Species asynchrony maintains community stability under different warming conditions

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This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination, and proofreading process, which may lead to differences between this Version and the Version of Record. Please cite this article as doi: 10.1093/jpe/rtae037.

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Abstract

Asymmetric seasonal warming, characterized by more pronounced temperature increases in winter than in summer, has become a critical feature of global warming, especially in cold and high-altitude regions. Previous studies have primarily focused on year-round warming, while comparatively less attention was paid to winter warming. However, a significant knowledge gap exists regarding the impacts of winter warming on ecosystem functions. To address this, we conducted an 8-year manipulated warming experiment in an alpine grassland on the Tibetan Plateau, employing three treatments: no warming, year-round warming, and winter warming. We found that neither year-round warming nor winter warming significantly alter species richness at the community-level. Notably, community biomass stability was maintained via species asynchrony. However, warming exerted significant effects on the plant abundance groups (dominant, common and rare species). Specifically, winter warming enhanced the stability of dominant species by increasing species asynchrony of dominant species, as the compensatory dynamics occurred between the grass and forbs. In contrast, year-round warming reduced the stability of common species, correlated with an increase in species richness and a decline in asynchrony among common species. Thus, our study underscores the capacity of alpine grassland to maintain community biomass stability via asynchrony dynamics of species under different warming conditions, although the stability of different abundance groups would be changed. Importantly, our results provide valuable insights for understanding the alpine grassland ecosystem on the Tibetan Plateau.

Keywords: Asymmetric seasonal warming; Dominants species; Ecological level; Species asynchrony; Temporal stability; Winter warming
1. Introduction

Global warming, one of the most significant global change elements in recent decades, has profoundly affected ecosystem structure and function, including biodiversity, plant productivity, and ecosystem stability (Klein et al., 2004; Liu et al., 2021; Mi et al., 2022). Elevated temperature can stimulate plant biomass via increasing soil available nitrogen (Rustad et al., 2001; Bai et al., 2013; Peng et al., 2016), while simultaneously altering soil temperature and humidity, and then affect the phenology of species (Wang et al., 2012; Henry et al., 2015; Suonan et al., 2017; Ganjurjav et al., 2020). These factors may lead to shifts in species composition and asynchronous dynamics, which in turn, may precipitate instability of plant productivity (Tilman et al., 1995; Yang et al., 2017; Muraina et al., 2021). The IPCC (2007) reported that asymmetric seasonal warming has been observed in most regions of the world, characterized by disproportionately greater temperature increases in winter than in summer (Wang et al., 2014; Xu et al., 2017), particularly in regions of high latitude and altitude. Previous studies have primarily focused on the effects of year-round or growing-season warming on ecosystems (Shi et al., 2016; Zhou et al., 2019; Li et al., 2021), while overlooking the implications of winter warming (but see Bokhorst et al., 2008; Natali et al., 2012; Suonan et al., 2017). Nevertheless, a few studies have demonstrated that simulated winter warming may have more substantial effects on plant community than simulated year-round warming, through greater changes in plant phenology (Suonan et al., 2017), or by boosting plant biomass (Natali et al., 2012; Grant et al., 2017). These suggested that community stability may respond differently to various warming conditions. However, the specific effects of winter warming on community stability are not yet fully comprehended (Han et al., 2023).

Temporal stability of plant biomass can indicate the ability of ecosystem function to maintain stable over time under external environmental perturbation (Grimm & Wissel, 1997; Donohue et al., 2016), which is defined here as the temporal mean of biomass divided by its standard deviation (Tilman, 1999). The debate over the relative contribution of mechanisms affecting community stability is ongoing. First, plant diversity has been generally considered to play a positive role in community stability, which is attributed to the higher likelihood of a more diverse community containing the appropriate species capable of withstanding external disturbances (Tilman, 1995; Loreau & Hector, 2001; Wang et al., 2012; Chen et al., 2022). Second, species asynchrony which may reflect a compensatory effect among species under environmental disturbance (Yachi & Loreau, 1999; Hautier et al., 2014; Pan et al., 2016; Wilcox et al., 2017), could stabilize community biomass. Third, there is a strong positive correlation between community and dominant species stability (Ma et al., 2017; Li et al., 2021), underscoring the significant role of dominant species as posited by the mass ratio hypothesis (Polley et al., 2007; Sasaki & Lauenroth, 2011). However, the relative contribution of these stabilizing mechanisms to community stability is uncertain under warming.

Different species exhibit different sensitivities to changes in environmental factors (Bai et al., 2004; Hector et al., 2010; Mariotte et al., 2014; Yang et al., 2017; Wang et al., 2019; Liu et al., 2021), which can exert various effects on community. Facing the environmental disturbances induced by climate warming, plant species often adopt alternative mechanisms to participate in
stabilizing community biomass (Zelikova et al., 2014; Shi et al., 2016; Ma et al., 2017; Wu et al., 2020; Zhu et al., 2020). Some studies have shown that warming-induced reductions in species richness compromise community stability (Klein et al., 2004; Post et al., 2013; Wang et al., 2012). Besides the loss of species, the asynchronous dynamics between co-occurring species are crucial, and warming could decrease community stability by reducing species asynchrony (Ma et al., 2017; Yang et al., 2017; Quan et al., 2021). Importantly, as components of the community, how plant abundance groups operate is generally explored. Wu et al. (2019) found that fluctuations in community biomass were associated with decline stability of dominant and common species. Ma et al. (2017) reported that community stability was strongly linked to dominant species under experimental warming. In addition, the effects of warming may vary within the abundance group levels (Dorji et al., 2013; Yang et al., 2017; Zhou et al., 2019). As a significant aspect of climate warming, winter warming may induce similar effects on plant communities. For instance, winter warming has a more significant impact on the phenology of mid- and late-flowering species than on the early-flowering species (Suonan et al., 2017), possibly leading to shifts in species composition and productivity dynamics. Given this, whether abundance groups respond differently under distinct warming conditions is rightly questioned. Nonetheless, the broader implications of winter warming on the relationship between the stability at abundance group- and community levels require further investigation.

The Tibetan Plateau, owing the largest alpine grasslands in the world, sustains approximately 5 million pastoralists for life and production (Li et al., 2017). As a unique high-altitude ecogeographic system, this region exhibits pronounced sensitivity to global climate change (Shen et al., 2011; Li et al., 2017). Over the past few decades, the Tibetan Plateau has experienced significant asymmetric seasonal warming (Liu & Chen, 2000; Wang et al., 2014; Xu et al., 2017). We collected temperature data from 1962 to 2020 in Damxung, which has revealed a trend towards more pronounced winter warming (Fig. S1, slope of lowest mean annual temperature > slope of mean annual temperature), thus serving as an ideal empirical system for examining the effects of asymmetric seasonal warming. However, prior warming experiments conducted in the Tibetan region have mostly focused on symmetric warming, lacking a comprehensive understanding of plant community responses to winter warming (Wang et al., 2012; Ganjurjav et al., 2020; Li et al., 2021). This knowledge gap calls for targeted research on the Tibetan Plateau (Zong et al., 2018; Han et al., 2023). Thus, we conducted an 8-year consecutive manipulative warming experiment involving asymmetric seasonal warming from 2013 to 2020 in an alpine grassland on the Tibetan Plateau. Our objectives were to address the following scientific questions: (1) How is the temporal stability of plant community biomass affected under different warming conditions? (2) How is the temporal stability of species at the abundance group level affected under different warming conditions? (3) What mechanisms may regulate community stability under winter and year-round warming?
2. Materials and methods

2.1. Study site

This experiment was conducted in an alpine meadow, located in Damxung grassland station, approximately 3 km north of Damxung County, Tibet Autonomous Region, China (91°05′ E, 30°29′ N). The study area, situated at an altitude of 4333 m above sea level, experiences a semi-arid continental climate. The average annual temperature is 1.3 °C, and the annual precipitation is 477 mm, with 85% of it occurring between June and August (Zong et al., 2023). This alpine steppe meadow is dominated by *Anaphalis xylorhiza*, *Carex montis-everestii*, *Kobresia pygmaea*, and *Stipa capillacea*. The soil in the area is sandy loam alpine meadow soil, with a depth of approximately 0.3-0.5 m. The majority of plant roots are distributed at the 10-15 cm of soil layer. Soil organic matter content ranges from 0.9% to 2.79%.

2.2. Experimental design

The field experiment was conducted in 2012 and followed a randomized block design with three replications for each treatment. The treatments included three warming conditions: no warming, year-round warming, and winter warming. To implement warming, we used passive heating in conjunction with open-top chambers (OTCs). The OTCs, made of 3 mm-thick polycarbonate plastic, had a top diameter of 100 cm, a bottom diameter of 140 cm, and a height of 40 cm. Winter warming treatment was applied from October to April of the following year, during which the OTCs were installed and removed for the rest of the year (Zong et al., 2018).

2.3. Measurements of meteorological factors and plant production

Air temperature data from 1962 to 2020 were collected from the Damxung National Meteorological Station (http://edc.cma.gov.cn). Soil moisture and temperature at a depth of 5 cm were monitored at 30-minute intervals simultaneously from 2012 to 2014 (HOBO weather station, Onset Inc., Bourne, MA, USA). Winter warming increased annual soil surface temperature (0-5 cm) by 0.8 °C, while year-round warming increased it by 1.4 °C (Fig. S2a). Winter warming decreased soil surface moisture (0-5 cm) by 2.4%, while year-round warming decreased it by 4.7% (Fig. S2b).

During the peak annual growing season (mid-August) from 2013 to 2020, the coverage of each plant species was visually estimated in three plots of each treatment. Permanent 1 m × 1 m quadrats were established, subdivided into 100 grids measuring 10 cm × 10 cm each for sampling. The percentage coverage of each plant species was calculated by summing the species coverage within each 10 cm × 10 cm grid (Zong et al., 2023). According to Ma et al. (2017), plant species were classified into three abundance groups based on relative abundance: dominant species (relative abundance > 5% under no warming), common species (relative abundance between 1% and 5%), and rare species (relative abundance < 1%). These three groups comprised 5, 4, and 14 species, accounting for 82.81%, 12.24%, and 4.95% of the total community coverage, respectively (Table S1). We have also partitioned species into two different plant functional groups: grass and non-grass forbs (Table S1).
2.4. Data calculation

In this study, we collected eight years of data from 2013 to 2020. Following previous work (Tilman, 1999; Loreau & de Mazancourt, 2008; Zhang et al., 2019), we calculated the temporal stability of plant biomass as $\mu/\alpha$, where $\mu$ and $\alpha$ are the inter-annual mean and standard deviation of plant biomass, respectively. Community-level stability was defined as the temporal stability of the whole community biomass of a plot, abundance group-level stability was defined as the temporal stability of each abundance group biomass of a plot, and species stability was defined as the temporal stability of individual species biomass of a plot. Species richness was calculated by the number of species in the plot.

Species asynchrony for each plot, the degree of asynchrony in the species dynamics of constituent species of its community was quantified as

$$1 - \frac{\alpha_T^2}{\sum_{i=1}^{N} \alpha_i}$$

where $\alpha_T$ is the temporal variance of community biomass, and $\alpha_i$ is the standard deviation of ANPP of species $i$ in the $N$-species community (Zhang et al., 2019). Furthermore, to measure community compensation dynamics better, we used a new variance ratio approach to calculate CPE (Compensatory Effect) refer to Zhao et al. (2022), which was quantified as

$$\sqrt{\sum_{i=1}^{N} \frac{\alpha_i^2}{\alpha_T}}$$

If CPE $> 1$, it reflects compensatory dynamics has occurred; if CPE $< 1$, then the changes between species are synchronized.

2.5. Statistical analyses

In this study, we performed all analyses in R version 4.2.1 (R Core Team, 2022). First, we applied a linear mixed-effects model using the "lme" function with package "NLME" to test the impact of winter warming and year-round warming treatments on community- and abundance group levels metrics. We set treatment as fixed effects, and block as a random effect in each model. Next, to explore the relationships between stability and other related variables, we conducted simple linear regression using the "lm" function among no warming, year-round warming, and winter warming treatments. Furthermore, multiple linear regression analysis was employed using the "lm" function to examine the associations between the stability of dominant species and its related metrics. All graphs were plotted in Origin Pro 2021, and all values were selectively logarithm transformed to meet the normality requirement for data analysis.

3. Results

Both winter warming and year-round warming treatments had no obvious effects on community stability, species stability, species asynchrony, or species richness, which are community-level metrics (Fig. 1a and b). However, winter warming significantly increased the stability of dominant species (Fig. 1a), and year-round warming significantly decreased the stability of
common species (Fig. 1b). When considering the dominant species alone, we found that winter warming significantly increased its species asynchrony, but decreased standard deviation (SD) of biomass production (Fig. 1a). As for the common species, year-round warming increased its species richness, and slightly decreased species asynchrony by 31% compared with the control (Fig. 1b).

The linear regression showed there was no significant relationship between community stability and the stability and asynchrony of dominant species (Fig. 2a and b), while positively correlated with species asynchrony (Fig. 2c). At abundance group level, the stability of dominant species was positively correlated with its species asynchrony (Fig. 2d), but negatively correlated with its SD of biomass production (Fig. 2e). However, no obvious relationship was found between the stability of dominant species and its species richness (Fig. 2f). Moreover, multiple linear regression revealed the stability of dominant species was not correlated with its SD of biomass, but positively correlated with its species asynchrony (Table S3). The stability of common species was positively correlated with its species asynchrony (Fig. 2g) but negatively correlated with its SD of biomass production (Fig. 2h) and slightly correlated with its richness (Fig. 2i).

We further divided the dominant species into two groups: grass and forbs. The cover of grass increased under winter warming in most years except for 2014 and 2015, whereas the cover of forbs decreased under winter warming except for 2020 (Fig. 3a). This result shows that winter warming treatment increased the cover of grass in a given year, while decreased the cover of forbs. However, the cover of grass and forbs consistently decreased under year-round warming in most years (Fig. 3b). Furthermore, we calculated the compensatory effect (CPE) between the dominant species (Table S4). The values of CPE were 1.45 and nearly 1 under winter warming and year-round warming, respectively, which indicated significant compensatory dynamics existed between the dominant species under winter warming.

4. Discussion

While currently experiencing global asymmetric seasonal warming, it is important to deeply understand how plant diversity and stability at the community- and abundance group levels respond to different warming conditions. Therefore, we conducted experiments with year-round and winter warming treatments on the Tibetan Plateau. Winter warming stabilized the biomass production of dominant species mainly by increasing its species asynchrony, that is, a compensatory dynamic occurred between the grass and forbs. However, both winter warming and year-round warming had no obvious impacts on community-level diversity and stability. Our findings point to the need to pay more attention to the diversity and stability of different ecological levels under global change, especially at the abundance group level.

4.1. The impacts of winter and year-round warming on community-level diversity and stability

In our study, both winter warming and year-round warming did not significantly alter plant community-level diversity and stability. Consistent with our results, some studies have also demonstrated low-level warming (+1~2°C) has no significant effects on community-level diversity and stability in similar regions (Zhu et al., 2020; Quan et al., 2021). Based on our findings as well as those of others, it can be inferred that alpine plants are less sensitive to low-
level warming with relatively minor temperature increases (Zhou et al., 2019; Zhu et al., 2020; Quan et al., 2021). However, in contrast, other experiments have yielded mixed impacts on diversity and stability (Grime et al., 2008; Zhu et al., 2020; Quan et al., 2021). Shi et al. (2016) reported that warming increased community diversity and stabilized biomass by promoting the productivity of the C4 functional group. Other studies reported that year-round warming decreased community stability through reduced species asynchrony (Ma et al., 2017) or lower species richness caused by resource competition (Brooker & Kikvidze, 2008). Furthermore, other winter warming experiments conducted on the Tibetan Plateau have demonstrated a decrease in community stability (Han et al., 2023). The inconsistent results may be attributed to variations in experimental duration, warming conditions, vegetation types, and environmental factors, such as precipitation and temperature among different study sites (Fu et al., 2019; Liu et al., 2021; Fu & Sun, 2022). In our study, the non-responsiveness of community stability may be due to the constant species asynchrony, as community stability and species asynchrony both remained stable under warming and showed a significant positive correlation. While the stability and asynchrony of dominant species contributed little to the community stability, we can infer that stabilized community biomass was mainly attributed to species asynchrony rather than dominant species.

4.2. The impacts of winter and year-round warming on abundance group-level diversity and stability

It is essential to explore how stability at abundance group level responded to external disturbances and its underlying mechanisms. In our experiments, winter warming enhanced the stability of the dominant species, mainly by increasing its species asynchrony. This finding is similar to other community-level studies that have shown high species asynchrony can stabilize plant biomass in response to fluctuating environmental factors (Bai et al., 2004; Baert et al., 2016; Muraina et al., 2021). This reflects that plant biomass stability results from compensatory dynamics among interspecific species with differing tolerance to environmental disturbances (Schindler, 1990; Doak et al., 1998; Gonzalez & Loreau, 2009; Hallett et al., 2014). Our study also found that there were asynchronous fluctuations in the cover of different plant functional groups within dominant species, specifically an increase in grass cover and a decrease in forbs cover. Furthermore, we calculated that the CPE (Compensatory Effect) value was greater than 1 under winter warming, suggesting that compensatory dynamics existed between dominant species thus contributing to its increased stability (Zhao et al., 2022).

The asynchronous dynamics between the cover of dominant grass and non-grass forbs under winter warming can be attributed to their different characteristics. Winter warming may advance the spring phenology of plants (Shen et al., 2016; Suonan et al., 2017; Signarbieux et al., 2017; Arfin Khan et al., 2018; Chen et al., 2023) by providing more heat to rapidly meet the requirements of plant heating accumulations, resulting in enhancing plant biomass by prolonged growing season in the alpine region (Parmesan & Yohe, 2003; Wang et al., 2012; Kreyling et al., 2019; Meng et al., 2019; Hu et al., 2020). Additionally, warming may stimulate soil nitrogen mineralization, therefore increasing the availability of nitrogen which may promote subsequent plant growth (Rustad et al., 2001; Malyshev & Henry, 2012; Peng et al., 2016; Zong et al.,
On the Tibetan Plateau, deep-rooted grass species with higher water use efficiency were less sensitive to drought induced by warming (Liu et al., 2018; Zhou et al., 2019) and exhibited advanced phenology, allowing them to more rapidly occupy a larger resource space under winter warming (Shen et al., 2002; Li et al., 2021). In contrast, sedges with a shallow-rooted nature were more sensitive to warming-induced drought causing a delay in their greening up (Klein et al., 2008; Dorji et al., 2013; Zhu et al., 2016; Liu et al., 2018; Ganjurjav et al., 2020). Additionally, grass group with a stronger stress-tolerator strategy (maintaining individual survival in resource-poor environments) tended to better adapt to warming stress than other forbs (Zhou et al., 2021; Yu et al., 2022). Subsequently, the taller and more productive grass species could shade lower forbs, limiting light competition (Fig. 4; Wang et al., 2012; Li et al., 2018; Kreyling et al., 2019). This means, perhaps often overlooked, that in addition to influencing community-level variables, future winter warming may favor the biomass production of grass and intensify inter-specific competition for limited resources in our studied alpine grassland.

However, under year-round warming, the cover of dominant grass and forbs both decreased, and there was no significant compensatory effect was observed among the dominant species. It could be explained by the fact that summer warming induced more loss of soil moisture and that also inhibited the growth of dominant grass. In addition, year-round warming reduced the stability of common species probably due to increasing common species that were more sensitive to warming after 2017 (Fig. S3), resulting in substantial biomass fluctuations.

5. Conclusions

Our study found that winter warming, but not year-round warming, enhanced the temporal stability of dominant species biomass by increasing its species asynchrony, which was facilitated by compensatory dynamics between grass and forbs. As dominant grass species serve as the main food source for livestock (Yang et al., 2016; Ganjurjav et al., 2019), it is favorable for grasslands to provide a stable food supply for livestock on the Tibetan Plateau under winter warming. In this study, we emphasize that the responses of plant community dynamics to winter warming differ from year-round warming. Moreover, we need to pay more attention to the temporal stability at different ecological levels, especially abundance group level. Under the ongoing global climate change, our study carries significant ecological implications for understanding the Tibetan Plateau ecosystem.
Funding

This work was supported by the National Natural Science Foundation of China (U20A2009, 41991234, 42077422, 41725003), the National Key Research and Development Program of China (2022YFF1301801), the Major Science and Technology Projects in Tibet (XZ202101ZD0007G and XZ202101ZD0003N).

Acknowledgements

We gratefully acknowledge the reviewers for spending their valuable time to provide constructive comments.

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


Mi J (2022) The loss of plant species diversity dominated by temperature promotes local productivity in the steppe of eastern Inner Mongolia. Ecological Indicators.


Figure legends:

Fig. 1 The effects of winter warming (a) and year-round warming (b) on different community- and abundance group levels variables of plant communities (n = 3). Winter warming and year-round warming represent the differences from the ambient plots without any warming treatment. Ds, Cs, and Rs represent dominant, common, and rare species, respectively. "*" indicates significance at the 0.1 level, "**" indicates significance at the 0.05 level. Dots are mean values estimated from linear mixed-effect models; error bars are 95% confidence intervals. See Table S2 for test statistics.

Fig. 2 Community stability in relation to (a) stability of dominant species, (b) species asynchrony of dominant species, (c) species asynchrony. Stability of dominant species in relation to (d) species asynchrony of Ds, (e) cover SD of Ds, (f) richness of Ds. Stability of common species in relation to (g) species asynchrony of Cs, (h) cover SD of Cs, (i) richness of Cs. The black solid lines represent significant regression relationships at 0.05 level. Ds and Cs represent dominant and common species, respectively. The filled dots represent year-round warming, half-filled dots represent winter warming, and empty dots represent no warming. Each dot represents an experimental plot (n = 3). Shaded areas represent 95% confidence intervals.

Fig. 3 Changes in the cover of different PFG groups of the dominant species under winter warming (a) and year-round warming (b) to no warming from 2013 to 2020. And incorporate standard error (SE) bars in the mean bar.

Fig. 4 The relationship between grass and forbs of the dominant species changes over time (created with BioRender.com).
Figure 1
Figure 2

(a) $R^2 = 0.2931 \quad P = 0.1322$

(b) $R^2 = 0.3742 \quad P = 0.0800$

(c) $R^2 = 0.6063 \quad P = 0.0134$

(d) $R^2 = 0.8433 \quad P = 0.0005$

(e) $R^2 = 0.6883 \quad P = 0.0057$

(f) $R^2 = 0.0242 \quad P = 0.8892$

(g) $R^2 = 0.6974 \quad P = 0.0051$

(h) $R^2 = 0.6395 \quad P = 0.0097$

(i) $R^2 = 0.4023 \quad P = 0.0666$
Figure 3

Changes in cover of PFGs versus NW

(a) Grass
(b) Forbs


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