Additive negative effects of decadal warming and nitrogen addition on grassland community stability

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Abstract

Much recent research has explored how global warming and increased nitrogen (N) deposition, two important components of global environmental changes, influence the structure and functioning of natural ecosystems. However, how ecosystem dynamics respond to the combination of long-term warming and N enrichment remains largely unexplored. The impact of warming and N addition on the temporal stability of plant communities were investigated in a decade-long field experiment. The study was conducted in northern China in a desert steppe, using a split-plot design with warming as the main-plot factor and N addition as the split-plot factor. Long-term warming and N addition had additive, negative effects on plant community stability. A warming-induced decrease in species richness was not a significant driver of decreased community stability, which was instead driven by the decreased stability of dominant species under warming. On the other hand, an N-induced decrease in community stability was ascribed to both decreased stability of dominant and common species and decreased asynchronous population dynamics under N addition. Our results suggest that ongoing anthropogenic environmental changes may have appreciable consequences for the stability of natural grassland functions and services while also highlighting the different mechanisms associated with the similar effects of climate warming and increased N deposition on grassland community stability.

Introduction

The stability of an ecosystem represents its ability to maintain consistent properties in the face of temporal variation in environmental conditions (Lehman and Tilman 2000; Pimm 1984). A stable ecosystem is critical for providing sustainable ecological goods and services to humanity (López et al. 2013). Numerous experimental studies have reported that increasing species diversity can enhance plant community stability (Gross et al. 2014; Tilman and Downing 1994). Besides species diversity, recent studies have revealed that community stability can be affected by other factors, such as the relative abundance of dominant species (Sasaki and Lauenroth 2011), the composition of plant functional groups (Shi et al. 2016), and the stability of constituent populations (Yang et al. 2011; Zhang et al. 2016). All of these may have the potential to be altered by climate warming and increased nitrogen (N) deposition, which is two of the most prominent global change stressors (Galloway et al. 2008; IPCC 2013).

Climate warming may have positive (Shi et al. 2016) or negative (Ma et al. 2017; Yang et al. 2017) effects on community stability. For instance, the increased temperature can enhance plant community stability by increasing the biomass of plant functional groups (Shi et al. 2016) or decreasing plant community stability via decreasing the degree of species asynchrony (Ma et al. 2017) and the relative abundance of dominant, stable species (Yang et al. 2017). Nitrogen addition may decrease community stability through decreasing plant diversity (Yang et al. 2012), the degree of species asynchrony (Xu et al. 2015; Zhang et al. 2016), population stability (Zhang et al. 2016) or the relative abundance of dominant species (Yang et al. 2011), as increased N supply can relieve plant species from N limitation, which may alter the response of species to environmental fluctuations.

Although studies on the effects of global environmental change on community stability have considered either warming (Ma et al. 2017) or N addition alone (Zhang et al. 2016), the combined effects of warming and N addition have not been studied. Furthermore, the existing studies have been conducted in various types of grasslands but not in the desert steppe, and the duration of most of these studies has been relatively short ($\leqslant$ 5 years; Chen et al. 2016; Ma et al. 2017). The desert steppe is a transitional ecosystem between grassland and desert and occurs only in the Eurasian temperate steppe (Chen et al. 2017). It plays an important role in carbon sequestration, biodiversity, animal husbandry, and regional economic development (Angerer et al. 2008). Therefore, it is important to understand how plant community stability responds to projected warming and increased N deposition, including their potentially interactive effects, on the stability of the desert steppe. In this study, we made a first attempt to investigate the long-term impacts of warming and N addition on plant

community stability in a species-poor desert steppe (averages 7.5 species/m^2), we examined the following questions: (a) What are the impacts of warming and N addition on the temporal stability of plant communities in the studied desert steppe? (b) What mechanisms drove the responses of community stability to warming and N addition? (c) Do warming and N addition interactively affect community stability?

Methods

The study was conducted in a desert steppe located at Siziwang Banner (41°46′43.6″ N, 111°53′41.7″ E, at 1456 m a.s.l.), in Inner Mongolia, northern China. Mean annual precipitation during the experimental period at the study site was about 229 mm, with 78% occurring from June to September.

The experiment used a split-plot design with warming applied to the main plot and N addition to the subplot. Six pairs of 3 × 4 m plots were established in a flat area at a distance of 3 m between the two plots in each pair. One main plot in each pair was assigned to warming (W1) and the other was maintained at ambient temperature (W0, or no warming). Each main plot was divided into two, 2 m × 3 m subplots, with one of them randomly assigned to receive supplemental N (N1) and the other to receive no N (N0, ambient N addition rate). Thus, 24 subplots were established with the following treatment combinations: no warming or N addition as the control, warming without N addition (W), N addition without warming (N), and warming plus N addition (WN). Each year, N was applied once prior to a rainfall event in about the third week of June in the form of NH$_4$NO$_3$, at a rate of 10 g N m^{-2} year^{-1}. Each warmed plot was heated continuously for 24 hr a day throughout the year, starting from May 2006. Heating was done using a 165 cm × 15 cm MSR-2420 infrared radiator (Kalgo Electronics, Bethlehem, PA, USA). The infrared radiator was hung 2.25 m above the ground in the warming plots and was set at an electrical power output of 2000 W. In the no-warming plots, a dummy radiator of the same physical size was hung at the same height to simulate the shading effect of the heater.

A permanent 1 × 1 m quadrat was established in each of the 24 subplots. In each quadrat, a visual estimate of canopy cover of each species was conducted in August at the peak of the growing season from 2006 to 2015. In conducting the measurement, each quadrat was subdivided into 100 grids of 10 × 10 cm. The percent cover of each plant species was estimated by summing the cover of the species in each 10 × 10 cm grid within the quadrat. Species richness was measured as the total number of species present in each subplot. Species were classified into three abundance groups: dominant, common and rare species (Chen et al. 2016; Clark and Tilman 2008).

We quantified the stability of the whole community, dominant, common and rare species as the ratio of mean plant coverage and its temporal *SD* in each subplot over the decade of the experiment (2006-2015) (Lehman and Tilman 2000; Tilman et al. 2006).

Species asynchrony was calculated as the community-wide asynchrony index (Loreau and de Mazancourt 2008):

$$1 - \varphi_x = 1 - \sigma^2 \Big/ \left(\sum\nolimits_{i=1}^{S} \sigma_i \right)^2$$

where φ_x is species synchrony, σ^2 is the variance of community coverage and σ_i is the *SD* of the coverage of species i in a plot with S species. The asynchrony index equals one when species fluctuations are perfectly asynchronized, and equals zero when they are perfectly synchronized.

Results and Discussion
Species richness

Species richness was decreased by 11.7% by warming ($F_{1,10} = 9.02$, $p = .013$; Figure 1), but was not affected by N addition; the effect of warming was independent of N treatment ($F_{1,10} = 0.09$, $p = .774$; Fig. 1).

Community stability and stability of different plant groups

In this study, both warming and N addition resulted in decreased community stability (Fig. 2). Community stability was decreased by warming by 9.7% ($F_{1,10} = 6.26$, $p = .031$) and by N addition by 15.8% ($F_{1,10} = 23.45$, $p = .001$; Figure 2), respectively. The stability of dominant species was decreased by warming by 5.1% ($F_{1,10} = 6.15$, $p = .033$) and by N addition by 9.9% ($F_{1,10} = 29.07$, $p < .001$; Figure 2). The stability of common species was decreased by N addition by 17.8% ($F_{1,10} = 50.56$, $p < .001$; Figure 2); but was not affected by warming ($F_{1,10} = 2.35$, $p = .156$; Fig. 2).

The stability of rare species was not affected by either warming or N addition (Figure 2). The decreased temporal stability of our study grassland communities under decadal experimental warming is consistent with findings from a five-year warming experiment conducted in an alpine grassland on the Tibetan Plateau, which showed that warming reduced community stability by decreasing the degree of asynchrony in population dynamics across species (Ma et al. 2017). In the present study, N addition also resulted in reduced grassland temporal stability. This finding is consistent with the results of studies of temperate semi-arid grasslands (Xu et al. 2015; Zhang et al. 2016).
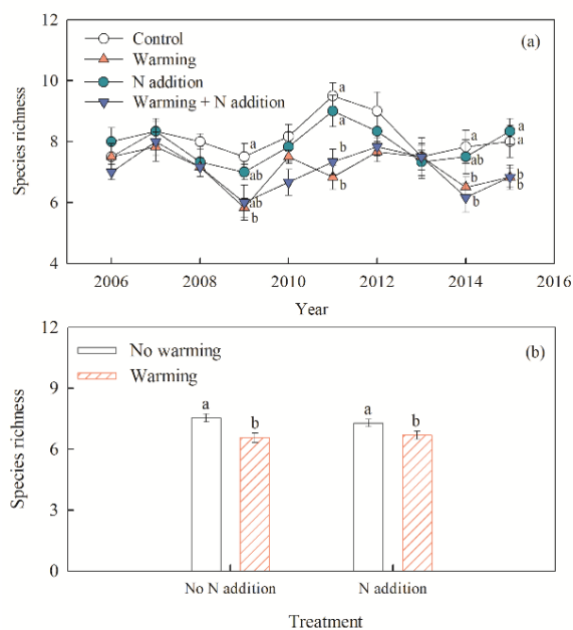

Figure 1. Effects of warming and nitrogen addition on species richness during a decade (2006-2015) of study in a desert steppe in China.
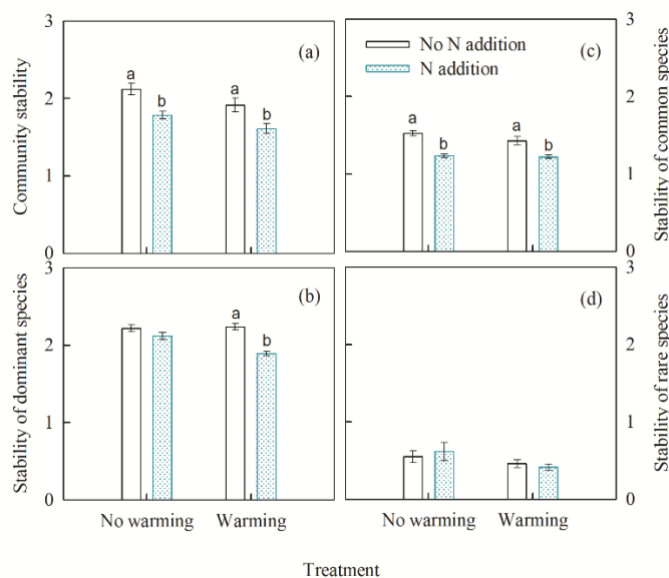

Figure 2. Effects of nitrogen addition on (a) mean (±SE) plant community stability and (b) the stability of dominant, (c) common and (d) rare species during a decade (2006-2015) of study in a desert steppe in China.

Species asynchrony

Species asynchrony was decreased by 7.2% by N addition ($F_{1,10} = 18.29$, $p = .002$; Fig. 3) but was not affected by warming; the effect of N addition was independent of warming treatment (Fig. 3).

Relationships among species asynchrony, species richness and plant stability

The SEM shows that warming decreased community stability by decreasing the stability of dominant species, whereas N addition decreased community stability by decreasing both the stability of dominant and common species and species asynchrony (Figure 4). Although warming had negative effects on species richness, species richness did not affect community stability (Figure 4). Warming may affect plant community stability through several mechanisms: (a) by influencing plant diversity (Klein et al. 2004); (b) by differential responses of species to environmental fluctuations which thus influence the degree of species asynchrony (Ma et al. 2017); or (c) by inducing changes in the stability of dominant species or plant functional/abundance groups (Sasaki and Lauenroth 2011; Shi et al. 2016; Yang et al. 2017). Our results point to the third mechanism, the decreased stability of dominant species, as playing a key role in the observed negative response of community stability to warming. The role of dominant species stability in community-level stability has been suggested to be most important in communities dominated by a small number of species (Sasaki and Lauenroth 2011; Yang et al. 2017), which is the case for our study grassland (Fig. 4). In our experiment, warming may reduce the stability of C_3 plants. The stability of C_3 plant species was more sensitive than that of C_4 plant species in the desert steppe, as C_4 plant species are generally better adapted to warmer and drier conditions (Gowik and Westhoff 2011). However, similar to these findings, some recent studies have also documented the lack of significant relationships between species richness and community stability (Xu et al. 2015; Yang et al. 2017). Our study was conducted at a single site where differences in species richness among treatments were small (1.5-9.5 species/m^2), which probably has made it difficult to detect the effects of species richness on community stability.
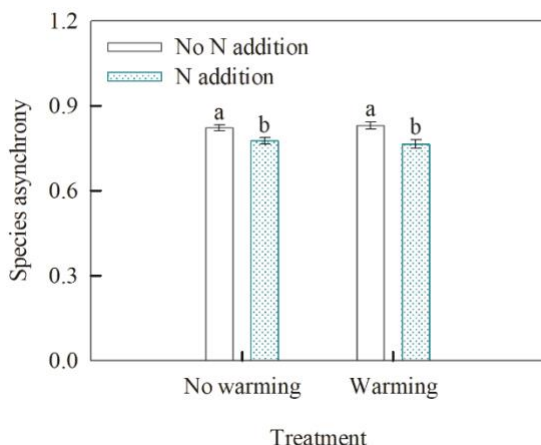
Figure 3. Effects of nitrogen addition on species asynchrony (M ± SE) across a decade (2006-2015) of study in a desert steppe in China.
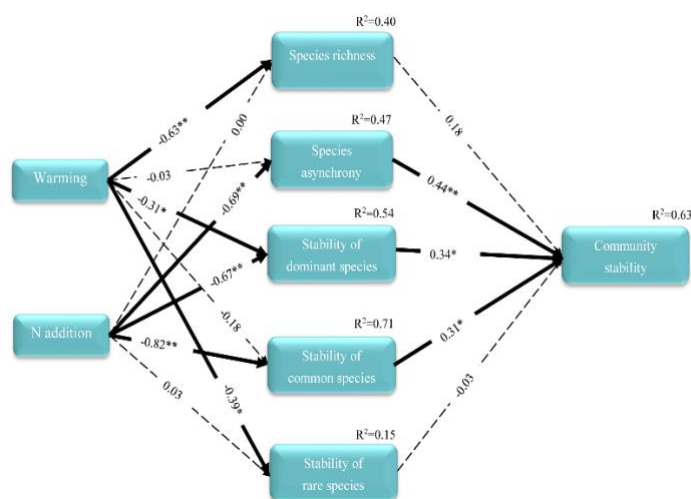
Figure 4. Structural equation modelling (SEM) illustrating the direct and indirect effects of warming and N addition on community stability. The R^2 values indicate the proportion of variance explained. Significance levels: * $p < .05$, ** $p < .01$. $\chi^2 = 19.540$, df = 12, $p = .076$.

Conclusions

The results indicate that warming and increased N deposition, two important components of global environmental change, may combine to threaten plant community stability in arid grassland ecosystems. These findings also highlight the different mechanisms associated with the similar effects of climate warming and increased N deposition on grassland community stability. The data combined with the reported adverse effects of ongoing anthropogenic environmental changes on the stability of other ecosystems, point to the need for immediate intervention to mitigate projected future global environmental changes, in order to conserve the stability of natural ecosystem functions and services provided for humanity.

Acknowledgements

References

Angerer, J., Han, G., Fujisaki, I., & Havstad, K. 2008. Climate change and ecosystems of Asia with emphasis on Inner Mongolia and Mongolia. *Rangelands*, 30: 46-51.

Chen, W., Zhang, Y., Mai, X., & Shen, Y. 2016. Multiple mechanisms contributed to the reduced stability of Inner Mongolia grassland ecosystem following nitrogen enrichment. *Plant and Soil*, 409: 283-296.

Chen, Y., Li, J., Ju, W., Ruan, H., Qin, Z., Huang, Y., ... Propastin, P. 2017. Quantitative assessments of water-use efficiency in Temperate Eurasian Steppe along an aridity gradient. *PLoS ONE*, 12: e0179875.

Clark, C. M., & Tilman, D. 2008. Loss of plant species after chronic low-level nitrogen deposition to prairie grasslands. *Nature*, 451: 712-715.

Galloway, J. N., Townsend, A. R., Erisman, J. W., Bekunda M., Cai, Z., Freney, J. R., ... Sutton, M. A. 2008. Transformation of the nitrogen cycle: Recent trends, questions, and potential solutions. *Science*, *320*, 889-892.

Gowik, U., & Westhoff, P. 2011. The path from C_3 to C_4 photosynthesis. *Plant Physiology*, 155: 56-63.

Gross, K., Cardinale, B. J., Fox, J. W., Gonzalez, A., Loreau, M., Polley, H. W., ... van Ruijven, J. 2014. Species richness and the temporal stability of biomass production: A new analysis of recent biodiversity experiments. *The American Naturalist*, 183: 1-12.

IPCC. 2013. *Climate Change 2013: The physical science basis. The contribution of working group I to the fifth assessment report of the Intergovernmental Panel on Climate Change*. Cambridge, UK: Cambridge University Press.

Klein, J. A., Harte, J., & Zhao, X. Q. 2004. Experimental warming causes large and rapid species loss, dampened by simulated grazing, on the Tibetan Plateau. *Ecology Letters*, 7: 1170-1179.

Lehman, C. L., & Tilman, D. 2000. Biodiversity, stability, and productivity in competitive communities. *The American*

Naturalist, 156: 534-552.

López, D. R., Brizuela, M. A., Willems, P., Aguiar, M. R., Siffredi, G., & Bran, D. 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. *The American Naturalist*, 172: E48-66.

Ma, Z., Liu, H., Mi, Z., Zhang, Z., Wang, Y., Xu, W., ... He, J. -S. 2017. Climate warming reduces the temporal stability of plant community biomass production. *Nature Communications*, 8: 15378.

Pimm, S. L. 1984. The complexity and stability of ecosystems. *Nature*, 307: 321-326.

Sasaki, T., & Lauenroth, W. K. 2011. Dominant species, rather than diversity, regulates temporal stability of plant communities. *Oecologia*, 166: 761-768.

Shi, Z., Xu, X., Souza, L., Wilcox, K., Jiang, L., Liang, J., ... Luo, Y. 2016. Dual mechanisms regulate ecosystem stability under decade-long warming and hay harvest. *Nature Communications*, 7: 11973.

Tilman, D. 1999. The ecological consequences of changes in biodiversity: A research for general principles. *Ecology*, 80: 1455-1474.

Tilman, D., & Downing, J. A. 1994. Biodiversity and stability in grasslands. *Nature*, 367: 363-365.

Tilman, D., Reich, P. B., & Knops, J. M. 2006. Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature*, 441: 629-632.

Xu, Z., Ren, H., Li, M. -H., van Ruijven, J., Han, X., Wan, S., ... MacDougall, A. 2015. Environmental changes drive the temporal stability of semi-arid natural grasslands through altering species asynchrony. *Journal of Ecology*, 103: 1308-1316.

Yang, H., Jiang, L., Li, L., Li, A., Wu, M., & Wan, S. 2012. Diversity-dependent stability under mowing and nutrient addition: evidence from a 7-year grassland experiment. *Ecology Letters*, 15: 619-626.

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

Yang, Z., Zhang, Q., Su, F., Zhang, C., Pu, Z., Xia, J., ... Jiang, L. 2017. Daytime warming lowers community temporal stability by reducing the abundance of dominant, stable species. *Global Change Biology*, 23: 154-163.

Zhang, Y., Loreau, M., Lu, X., He, N., Zhang, G., & Han, X. 2016. Nitrogen enrichment weakens ecosystem stability through decreased species asynchrony and population stability in a temperate grassland. *Global Change Biology*, 22: 1445-1455.