

Research Article

Diversity and productivity of a natural grassland decline with the number of global change factors

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Abstract

Grasslands are highly diverse ecosystems providing important ecosystem services, but they currently face a variety of anthropogenic stressors simultaneously. Quantifying grassland responses to global change factors (GCFs) is crucial for developing effective strategies to mitigate the negative impacts of global change on grassland communities and to promote their resilience in the face of future environmental challenges. We conducted a field experiment in the Songnen grassland, northeastern China, to test the combined effects of 0, 1, 2, 4, 6 and 8 GCFs, including fungicide, herbicide, insecticide, antibiotic stress, heavy metal pollution, light pollution, microplastic pollution, nitrogen deposition, tillage disturbance and increased precipitation. We found that within one year, the increasing number of GCFs negatively impacts both the productivity and diversity of grassland communities. In comparison to exposure to a single GCF, exposure to 8 GCFs led to a reduction in productivity and species richness by 42.8% and 42.9%, respectively. Furthermore, these negative effects seem to be linked to the reduction of dominant species and the concurrent increase in neonative species (i.e., species that have expanded their geographic range into a new area without direct human assistance, but as an indirect consequence of human-induced environmental changes). The results of hierarchical diversity-interaction modeling suggested that the adverse impacts of an increasing number of GCFs on community productivity and diversity are attributable to both the specific identities of GCFs involved and their unique pairwise interactions. The results suggest that grasslands may quickly lose stability and degrade more rapidly in response to multiple co-occurring GCFs. Greater efforts should be made to conserve the functions and services of grassland ecosystems by reducing the impacts of human activities.

Keywords: community composition, grassland ecosystems, grassland management, multiple global change factors, productivity

全球变化多因子耦合降低天然草地植物群落多样性和生产力

摘要：草地具有较高的生物多样性并能提供重要的生态系统服务功能，然而草地生态系统正受到多种人为干扰的威胁。量化草地生态系统对全球变化因子(GCF)的响应，对制定有效管理策略、减缓全球变化对草地的负面影响，并提升其环境抵抗力至关重要。本研究以中国东北松嫩草地为对象，基于包含杀菌剂、除草剂、杀虫剂、抗生素胁迫、重金属污染、光污染、微塑料污染、氮沉降、耕作干扰和降水增加等10种GCF的因子库，构建了包含0、1、2、4、6和8种GCF的不同组合处理。研究发现，即使在处理的第一年，随着GCF数量的增加，草地群落生产力与多样性均呈现显著下降趋势。与单一GCF处理相比，8种GCF组合处理导致生产力降低约42.8%，物种丰富度下降约42.9%。这种负效应主要与优势物种丰度的下降以及非本地物种(指非经人类直接引入，而是因人类活动导致的环境变化而间接扩张至新地理范围的物种)的增加相关。层次多样性互作模型分析表明，GCF数量增加对草地生产力和多样性的不利影响可归因于所涉及的特定GCF的独立贡献以及GCF之间的协同效应。上述研究表明，在多重GCF共同作用下，草地生态系统可能迅速丧失稳定性并加速退化，未来亟需减少人类活动干扰，以维持草地生态系统功能和服务能力。

关键词：群落组成，草地生态系统，草地管理，多重全球变化因子，生产力

INTRODUCTION

Grasslands, encompassing a diverse range of ecosystems such as open grassland, grassy shrublands and savannas, cover a vast area of 52.5 million km², representing ~40.5% of the Earth's land surface (excluding Greenland and Antarctica) (Bardgett *et al.* 2021). Grasslands are crucial for preserving biodiversity, hosting numerous iconic and endemic species and offering a multitude of services to humans. These services include food production, water regulation, carbon sequestration for climate regulation, pollination and numerous cultural services (Bai and Cotrufo 2022; Bardgett *et al.* 2021; Petermann and Buzhdygan 2021). In fact, around 1.5 billion people worldwide rely on grasslands for their livelihoods (Sun *et al.* 2022). Despite their vital importance as global reservoirs of biodiversity and providers of essential ecosystem services, grasslands are experiencing widespread and accelerating degradation across the globe due to ongoing and expanding human-caused global environmental changes (Bardgett *et al.* 2021).

Responses of grassland ecosystems to individual global change factors (GCFs) have been widely studied, providing valuable insights into how these ecosystems react to specific environmental changes. For instance, nitrogen enrichment, due to atmospheric nitrogen deposition and agricultural activities, has been shown to reduce plant species richness in grasslands by favoring fast-growing, competitive species over slower-growing, stress-tolerant ones (Suding *et al.* 2005; Zheng *et al.* 2023). Similarly,

changes in rainfall patterns, such as increased drought frequency or intensity, can alter competitive dynamics, leading to shifts in community composition (Wilcox *et al.* 2017). Even management practices like mowing can influence plant community structure by removing biomass and creating opportunities for less competitive species (Ding *et al.* 2024; Socher *et al.* 2012). However, the challenge lies in the fact that natural ecosystems rarely experience single isolated GCFs. Multiple GCFs, such as nitrogen enrichment, altered rainfall and microplastic pollution, often act concurrently, creating a complex web of possible interactions (Rillig *et al.* 2019; Speißen *et al.* 2022; Xue *et al.* 2024).

The combined effects of multiple GCFs on grassland ecosystems can be additive, where the overall impact is simply the sum of the individual effects, synergistic, where the combined impact is greater than the sum of individual effects, or antagonistic, where the combined impact is less than the sum (Côté *et al.* 2016). Complex interactions can lead to unpredictable "ecological surprises", where the observed responses of grassland communities to multiple GCFs deviate significantly from expectations based on single-factor studies (Darling and Côté 2008). For example, the combined effects of nitrogen enrichment and altered rainfall patterns can cause more dramatic shifts in grassland community composition than would be predicted by considering each factor independently (Zavaleta *et al.* 2003). Such synergistic global change effects pose a substantial threat to biodiversity and ecosystem functioning (Oliver *et al.* 2015; van der Plas 2019; Xu *et al.* 2024). Despite extensive knowledge on

the responses of grasslands to single GCFs, our understanding of how multiple simultaneously acting factors affect these ecosystems remains limited (Speißer *et al.* 2022; Zandalinas *et al.* 2021). This knowledge gap is particularly concerning given the increasing prevalence of multiple, simultaneously acting GCFs (Steffen *et al.* 2015).

Multiple GCFs acting simultaneously can influence grassland communities through both direct and indirect pathways. Directly, the number of co-occurring GCFs can alter niche availability, either by shifting existing niches or creating new ones (Komatsu *et al.* 2019). Such changes can drive shifts in plant community composition, as different species respond uniquely to the altered environmental conditions. Global change factors can also directly affect plant growth, reproduction and interactions with other species (Zandalinas *et al.* 2021; Zhou and Wang 2023). For instance, the presence of multiple stressors may weaken competition or promote facilitation among species, potentially increasing stress tolerance and influencing community dynamics. Moreover, as the number of GCFs increases the likelihood of crossing ecological tipping points also rises, potentially leading to abrupt and irreversible shifts in ecosystem states (Suding and Hobbs 2009). Thus, even low-intensity additions of new GCFs could precipitate rapid ecosystem collapse if they interact synergistically with existing stressors (Zandalinas *et al.* 2021). Indirectly, the number of GCFs can alter top-down and bottom-up effects, impacting plant communities through trophic interactions and soil legacies. For example, GCFs that affect herbivory (e.g., insecticide and light pollution) can influence plant communities via top-down effects by modifying herbivore behavior and abundance (Liu and Heinen 2024; Xu *et al.* 2024). Similarly, changes in the number of GCFs can alter interactions between plants and soil biota, thereby influencing plant communities (Xue *et al.* 2024). These altered plant–soil biota interactions can lead to reduced microbial diversity and shifts toward more generalist and stress-tolerant plant species (Rillig *et al.* 2019; Xu *et al.* 2024). While these mechanisms have been explored in various contexts, the impacts of multiple GCFs on natural grasslands remain largely unknown, highlighting the need for further research in this critical area.

Currently, studies exploring the responses of natural grassland communities to an increasing number of co-occurring GCFs are limited (Komatsu *et al.* 2019). Such studies, however, are crucial for developing effective strategies to conserve and

manage ecosystems that are increasingly subjected to multiple environmental stressors (Bowler *et al.* 2020; Rillig *et al.* 2019). In particular, by conducting field experiments, researchers can gain valuable insights into the complex interactions between GCFs and their impacts on plant communities in real-world contexts. Therefore, we conducted a field experiment in a natural grassland to investigate how plant communities respond to an increasing number of simultaneously acting GCFs. We selected 10 GCFs that either already frequently occur simultaneously in grasslands or are predicted to become more common in the future: exposure to fungicide, herbicide, insecticide and antibiotics, heavy metal pollution, light pollution, microplastic pollution, nitrogen deposition, disturbance by tillage and increased precipitation (Bardgett *et al.* 2021). We exposed natural grassland communities to one, two, four, six, or eight GCFs chosen randomly from this pool, alongside a control group with no GCFs. We addressed the question: Does the increasing number of GCFs affect the productivity, composition and diversity of natural grassland communities?

MATERIALS AND METHODS

Site description

We conducted the experiment in the Songnen grassland, located in Changling County (44°45' N, 123°45' E), Jilin Province, in northeastern China. This region experiences a semiarid continental and monsoonal climate characterized by cold, dry winters and warm, moist summers. The average annual temperature ranges from 4.6 to 6.4 °C, while annual precipitation varies between 253.2 and 716.2 mm, with ~70% falling during the growing season from July to September in the last six decades (1953–2017, Wang 2023). Soil salinization and alkalization are the main limiting factors for vegetation development in this area. The major vegetation type is meadow steppe dominated by *Leymus chinensis* (Trin.) Tzvel.

Experimental design and plot lay-outs

We selected these GCFs based on their current prevalence or emerging threat potential in the Songnen grassland region. Several factors are already well-documented stressors in this ecosystem. The Songnen Meadow Steppe has seen a sharp rise in atmospheric nitrogen deposition, averaging

approximately $10.5 \text{ g N m}^{-2} \text{ year}^{-1}$ (equivalent to $105 \text{ kg N ha}^{-1} \text{ year}^{-1}$), and this rate is increasing annually (Zhang *et al.* 2013). Long-term analyses of precipitation in Northeast China for the period 1961–2020 reported significant increases in total precipitation during the cold season and early warm season, indicating an overall upward trend in precipitation amounts (Wang *et al.* 2023). These precipitation changes have had direct consequences for the Songnen grassland ecosystem, affecting vegetation cover and plant community composition (Niu *et al.* 2023). Tillage from cropland expansion has fragmented over 2.8 million hectares of Songnen grasslands, with annual conversion rates of 1.2% threatening remaining intact grasslands (Huang *et al.* 2012). Chemical pesticide uses in China from 1991 to 2021 primarily consisted of fungicides, herbicides and insecticides, with herbicides accounting for over 60% of total pesticide consumption (Wang *et al.* 2022). Average chemical fertilizer (nitrogen, phosphorus and potassium) and pesticides use per hectare of cropland in China are two to four and two to seven times those of other countries/regions, respectively (Zhan 2021). Studies have found microplastics in farmland soils of northeast China (Zhang *et al.* 2020). These empirically confirmed pressures have led to significant biodiversity losses and ecosystem function alterations across the region (Yu *et al.* 2020).

To investigate the effects of increasing numbers of co-occurring GCFs on grassland plant communities, we designed six levels of GCFs diversity. These levels included zero (control with no GCF), one (a single GCF), two, four, six and eight GCFs (*sensu* Rillig *et al.* 2019; SpeiBer 2021). We randomly assigned individual GCFs from our pool of 10 to these groups. The control and single GCF groups had six replicates each. For groups with two, four, six, or eight GCFs, we randomly created combinations, while ensuring that each GCF was evenly represented across the different factor-number levels, with 10 replicates each (Supplementary Fig. S1). This experimental design parallels methods used in biodiversity research (e.g., Tilman *et al.* 1997), focusing on GCFs diversity rather than the specific identity or combination of GCFs (Rillig *et al.* 2019). This design resulted in a total of 106 experimental plots (Supplementary Fig. S2a), each measuring $2.8 \text{ m} \times 2.8 \text{ m}$. To prevent interference of the treatment applications between plots, a 2.0-m buffer zone separated each plot. In addition, to contain the GCFs within their designated plots, we enclosed each plot with iron sheets buried

40 cm deep and extending 20 cm aboveground (Supplementary Fig. S2b).

The implementation of GCFs

Between 11 May and 25 June 2023, we implemented the 10 GCFs in various combinations to the plots. For the antibiotic stress treatment, 3.5 mg of oxytetracycline per kg of soil was added to the top 20 cm of soil (soil bulk density: 1.65 g cm^{-3}), resulting in a final concentration of 3.5 mg kg^{-1} . This dosage is within the range used in previous studies and reflects antibiotic exposure levels common in agriculture. We dissolved 9.42 g of oxytetracycline (94.2% purity) in 3 L of water and distributed it evenly over the soil surface using a watering can. For the microplastic pollution treatment, we used polybutylene succinate (PBS) granules (3.0–4.0 mm in diameter) at a concentration of 0.1% (w/w, granules/dry soil). PBS is commonly found in packaging, medical supplies, agricultural mulching and household items, making it relevant for studying microplastic effects on plants. In each designated plot, 2.60 kg of PBS was sprinkled evenly over the soil surface. For the heavy metal (cadmium) pollution treatment, CdCl_2 was added to the top 20 cm of the soil. We dissolved 26.13 g of CdCl_2 in 3 L of water and evenly distributed it over the soil surface, achieving a concentration of 10.0 mg kg^{-1} . For pollution by fungicides, 0.9 g of Score® (10% difenoconazole) and 0.225 g of Ortiva® (250 g L^{-1} azoxystrobin) were dissolved in 0.5 L of water and sprayed evenly onto the plants in each plot. For pollution by an herbicide, 0.235 mL of glyphosate (30%) was diluted in 0.5 L of water and sprayed onto the plants. Insecticide application involved spraying 0.27 mL of Karate Zeon® (25 g L^{-1} lambda-cyhalothrin) diluted in 0.5 L of water onto the plants. For the nitrogen deposition treatment, 169.7 g of slow-release urea (46.2% N) was evenly spread in each plot, corresponding to an input of 10.0 g N m^{-2} , similar to the annual atmospheric nitrogen deposition in northern China (Wen *et al.* 2020). For the light-pollution treatment, LED spotlights mounted on 120 cm high metal frames were used (Supplementary Fig. S2c), providing an average light intensity of 30.0 lux at ground level from sunset to sunrise, which is within the range of light intensities found below light poles (SpeiBer *et al.* 2022). To achieve full inversion tillage, a small rotary tiller was used to plow the entire plot to a depth of 20 cm (Supplementary Fig. S2d). For the increased precipitation treatment, 258.4 L of water were added

per plot, simulating a 30% increase above the average rainfall received between May and September over the past two decades in this region (Wang 2023). For each treatment involving the application of solutions to specific plots, an equivalent amount of water was applied to the remaining plots. A summary of the levels of the individual GCFs used in this experiment is provided in [Supplementary Table S1](#).

Measurements

We carried out sampling and measurements in all the 106 plots on 3 October 2023 (i.e. 4 months after the start of the GCFs treatments). To assess above-ground vegetation biomass, we randomly placed a 50 cm × 200 cm quadrat in each plot and clipped all vegetation at ground level. Immediately after clipping, we identified each plant species present in the sample. We then randomly selected five harvested individuals of each species and measured their height. The collected plant material was placed in paper bags, flash-dried at 105 °C in a forced-air oven for 2 h, and then oven-dried at 65 °C for 72 h until a constant weight was achieved.

We assessed plant diversity and composition in each of the 106 plots. Plot-level plant species richness (S) was calculated by counting the total number of species present in the sampled quadrat. We also calculated plot-level diversity using the Shannon-Wiener diversity index (H') and Simpson's diversity index (D), and evenness using Pielou's evenness ($J = H' / \ln[S]$), based on the total aboveground biomass of each species within the sampled quadrat. These calculations were done using the diversity function in the "vegan" package (version 2.5-7) (Oksanen *et al.* 2022). We also estimated total vegetation coverage in each plot. As plant height is a key indicator of light utilization strategy and competitive ability, we calculated the community-weighted mean (CWM) of plant height using the following equation:

$$\text{CWM}_{\text{height}} = \sum_{i=1}^S P_i \times H_i \quad (1)$$

Where S is the species richness, H_i is the average height of five individuals of species i and P_i represents the relative abundance of species i .

Statistical analyses

All statistical analyses were done in R 4.2.2 (R Core Team 2022). To examine the combined effects of GCFs on community aboveground biomass, total

coverage and community-weighted mean (CWM) plant height, we fitted linear mixed-effects models using the "lme" function from the "nlme" package (Pinheiro *et al.* 2021). In these models, aboveground biomass, total coverage and plant height per plot were used as response variables, with GCFs number included as a continuous fixed effect. To account for the non-independence of plots sharing the same GCFs combination, GCFs combination was included as a random effect. To improve the normality of residuals, aboveground biomass and coverage were square-root transformed, while plant height was natural log-transformed. Additionally, we assessed the effects of individual GCFs on these variables using separate linear mixed-effects models, which included only the control and single-GCF treatment data. In these models, GCF identity was specified as a fixed effect, and plot was included as a random effect.

We also used linear mixed-effects models to analyze the effects of single GCFs and increasing GCFs number on plant community diversity and evenness, treating these indices as response variables. For species richness, we fitted a generalized linear mixed-effects model with a Poisson error distribution using the "glmmPQL" function from the "MASS" package. In all models, the fixed and random effects were structured as described above. The significance of fixed effects in all models was evaluated using Type II analysis of variance (ANOVA) with the "Anova" function from the "car" package.

A significant effect observed in relation to the number of GCFs could be due to the increased likelihood of including a dominant GCF when more factors are present, a phenomenon known as the "sampling effect". However, this effect could also stem from interactions among multiple GCFs, where these interactions might either be specific to certain GCFs or represent a more generalized effect. Since our experiment did not encompass all possible combinations of GCFs, we could not directly test the impact of each potential multi-way GCFs interaction. Therefore, to determine whether GCF identities or specific/general interactions underlie the significant GCF-number effects observed, we employed the hierarchical diversity-interaction modeling framework developed by Kirwan *et al.* (2009), specifically adapted to GCF identities and interactions. For each response variable with a significant GCF-number effect, we ran five hierarchical models, each with different assumptions regarding the contributions of single GCFs and their

interactions. We then compared these models using likelihood-ratio tests, and the best model was determined using AIC (Supplementary Fig. S3; Table 1). This approach allowed us to discern the relative importance of GCF identity versus interactions in driving the observed responses of grassland communities to increasing GCF numbers.

We also performed PERMANOVA, using the “*adonis2*” function in the “*vegan*” package, to test whether plant community composition could be explained by the number and the identity of GCFs; significance was based on a permutation test (999 permutations). Differences in plant community composition among the GCF treatments were visualized using non-metric multidimensional scaling (NMDS) plots based on the Bray-Curtis dissimilarity matrix (Schroeder and Jenkins 2018).

RESULTS

Effects of GCFs on productivity, total coverage and plant height within the grassland community

The individual GCFs significantly impacted the productivity, total coverage and plant height within the grassland community, but the direction and magnitude of these effects varied considerably among the GCFs (Fig. 1; Table 1). Compared with the control, herbicide application and soil disturbance from tillage significantly decreased the mean community above-ground biomass per plot (Fig. 1a). Conversely, increased nitrogen input significantly increased the mean community above-ground biomass (Fig. 1a). Moreover, herbicide application and soil disturbance from tillage significantly decreased, and fungicide application marginally decreased the community coverage per plot (Fig. 1b). Soil disturbance from tillage significantly increased mean plant height within the communities (Fig. 1c). As the number of simultaneously acting GCFs increased, we observed a significant decrease in both community productivity and total coverage (Fig. 1a, b). Conversely, plant height increased significantly with the number of GCFs (Fig. 1c).

The hierarchical diversity–interaction modeling framework for productivity and total coverage revealed that models incorporating specific pairwise GCF interactions provided the best fit. Specifically, Model 2 outperformed Model 3, as indicated by lower AIC values (Table 1). This finding suggests that the negative effects of increasing GCF number on community productivity and coverage are driven not

only by the identities of the individual GCFs but also by their unique pairwise interactions. In contrast, for mean plant community height, Model 5 showed the best fit among all models (Table 1). This model includes additive, factor-specific interaction contributions, indicating that the observed positive relationship between the number of GCFs and plant height is largely attributable to specific interactions among the GCFs.

Effects of GCFs on plant community composition and diversity

Single-factor treatments significantly influenced species richness and diversity (Shannon-Wiener and Simpson indices) within the grassland community (Fig. 2), but had no effect on evenness. Soil disturbance from tillage significantly decreased species richness, and the Shannon-Wiener and Simpson indices (Fig. 2a–c). Moreover, light pollution significantly reduced the Shannon-Wiener and Simpson indices (Fig. 2b, c). Fungicide application tended to decrease species richness (Fig. 2a). Mirroring the trends observed in community productivity, we found significant directional changes linked to the number of GCFs: a reduction in species richness, evenness, Shannon-Wiener index and Simpson index (Fig. 2). The identity and number of GCFs both had significant effects on plant community composition (Fig. 3a, b).

Based on the hierarchical diversity–interaction modeling framework, Model 3 outperformed Model 4 for species richness, diversity and evenness, indicating that specific pairwise interactions among factors had a stronger influence than averaged interaction effects. The best-fitting model for species richness, diversity and evenness was the one incorporating separate pairwise GCF interactions (Table 1). This suggests that the negative impact of increasing GCF number on these variables stems from both the identities of the GCFs themselves and their strong, specific pairwise interactions.

DISCUSSION

Our field experiment in a natural grassland showed that most of the 10 GCFs applied individually had weak or minimal impacts on the productivity, species composition and diversity of the grassland community. Additionally, the effects of single GCFs varied depending on the specific community variables examined (Figs 1 and 2). However, despite

Table 1: Results of statistical tests that examined how the identity and interactions of global change factors (GCFs) influence various aspects of grassland plant communities, including productivity, coverage, plant height, diversity, and evenness

Model (reference model number)	Above-ground biomass per plot			Total coverage per plot			Average plant height per plot						
	DF	AIC	χ^2	LogLik	χ^2	P	AIC	LogLik	χ^2	AIC	LogLik	χ^2	P
1. Null	—	104.55	—	-49.28	—	—	84.93	-39.46	—	9.64	-1.82	—	—
2. Identity of factors (1)	9	61.45	61.11 (+)	-18.72	<0.001	<0.001	82.08	-29.04	20.85 (+)	0.013	25.21	54.06 (+)	<0.001
3. Separate-pairwise factor interactions (4)	37	-15.03	152.40(+)	57.52	<0.001	<0.001	-96.21	98.10	252.72(+)	<0.001	-33.58	66.79	78.48 (+) <0.001
4. Average factor interaction (2)	1	63.37	0.08	-18.69	0.781	0.212	82.52	-28.26	1.56	-29.10	27.55	4.69 (+)	0.030
5. Additive factor-specific interaction contributions (3)	28	47.64	118.68 (-)	-1.82	<0.001	<0.001	67.60	-11.80	219.8 (-)	-35.23	39.61	54.36 (+)	0.002
Model (reference model number)	DF	Species number			Shannon-Wiener's diversity index			Simpson's diversity index					
		AIC	LogLik	χ^2	P	AIC	LogLik	χ^2	P	AIC	LogLik	χ^2	P
1. Null	—	74.58	-34.29	—	—	18.27	-6.13	—	—	-94.66	50.33	—	—
2. Identity of factors (1)	9	76.38	-26.19	16.21	0.063	4.62	9.69	31.65 (+)	<0.001	-109.03	66.51	32.37 (+)	<0.001
3. Separate-pairwise factor interactions (4)	37	27.41	36.29	124.83(+)	<0.001	-45.04	72.52	125.35 (+)	<0.001	-156.55	128.28	123.51 (+)	<0.001
4. Average factor interaction (2)	1	78.24	-26.12	0.13	0.714	6.31	9.84	0.31	0.580	-107.04	66.52	0.01	0.918
5. Additive factor-specific interaction contributions (3)	28	60.42	-8.21	89.01 (-)	<0.001	-10.65	27.33	90.38 (-)	<0.001	-132.40	88.20	80.15 (-)	<0.001
Model (reference model number)	DF	Pielou's evenness index											
		AIC	LogLik	χ^2									
1. Null	—	-88.60	47.30	—									
2. Identity of factors (1)	9	-83.62	53.81	13.02									
3. Separate-pairwise factor interactions (4)	37	-108.17	104.08	100.53 (+)									
4. Average factor interaction (2)	1	-81.63	53.82	0.01									
5. Additive factor-specific interaction contributions (3)	28	-87.90	65.95	76.27 (-)									

Notes: Results are based on the hierarchical diversity-interaction comparisons between the model of interest and a reference model (indicated by the numbers in brackets) using log-likelihood ratio tests (χ^2 statistics). The numbers and names of the models correspond to those in Supplementary Fig. S3. For each model, we show its AIC and log-likelihood (logLik). To answer the four questions shown in Supplementary Fig. S3, we made four model comparisons based on log-likelihood ratio tests. The number of the reference model is shown in brackets after the model of interest. For the model comparisons, we provide the degrees of freedom (DF), the χ^2 test statistic and the P value. The P values <0.05 are indicated in bold. The + and - in brackets after the χ^2 value indicate whether the model was better or worse than its reference model.

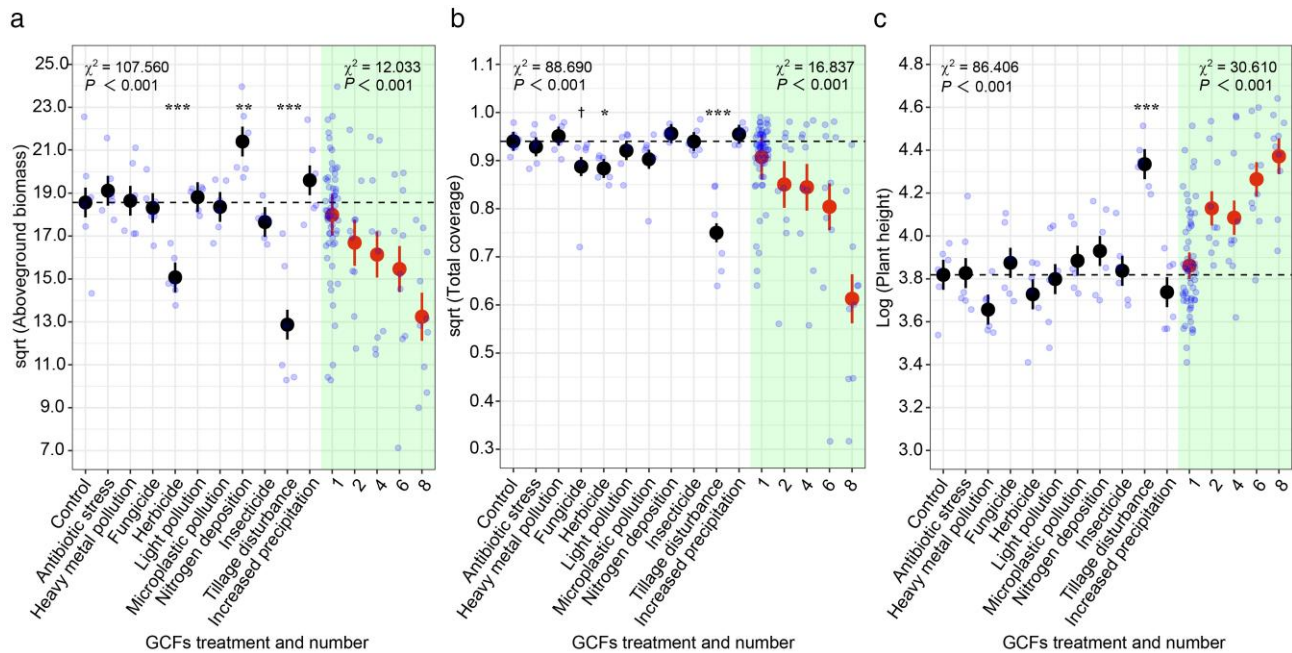


Figure 1: Effects of single and multiple global change factors (GCFs) on (a) community productivity, (b) vegetation coverage, and (c) community-weighted mean plant height in the Songnen grassland in northeastern China. Black circles represent responses to individual GCF treatments, while red circles represent responses to varying numbers of simultaneously acting GCFs (1, 2, 4, 6 and 8). The red circles marked with value '1' represent the average values across all individual GCF applications. Significant deviations of the individual GCF treatments from the control are indicated as follows: † ($0.05 < P < 0.1$), * ($P < 0.05$), ** ($P < 0.01$), and *** ($P < 0.001$). Error bars depict standard errors, and light blue circles show the raw data distribution. Horizontal dashed lines represent the mean values of the control group (no GCF treatment).

the weak individual effects of most GCFs, our study showed that an increase in the number of GCFs led to more pronounced directional changes in the grassland-community attributes. Consistent with previous mesocosm studies (Rillig *et al.* 2019; SpeiBer *et al.* 2022; Yang *et al.* 2022), our findings thus indicate that the presence of multiple GCFs acting in concert can lead to more severe consequences for grassland communities compared with the additive effects of individual factors. The synergistic interactions among GCFs potentially lead to more rapid and extensive degradation of grassland productivity and diversity, and changes in species composition. These findings align with the growing body of evidence that underscore the importance of considering the joint effects of multiple GCFs when assessing the vulnerability of ecosystems to global change (Orr *et al.* 2020).

Previous research has demonstrated that an increasing number of simultaneously acting GCFs can negatively affect soil microbial diversity and the growth, survival and diversity of plants (Fu *et al.* 2024; Rillig *et al.* 2019; SpeiBer 2021; Yang *et al.* 2022; Zandalinas *et al.* 2021). A more recent study also found that increasing numbers of GCFs can modify

plant-soil feedbacks by altering the fungal legacies left by plants in the soil (Xue *et al.* 2024). These studies underscore the critical role of multiple GCFs in influencing plant and soil systems, as well as in regulating ecological processes such as plant-microbe interactions, which can in turn affect community structure and ecosystem functions. For example, the application of fungicides and insecticides may directly impact microorganisms and insects, thereby disrupting the structure and functioning of ecosystems (e.g. Ni *et al.* 2025; Steiner *et al.* 2024). Our study builds upon this body of knowledge, which has largely been derived from artificial microcosm and mesocosm experiments, by providing evidence from a natural grassland community. We show that an increasing number of co-occurring GCFs not only affects individual plants and soil components but also leads to a significant reduction in both the productivity and diversity of entire grassland communities. This occurs despite the fact that GCFs explain only a limited portion of the variation in community composition (Fig. 3b; $R^2 = 0.239$, stress value = 0.102, $P = 0.001$).

Our study's findings differ from those of a previous study by SpeiBer *et al.* (2022), which found that an increasing number of GCFs led to greater

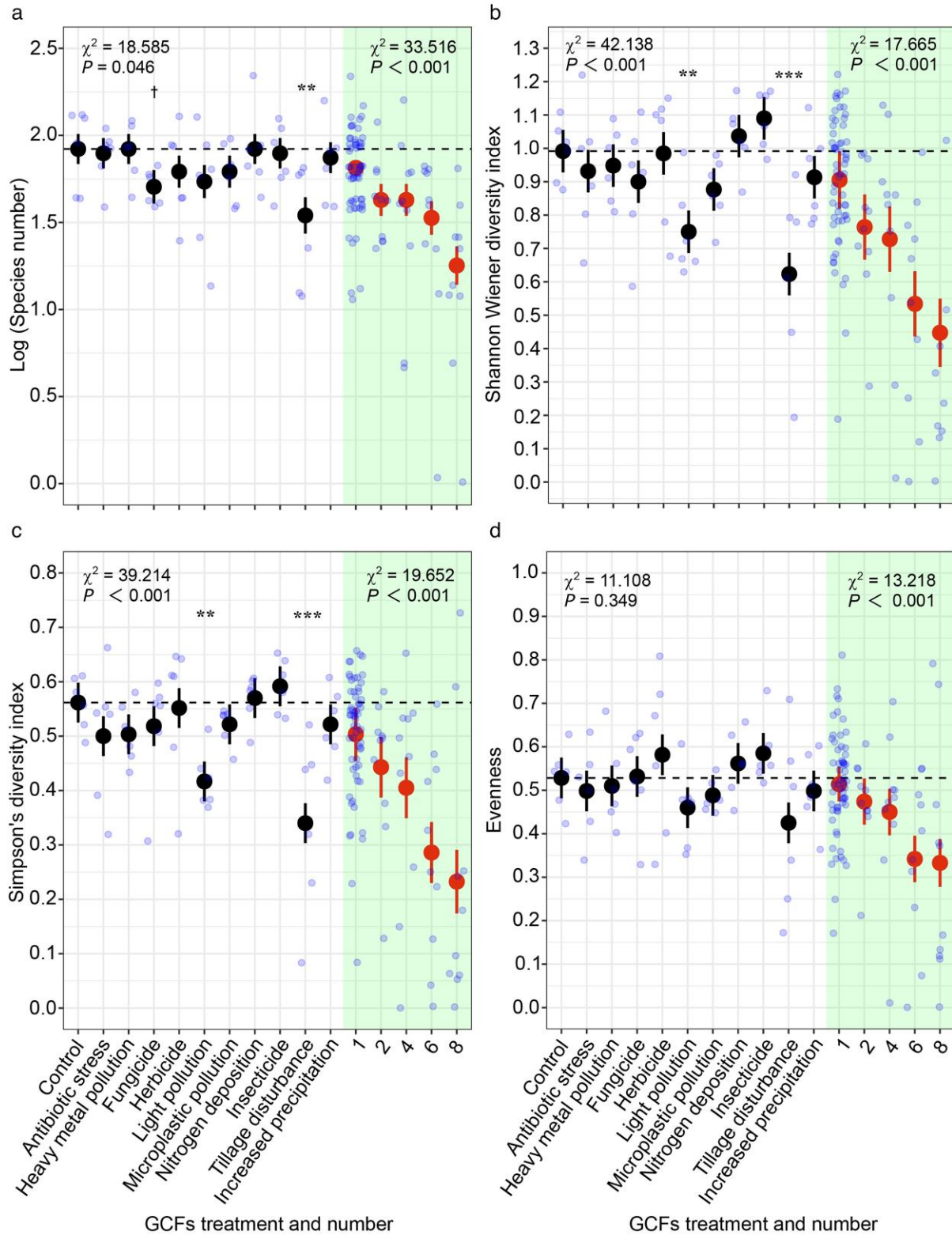


Figure 2: Effects of single and multiple global change factors (GCFs) on (a) species richness, (b) Shannon-Wiener diversity index, (c) Simpson’s diversity index, and (d) Evenness in the Songnen grassland in northeastern China. Black circles represent responses to individual GCF treatments, while red circles represent responses to varying numbers of simultaneously acting GCFs (1, 2, 4, 6, and 8). The red circles marked with value ‘1’ represent the average values across all individual GCF applications. Significant deviations of the individual GCF treatments from the control are indicated as follows: † ($0.05 < P < 0.1$), * ($P < 0.05$), ** ($P < 0.01$), and *** ($P < 0.001$). Error bars depict standard errors, and light blue circles show the raw data distribution. Horizontal dashed lines represent the mean values of the control group (no GCF treatment).

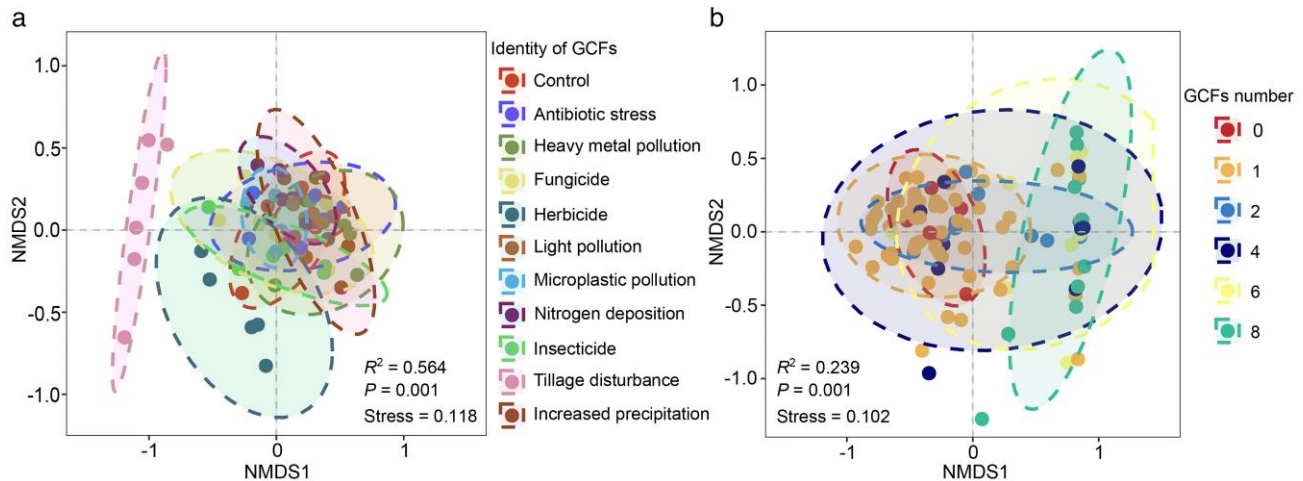


Figure 3: Nonmetric multidimensional scaling (NMDS) plots showing the grassland community composition under (a) different single global change factors (GCFs), and (b) under treatment combinations involving one, two, four, six, and eight GCFs and a control without any GCF. The R^2 and P values shown in the figures are based on the PERMANOVA analysis.

productivity in a grassland mesocosm. This was primarily driven by a strong positive influence of nitrogen enrichment in that study, which was, due to the limited pool of GCFs in that study, more likely to be included in the high GCF-number treatments. Moreover, in contrast to [Speißer et al. \(2022\)](#), our study was conducted in a natural grassland where complex conditions may weaken the concurrent effects of N addition with other GCFs on plant communities. Many previous studies have been conducted under greenhouse conditions or in experimental mesocosms ([Speißer et al. 2022](#); [Yang et al. 2022](#)), where the experimental conditions do not fully mirror the natural habitats of the plants and may not accurately represent the complex interactions and feedbacks that occur in real-world ecosystems ([De Boeck et al. 2015](#); [Leuzinger et al. 2011](#)). To address the gap in knowledge on real-world impacts of multiple global change factors (GCFs), long-term, field-based studies in natural habitats are crucial. This research will enhance our understanding of the cumulative effects of GCFs on biodiversity, ecosystem functioning and services, while also revealing potential tipping points, regime shifts and the overall resilience of ecosystems to global change ([Blowes 2019](#); [Ratajczak et al. 2018](#)).

The significant effects of the various GCFs on the plant community observed in our study may be attributed to several mechanisms. First, changes in resource availability can affect niche dimensionality, with large consequences for plant communities. For example, light pollution and N enrichment may reduce the heterogeneity of limiting resources,

thereby diminishing the niche space available for species coexistence—even without decreasing the number of limiting resources ([Harpole and Tilman 2007](#)). Combinations of GCFs that synergistically enhance resource availability tend to reduce niche dimensionality, while those that limit resource availability can increase it. Second, a higher number of GCFs increases the probability of including at least one factor with strong ecological effects—a phenomenon known as the sampling effect. In our study, the presence of tillage disturbance as a single-factor treatment significantly promoted the proliferation of the nonnative species *Phragmites australis* ([Supplementary Fig. S4](#)), which in turn negatively impacted the growth of other plant species. Additionally, tillage disturbance likely disrupted essential soil biological networks (e.g., microbial trophic interactions) and decoupled aboveground–belowground feedbacks. Such disruptions compromise ecosystem structure and function, reducing resilience and adaptive capacity in response to environmental stressors ([Czerwiński et al. 2018](#); [Lawrence-Smith et al. 2021](#)). Light pollution, which also exhibited strong negative effects on multiple diversity metrics, can alter plant communities both by affecting herbivores and by increasing resource availability. Although it is impractical to study all possible interactions among numerous global change factors, our findings align with a recent meta-analysis indicating that plant communities are more likely to be significantly altered when exposed to three or more GCFs simultaneously ([Cheng et al. 2024](#)). Third, co-occurring GCFs can modify each other's effects,

with net ecosystem responses depending on the nature of their interactions (i.e. interaction effects). In our study, hierarchical diversity-interaction models revealed that, beyond the main effects of individual GCFs (e.g. N enrichment or tillage), specific pairwise interactions also contributed to the observed decline in productivity and diversity as the number of GCFs increased (Table 1). This suggests that the ecological impacts of multiple GCFs may diverge substantially from predictions based solely on single-factor effects.

Our results show that multiple, simultaneously applied GCFs had differential impacts on *Leymus chinensis*—the dominant species in this grassland, and *P. australis*. While *P. australis* is native to most parts of China, it has recently begun expanding into the meadow steppe where our study was conducted, making it a neonative species (*sensu* Essl *et al.* 2019). As the number of GCFs increased, the biomass of *L. chinensis* declined, whereas *P. australis* increased its relative biomass. This shift suggests that the overall negative effect of multiple GCFs on community biomass is primarily driven by the decline of the dominant species, coupled with the concurrent rise of the neonative species. The contrasting responses of *L. chinensis* and *P. australis* to GCF exposure suggest that in meadow steppes dominated by the more sensitive *L. chinensis*, aboveground productivity is likely to decline under increasing pressure of multiple GCFs. In contrast, in ecosystems where *P. australis* is already dominant, such as arid regions of northwestern China or coastal wetlands, GCFs may not reduce aboveground productivity. This highlights that the impacts of GCFs on ecosystem functions are highly system- or context dependent.

Plant community composition varied significantly across the different single-GCF treatments, with tillage disturbance exerting the most pronounced effect (Fig. 3a). This disturbance particularly favored the growth of *P. australis*, a much taller species compared with others in the grassland community (Supplementary Fig. S4). *Phragmites australis* is a widely distributed and highly polymorphic species. It typically inhabits riverbanks and lake margins, where it contributes to wetland ecosystem diversity, but it also thrives in arid environments such as deserts and drylands in western and northwestern China (An *et al.* 2012). The post-tillage increase in this tall species likely explains the positive relationship observed between the number of GCFs and overall plant height at the community level (Fig. 1c; Supplementary Fig. S5). Although we did not

perform detailed analyses of direct competitive interactions between *P. australis* and other species, the observed changes in biomass distribution suggest that *P. australis* exerts strong negative effects on neighboring plant species, resulting in cascading impacts on community structure.

In summary, this study is the first to examine the joint effects of multiple co-occurring GCFs on a natural grassland community. We found that an increasing number of GCFs can significantly reduce grassland productivity and biodiversity within a single growing season, through both individual GCF effects and their specific interactions. These findings suggest that natural ecosystems, particularly those dominated by perennials, may be more sensitive to GCFs than previously assumed. These results also imply that grassland ecosystems may possess lower stability and degrade more rapidly under the pressure of multiple GCFs than previously recognized. Altogether, our findings underscore the urgent need for studies that investigate the compound effects of multiple GCFs on natural ecosystems—an area of growing concern as highlighted by recent research (Rillig *et al.* 2019; SpeiBer *et al.* 2022; Xu *et al.* 2024). To advance this field, we recommend that future research prioritize long-term field experiments in natural habitats to capture the temporal dynamics, resilience and potential adaptation of plant communities to sustained global change.

Supplementary Material

Supplementary material is available at *Journal of Plant Ecology* online.

Table S1: Single GCF treatment implementation. Summary of the materials or equipment used to implement the single GCF treatments, and the intensity of concentration of each GCF.

Figure S1: Combinations of global change factors (GCFs) applied at various levels in this experiment.

Figure S2: An overview of the experimental plot layout.

Figure S3: Hierarchical framework for analyzing individual and interactive effects of global change factors (GCFs).

Figure S4: Effects of single GCF treatments on the biomass proportion of the dominant plant species: (a) *Phragmites australis* and (b) *Leymus chinensis*.

Figure S5: Effects of increasing numbers of simultaneously acting global change factors (GCFs) on the mean biomass proportions of plant species within the community.

Authors' Contributions

Yanjie Liu conceived the idea and designed the experiment. Jianyong Wang and Yingxia Liu performed the experiment. Yingxia Liu and Jianyong Wang analyzed and visualized the data. Jianyong Wang and Yingxia Liu wrote the draft of the manuscript, with major inputs from Ayub M. O. Oduor, Mark van Kleunen and Yanjie Liu.

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Conflict of interest statement. The authors declare that they have no conflict of interest.

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