Response of temporal stability of plant community biomass in alpine meadows of the Qinghai-Xizang Plateau, China to climate warming and nitrogen deposition (Postprint)

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Abstract

In recent years, numerous studies have focused on the effects of global climate warming and increased nitrogen deposition on the structure and function of grassland ecosystems. However, considerable uncertainties remain regarding the response mechanisms of plant community biomass stability to these two major climate factors in alpine meadows of the Qinghai-Xizang Plateau, China. In light of this, the present study, based on field control experiments, systematically evaluated the effects of different levels of climate warming (W0 (no warming), W1 (air temperature increased by 0.47°C or soil temperature increased by 0.61°C), W2 (air temperature increased by 0.92°C or soil temperature increased by 1.09°C), W3 (air temperature increased by 1.44°C or soil temperature increased by 1.95°C)), nitrogen deposition (N0 (0 kg N/($hm^2 \cdot a$)), N16 (16 kg N/($hm^2 \cdot a$)), and N32 (32 kg N/($hm^2 \cdot a$))), and their interactions on plant community biomass and its temporal stability, and explored the underlying regulatory mechanisms. The results demonstrated that with increasing temperature, the biomass of the total community, Gramineae, and dominant species increased significantly, whereas the biomass of common and rare species decreased significantly. Nitrogen deposition also significantly promoted biomass accumulation in the community and gramineous plants. Under the W3N32 treatment, the biomass of the plant community, Gramineae, and dominant species reached maximum values, indicating a synergistic effect. Structural equation modeling revealed that warming significantly decreased the stability of plant community biomass by reducing the stability of Gramineae and dominant species biomass and weakening species asynchrony. The interaction between nitrogen deposition and warming increased biomass fluctuations in the gramineous functional group, thereby amplifying its negative impact on community stability. Greater atten-

tion should be devoted to the response and regulatory mechanisms of dominant species and functional groups under global climate change. This study provides a theoretical basis for elucidating the stability maintenance mechanisms of alpine grasslands and offers scientific support for developing future grassland ecosystem management and assessment strategies.

Full Text

Preamble

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Response of Temporal Stability of Plant Community Biomass in Alpine Meadows of the Qinghai-Xizang Plateau, China to Climate Warming and Nitrogen Deposition

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Abstract

In recent years, numerous studies have examined how global climate warming and increased nitrogen deposition affect grassland ecosystem structure and function. However, significant uncertainties remain regarding the response mechanisms of plant community biomass stability in alpine meadows of the Qinghai-Xizang Plateau to these two major climate factors. To address this knowledge gap, we conducted field control experiments to systematically evaluate the effects of different levels of climate warming (W0: no warming; W1: air temperature increased by 0.47°C or soil temperature increased by 0.61°C; W2: air temperature increased by 0.92°C or soil temperature increased by 1.09°C; W3: air temperature increased by 1.44°C or soil temperature increased by 1.95°C), nitrogen deposition (N0: 0 kg N/($hm^2 \cdot a$), N16: 16 kg N/($hm^2 \cdot a$), and N32: 32 kg N/($hm^2 \cdot a$)), and their interactions on plant community biomass and its temporal stability, while exploring potential regulatory mechanisms.

Our results showed that total community biomass, Gramineae biomass, and dominant species biomass increased significantly with rising temperature, whereas common and rare species biomass decreased significantly. Nitrogen deposition also significantly promoted biomass accumulation in the community and gramineous plants. Under the W3N32 treatment, biomass of the plant community, Gramineae, and dominant species reached maximum values, indicating a synergistic effect. Structural equation modeling revealed that increasing temperature significantly decreased plant community biomass stability by reducing the stability of grass and dominant species biomass and weakening species asynchrony. The interaction between nitrogen deposition and temperature increased biomass fluctuation in the grass functional group, thereby amplifying its negative influence on community stability. These findings underscore the need for greater attention to the responses and regulatory mechanisms of dominant species and functional groups under global climate change. This study provides a theoretical basis for revealing stability maintenance mechanisms in alpine grasslands and offers scientific support for future grassland ecosystem management and assessment strategies.

Keywords: alpine meadows; climate change; plant community biomass; dominant species; species asynchrony

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Introduction

The temporal stability of plant biomass reflects an ecosystem's capacity to maintain functional stability over time under external environmental disturbances [?]. Stable ecosystems are essential for providing sustainable ecological services to humans [?]. However, global climate change is affecting ecosystem structure and function at an unprecedented rate, with climate warming and increased nitrogen deposition emerging as two of the most important factors in contemporary global change [?, ?, ?].

Climate warming influences the stability of plant community productivity through both direct and indirect pathways. On one hand, increased temperature can alter plant phenology and interspecific competition, thereby changing community productivity [?, ?]. On the other hand, climate warming may lead to plant species loss, shifts in community composition, and reduced species asynchrony, which collectively weaken the community' s buffering capacity against environmental disturbances [?]. Previous studies have shown that the stability of plant communities under climate warming exhibits regional heterogeneity, with the direction and magnitude of its influence regulated by plant community diversity levels, soil resource limitation, and community structure [?, ?]. Simultaneously, the significant increase in atmospheric nitrogen deposition caused by human activities has altered soil nutrient status and profoundly impacted plant community function and stability [?]. Previous research on nitrogen deposition effects has yielded inconsistent results regarding temporal stability of plant communities, with studies showing positive effects [?], negative effects [?], and even neutral effects [?]. These divergent outcomes may be closely related to ecosystem type, nitrogen application intensity, and experimental duration.

Although progress has been made in understanding how climate warming and nitrogen deposition independently affect plant community stability, most studies have focused on single-factor effects, and a systematic understanding of their interactive mechanisms on community biomass temporal stability remains lacking [?, ?]. Given that climate warming and nitrogen deposition, as two key factors of global change, often occur synergistically in natural environments, their potential synergistic or antagonistic effects may trigger nonlinear ecological responses with far-reaching impacts on plant community structure, functional properties, and stability. Therefore, systematically assessing the comprehensive effects of climate warming and nitrogen deposition interactions on plant community biomass stability has important theoretical significance and practical value for deepening our understanding of dynamic regulation mechanisms of grassland ecosystem structure and function under global change and improving predictive capacity regarding ecosystem response and adaptability.

In recent decades, substantial research has examined potential mechanisms underlying plant community stability [?, ?]. Plant diversity plays a positive role in community stability, as more diverse communities are often better able to withstand external disturbances [?, ?]. Studies indicate that communities with higher diversity exhibit greater temporal stability [?]. Additionally, species asynchrony—driven by compensatory interactions among species—can also influence temporal stability in plant communities [?]. A strong positive relationship exists between the stability of plant communities and that of plant functional groups [?]. The mass ratio hypothesis highlights the importance of dominant species in ecosystem functioning [?]. However, variations in species sensitivity to environmental changes introduce uncertainty in their effects on plant community stability [?]. Considering the complex responses of community biomass stability, an in-depth examination of direct and indirect factors influencing community biomass stability under climate warming and nitrogen deposition is essential for accurately predicting grassland ecosystem dynamics in a changing climate. This understanding will aid in formulating effective conservation and management strategies to address ecological challenges posed by global climate change.

As one of the largest alpine ecosystems in the world, alpine meadows on the Qinghai-Xizang Plateau play a crucial role in regional water conservation, carbon sink maintenance, and plateau animal husbandry development [?, ?]. However, due to high altitude, low temperature, and nutrient limitation, this ecosystem is highly vulnerable to external disturbances [?, ?]. In recent years, continuous climate warming and nitrogen deposition have posed serious threats to alpine meadow ecosystem functions, particularly the structure and stability of plant communities [?]. Given that the temporal stability of plant communities can more accurately reflect ecosystem responses to global change, in-depth research on this topic is helpful for scientifically assessing degradation risk and restoration potential of grasslands and provides a scientific basis for formulating adaptive ecological protection and management strategies.

In summary, this study aims to simulate temperature increase and nitrogen deposition at different levels in typical alpine meadows on the Qinghai-Xizang Plateau through field control experiments, and systematically explore the following scientific questions: (1) How does biomass stability of alpine meadow plant communities respond to the interaction of climate warming and nitrogen deposition? (2) Is the response of plant community biomass stability to climate change primarily driven by species asynchrony, stability of dominant species, or stability of functional groups? and (3) Do these driving mechanisms change under the interaction between climate warming and nitrogen deposition? Through in-depth discussion of these issues, we aim to reveal the internal mechanisms of alpine meadow ecosystem stability changes under global change, improve our ability to predict future evolution trends of ecosystem function, and provide theoretical support for sustainable utilization and ecological security of plateau grasslands.

2.1 Study Area

The study was conducted at the Ministry of Education Field Scientific Observation Station of the Sanjiangyuan Ecosystem, located in Chengduo County, Yushu Autonomous Prefecture, Qinghai Province, China (33°24 30 N, 97°18 00 E; 4270 m a.s.l.). The study area has a typical high-altitude continental climate, with an annual average temperature ranging from -5.60°C to 3.80°C and average annual precipitation of 562.2 mm. Most precipitation (approximately 75.00%) falls from July to September, coinciding with peak grass growth. Vegetation is dominated by sedges and grasses, with main dominant species including *Kobresia humilis* (C.A. Mey ex Trauvt) Serg., *Kobresia pygmaea* Clarke, *Elymus nutans* Griseb., and *Poa annua* L.

2.2 Experimental Design and Soil Sampling

Temperature control devices used in field experiments fall into four main categories: open-top chambers (OTCs), soil heating cables, infrared reflectors, and infrared radiators. OTCs, which are simple in design and widely used, are particularly suitable for low-stature plants [?]. OTCs are also applicable for long-term positioning observation of alpine ecosystems, especially in resource-limited and environmentally sensitive field conditions, as they provide a relatively stable passive warming environment without introducing external energy sources.

In this study, a field experiment was established in a 50 m × 50 m fenced flat area in May 2023. Climate projections indicate that the Qinghai-Xizang Plateau may experience additional warming of up to 2.00°C by 2035 and 4.90°C by 2100

[?]. Therefore, we applied four warming treatments (W0 as control and three incremental warming levels) using OTCs to create a controlled temperature gradient (Table 1). Soil temperature at 5 cm depth and air temperature at 10 cm height were continuously measured from June to October using HOBO S-TMB-M006 temperature sensors (Onset Computer Corporation, Bourne, USA), with data recorded every 120 minutes.

During the growing season, both air temperature (10 cm height) and soil temperature (5 cm depth) in the study area showed significant fluctuations (Fig. 1a [Figure 1: see original paper] and 1b). Under control treatment, mean soil temperature was 10.83°C, with a maximum of 21.93°C and a minimum of 5.37°C. Compared with the control, W1, W2, and W3 treatments increased soil temperature by 0.61°C, 1.09°C, and 1.95°C, respectively. Mean air temperature under control treatment was 8.73°C, with a maximum of 16.92°C and a minimum of 1.02°C. Under W1, W2, and W3 treatments, air temperature increased by 0.47°C, 0.92°C, and 1.44°C, respectively. Overall, the OTCs effectively increased temperatures in this alpine meadow, with significant differences observed across warming gradients, achieving the desired warming effect (Table 1).

Atmospheric nitrogen deposition on the Qinghai-Xizang Plateau is approximately 8 kg N/(hm^2·a), primarily in the form of ammonium and nitrate nitrogen [?]. To simulate future nitrogen deposition scenarios, we applied three nitrogen levels: N0 (0 kg N/(hm^2·a)), N16 (16 kg N/(hm^2·a)), and N32 (32 kg N/(hm^2·a)). Ammonium nitrate (NH_4NO_3) was used to simulate nitrogen deposition during the growing season by dissolving NH_4NO_3 in water and spraying it evenly on each plot, with an equal amount of water also sprayed in the control plots.

The experiment used a randomized block design with 12 treatments and 4 replicates for each: W0N0, W0N16, W0N32, W1N0, W1N16, W1N32, W2N0, W2N16, W2N32, W3N0, W3N16, and W3N32.

2.3 Plant Community Composition and Biomass Measurement

Surveys were conducted in mid-August from 2023 to 2024. In each plot, a 0.5 m × 0.5 m quadrat was placed at the center to assess plant coverage and biomass. To estimate aboveground biomass for the plant community and functional groups (grasses, sedges, and forbs), we clipped all aboveground vegetation, sorted it by species, and oven-dried it at 65.00°C to a constant weight [?]. Across the study period, 19 plant species were recorded, categorized into the following functional groups: sedges (2 species), grasses (3 species), and forbs (14 species) (Fig. S1a).

Additionally, based on the relative biomass of each species in the control plots, we categorized species within the community by dominance [?]. Dominant species were defined as those with a relative abundance of >10.00%. Throughout the study period in the control plots, common species had a relative abundance between 1.00% and 10.00%, and rare species had a relative abundance of <1.00%

[?]. These three categories comprised 4, 5, and 3 species, respectively, accounting for 83.51%, 15.14%, and 1.35% of the total community relative biomass (Fig. S1b).

2.4 Data Analysis and Calculation

In this study, inter-annual variation in aboveground biomass from 2023 to 2024 was used as an indicator of plant community temporal stability [?]. Temporal stability of plant communities was calculated as the coefficient of variation (CV). Additionally, temporal stability of aboveground biomass was calculated for species grouped by dominance categories (dominant, common, and rare species) as well as by functional groups (sedge, grass, and forb). Species biomass temporal stability was determined as the mean temporal stability of individual species biomass within the community.

Species asynchrony, a potential mechanism regulating community temporal stability [?], was quantified as follows:

$$\phi_x = 1 - \frac{\sigma^2}{\left(\sum_{i=1}^{S} \sigma_i\right)^2}$$

where ϕ_x is the species synchrony; σ^2 is the variance of community aboveground biomass; and σ_i is the standard deviation of the biomass of species i in a community of S species. The species asynchrony index ranges from 0 (completely synchronous) to 1 (completely asynchronous).

The Simpson dominance index (D) was used to assess changes in community dominance, which may influence temporal stability [?]. The equation is as follows:

$$D = \sum_{i=1}^{S} P_i^2$$

where P_i is the relative aboveground biomass of species i in a community of S species.

2.5 Statistical Analysis

Data were naturally log-transformed to meet normality assumptions for statistical analysis. A mixed-effect model was used to analyze the effects of nitrogen deposition and climate warming on plant biomass, community biomass stability, stability of dominant, common, and rare species, stability of grasses, sedges, and forb biomass, as well as species asynchrony and dominance. Year, climate warming, and nitrogen deposition treatments, along with all their interactions, were included as fixed effects, while experimental plots were treated as random effects.

One-way analysis of variance (ANOVA) and Tukey' s multiple comparison tests were conducted to evaluate the impacts of climate warming and nitrogen deposition on each variable. Linear regression was used to examine the relationships between species asynchrony, species dominance, stability of the three abundance groups, stability of the three functional groups, and community biomass temporal stability. All statistical analyses were performed using SPSS v.24.0 software (SPSS Inc., Chicago, USA). Based on linear regression results, we constructed a structural equation model (SEM) using SPSS software. To build the SEM, we excluded biological factors unaffected by warming and nitrogen changes, then selected the best-fitting model based on a non-significant Chi-square test ($P > 0.050$), low Akaike information criterion (AIC), and low root mean square error of approximation (RMSEA) values. To comprehensively investigate causal relationships and underlying mechanisms among variables, we estimated path coefficients within the SEM framework to differentiate direct effects (i.e., the effect of variable A on variable C not mediated by other variables) from indirect effects (i.e., the effect of variable A on variable C mediated through variable B). Based on the significance of individual path coefficients, we systematically removed non-significant paths to refine the model structure and enhance overall model fit.

3.1 Plant Biomass of Alpine Meadow

Climate warming significantly impacted the biomass of plant community, dominant species, common species, and rare species ($P < 0.050$). Compared with W0, plant community biomass in 2023 increased by 6.68% and 8.81% under W2 and W3 treatments, respectively, and in 2024, it increased by 9.05% and 17.87%, respectively. Grass biomass, relative to W0, showed a significant increase of 38.70% and 115.23% in 2023 under W2 and W3 treatments, respectively, and increases of 12.61%, 37.31%, and 88.60% in 2024 under W1, W2, and W3 treatments, respectively. In 2024, biomass of dominant species under W2 and W3 treatments increased by 5.13% and 30.18%, respectively, while biomass of common and rare species decreased by 12.43% and 26.04% under W3 treatment (Fig. 2 [Figure 2: see original paper]; Table S1).

Nitrogen deposition significantly influenced the biomass of plant community, grass, and dominant species ($P < 0.001$). Under N32 treatment, plant community biomass increased by 19.96% in 2023 and 24.90% in 2024 compared with N0 treatment. Similarly, grass biomass increased by 74.42% in 2023 and 51.64% in 2024 under N32 treatment, and dominant species biomass increased by 9.90% in 2024.

The interaction of climate warming and nitrogen deposition had a significant effect on the biomass of plant community, grass, forb, dominant species, and common species ($P < 0.050$). Biomass of plant community, grass, and dominant species peaked under W3N32 treatment, whereas biomass of forb and common species reached their lowest levels under W3N32 treatment. Additionally, interactions among the three factors had no significant effects on the biomass of plant community, the three abundance groups (dominant, common, and rare species), or the three functional groups (sedge, grass, and forb).

3.2 Stability of Alpine Meadow Community Biomass

Climate warming significantly affected the stability of plant communities, grass, dominant species, and common species biomass, as well as species asynchrony ($P < 0.050$). Specifically, compared with W0 treatment, stability of plant community biomass decreased by 14.10% and 48.87% under W2 and W3 treatments, respectively. Species asynchrony decreased significantly by 22.81% and 50.57% under W2 and W3 treatments, respectively. Stability of grass, dominant species, and common species biomass decreased by 40.73%, 63.49%, and 53.99%, respectively, under W3 treatment. Nitrogen deposition significantly impacted stability of grass biomass ($P < 0.050$), with a notable reduction of 22.51% under N32 treatment. Additionally, the interaction between climate warming and nitrogen deposition significantly influenced stability of grass and dominant species biomass, and species asynchrony, with minimum values of 5.24, 43.85, and 0.12, respectively, under W3N32 treatment (Fig. 3 [Figure 3: see original paper]; Table S2).

3.3 Relationship Between Stability of Plant Community Biomass and Driving Factors

The primary factors influencing stability of grassland plant community biomass under climate warming and nitrogen deposition were evident. Linear regression analyses revealed significant positive correlations between stability of plant community biomass and that of grass ($R^2 = 0.32$, $P < 0.001$), forb ($R^2 = 0.11$, $P = 0.030$), and dominant species biomass ($R^2 = 0.38$, $P < 0.001$), as well as species asynchrony ($R^2 = 0.24$, $P < 0.001$) (Fig. 4 [Figure 4: see original paper]). The SEM indicated that stability of grass and dominant species biomass, and species asynchrony under climate warming and nitrogen deposition jointly explained 40.00% of the stability of plant community biomass (Fig. 5a [Figure 5: see original paper]).

Climate warming could indirectly reduce stability of plant community biomass by directly lowering stability of grass biomass (with a path coefficient of -0.62), stability of dominant species biomass (with a path coefficient of -0.74), and species asynchrony (with a path coefficient of -0.24). Meanwhile, nitrogen deposition could also reduce stability of plant community biomass by directly affecting stability of grass biomass (with a path coefficient of -0.34) (Fig. 5b). Therefore, both climate warming and nitrogen deposition could affect the stability of plant community biomass.

4.1 Effects of Climate Warming and Nitrogen Deposition on Plant Community Biomass

Grassland community biomass serves as a crucial indicator of plant community structure and function, reflecting vegetation growth conditions and responses to external environmental changes [?]. Temperature is a critical limiting factor influencing plant growth [?, ?]. Some studies have indicated that climate warming can decrease biomass by reducing soil moisture and inhibiting plant growth [?], while others have shown that it can enhance biomass through increased mineral nutrient absorption and organic matter accumulation [?]. Our results indicated that climate warming significantly increased the biomass of community, grass, and dominant species, while notably decreasing the biomass of common and rare species. This pattern can be explained by the following reasons: (1) different species exhibit varying sensitivities to changes in environmental factors [?]. Grass species and other dominant species typically possess higher photosynthetic efficiencies and heat tolerance, while common and rare species may exhibit weaker growth under climate warming conditions [?]; and (2) climate warming may alter patterns of ecological niche overlap and differentiation among species within the community. Under climate warming conditions, the growth space and resource acquisition of common and rare species become limited, exacerbating the ecological exclusion effect and further contributing to the decline in their biomass [?].

Nutrient availability can limit primary productivity in grasslands, while fertilization improves soil quality and nutrient bioavailability, positively impacting grassland ecosystem productivity [?]. Our findings indicated that at a nitrogen addition rate of 32 kg N/hm^2, biomass of plant community, grass species, and dominant species significantly increased. This result aligns with previous studies on grassland ecosystems in the Xizang Plateau [?, ?]. Variability in nitrogen utilization strategies and efficiencies among different functional groups leads to varying responses to nitrogen, ultimately affecting plant community biomass [?]. Research has shown that nitrogen deposition allows dominant species to acquire more nutrients for rapid growth [?]. This phenomenon can be attributed to the following factors: (1) intense competition within plant communities enables nitrogen-preferring species to access more light and water resources, with most grass species tending to prefer nitrogen compared with sedge species [?]; and (2) nitrogen addition can increase aboveground light limitation for low-stature plants through the accumulation of plant biomass and litter [?]. This asymmetry in light availability enhances the competitive advantage of resource-acquiring species that exhibit rapid growth [?]. As a result, plant communities tend to retain species belonging to similar functional groups, leaving smaller plant species unable to capture enough light to compensate for their limitation, thus affecting plant community biomass.

The results also showed that the interaction between climate warming and nitrogen deposition significantly affected the biomass of plant community, Gramineae, and dominant species, with the strongest promoting effect observed under W3N32 treatment. However, the biomass of various grasses and common species decreased to the lowest value under this treatment. This response indicates that the combined effect of temperature increases and nitrogen deposition is not simply additive but exhibits significant nonlinear characteristics. Previous studies have shown that climate warming and nitrogen deposition stimulate plant biomass and enhance key plant photosynthesis [?]. Increased soil nutrient availability (particularly nitrogen) allows grass species and dominant plants, known for their strong resource acquisition capabilities and adaptability to environmental changes, to quickly utilize these enhanced resources, further increasing their biomass. Simultaneously, climate warming and nitrogen deposition may amplify the competitive advantages of grass and dominant species within the community, intensifying their competitive exclusion of other plants. This competition limits the growth space and resource utilization of mixed grasses and common species, resulting in decreased biomass for these plants [?, ?].

4.2 Mechanisms of Temporal Stability of Plant Community Biomass in Alpine Meadows to Climate Warming and Nitrogen Deposition

Numerous studies have demonstrated that dominant species, functional groups, and species asynchrony play critical roles in maintaining grassland community stability [?, ?]. The results of this study showed that increasing temperature affects the stability of plant community biomass by reducing the stability of grass and dominant species. This finding is consistent with research on alpine meadows of the Xizang Plateau [?]. Dominant species [?] or plant functional groups under climate change [?, ?] play an important role in maintaining grassland productivity stability. There is increasing evidence that community biomass stability is often closely related to the stability of dominant species [?, ?]. The mass ratio hypothesis suggests that ecosystem stability is primarily regulated by the characteristics of dominant species or functional groups [?]. The degree of interspecific interaction in a given community is determined by plant species that exhibit the highest productivity [?].

Previous studies have shown that increasing temperature can weaken plant community stability by reducing species asynchrony and the relative abundance of dominant species [?, ?]. Species asynchrony is one of the key mechanisms maintaining community stability, as it effectively buffers adverse effects of the external environment through asynchronous responses of different species on the temporal scale [?]. This phenomenon reflects that the stability of plant biomass arises from compensation dynamics among interspecific species with different tolerances to environmental disturbances [?]. The results of this study also indicate that increasing temperature affects the stability of plant community biomass by reducing species asynchrony. The existence of species asynchrony enables different species in a community to occupy their specific ecological niches, reduces interspecific competition, and helps enhance the buffer capacity of plant communities against environmental disturbances, thereby improving biomass stability [?]. In this study area, *K. humilis* (sedge) and *E. nutans* (grass) are the main dominant species, which occupy a high biomass proportion in the plant community and have strong resource competitive advantages and adaptability. To adapt to environmental changes, dominant species ensure effective water use and nutrient acquisition through well-developed roots, higher canopy, increased branching, and larger specific leaf area [?, ?]. However, due to the small number of non-dominant species in the alpine meadow plant community, their impact on overall community productivity is relatively limited. Therefore, once the stability of dominant species declines, the buffer capacity of the whole community to environmental fluctuations will be significantly weakened, resulting in decreased community stability. Increasing temperature may further promote some high-temperature-tolerant and fast-growing dominant species (such as Gramineae) to occupy more resources and space in the community, strengthening their dominant position. This trend will reduce community species uniformity [?] and lead to the phenomenon of "mono-dominant species,"which makes species with similar functions dominate the community and weakens the role of asynchronous regulation mechanisms between species. Ultimately, the decline in species asynchrony will lead to reduced community responsiveness in the face of environmental fluctuations or extreme climate events, thereby reducing overall plant community stability [?]. These results confirm the important role of asynchronous mechanisms in maintaining community functional stability and suggest that we should pay attention to the dynamics of dominant species and their potential effects on community structure and functional stability in the context of climate warming.

The results of this study also showed that single nitrogen addition did not significantly affect the overall stability of plant community biomass. However, the interaction of nitrogen addition and climate warming (under W3N32 treatment) reduced the stability of grass biomass to the minimum value. These results suggest that nitrogen deposition and climate warming may indirectly regulate overall community stability by affecting the biomass stability of key functional groups such as grass. In alpine meadow ecosystems, grasses are important for maintaining community structure and function due to their strong resource utilization capacity and high biomass output [?]. However, under the interaction of climate warming and nitrogen deposition, biomass fluctuation of grass functional groups increased, which not only directly affected the stability of the group itself but also weakened the response ability of the whole community to external disturbances by changing the structural status of dominant species in the community [?]. In other words, the instability of key functional groups has an amplifying effect, resulting in a decline in stability at the community scale [?]. This trend suggests that changes in community stability may not be driven solely by species diversity or richness but more by the synergistic relationship of functional groups in the community. In conclusion, although nitrogen deposition alone has a weak effect on community stability, it can indirectly affect community stability by regulating biomass fluctuation of key functional groups under the background of temperature increase. These findings highlight the complexity of ecosystem response mechanisms under multiple climate changes and suggest that dynamic changes of key functional groups and their roles in maintaining community stability should receive more attention in future grassland ecological management and policy making.

5 Conclusions

Based on control experiments, this study systematically evaluated the effects of temperature increase, nitrogen deposition, and their interactions on the temporal stability of plant community biomass in alpine meadows of the Xizang Plateau. The results showed that increasing temperature significantly decreased the stability of plant community biomass by decreasing the stability of grass and dominant species biomass and weakening species asynchrony. Further analysis showed that there was a significant interaction between nitrogen deposition and temperature increase, which could aggravate the fluctuation of grass functional group biomass, thus amplifying its negative effect on community stability. These results indicate that the response of community stability to climate change is not only determined by species richness or diversity but also by key functional group stability and interspecific dynamic relationships. In the future, dynamic monitoring and regulation of dominant functional groups should be strengthened to enhance their ecological adaptability to multiple stress factors. Additionally, it should be pointed out that this study mainly revealed the short-term response process of plant communities to temperature increase and nitrogen deposition, and the relevant mechanisms need to be verified through long-term monitoring and multi-spatiotemporal scale studies to better understand the stability regulation mechanism of grassland ecosystems in the context of global change.

Conflict of Interest: The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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References

Baert J M, De Laender F, Sabbe K, et al. 2016. Biodiversity increases functional and compositional resistance, but decreases resilience in phytoplankton communities. *Ecology*, 97: 3433-3440.

Bai Y F, Han X G, Wu J G, et al. 2004. Ecosystem stability and compensatory effects in the Inner Mongolia grassland. *Nature*, 431: 181-184.

Chen J, Luo Y Q, Xia J Y, et al. 2017. Warming effects on ecosystem carbon fluxes are modulated by plant functional types. *Ecosystems*, 20: 515-526.

Chen Q Q, Wang S P, Seabloom E W, et al. 2022. Nutrients and herbivores impact grassland stability across spatial scales through different pathways. *Global Change Biology*, 28(8): 2678-2688.

DeMalach N, Kadmon R. 2017. Light competition explains diversity decline better than niche dimensionality. *Functional Ecology*, 31(9): 1834-1838.

Dong S K, Shang Z H, Gao J X, et al. 2022. Enhancing the ecological services of the Qinghai-Tibetan Plateau' s grasslands through sustainable restoration and management in era of global change. *Agriculture Ecosystems & Environment*, 326: 107756, doi: 10.1016/j.agee.2021.107756.

Donohue I, Hillebrand H, Montoya J M, et al. 2016. Navigating the complexity of ecological stability. *Ecology Letters*, 19(9): 1172-1185.

Fu G, Shen Z X. 2016a. Environmental humidity regulates effects of experimental warming on vegetation index and biomass production in an alpine meadow of the northern Tibet. *PLoS ONE*, 11(10): e0165643, doi: 10.1371/journal.pone.0165643.

Fu G, Shen Z X. 2016b. Response of alpine plants to nitrogen addition on the Tibetan Plateau: A meta-analysis. *Journal of Plant Growth Regulation*, 35: 974-979.

Galloway J N, Dentener F J, Capone D G, et al. 2004. Nitrogen cycles: Past, present, and future. *Biogeochemistry*, 70: 153-226.

Grime J P. 1998. Benefits of plant diversity to ecosystems: Immediate, filter and founder effects. *Journal of Ecology*, 86(6): 902-910.

Grman E, Lau J A, Schoolmaster D R, et al. 2010. Mechanisms contributing to stability in ecosystem function depend on the environmental context. *Ecology Letters*, 13(11): 1400-1410.

Guo H B, Quan Q, Niu S L, et al. 2023. Shifting biomass allocation and light limitation co-regulate the temporal stability of an alpine meadow under eutrophication. *Science of the Total Environment*, 860: 160411, doi: 10.1016/j.scitotenv.2022.160411.

Han F S, Yu C Q, Fu G. 2023. Non-growing/growing season non-uniform-warming increases precipitation use efficiency but reduces its temporal stability in an alpine meadow. *Frontiers in Plant Science*, 14: 1090204, doi: 10.3389/fpls.2023.1090204.

Harpole W S, Sullivan L L, Lind E M, et al. 2016. Addition of multiple limiting resources reduces grassland diversity. *Nature*, 537: 93–96.

Hautier Y, Seabloom E W, Borer E T, et al. 2014. Eutrophication weakens stabilizing effects of diversity in natural grasslands. *Nature*, 508: 521–525.

Houlahan J E, Currie D J, Cottenie K, et al. 2018. Negative relationships between species richness and temporal variability are common but weak in natural systems. *Ecology*, 99(11): 2592–2604.

Jiang Q X, Zhu J T, Shi P L, et al. 2024. Species asynchrony maintains community stability under different warming conditions. *Journal of Plant Ecology*, 17(3): rtae037, doi: 10.1093/jpe/rtae037.

Kwaku E A, Dong S K, Shen H, et al. 2021. Biomass and species diversity of different alpine plant communities respond differently to nitrogen deposition and experimental warming. *Plants*, 10(12): 2719, doi: 10.3390/plants10122719.

Li C L, Li Y H, Li X W, et al. 2021a. Differential responses of plant primary productivity to nutrient addition in natural and restored alpine grasslands in the Qinghai Lake Basin. *Frontiers in Plant Science*, 12: 792123, doi: 10.3389/fpls.2021.792123.

Li C Y, Peng F, Xue X, et al. 2018a. Productivity and quality of alpine grassland vary with soil water availability under experimental warming. *Frontiers in Plant Science*, 9: 01790, doi: 10.3389/fpls.2018.01790.

Li C Y, Lai C M, Peng F, et al. 2021b. Dominant plant functional group determine the response of the temporal stability of plant community biomass to 9-year warming on the Qinghai-Tibetan Plateau. *Frontiers in Plant Science*, 12: 704138, doi: 10.3389/fpls.2021.704138.

Li X E, Zhu X X, Wang S P, et al. 2018b. Responses of biotic interactions of dominant and subordinate species to decadal warming and simulated rotational grazing in Tibetan alpine meadow. *Science China-Life Sciences*, 61: 849–859.

Liu X D, Ma Q H, Yu H Y, et al. 2021. Climate warming-induced drought constrains vegetation productivity by weakening the temporal stability of the plant community in an arid grassland ecosystem. *Agricultural and Forest Meteorology*, 307: 108526, doi: 10.1016/j.agrformet.2021.108526.

López D R, Brizuela M A, Willems P, et al. 2013. Linking ecosystem resistance, resilience, and stability in steppes of North Patagonia. *Ecological Indicators*, 24: 1–11.

Loreau M, de Mazancourt C. 2008. Species synchrony and its drivers: Neutral and nonneutral community dynamics in fluctuating environments. *American Naturalist*, 172(2): 48–66.

Loreau M, de Mazancourt C. 2013. Biodiversity and ecosystem stability: A synthesis of underlying mechanisms. *Ecology Letters*, 16: 106–115.

Ma F F, Chen W N, Wang J S, et al. 2023. Below-ground net primary productivity stability in response to a nitrogen addition gradient in an alpine meadow. *Functional Ecology*, 37: 315–326.

Ma Z Y, Liu H Y, Mi Z R, et al. 2017. Climate warming reduces the temporal stability of plant community biomass production. *Nature Communications*, 8: 15378, doi: 10.1038/ncomms15378.

Muraina T O, Xu C, Yu Q, et al. 2021. Species asynchrony stabilises productivity under extreme drought across northern China grasslands. *Journal of Ecology*, 109(4): 1665–1675.

Pang Z, Jiang L L, Wang S P, et al. 2019. Differential response to warming of the uptake of nitrogen by plant species in non-degraded and degraded alpine grasslands. *Journal of Soils and Sediments*, 19: 2212–2221.

Peng Y F, Li F, Zhou G Y, et al. 2017. Nonlinear response of soil respiration to increasing nitrogen additions in a Tibetan alpine steppe. *Environmental Research Letters*, 12(2): 024018, doi: 10.1088/1748-9326/aa5ba6.

Polley H W, Wilsey B J, Derner J D. 2007. Dominant species constrain effects of species diversity on temporal variability in biomass production of tallgrass prairie. *Oikos*, 116(2): 2044–2052.

Shen H, Dong S K, Li S, et al. 2019. Effects of simulated N deposition on photosynthesis and productivity of key plants from different functional groups of alpine meadow on Qinghai-Tibetan Plateau. *Environmental Pollution*, 251: 731–737.

Shi Z, Xu X, Souza L, et al. 2016. Dual mechanisms regulate ecosystem stability under decade-long warming and hay harvest. *Nature Communications*, 7: 11973, doi: 10.1038/ncomms11973.

Smith B, Wilson J B. 1996. A consumer' s guide to evenness indices. *Oikos*, 76(1): 70–82.

Tao H F, Hao L W, Li S T, et al. 2021. Geochemistry and petrography of the sediments from the marginal areas of Qinghai Lake, northern Tibet Plateau, China: Implications for weathering and provenance. *Frontiers in Earth Science*, 9: 725553, doi: 10.3389/feart.2021.725553.

Wan Z Q, Gu R, Ganjurjav H, et al. 2024. The stability of aboveground productivity in a semiarid steppe in China is influenced by the plant community structure. *Communications Earth & Environment*, 5: 523, doi: 10.1038/s43247-024-01702-2.

Wang C Y, Wang J B, Zhang F W, et al. 2022. Stability response of alpine meadow communities to temperature and precipitation changes on the northern Tibetan Plateau. *Ecology and Evolution*, 12(2): e8592, doi: 10.1002/ece3.8592.

Wang J F, Knops J M H, Brassil C E, et al. 2017. Increased productivity in wet years drives a decline in ecosystem stability with nitrogen additions in arid grasslands. *Ecology*, 98(7): 1779–1786.

Wang S P, Duan J C, Xu G P, et al. 2012. Effects of warming and grazing on soil N availability, species composition, and ANPP in an alpine meadow. *Ecology*, 93(11): 2365–2376.

Wang Y H, Niu X X, Zhao L Q, et al. 2020. Biotic stability mechanisms in Inner Mongolian grassland. *Proceedings of the Royal Society B-Biological Sciences*, 287(1928): 20200675, doi: 10.1098/rspb.2020.0675.

Wei H X, Zhao J X, Luo T X. 2019. The effect of pika grazing on *Stipa purpurea* is amplified by warming but alleviated by increased precipitation in an alpine grassland. *Plant Ecology*, 220: 371–381.

Wu Q, Ren H Y, Wang Z W, et al. 2020. Additive negative effects of decadal warming and nitrogen addition on grassland community stability. *Journal of Ecology*, 108(4): 1442–1452.

Xu M H, Liu M, Xue X, et al. 2016. Warming effects on plant biomass allocation and correlations with the soil environment in an alpine meadow, China. *Journal of Arid Land*, 8(5): 773–786.

Xu Z W, Ren H Y, Li M H, et al. 2015. Environmental changes drive the temporal stability of semi-arid natural grasslands through altering species asynchrony. *Journal of Ecology*, 103(5): 1308–1316.

Yang G J, Lü X T, Stevens C J, et al. 2019. Mowing mitigates the negative impacts of N addition on plant species diversity. *Oecologia*, 189: 769–779.

Yang H J, Jiang L, Li L H, et al. 2012. Diversity-dependent stability under mowing and nutrient addition: Evidence from a 7-year grassland experiment. *Ecology Letters*, 15(6): 619–626.

Yang Z L, van Ruijven J, Du G Z. 2011. The effects of long-term fertilization on the temporal stability of alpine meadow communities. *Plant and Soil*, 345: 315–324.

Yang Z L, Zhang Q, Su F L, et al. 2017. Daytime warming lowers community temporal stability by reducing the abundance of dominant, stable species. *Global Change Biology*, 23(1): 154–163.

Zhang D Y, Peng Y F, Li F, et al. 2019. Trait identity and functional diversity co-drive response of ecosystem productivity to nitrogen enrichment. *Journal of Ecology*, 107(5): 2402–2414.

Zhang G Y, Shen Z X, Fu G. 2021. Function diversity of soil fungal community has little exclusive effects on the response of aboveground plant production to experimental warming in alpine grasslands. *Applied Soil Ecology*, 168: 104153, doi: 10.1016/j.apsoil.2021.104153.

Zhang J, Zuo X A, Lü P. 2023. Effects of grazing, extreme drought, extreme rainfall and nitrogen addition on vegetation characteristics and productivity of semi-arid grassland. *International Journal of Environmental Research and Public Health*, 20(2): 960, doi: 10.3390/ijerph20020960.

Zhang R, Shen H, Dong S K, et al. 2022. Effects of 5-year nitrogen addition on species composition and diversity of an alpine steppe plant community on Qinghai-Tibetan Plateau. *Plants*, 11(7): 966, doi: 10.3390/plants11070966.

Zhang T, Guo R, Gao S, et al. 2015. Responses of plant community composition and biomass production to warming and nitrogen deposition in a temperate meadow ecosystem. *PLoS ONE*, 10(4): e0123160, doi: 10.1371/journal.pone.0123160.

Zhang Y H, Loreau M, Lü X T, et al. 2016. Nitrogen enrichment weakens ecosystem stability through decreased species asynchrony and population stability in a temperate grassland. *Global Change Biology*, 22(4): 1445–1455.

Zhang Y H, Loreau M, He N P, et al. 2017. Mowing exacerbates the loss of ecosystem stability under nitrogen enrichment in a temperate grassland. *Functional Ecology*, 31(8): 1637–1646.

Zhao Y N, Yang B, Li M X, et al. 2019. Community composition, structure and productivity in response to nitrogen and phosphorus additions in a temperate meadow. *Science of the Total Environment*, 654: 863–871.

Zhou B R, Li S, Li F, et al. 2019. Plant functional groups asynchrony keep the community biomass stability along with the climate change–a 20-year experimental observation of alpine meadow in eastern Qinghai-Tibet Plateau. *Agriculture Ecosystems & Environment*, 282: 49–57.

Zong N, Hou G, Shi P L, et al. 2023. Winter warming alleviates the severely negative effects of nitrogen addition on ecosystem stability in a Tibetan alpine grassland. *Science of the Total Environment*, 855: 158923, doi: 10.1016/j.scitotenv.2022.158923.

Zwolicki A, Zmudczynska-Skarbek K, Richard P, et al. 2016. Importance of marine-derived nutrients supplied by planktivorous seabirds to high arctic tundra plant communities. *PLoS ONE*, 11(5): e0154950, doi: 10.1371/journal.pone.0154950.

Appendix

Fig. S1 Vegetation coverage (a) and relative biomass (b) of different plant functional groups and categories under different treatments. W0, no warming; W1, air temperature increased by 0.47°C or soil temperature increased by 0.61°C; W2, air temperature increased by 0.92°C or soil temperature increased by 1.09°C; W3, air temperature increased by 1.44°C or soil temperature increased by 1.95°C; N0, 0 kg N/($hm^2 \cdot a$); N16, 16 kg N/($hm^2 \cdot a$); N32, 32 kg N/($hm^2 \cdot a$).

Table S2 Results of linear mixed model assessing individual or interactive effects of climate warming (W) and nitrogen deposition (N) on the temporal stability of the biomass of plant community and different functional groups, as well as on species asynchrony and degree of species dominance.

Note: Figure translations are in progress. See original paper for figures.