecosystem functions via facilitative interaction, sampling effect and niche complementarity (Hector et al., 1999; Hong et al., 2022; Reich et al., 2001). In contrast to the strong and stabilizing effects of biodiversity on ecosystem functioning in stressed environments, including drought (Hong et al., 2022; Kreyling et al., 2017; Wagg et al., 2017), we found that changes in grassland productivity and stability were unrelated to those in plant diversity under precipitation decrease at the global scale.

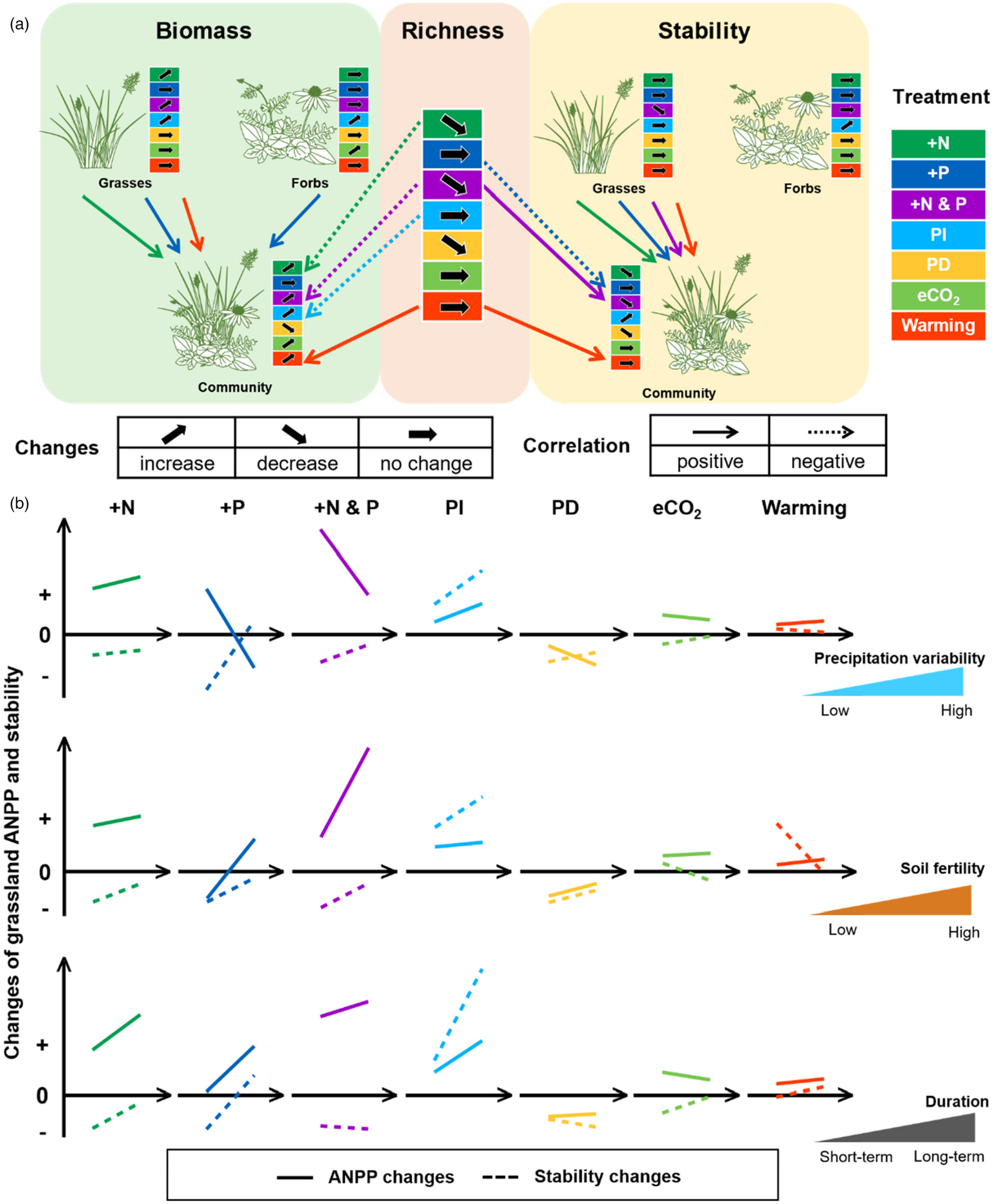

FIGURE 5 Graphical illustration of the changes in productivity, diversity and stability and their changing tendencies along the gradients of precipitation variability, soil fertility and experimental duration. In panel (a), the arrows indicate increase (up), decrease (down), and no change (horizontal) in target variables, and the connectors with arrows indicate positive (solid) and negative (dashed) relationships between two variables. In panel (b), '+' and '−' indicate the increase and decrease of variables, respectively. Solid and dashed lines indicate the changes in above-ground net primary productivity and the stability of community, respectively. The colour of the connectors with arrows (in panel (a)) and lines (in panel (b)) correspond to the global change drivers in Figure 1. See Figure 1 for the abbreviations of the global change drivers.

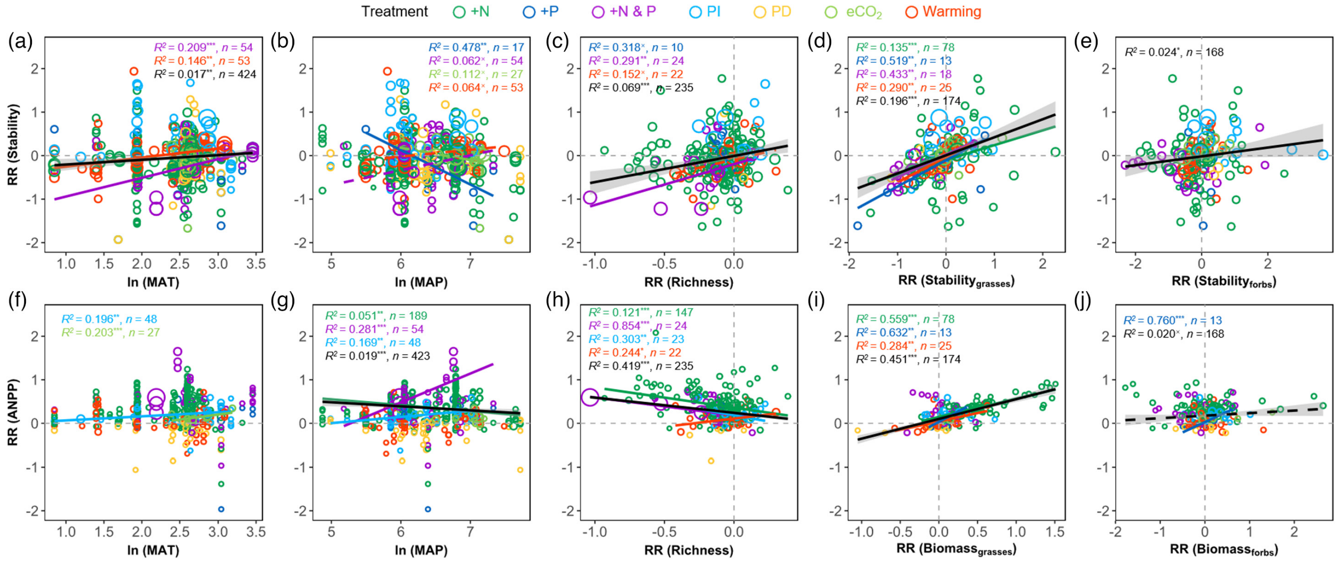

FIGURE 6 Relationship of the response ratios (RRs) of community stability and above-ground net primary productivity (ANPP) with climatic and biotic factors under different global change drivers. We determined the RRs of community stability and ANPP with MAT (a, f), MAP (b, g) and RRs of richness (c, h), grasses (d, i) and forbs (e, j). Circle size represents the inverse of variance, and only the significant fitted regressions ($p < 0.1$) are shown. Colours of circles and regression lines correspond to the global change drivers in Figure 1. Black lines represent the overall relationship across all global change drivers, and the 95% confidence intervals are shaded.

On the other hand, global changes could indirectly affect ecosystem stability via modifying biodiversity (Hautier & Van der Plas, 2022). For instance, a wide range of global environmental changes have been shown to affect ecosystem stability via changing biodiversity in grasslands, regardless of the attribute of global change driver (Hautier et al., 2015). In our study, N addition, N and P addition and precipitation decrease may destabilise primary productivity by reducing species richness. However, the positive relationship between the changes in species richness and stability can only be applied to N and P addition and warming in this study (Figure 6c), implying that the effects of global change on grassland stability may be mediated by factors other than diversity. Moreover, global change could indirectly affect stability by modifying the diversity–stability relationship (Hautier & Van der Plas, 2022). Hautier et al. (2014) demonstrated that fertilization weakened the positive relationship between biodiversity and stability, whereas the effects of other global change drivers on the diversity–stability relationship remain uncharacterised. Contrary to the widely recognised positive diversity–productivity relationship (Tilman et al., 2006), we found that changes in plant productivity were negatively related to changes in species richness, which implies a directional shift in community composition towards highly productive species under global changes (Carroll et al., 2022).

The stabilizing effects of diversity on temporal stability may be dampened by the dynamics of the dominant species (Chen et al., 2016; Ma et al., 2017; Yang et al., 2011) and plant functional groups (Mackie et al., 2019; Shi et al., 2016). We found that community stability was largely controlled by the stability of grasses, particularly under nutrient additions and warming. The predominant effects of grasses on grassland stability under global changes may have arisen from their greater contributions to the changes in community productivity (Bai et al., 2004; DeMalach et al., 2017; You et al., 2017), supporting the 'mass ratio' hypothesis (Grime, 1998). Grasses typically have a shallow and fibrous root system (Mackie et al., 2019), which enables them to be the superior competitors in the surface soil layer under global changes and helps to track environmental fluctuations. As a result, the stability of grasses was only decreased under N and P addition, indicating that the growth of grasses was co-limited by both N and P nutrients. Forbs, in contrast, are often characterised by their deep taproot system and resource-conservative strategy (Yang et al., 2011). Based on multisite grassland experiments, recent studies demonstrated that forbs mediated drought resistance, while grasses governed drought recovery (Mackie et al., 2019; Stampfli et al., 2018). In our study, precipitation increase enhanced the stability of forbs by increasing productivity, and other global changes drivers showed no effect on the stability of forbs. Forbs often exhibit a higher temporal stability than grasses, possibly due to the inherently high phylogenetic diversity and functional diversity among the forb species (Cadotte et al., 2008).

We found a positive relationship between changes in community stability and species asynchrony under various global changes. As asynchronous responses among species can help stabilise productivity in grasslands with high diversity (Hector et al., 2010; Tilman, 1996), variations in species asynchrony caused by global changes may translate into alterations in community stability (Hautier et al., 2014). These results were partially supported by a recent synthesis study that showed that species asynchrony was the most crucial factor controlling positive biodiversity–stability relationships (Hautier & Van der Plas, 2022). Notably, synchrony dynamics among dominant species matter more than species richness in determining plant community stability in global grasslands, and these findings emphasise the importance of community evenness to regulate the effects of species richness on stability (Valencia et al., 2020; Wang et al., 2021). Furthermore, global change drivers could further disrupt the interplay between species richness, synchrony and stability, and this disruption highlights the necessity for more experiments with the interactive manipulation of biodiversity and global changes.

4.3 | Effects of climate and soil conditions

Environmental (e.g. climate, soil) factors mediate the responses of community stability to global changes (Fernandez-Going et al., 2012; Garcia-Palacios et al., 2018). For example, the negative effects of warming on community stability decreased with increasing MAT, suggesting that grasslands in cold regions are more vulnerable to warming due to higher sensitivity (Ma et al., 2017). Our findings also showed that eCO_2, P addition and precipitation decrease tended to lower community stability in wetter grasslands, which may have arisen from intensified N limitation under eCO_2 (Luo et al., 2004) and higher P limitation in wetter regions (Li et al., 2016). The negative effect of precipitation decrease on community stability only occurred in wetter regions, as drought tolerance traits (e.g. higher leaf dry matter content and lower specific leaf area) are typically favoured by plants in arid regions, and this increases their resistance to drought (Wilcox et al., 2021). However, a recent meta-analysis showed that the climatic sensitivity of global grassland vegetation productivity was greater in dry habitats (Liu et al., 2021). Hence, more studies are required to evaluate how grassland stability varies under global changes along a precipitation gradient. Consistent with previous studies (Ciemer et al., 2019; Kreyling et al., 2017), we found that the historical precipitation variability could mitigate the negative effects of nutrient- and water-related global changes on community stability in grasslands. This finding partially supported our third hypothesis that community stability would be less affected in grasslands with higher climate variability. Higher precipitation variability could increase plant functional diversity due to trade-offs in the species responses to water availability (Gherardi & Sala, 2015), which in turn ameliorates the negative impacts on productivity and its stability (Perez-Ramos et al., 2017).

Moreover, in contrast to the third hypothesis that community stability might be less affected by global changes in grasslands with lower soil fertility, we found that community stability in infertile soils was reduced more under nutrient additions, which agrees with previous studies (Carroll et al., 2022; Shovon et al., 2020). Plant communities in nutrient-poor soils are usually characterised by conservative species with slow growth rates and resource uptake, and these species may be replaced by exploitative species capable of rapid growth and resource uptake under nutrient additions (Eskelinen & Harrison, 2015; Martinez-Almoyna et al., 2020), thus destabilizing community productivity under environmental fluctuations. In an era of increased climatic variability (IPCC, 2013), it is important to better understand the response patterns of plant functional traits and soil fertility to global changes and their subsequent roles in driving ecosystem processes so that ecosystem functions can be effectively promoted and maintained under variable environments.

5 | CONCLUSIONS

Our meta-analysis has provided a comprehensive synthesis of the effects of seven global change drivers on primary productivity and community stability in global grasslands. Despite increased productivity, N-based nutrient additions reduced community stability whereas neither elevated CO_2 nor warming affected community stability. Precipitation increase and decrease showed positive and negative effects on community stability, respectively, due to changes in productivity. In contrast, P addition had little effect on grassland productivity and stability. Our results also highlighted the importance of plant diversity and functional group, environment characteristics and experimental setup in regulating community stability responses to various global changes. Nevertheless, our study has several limitations. First, the effects of global change drivers on productivity, stability and species richness may be confounded by the inherent heterogeneity in the plant community characteristics, environment conditions and treatment setup among different studies. Second, the small sampling size regarding changes in species diversity under eCO_2 limits our ability to evaluate the species richness effects on productivity and stability. Third, global change-induced alterations in nutrient availability (Li et al., 2016; Liu et al., 2018; Luo et al., 2004) and nutrient cycling (Xiao et al., 2018) may mediate stability responses to environmental fluctuations. Furthermore, given that grasslands are simultaneously influenced by multiple global change drivers, their interactive effects on grassland productivity may potentially modify the stability response (Komatsu et al., 2019), which requires further investigation.

AUTHOR CONTRIBUTIONS

Yongfei Bai designed the study; Jishuai Su, Yujin Zhao, Fengwei Xu and Yongfei Bai carried out data compilation and analysis; Jishuai Su and Yongfei Bai wrote the manuscript. All authors contributed critically to the manuscript drafts and gave final approval for publication.

ACKNOWLEDGEMENTS

We thank the handling editors Dr. Jane Catford and Dr. Adam Clark and two reviewers (Dr. Yann Hautier and one anonymous reviewer) for their valuable comments on the manuscript. We also thank all the researchers whose data were used in this meta-analysis. This work was supported by the National Key R&D Program of China (2017YFA0604702) and National Natural Science Foundation of China (32192464).

CONFLICT OF INTEREST

All authors declare no conflict of interests.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/1365-2745.13983.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available at Dryad Digital Repository https://doi.org/10.5061/dryad.5x69p8d5d (Su et al., 2022).

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SUPPORTING INFORMATION

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How to cite this article: Su, J., Zhao, Y., Xu, F., & Bai, Y. (2022). Multiple global changes drive grassland productivity and stability: A meta-analysis. *Journal of Ecology*, *110*, 2850–2869. https://doi.org/10.1111/1365-2745.13983