META ANALYSIS

Warming effects on grassland productivity depend on plant diversity

Junjiong Shao[1] | **Xuhui Zhou**[2,3] | **Kees Jan van Groenigen**[4,5] | **Guiyao Zhou**[3] | **Huimin Zhou**[3] | **Lingyan Zhou**[3] | **Meng Lu**[6] | **Jianyang Xia**[3] | **Lin Jiang**[7] | **Bruce A. Hungate**[5] | **Yiqi Luo**[5] | **Fangliang He**[3,8] | **Madhav P. Thakur**[9]

[1]State Key Laboratory of Subtropical Silviculture, Zhejiang A&F University, Hangzhou, China

[2]Center for Ecological Research, Key Laboratory of Sustainable Forest Ecosystem Management-Ministry of Education, School of Forestry, Northeast Forestry University, Harbin, China

[3]Center for Global Change and Ecological Forecasting, Tiantong National Station for Forest Ecosystem Research, Shanghai Key Lab for Urban Ecological Processes and Eco-Restoration, School of Ecological and Environmental Sciences, East China Normal University, Shanghai, China

[4]Geography, College of Life and Environmental Sciences, University of Exeter, Exeter, UK

[5]Center for Ecosystem Science and Society, Northern Arizona University, Flagstaff, Arizona, USA

[6]School of Ecology and Environmental Sciences, Yunnan University, Kunming, China

[7]School of Biological Sciences, Georgia Institute of Technology, Atlanta, Georgia, USA

[8]Department of Renewable Resources, University of Alberta, Edmonton, Alberta, Canada

[9]Terrestrial Ecology Group, Institute of Ecology and Evolution, University of Bern, Bern, Switzerland

Correspondence
Xuhui Zhou, Center for Ecological Research, School of Forestry, Northeast Forestry University, 26 Hexing Road, Harbin, 150006, China.
Email: xhzhou@nefu.edu.cn

Funding information
National Natural Science Foundation of China, Grant/Award Number: 31600387, 31770559 and 31930072

Editor: Margaret Mayfield

Abstract

Aim: Climate warming and biodiversity loss both alter plant productivity, yet we lack an understanding of how biodiversity regulates the responses of ecosystems to warming. In this study, we examine how plant diversity regulates the responses of grassland productivity to experimental warming using meta-analytic techniques.

Location: Global.

Major taxa studied: Grassland ecosystems.

Methods: Our meta-analysis is based on warming responses of 40 different plant communities obtained from 20 independent studies on grasslands across five continents.

Results: Our results show that plant diversity and its responses to warming were the most important factors regulating the warming effects on plant productivity, among all the factors considered (plant diversity, climate and experimental settings). Specifically, warming increased plant productivity when plant diversity (indicated by effective number of species) in grasslands was lower than 10, whereas warming decreased plant productivity when plant diversity was greater than 10. Moreover, the structural equation modelling showed that the magnitude of warming enhanced plant productivity by increasing the performance of dominant plant species in grasslands of diversity lower than 10. The negative effects of warming on productivity in grasslands with plant diversity greater than 10 were partly explained by diversity-induced decline in plant dominance.

Main conclusions: Our findings suggest that the positive or negative effect of warming on grassland productivity depends on how biodiverse a grassland is. This may mainly be due to differences in how warming may affect plant dominance and subsequent shifts in interspecific interactions in grasslands of different plant diversity levels.

KEYWORDS

aboveground plant biomass, biodiversity loss, climate change, grassland, species dominance, stability

1 | INTRODUCTION

Climate warming is affecting ecosystems worldwide, often with detrimental effects on biodiversity (Gruner et al., 2017; Trisos et al., 2020) and on a range of ecosystem functions such as plant growth (Rustad et al., 2001), carbon sequestration (Lu et al., 2013), and disease suppression (Altizer et al., 2013). Greater plant diversity generally enhances ecosystem productivity as it represents greater trait diversity that make a community more likely to efficiently use resources (e.g., complementarity effects), or through a greater likelihood of the presence of more productive species, also referred to as selection effects (Tilman et al., 2014). Biodiversity loss may amplify the negative effects of climate warming on ecosystem functions, and thereby reduce the stability of ecosystem functioning, such as productivity (Hautier et al., 2015; Liu et al., 2018). Given the importance of biodiversity in regulating ecosystem functioning, understanding whether and how biodiversity mediates the responses of ecosystem functioning to climate warming would facilitate the integration of biodiversity into ecosystem models and help produce more realistic simulations of ecosystem processes in a changing world (Grace et al., 2016; Mokany et al., 2016).

Recent evidence suggests that warming can affect plant diversity and biomass differently. For example, warming-induced changes in plant diversity and biomass were positively correlated in a temperate steppe (Zhu et al., 2015) and a desert steppe (Wang et al., 2014). In contrast, experimental warming increased plant diversity but decreased plant biomass in a temperate meadow (Zhang et al., 2015). Moreover, an experiment conducted on a Tibetan Plateau grassland suggested that warming altered the composition of plant species without affecting the total production of plant biomass (Liu et al., 2018). We still know little about underlying mechanisms that drive such contrasting effects of warming on plant diversity and plant biomass.

One of the possible mechanisms for variations in warming effects on plant diversity and biomass is how warming may alter the stabilization effects of diversity (higher resistance to environmental changes or less temporal variation of environmental fluctuations in plant communities). High-diversity plant communities usually exhibit smaller temporal fluctuations in total biomass production despite the year-to-year environmental fluctuations and changes in species compositions (Tilman et al., 2014). In fact, this so-called stabilization effect of plant diversity on production could arise from several mechanisms (Loreau & de Mazancourt, 2013). For instance, when a set of plant species performs worse in a given year owing to unfavourable climatic conditions, other plant species thrive, and thereby the total biomass production is relatively invariant (Hector et al., 2010; Tilman, 1996). This asynchrony of species' responses makes any given species less likely to become dominant in the backdrop of changing environments (Wittebolle et al., 2009). Moreover, the overyielding effect induced by high diversity can reduce the strength of demographic stochasticity and thus stabilize the community productivity (Loreau & de Mazancourt, 2013). Owing to these mechanisms, high biodiversity can buffer ecosystem responses and thereby enhance resistance to climatic changes such as extreme drought (Isbell et al., 2015; Wagg et al., 2017).

High diversity does not always imply a high stability of productivity. Species-rich grasslands could have low resistance to environmental perturbations (Pfisterer & Schmid, 2002). A recent experiment involving micro-ecosystems (i.e., using microcosms) also indicated that the ecosystem resistance to warming decreased with species richness (Pennekamp et al., 2018). The destabilizing effect of plant diversity (lower resistance to environmental changes or greater temporal variation of environmental fluctuations in plant communities) could depend on biotic interactions, such as interspecific competition. Although competition among species is often considered as a stabilizing factor, recent evidence suggests that it could induce a destabilizing effect on community properties, through greatly increasing the population variability (Loreau & de Mazancourt, 2008, 2013).

To probe whether the observed variation of warming effects on plant productivity is regulated by different levels of plant diversity, and if plant diversity levels have stabilizing (weaker response to warming) or destabilizing effects (stronger response to warming), we synthesized warming effects on plant diversity and productivity (more precisely community biomass) for 40 different plant communities in grasslands across five continents. We used structural equation modelling to delineate direct and indirect effects of warming on plant community biomass via shifts in plant community characteristics.

2 | MATERIALS AND METHODS

2.1 | Data sources

The data used in this study were from peer-reviewed papers published before 2018. We searched for papers in Web of Science (http://www.webofknowledge.com) and China National Knowledge Infrastructure (http://www.cnki.net, Chinese

literature). Keywords included "warming", "elevated temperature", "temperature rising/raising", "temperature increase", "increasing temperature" and "temperature regime", and words describing relevant variables, such as "biomass", "production" and "productivity". Other relevant papers were also included by surveying the citations of the above searched papers. To be included in our analyses, the studies had to meet several criteria: (a) the research was on grassland ecosystems; (b) the research included two or more growth temperature regimes, and the alternation of temperature was achieved by warming rather than cooling; (c) the warming experiment was carried out for at least one growing season; (d) the warming effects on biomass and biodiversity were directly reported or could be calculated. When a study included other treatments (e.g., CO_2 enrichment, nitrogen addition, water manipulation and grazing), only the data from ambient and warming plots were used to avoid the possible confounding effects of other factors on plant diversity or community stability (Hautier et al., 2015). Furthermore, to minimize the (temporal) autocorrelation problem, when there were multiple published papers for a certain experiment, only the latest one was included. Similarly, for those studies reporting multi-year results, only the values from the last year were extracted. We also tabulated the auxiliary information, such as the location of the experiment, mean annual temperature and precipitation, warming facility (active or passive), warming magnitude, warming duration. In total, our dataset included 20 papers (a list of the data sources is given in Text S1.1 of Supporting Information Appendix S1), describing 40 different plant communities (Supporting Information Figure S1.1 and Data S1).

2.2 | Biodiversity and warming response metrics

The plant diversity was quantified by the effective number of species (ENS), which indicate the species richness of a perfectly even community with the same diversity index (Shannon's diversity index, SDI) as the original community (Jost, 2006):

$$ENS = e^{SDI} \quad (1)$$

where SDI is:

$$SDI = - \sum_{i=1}^{n} p_i \log p_i \quad (2)$$

where p_i is the biomass proportion of species i relative to the total community biomass. Species richness, SDI and ENS were all used to explore the relationship between plant diversity and the responses of plant biomass to warming, but the results reported here are mainly focused on ENS, because (a) ENS had a significant relationship with biomass responses, (b) the SDI can be transformed to ENS and (c) ENS as a measure of biodiversity is least affected by the rarity or the commonness of species present within a community (Jost, 2006). Essentially, the results based

on ENS are consistent with those based on SDI, because ENS is a monotonic function of SDI (Equation 1). We are aware that species richness is commonly used as the diversity index in other studies (e.g., Hautier et al., 2015; Isbell et al., 2015). As long as the variation in community evenness is constrained within a small range (which was the case for most of the studied biodiversity manipulative experiments), results based on ENS do not largely deviate from those based on richness. For situations with large variation in community evenness (Supporting Information Figure S1.2), ENS might be a more effective measure of biodiversity, probably because one or two species might still be dominant in a community despite the high level of richness (Grime, 1998).

To investigate the warming-induced changes in community composition, the Simpson's dominance index was used to indicate the contribution of dominant species to the total biomass (Smith & Wilson, 1996):

$$Dominance = - \sum_{i=1}^{n} p_i^2 \quad (3)$$

Higher dominance means that an ecosystem is largely composed of a few dominant species, implying lower community evenness. Note that a few studies reported the SDI but not the biomass of every species, which reduced the plant communities to 27 when the analysis involved the dominance.

The response of each variable to experimental warming was quantified by the natural logarithm of the response ratio (lnRR; Hedges et al., 1999):

$$lnRR = \ln\left(\frac{\overline{X}_t}{\overline{X}_c}\right) = \log(\overline{X}_t) - \log(\overline{X}_c) \quad (4)$$

where $\overline{X}_t$ and $\overline{X}_c$ are the means of a certain variable in the warming and control groups, respectively. lnRR can be converted to the percentage change by

$$Percentage\ change = (e^{lnRR} - 1) \times 100\% \quad (5)$$

The lnRR was also an indicator of ecosystem resistance to warming, with values close to zero indicating high resistance (implying weak response to warming). Therefore, the plant diversity showed a stabilization effect on productivity if the lnRR was closer to zero, whereas it exerted a destabilization effect if the lnRR was more positive or negative. Note that all the biodiversity and warming response metrics refer to the average values aggregated from experiment replicates.

2.3 | Generalized additive mixed-effects model

The overall responses of plant diversity (ENS) and (community) aboveground biomass (AGB), the relationships between AGB, ENS and their responses to warming were examined by a generalized

additive mixed-effects model (GAMM). Generalized additive mixed-effects modelling is a technique combining generalized additive and linear mixed-effects modelling into a single statistical framework, which can flexibly simulate nonlinear patterns and incorporate random effects (Zuur et al., 2009). Community ID (experiments conducted in the same community shared the same community ID) was considered as a random effect while other explanatory variables (e.g. warming and diversity) were used as fixed effects. As an example, the R code of the GAMM model (the R package details are provided in the Software section below) for the relationship between the AGB response and plant diversity was:

$$mod < - gamm(AGB\_yi \sim s(ENS), \; random = list(CommunityID = \sim 1),$$
$$data = Data) \tag{6}$$

where AGB_yi is the AGB response and s() is the smoother of the GAMM. The marginal r^2, which is the proportion of variance explained by the fixed effects, was used to indicate the predictive power of the explanatory variables. The total predictive power of both fixed and random effects was represented by the conditional r^2. The normality assumption of model residuals was tested by the Shapiro–Wilk test. The variance homogeneity assumption of model residuals was tested by Fligner–Killeen tests between low- and high-diversity communities. p values larger than .05 indicate no violation of normality or homogeneity assumptions.

2.4 | Relative importance of multiple factors

Besides plant diversity effects, we also examined the effects of other confounding factors such as site-specific climatic characteristics (e.g., temperature, precipitation and aridity) and warming conditions used in the experiments (e.g., warming facility, magnitude and duration) to better understand the variation in AGB responses to warming (Lu et al., 2013; Shao et al., 2019). Moreover, the plant diversity was measured based on different plot sizes among study sites. As the sampled species may increase with sampling area at small spatial scales (Connor & McCoy, 1979), the plot size was also considered as a potential covariate in order to account for the imperfect estimate of plant diversity. As there was no nonlinear pattern observed based on GAMM results for the separated low- and high-diversity communities, linear mixed-effects models (LMMs) were conducted to investigate the relative importance of potential factors (including plant diversity) in explaining AGB responses to warming. Because of the insufficient data, we were unable to conduct a multiple LMM with all the explanatory variables. Therefore, to avoid the overfitting problem, a two-step approach was applied. In the first step, the relationship between lnRR(AGB) and each variable was investigated separately by simple LMMs. The result suggested that only the ENS, the lnRR(ENS) and the (ΔT) were significantly related to lnRR(AGB). In the second step, a multiple LMM was conducted with ENS, lnRR(ENS) and ΔT as three explanatory variables. The difference in the marginal

r^2 between multiple LMMs with and without a given variable was considered as the partial r^2, which quantified the relative importance of that variable (Hu et al., 2018). Similar to the GAMMs, the normality and homogeneity assumptions were tested for simple and multiple LMMs. In simple LMMs, the homogeneity test was conducted by applying the Fligner–Killeen test between groups with low and high values of corresponding explanatory variables. In multiple LMMs, the Fligner–Killeen test was applied between groups with low and high fitted values. These low and high value groups were determined by the median. The variance inflation factor (VIF) was also calculated in the multiple LMMs in order to examine multicollinearity among the explanatory variables.

2.5 | Direct and indirect effects on warming responses

To further investigate the direct and indirect effects of ΔT, ENS, lnRR(ENS) and lnRR(Dominance) on lnRR(AGB), we used a multiple group structural equation model (SEM; Shipley, 2004). The AGB response was linked to warming magnitude, diversity, and the dominance response. The dominance response was regulated by diversity and warming magnitude, while the diversity response was regulated by warming magnitude and the dominance response. The covariation between the diversity response and the AGB response was also included in the SEMs. The maximum likelihood method was used to obtain the SEM results. A χ^2 test was used to examine if the hypothesized SEM was rejected by the data. The standardized path coefficient (ρ, the path coefficient when all the variables were standardized), which is analogous to the correlation coefficient, was used to quantify the effect size of one variable on another. To test whether causal relationships were comparable between ENS < 10 and ENS > 10 (these two categories of diversity levels emerged in our GAMM, details in Section 3.1), two multiple group SEMs were used. The ρ of a concerned relationship was set to be different between groups for the first SEM and be the same for the second SEM. If the difference between the Akaike information criterion (AIC) values of the two SEMs was smaller than 2, the SEM with the same ρ was considered as a better model. Residual correlation matrices were calculated to examine if the interrelationships between different variables were appropriately explained by the SEM.

2.6 | Software

All the analyses were conducted in the R software environment (version 3.2.1, R Core Team, 2015). The LMMs, GAMMs, and the calculation of their test-statistics and fit to data were conducted with the R packages *lme4* (Bates et al., 2015), *mgcv* (Wood, 2004), *lmerTest* (Kuznetsova et al., 2017), *MuMIn* (Bartoń, 2020), respectively. We ran the SEMs with the *lavaan* package (Rosseel, 2012).

3 | RESULTS

3.1 | Responses of plant diversity and aboveground biomass to warming

The responses of biodiversity to warming were −3.6% [the 95% confidence interval (CI) was −43.3% to 13.4%, the percentage change was based on Equation 5], −5.0% (CI: −27.2% to 16.9%) and −8.3% (CI: −48.3% to 31.5%) for species richness, SDI and ENS, respectively (Figure 1). The response of AGB to warming was 2.6% (CI: −23.6% to 82.7%, Figure 1a). The AGB response to warming was not correlated to species richness but showed hump-shaped relationships with both SDI and ENS according to the GAMMs (Figure 2). Because the studied communities appeared to be divided naturally along the ENS axis into two clusters (Figure 2a,b), we classified them as either low- (ENS < 10) or high-diversity plant communities (ENS > 10).

When the dataset was analysed for low- and high-diversity plant communities separately, GAMM results suggested that the degrees of freedom (df) value of the smoother was close to 1, indicating linear models were sufficient to describe the pattern. Therefore, LMMs were applied and the results showed that with the increase in ENS, the warming effects on AGB dramatically increased in low-diversity grasslands (marginal $r^2 = .47$, conditional $r^2 = .62$, $p = .002$), but decreased in high-diversity grasslands (marginal $r^2 = .38$, conditional $r^2 = .38$, $p = .004$, Figure 2b).

3.2 | Influence of other factors

Overall, factors other than plant diversity had little influence on the AGB responses to warming (Supporting Information Table S1.1). According to simple LMMs, ENS explained much larger variance in

AGB response of low-diversity ecosystems than other climatic and experimental factors did (Figure 3a). In high-diversity plant communities, ENS, response of ENS to warming and warming magnitude were significantly related to the AGB response while other factors were not (Figure 3b).

To further quantify the relative contributions of ENS, the response of ENS and warming magnitude to explaining the variation in AGB responses to warming, multiple LMMs were applied. The results highlighted the importance of ENS in low-diversity plant communities (partial $r^2 = .325$, $p = .011$, Table 1). In high-diversity plant communities, however, all three of the factors were significant, although again the ENS response was the most important one (partial $r^2 = .428$, $p < .001$), followed by warming magnitude (partial $r^2 = .119$, $p = .004$) and ENS (partial $r^2 = .055$, $p = .036$, Table 1). We did not find any violation of normality or homogeneity assumptions for the simple or multiple LMMs used in our analyses, except for the simple LMM relationships between lnRR(AGB) and 'Facility', as well as among warming magnitude, MAT and MAP; both were only presented in high-diversity communities (Supporting Information Table S1.2). The VIFs were 1.00, 1.06 and 1.06 for ENS, lnRR(ENS) and ΔT, respectively, in the multiple LMM for low-diversity communities, and the values were 1.45, 1.08 and 1.37 for high-diversity communities, suggesting no multicollinearity in our mixed models.

3.3 | Direct and indirect effects of multiple factors

Multiple group structural equation modelling showed that in low-diversity plant communities (ENS < 10), the plant diversity directly regulated the AGB response (path coefficient $\rho = .63$, $p < .001$, Figure 4a). Warming magnitude strongly regulated the plant
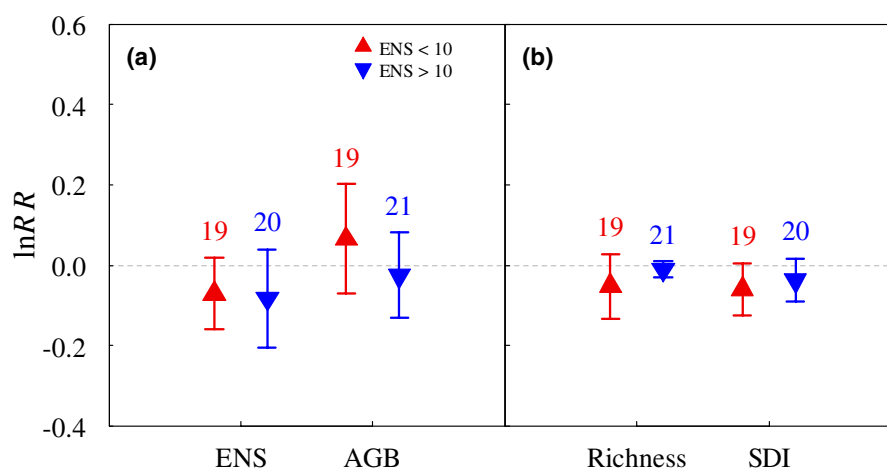

FIGURE 1 Summary of the responses of plant diversity and aboveground biomass (AGB) to warming. (a) Responses of effective number of species (ENS) and AGB to warming in low- (ENS < 10) and high-diversity (ENS > 10) communities. (b) Responses of species richness and Shannon's diversity index (SDI) to warming. Error bars represent the 95% confidence intervals (CIs) derived from the linear random effects models. Numbers above the error bars are the sample sizes. In high-diversity communities, the sample size for ENS and SDI (20) is smaller than that for AGB and richness (21) because there was no report of ENS or SDI change in one community. lnRR, natural logarithm of the response ratio

FIGURE 2 Relationship between biodiversity and responses of aboveground biomass (AGB) to warming. (a) Relationship between effective number of species (ENS) and the natural logarithm of the response ratio of AGB [lnRR(AGB)] in low- and high-diversity communities. The regression line is based on the generalized additive mixed-effect model (GAMM). Conditional $r^2 = .65$. (b) The same as (a) but the regression lines are derived from separate linear mixed-effects models (LMMs). The conditional r^2 was .62 and .38 for low- and high-diversity communities, respectively. (c) Relationship between richness and lnRR(AGB). No significant relationship was found. (d) Relationship between Shannon's diversity index (SDI) and lnRR(AGB). The regression line is based on the GAMM. Conditional $r^2 = .71$. Black, red and blue dashed lines indicate the 95% confidence intervals (CIs). *$p < .05$
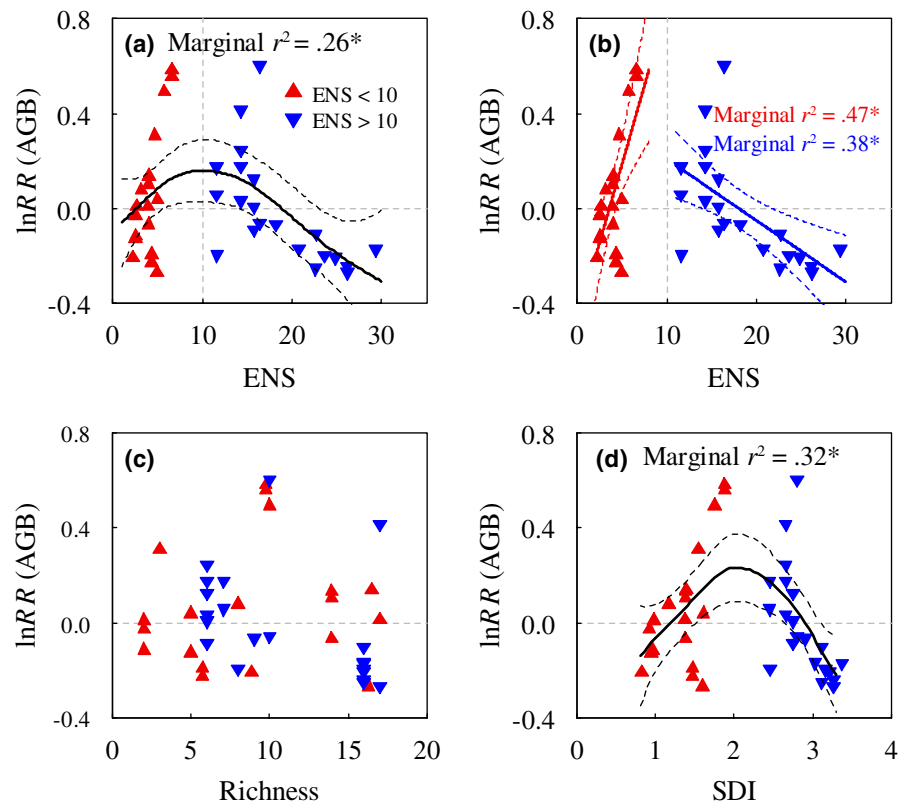
dominance responses ($\rho = .56$, $p = .002$), which in turn, negatively affected the diversity responses ($\rho = -.44$, $p = .001$) and positively affected the AGB response to warming ($\rho = .24$, $p = .036$). Overall, our model explained 36%, 22% and 53% of the variance in the responses of community dominance, diversity and AGB, respectively.

In high-diversity grasslands (ENS > 10), the diversity did not affect the AGB response directly but indirectly via decreasing the dominance response ($\rho = -.42$, $p = .017$, Figure 4b). The plant dominance was relatively stable as warming magnitude did not have any significant effects on it ($\rho = -.19$, $p = .274$). AGB response was directly regulated by warming magnitude ($\rho = -.44$, $p = .001$) in contrast to indirect warming effects in low-diversity grasslands. A negative correlation was found between responses of diversity and AGB ($\rho = -.41$, $p = .002$). Overall, the SEM explained 25%, 20% and 42% of the variance in the responses of community dominance, diversity and AGB, respectively. The residual correlation matrices of the SEMs in low- and high-diversity communities indicated the SEMs appropriately represented the interrelationship among different variables (Supporting Information Tables S1.3 and S1.4).

4 | DISCUSSION

Climate warming can have profound effects on both biodiversity and ecosystem functions (Lu et al., 2013; Rustad et al., 2001; Trisos et al., 2020). But how the responses of biodiversity and ecosystem functions to warming are linked, and what mechanisms underlie this

relationship remain unclear (De Laender et al., 2016). Indeed, the responses of ecosystem functions to warming can be influenced by a number of factors, such as climatic conditions, biodiversity levels and even the experimental design (Liu et al., 2018; Lu et al., 2013). Our meta-analysis suggests that the level of plant diversity itself and how the plant diversity respond to warming collectively determine grassland AGB responses to experimental warming (Figure 3 and Table 1). Specifically, diversity nonlinearly regulated the AGB responses to warming, with a positive effect in low-diversity communities (ENS < 10) and a negative effect in high-diversity ones (ENS > 10) (Figure 2a,b). Moreover, our results suggest the importance of shifts in plant dominance due to warming (or a lack of it) in determining how warming may affect plant biomass in grasslands (Figure 4).

Several possible mechanisms can be suggested for the increasing AGB responses to warming in low-diversity plant communities. First, the selection effect might make the presence likelihood of species with strong responses increase with plant diversity (Tilman et al., 2014). Second, the gradual addition of species to low-diversity communities will likely enhance the niche hypervolume and improve resource acquisition, and thereby an overall efficient utilization of resources for the whole plant community (Liang et al., 2015; Tilman et al., 2001). As a result, the enriched nutrient availability due to warming (Bai et al., 2013) could increase the complementarity effect with increasing plant diversity (van Zuidam et al., 2019). Third, increases in plant diversity could enhance the biomass responses to warming through increases in soil moisture (Cowles et al., 2016).

The increasing AGB will eventually induce a stabilizing effect called the 'overyielding effect', that is, the enhanced total biomass will reduce the strength of demographic stochasticity (Tilman, 1999). We suspect that if the increase in plant diversity consistently reduces the demographic stochasticity, it could eventually partly contribute to the decreasing AGB responses in plant communities with ENS lower than 20 (Figure 2a,b). Moreover, the stabilizing pattern might
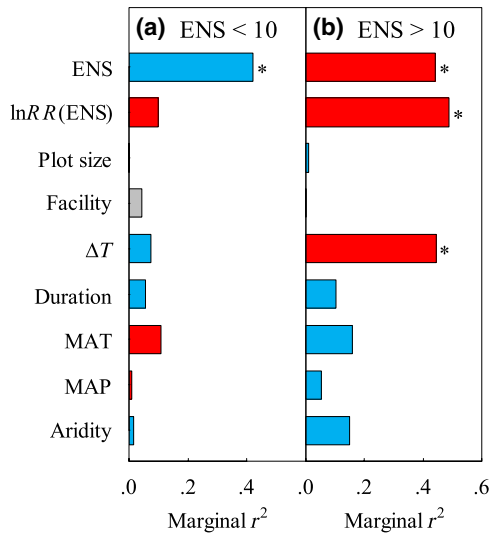
also be derived from the insurance effect, that is, the synchrony in species responses to warming may decrease at high plant diversity (Loreau & de Mazancourt, 2013; Yachi & Loreau, 1999).

However, our speculations concerning the overyielding and insurance effects do not apply to the results when ENS was larger than *c.* 20, where we observed a destabilizing pattern in plant biomass (i.e., stronger negative biomass response to warming: Figure 2a,b). We suspect that this finding may be related to interspecific competition in high-diversity plots. While interspecific competition has traditionally been treated as a stabilizing factor within diverse plant communities, recent studies indicate that it can decrease the community temporal stability by increasing the variability of individual species responses (de Mazancourt et al., 2013; Loreau & de Mazancourt, 2008, 2013). Therefore, we suspect that, in communities with ENS larger than 20, species with small population sizes were potentially more vulnerable to environmental perturbations, eventually decreasing the resistance of such plant communities (in terms of biomass production) to warming (Loreau & de Mazancourt, 2013).

The structural equation modelling showed that plant diversity can indirectly regulate AGB responses through the variation in community dominance in high- but not in low-diversity communities (Figure 4). Warming-induced shifts in plant dominance may depend on species-specific responses to higher temperatures. Indeed, we cannot conclude if dominance-driven biomass responses in high-diversity communities could be entirely independent of shifts in species interactions, given that interspecific interactions can determine both overyielding and insurance effects (Loreau et al., 2021). Moreover, the exhausted soil resources and increased water stress due to high transpiration (Paquette et al., 2018) could intensify the interspecific competition and thereby destabilizing the community biomass, at least when the ENS > *c.* 20 (Figure 2a,b).

There are several uncertainties around the main finding of our study. First, in the context of nutrient enrichment, it has been reported that the increase of nutrient availability can initially enhance plant biomass and reduce plant diversity, but the loss of diversity over time eventually can diminish the positive effect of nutrient enrichment on biomass (Isbell et al., 2013). We still know little about whether such a temporally dependent relationship exists for climate warming effects on plant diversity and productivity given the

FIGURE 3 Importance of biodiversity, experimental design and climate to the variance in the natural logarithm of the response ratio of aboveground biomass [lnRR(AGB)] in low- (a) and high-diversity (b) plant communities. The importance was quantified by the marginal r^2 of linear mixed effects models with lnRR(AGB) as the response variable and biodiversity measures, experimental duration and climatic factors as the explanatory variables. The blue and red bars indicate positive and negative effects, respectively. Note that grey bars are drawn for only facility, because it is a categorical factor. ENS, effective number of species; Plot size, size of the experimental plot; Facility, warming facility (active or passive); ΔT, warming magnitude; Duration, experimental duration (days); MAT, mean annual temperature; MAP, mean annual precipitation; Aridity, aridity index as the ratio between precipitation and potential evapotranspiration. *$p < .05$

	ENS < 10			ENS > 10		
	Coefficient	95% CI	r^2	Coefficient	95% CI	r^2
Fixed						
ΔT	.051	[−.039, .142]	.049	−.086	[−.131, −.040]	.119
ENS	.164	[.063, .264]	.325	−.051	[−.094, −.009]	.055
lnRR(ENS)	−.017	[−.111, .076]	.000	−.111	[−.146, −.075]	.428
Total			.428			.853
Random			.257			.067
Total			.685			.920

TABLE 1 Standardized coefficients, 95% confidence intervals (CIs) and partial r^2 of multiple linear mixed-effects models for responses of aboveground biomass to warming. r^2 of each fixed factor represents the relative contribution after controlling the other variables

Abbreviations: ENS, effective number of species; lnRR, natural logarithm of the response ratio; ΔT, warming magnitude.
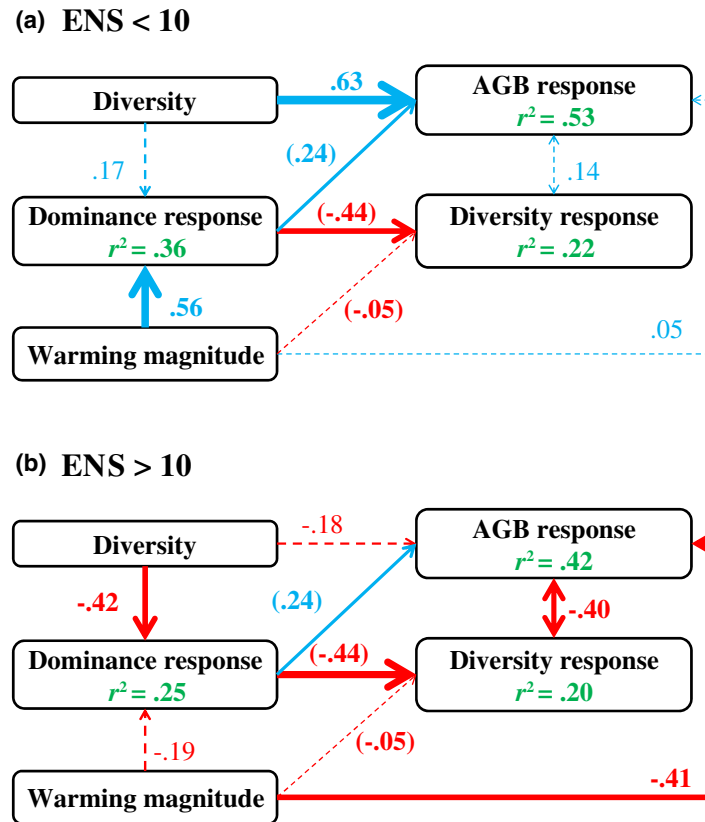
(a) ENS < 10

(b) ENS > 10

FIGURE 4 The direct and indirect effects of diversity, community dominance and warming magnitude on warming-induced changes in aboveground biomass (AGB) in low- (a) and high-diversity communities (b). The results are based on the multiple group structural equation model ($df = 11$, $\chi^2 = 10.45$, $p = .491$, CFI (comparative fit index) = 1.00, RMSEA (root mean square error of approximation) = 0.00). Single arrows are causal relationships while double arrows represent covarying ones. Blue and red lines represent positive and negative relationships, respectively, while solid and dashed lines indicate significant ($p < .05$) and non-significant ($p > .05$) relationships, respectively. The thickness of the arrows is proportional to the magnitude of the relationships. The values beside the arrows are the standardized path coefficients, which represent the effect size of one variable on another. Parentheses around a path coefficient indicate that there was no difference between low- and high-diversity communities according to the Akaike information criterion

paucity of long-term warming studies. In some systems, the plant diversity was shown to be resistant to warming in the first several years, but changed in the later years (Shi et al., 2015). A long-term experiment (it ran for 18 years) showed that the plant diversity in warmed plots was comparable to that in ambient temperature plots but with different community composition (Zhang et al., 2017). Therefore, although both our study and an earlier meta-analysis (Gruner et al., 2017) indicated non-significant effects of experimental duration on the responses of diversity or biomass to warming (Supporting Information Table S1.1), we cannot rule out the possibility of temporal dependency of warming effects on plant diversity or plant biomass production, given that temporal effects of plant diversity themselves can affect diversity–productivity relationships through several biotic processes (Thakur et al., 2021).

Second, the grasslands included in this study had an ENS up to 30, which is in general lower than the species richness in many natural grasslands, especially in tropical areas where species richness can be more than 70 per 100–1,000 m² (Faber-Langendoen & Josse, 2010). Given the recent insights about the varying role

of interspecific competition in (de)stabilizing ecosystem functions (de Mazancourt et al., 2013; Loreau & de Mazancourt, 2008, 2013), we encourage future studies to examine how the role of interspecific competition may vary among grasslands that are highly species-rich versus ones that are moderately rich (as in our study). Moreover, we need studies with a longer gradient of biodiversity especially in tropical areas, along with a sophisticated experimental design consisting of additional monocultures of each plant species, in order to disentangle and quantify the exact contribution of interspecific competition to ecosystem functioning under climate change.

Finally, we also caution readers that owing to the limited sample size (40 plant communities from 20 studies) and the uneven distribution of warming experiments (only one experiment each in Australia and Antarctica), our main results are premature for any generalization at the global scale. Despite the hundreds of manipulative warming experiments that have examined plant productivity responses to warming across the world (Song et al., 2019), many of these experiments do not report the productivity (or biomass) of every plant

species, which subsequently prevented us from conducting any detailed analyses on stabilization effects of plant diversity on productivity in warming experiments. Nevertheless, the nonlinear diversity effect and corresponding mechanisms (e.g., shifts in dominant plant species in response to warming and diversity) found in this study provide a potential explanation for the diversity–ecosystem function relationships obverved in warmer environments (Ammer, 2019; Paquette et al., 2018).

The paramount importance of biodiversity in regulating ecosystem functions under climate change found in our and other studies (Hautier et al., 2015; Hooper et al., 2012; Liu et al., 2018; Thakur et al., 2015) highlights the necessity of incorporating diversity effects into current ecosystem models for predicting ecosystem functions in a changing world (Grace et al., 2016). Climate warming generally causes species loss, which has been shown to threaten the provisioning of various ecosystem functions (Harrison, 2020; Klein et al., 2004). The link between biodiversity and ecosystem functions in responses to warming could in fact depend on biodiversity itself, at least across grasslands. The nonlinear diversity effect found in this study could very well depend on how underlying biotic and abiotic mechanisms differ between low (less than ENS *c.* 10 in our study) and high (higher than ENS *c.* 10 in our study) diversity grassland systems. We have speculated that mechanisms involving species interactions through shifts in plant dominance might become relatively more important in grasslands, which will need both theoretical and experimental scrutiny in future studies. We therefore encourage the incorporation of both plant diversity and dynamics of species interactions as two crucial biotic factors to help improve predictions of warming effects on grassland productivity and stability.

ACKNOWLEDGMENTS

AUTHOR CONTRIBUTIONS

J.S. and X.Z. conceived the study and analysed the data. H.Z., J.X. and M.L. compiled the dataset. J.S., X.Z. and M.P.T. led the writing with contributions from all the authors.

DATA AVAILABILITY STATEMENT

Data are available via the Dryad Digital Repository: https://doi.org/10.5061/dryad.gtht76hms.

ORCID

Xuhui Zhou https://orcid.org/0000-0002-2038-9901

Kees Jan van Groenigen https://orcid.org/0000-0002-9165-3925

Guiyao Zhou https://orcid.org/0000-0002-1385-3913

Jianyang Xia https://orcid.org/0000-0001-5923-6665

Madhav P. Thakur https://orcid.org/0000-0001-9426-1313

REFERENCES

Altizer, S., Ostfeld, R. S., Johnson, P. T. J., Kutz, S., & Harvell, C. D. (2013). Climate change and infectious diseases: From evidence to a predictive framework. *Science*, 341, 514–519. https://doi.org/10.1126/science.1239401

Ammer, C. (2019). Diversity and forest productivity in a changing climate. *New Phytologist*, 221, 50–66. https://doi.org/10.1111/nph.15263

Bai, E., Li, S., Xu, W., Li, W., Dai, W., & Jiang, P. (2013). A meta-analysis of experimental warming effects on terrestrial nitrogen pools and dynamics. *New Phytologist*, 199, 441–451. https://doi.org/10.1111/nph.12252

Bartoń, K. (2020). MuMIn: Multi-model inference. R package version 1.43.17. https://CRAN.R-project.org/package=MuMIn

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

Connor, E. F., & McCoy, E. D. (1979). The statistics and biology of the species-area relationship. *The American Naturalist*, 113, 791–833. https://doi.org/10.1086/283438

Cowles, J. M., Wragg, P. D., Wright, A. J., Powers, J. S., & Tilman, D. (2016). Shifting grassland plant community structure drives positive interactive effects of warming and diversity on aboveground net primary productivity. *Global Change Biology*, 22, 741–749. https://doi.org/10.1111/gcb.13111

De Laender, F., Rohr, J. R., Ashauer, R., Baird, D. J., Berger, U., Eisenhauer, N., Grimm, V., Hommen, U., Maltby, L., Meliàn, C. J., Pomati, F., Roessink, I., Radchuk, V., & Van den Brink, P. J. (2016). Reintroducing environmental change drivers in biodiversity–ecosystem functioning research. *Trends in Ecology and Evolution*, 31, 905–915. https://doi.org/10.1016/j.tree.2016.09.007

de Mazancourt, C., Isbell, F., Larocque, A., Berendse, F., De Luca, E., Grace, J. B., Haegeman, B., Wayne Polley, H., Roscher, C., Schmid, B., Tilman, D., van Ruijven, J., Weigelt, A., Wilsey, B. J., & Loreau, M. (2013). Predicting ecosystem stability from community composition and biodiversity. *Ecology Letters*, 16, 617–625. https://doi.org/10.1111/ele.12088

Faber-Langendoen, D., & Josse, C. (2010). World grasslands and biodiversity patterns. NatureServe. + Appendices. https://www.natureserve.org/biodiversity-science/publications/world-grasslands-and-biodiversity-patterns

Grace, J. B., Anderson, T. M., Seabloom, E. W., Borer, E. T., Adler, P. B., Harpole, W. S., Hautier, Y., Hillebrand, H., Lind, E. M., Pärtel, M., Bakker, J. D., Buckley, Y. M., Crawley, M. J., Damschen, E. I., Davies, K. F., Fay, P. A., Firn, J., Gruner, D. S., Hector, A., … Smith, M. D. (2016). Integrative modelling reveals mechanisms linking productivity and plant species richness. *Nature*, 529, 390–393. https://doi.org/10.1038/nature16524

Grime, J. P. (1998). Benefits of plant diversity to ecosystems: Immediate, filter and founder effects. *Journal of Ecology*, 86, 902–910. https://doi.org/10.1046/j.1365-2745.1998.00306.x

Gruner, D. S., Bracken, M. E. S., Berger, S. A., Eriksson, B. K., Gamfeldt, L., Matthiessen, B., Moorthi, S., Sommer, U., & Hillebrand, H. (2017). Effects of experimental warming on biodiversity depend on ecosystem type and local species composition. *Oikos*, 126, 8–17. https://doi.org/10.1111/oik.03688

Harrison, S. (2020). Plant community diversity will decline more than increase under climatic warming. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 375, 20190106.

Hautier, Y., Tilman, D., Isbell, F., Seabloom, E. W., Borer, E. T., & Reich, P. B. (2015). Anthropogenic environmental changes affect ecosystem stability via biodiversity. *Science*, 348, 336–340. https://doi.org/10.1126/science.aaa1788

Hector, A., Hautier, Y., Saner, P., Wacker, L., Bagchi, R., Joshi, J., Scherer-Lorenzen, M., Spehn, E. M., Bazeley-White, E., Weilenmann, M., Caldeira, M. C., Dimitrakopoulos, P. G., Finn, J. A., Huss-Danell,

K., Jumpponen, A., Mulder, C. P. H., Palmborg, C., Pereira, J. S., Siamantziouras, A. S. D., ... Loreau, M. (2010). General stabilizing effects of plant diversity on grassland productivity through population asynchrony and overyielding. *Ecology*, 91, 2213–2220. https://doi.org/10.1890/09-1162.1

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

Hooper, D. U., Adair, E. C., Cardinale, B. J., Byrnes, J. E. K., Hungate, B. A., Matulich, K. L., Gonzalez, A., Duffy, J. E., Gamfeldt, L., & O'Connor, M. I. (2012). A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature*, 486, 105–108. https://doi.org/10.1038/nature11118

Hu, Z., Michaletz, S. T., Johnson, D. J., McDowell, N. G., Huang, Z., Zhou, X., & Xu, C. (2018). Traits drive global wood decomposition rates more than climate. *Global Change Biology*, 24, 5259–5269. https://doi.org/10.1111/gcb.14357

Isbell, F., Craven, D., Connolly, J., Loreau, M., Schmid, B., Beierkuhnlein, C., Bezemer, T. M., Bonin, C., Bruelheide, H., de Luca, E., Ebeling, A., Griffin, J. N., Guo, Q., Hautier, Y., Hector, A., Jentsch, A., Kreyling, J., Lanta, V., Manning, P., ... Eisenhauer, N. (2015). Biodiversity increases the resistance of ecosystem productivity to climate extremes. *Nature*, 526, 574–577. https://doi.org/10.1038/nature15374

Isbell, F., Reich, P. B., Tilman, D., Hobbie, S. E., Polasky, S., & Binder, S. (2013). Nutrient enrichment, biodiversity loss, and consequent declines in ecosystem productivity. *Proceedings of the National Academy of Sciences USA*, 110, 11911–11916. https://doi.org/10.1073/pnas.1310880110

Jost, L. (2006). Entropy and diversity. *Oikos*, 113, 363–375.

Klein, J. A., Harte, J., & Zhao, X.-Q. (2004). Experimental warming causes large and rapid species loss, dampened by simulated grazing, on the Tibetan Plateau. *Ecology Letters*, 7, 1170–1179. https://doi.org/10.1111/j.1461-0248.2004.00677.x

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest package: Tests in linear mixed effects models. *Journal of Statistical Software*, 82, 1–26.

Liang, J., Zhou, M., Tobin, P. C., McGuire, A. D., & Reich, P. B. (2015). Biodiversity influences plant productivity through niche–efficiency. *Proceedings of the National Academy of Sciences USA*, 112, 5738–5743. https://doi.org/10.1073/pnas.1409853112

Liu, H., Mi, Z., Lin, L. I., Wang, Y., Zhang, Z., Zhang, F., Wang, H., Liu, L., Zhu, B., Cao, G., Zhao, X., Sanders, N. J., Classen, A. T., Reich, P. B., & He, J.-S. (2018). Shifting plant species composition in response to climate change stabilizes grassland primary production. *Proceedings of the National Academy of Sciences USA*, 115, 4051–4056. https://doi.org/10.1073/pnas.1700299114

Loreau, M., Barbier, M., Filotas, E., Gravel, D., Isbell, F., Miller, S. J., Montoya, J. M., Wang, S., Aussenac, R., Germain, R., Thompson, P. L., Gonzalez, A., & Dee, L. E. (2021). Biodiversity as insurance: From concept to measurement and application. *Biological Reviews*, 96(5), 2333–2354. https://doi.org/10.1111/brv.12756

Loreau, M., & de Mazancourt, C. (2008). Species synchrony and its drivers: Neutral and nonneutral community dynamics in fluctuating environments. *The American Naturalist*, 172, E48–E66. https://doi.org/10.1086/589746

Loreau, M., & de Mazancourt, C. (2013). Biodiversity and ecosystem stability: A synthesis of underlying mechanisms. *Ecology Letters*, 16, 106–115. https://doi.org/10.1111/ele.12073

Lu, M., Zhou, X., Yang, Q., Li, H., Luo, Y., Fang, C., Chen, J., Yang, X., & Li, B. O. (2013). Responses of ecosystem carbon cycle to experimental warming: A meta-analysis. *Ecology*, 94, 726–738. https://doi.org/10.1890/12-0279.1

Mokany, K., Ferrier, S., Connolly, S. R., Dunstan, P. K., Fulton, E. A., Harfoot, M. B., Harwood, T. D., Richardson, A. J., Roxburgh, S. H., Scharlemann, J. P. W., Tittensor, D. P., Westcott, D. A., & Wintle, B. A. (2016). Integrating modelling of biodiversity composition and ecosystem function. *Oikos*, 125, 10–19. https://doi.org/10.1111/oik.02792

Paquette, A., Vayreda, J., Coll, L., Messier, C., & Retana, J. (2018). Climate change could negate positive tree diversity effects on forest productivity: A study across five climate types in Spain and Canada. *Ecosystems*, 21, 960–970. https://doi.org/10.1007/s10021-017-0196-y

Pennekamp, F., Pontarp, M., Tabi, A., Altermatt, F., Alther, R., Choffat, Y., Fronhofer, E. A., Ganesanandamoorthy, P., Garnier, A., Griffiths, J. I., Greene, S., Horgan, K., Massie, T. M., Mächler, E., Palamara, G. M., Seymour, M., & Petchey, O. L. (2018). Biodiversity increases and decreases ecosystem stability. *Nature*, 563, 109–112. https://doi.org/10.1038/s41586-018-0627-8

Pfisterer, A. B., & Schmid, B. (2002). Diversity-dependent production can decrease the stability of ecosystem functioning. *Nature*, 416, 84–86. https://doi.org/10.1038/416084a

R Core Team. (2015). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Rosseel, Y. (2012). lavaan: An R package for structural equation modeling. *Journal of Statistical Software*, 48, 1–36.

Rustad, L., Campbell, J., Marion, G., Norby, R., Mitchell, M., Hartley, A., Cornelissen, J., Gurevitch, J., & GCTE-NEWS. (2001). A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia*, 126, 543–562. https://doi.org/10.1007/s004420000544

Shao, J., Yuan, T., Li, Z., Li, N., Liu, H., Bai, S. H., Xia, J., Lu, M., & Zhou, X. (2019). Plant evolutionary history mainly explains the variance in biomass responses to climate warming at a global scale. *New Phytologist*, 222, 1338–1351. https://doi.org/10.1111/nph.15695

Shi, Z., Sherry, R., Xu, X., Hararuk, O., Souza, L., Jiang, L., Xia, J., Liang, J., & Luo, Y. (2015). Evidence for long-term shift in plant community composition under decadal experimental warming. *Journal of Ecology*, 103, 1131–1140. https://doi.org/10.1111/1365-2745.12449

Shipley, B. (2004). *Cause and correlation in biology: A user's guide to path analysis, structural equations and causal inference*. Cambridge University Press.

Smith, B., & Wilson, J. B. (1996). A consumer's guide to evenness indices. *Oikos*, 76, 70–82. https://doi.org/10.2307/3545749

Song, J., Wan, S., Piao, S., Knapp, A. K., Classen, A. T., Vicca, S., Ciais, P., Hovenden, M. J., Leuzinger, S., Beier, C., Kardol, P., Xia, J., Liu, Q., Ru, J., Zhou, Z., Luo, Y., Guo, D., Adam Langley, J., Zscheischler, J., ... Zheng, M. (2019). A meta-analysis of 1,119 manipulative experiments on terrestrial carbon-cycling responses to global change. *Nature Ecology and Evolution*, 3, 1309–1320. https://doi.org/10.1038/s41559-019-0958-3

Thakur, M. P., Milcu, A., Manning, P., Niklaus, P. A., Roscher, C., Power, S., Reich, P. B., Scheu, S., Tilman, D., Ai, F., Guo, H., Ji, R., Pierce, S., Ramirez, N. G., Richter, A. N., Steinauer, K., Strecker, T., Vogel, A., & Eisenhauer, N. (2015). Plant diversity drives soil microbial biomass carbon in grasslands irrespective of global environmental change factors. *Global Change Biology*, 21, 4076–4085. https://doi.org/10.1111/gcb.13011

Thakur, M. P., van der Putten, W. H., Wilschut, R. A., Veen, G. F. (C.), Kardol, P., van Ruijven, J., Allan, E., Roscher, C., van Kleunen, M., & Bezemer, T. M. (2021). Plant–soil feedbacks and temporal dynamics of plant diversity–productivity relationships. *Trends in Ecology and Evolution*, 36, 651–661. https://doi.org/10.1016/j.tree.2021.03.011

Tilman, D. (1996). Biodiversity: Population versus ecosystem stability. *Ecology*, 77, 350–363. https://doi.org/10.2307/2265614

Tilman, D. (1999). The ecological consequences of changes in biodiversity: A search for general principles. *Ecology*, 80, 1455–1474. https://doi.org/10.2307/176540

Tilman, D., Isbell, F., & Cowles, J. M. (2014). Biodiversity and ecosystem functioning. *Annual Review of Ecology, Evolution, and Systematics, 45*, 471–493. https://doi.org/10.1146/annurev-ecolsys-120213-091917

Tilman, D., Reich, P. B., Knops, J., Wedin, D., Mielke, T., & Lehman, C. (2001). Diversity and productivity in a long-term grassland experiment. *Science, 294*, 843–845. https://doi.org/10.1126/science.1060391

Trisos, C. H., Merow, C., & Pigot, A. L. (2020). The projected timing of abrupt ecological disruption from climate change. *Nature, 580*, 496–501. https://doi.org/10.1038/s41586-020-2189-9

van Zuidam, J. P., Leeuwen, C. H. A., Bakker, E. S., Verhoeven, J. T. A., Ijff, S., Peeters, E. T. H. M., Zuidam, B. G., & Soons, M. B. (2019). Plant functional diversity and nutrient availability can improve restoration of floating fens via facilitation, complementarity and selection effects. *Journal of Applied Ecology, 56*, 235–245. https://doi.org/10.1111/1365-2664.13256

Wagg, C., O'Brien, M. J., Vogel, A., Scherer-Lorenzen, M., Eisenhauer, N., Schmid, B., & Weigelt, A. (2017). Plant diversity maintains long-term ecosystem productivity under frequent drought by increasing short-term variation. *Ecology, 98*, 2952–2961. https://doi.org/10.1002/ecy.2003

Wang, C., Wang, Z., Zhang, X., Li, Y., Liu, J., & Han, G. (2014). Effect of warming on plant community composition and plant species diversity in the desert steppe. *Ecology and Environmental Sciences, 23*, 43–49.

Wittebolle, L., Marzorati, M., Clement, L., Balloi, A., Daffonchio, D., Heylen, K., De Vos, P., Verstraete, W., & Boon, N. (2009). Initial community evenness favours functionality under selective stress. *Nature, 458*, 623–626. https://doi.org/10.1038/nature07840

Wood, S. N. (2004). Stable and efficient multiple smoothing parameter estimation for generalized additive models. *Journal of the American Statistical Association, 99*, 673–686. https://doi.org/10.1198/016214504000000980

Yachi, S., & Loreau, M. (1999). Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis. *Proceedings of the National Academy of Sciences USA, 96*, 1463–1468. https://doi.org/10.1073/pnas.96.4.1463

Zhang, C., Willis, C. G., Klein, J. A., Ma, Z., Li, J., Zhou, H., & Zhao, X. (2017). Recovery of plant species diversity during long-term experimental warming of a species-rich alpine meadow community on the Qinghai-Tibet plateau. *Biological Conservation, 213*, 218–224. https://doi.org/10.1016/j.biocon.2017.07.019

Zhang, T., Guo, R., Gao, S., Guo, J., & Sun, W. (2015). Responses of plant community composition and biomass production to warming and nitrogen deposition in a temperate meadow ecosystem. *PLoS One, 10*, e0123160. https://doi.org/10.1371/journal.pone.0123160

Zhu, H., Zou, X., Wang, D., Wan, S., Wang, L., & Guo, J. (2015). Responses of community-level plant-insect interactions to climate warming in a meadow steppe. *Scientific Reports, 5*, 18654.

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. Springer.

BIOSKETCHES

Junjiong Shao, Xuhui Zhou, Lin Jiang, Fangliang He and Madhav P. Thakur are career scientists mainly interested in the effects of biodiversity on ecosystem functions.

Kees Jan van Groenigen, Guiyao Zhou, Lingyan Zhou, Meng Lu, Jianyang Xia, Bruce A. Hungate and **Yiqi Luo** are career scientists mainly interested in ecosystem carbon cycles.

Huimin Zhou is a student in Prof. Xuhui Zhou's research group.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Shao, J., Zhou X., van Groenigen K. J., Zhou G., Zhou H., Zhou L., Lu M., Xia J., Jiang L., Hungate B. A., Luo Y., He F., & Thakur M. P. (2022). Warming effects on grassland productivity depend on plant diversity. *Global Ecology and Biogeography*, 31, 588–598. https://doi.org/10.1111/geb.13441