

Nitrogen addition and mowing alter drought resistance and recovery of grassland communities

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Nitrogen enrichment and land use are known to influence various ecosystems, but how these anthropogenic changes influence community and ecosystem responses to disturbance remains poorly understood. Here we investigated the effects of increased nitrogen input and mowing on the resistance and recovery of temperate semiarid grassland experiencing a three-year drought. Nitrogen addition increased grassland biomass recovery but decreased structural recovery after drought, whereas annual mowing increased grassland biomass recovery and structural recovery but reduced structural resistance to drought. The treatment effects on community biomass/structural resistance and recovery were largely modulated by the stability of the dominant species and asynchronous dynamics among species, and the community biomass resistance and recovery were also greatly driven by the stability of grasses. Community biomass resistance/recovery in response to drought was positively associated with its corresponding structural stability. Our study provides important experimental evidence that both nitrogen addition and mowing could substantially change grassland stability in both functional and structural aspects. Our findings emphasize the need to study changes across levels of ecological organization for a more complete understanding of ecosystem responses to disturbances under widespread environmental changes.

biomass stability, dominant species, drought, functional stability, species asynchrony, structural stability

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INTRODUCTION

Human activities have resulted in substantial increases in the

frequency and intensity of extreme climate events, such as drought, worldwide (IPCC, 2014; Meehl et al., 2000). These climate extremes, which are projected to increase in the next decades, may exert large impact on the structure and functioning of plant communities, as observed for various regions

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following naturally occurring precipitation extremes (Buckland et al., 1997; Ciais et al., 2005; Knapp et al., 2015) and in studies experimentally imposing precipitation deficits (de Boeck et al., 2011; Dreesen et al., 2014; Heitschmidt et al., 2005). Considerable efforts have been directed towards assessing the stability of ecological communities experiencing extreme climate events (Hoover et al., 2014; Tilman and Downing, 1994; Van Ruijven and Berendse, 2010). A major component of this work has focused on two elements of ecological stability: resistance (the ability of an ecological system to withstand disturbance (Pimm, 1984)), and recovery (the ability of an ecological system to recover from disturbance (Lloret et al., 2011)). However, until recently research on this topic has mainly focused on the resistance and/or recovery of ecosystem functions (particularly biomass), paying far less attention to the resistance and recovery of the structure (i.e., species composition and abundance) of ecological communities. This one-dimensional approach, however, precludes a comprehensive understanding of ecological stability across levels of ecological organization.

On the one hand, community functional and structural stability may be positively associated with each other, a scenario that may arise when functional resistance/recovery of an ecosystem is closely linked to the resistance/recovery of community structure (Baert et al., 2016; Hillebrand et al., 2018; Polazzo and Rico, 2021). On the other hand, ecosystem functions may be less responsive to disturbance than community structure, as functional redundancy among species may allow communities to mitigate their functional changes despite potentially substantial structural deviation from their pre-disturbance states (Allison and Martiny, 2008; Yachi and Loreau, 1999). Within this context, accumulating theoretical and empirical evidence suggests asynchronous population dynamics among species as a potentially important mechanism stabilizing ecosystem function (Hautier et al., 2014; Hector et al., 2010; Ives et al., 1999; Loreau and de Mazancourt, 2008). However, greater asynchrony also indicates lower community structural stability, as it corresponds to greater change in species composition (Allan et al., 2011; Hillebrand et al., 2018). Thus, it is possible for structural and functional stability to be decoupled or even negatively associated with each other.

Empirical studies have reported that ecosystem stability in response to drought could have been mediated by composition (Carlsson et al., 2017; Fry et al., 2013) or identity (Mackie et al., 2019; Xu et al., 2021) of plant functional groups. However, the relative contributions of composition and identity of plant functional groups, together with other factors, to community resistance and recovery to drought have rarely been identified. Moreover, species diversity is often thought as an important factor influencing plant community drought resistance (Baert et al., 2016; Vogel et al., 2012) and recovery (Kreyling et al., 2017; Van Ruijven and

Berendse, 2010). Nevertheless, empirical studies of the diversity-resistance/recovery relationships have reported mixed results. For instance, ecosystem functional resistance has been found to increase (Isbell et al., 2015; Kahmen et al., 2005; Tilman and Downing, 1994), decrease (Allison, 2004; de Boeck et al., 2008; Pfisterer and Schmid, 2002), or remain unchanged (Carter and Blair, 2012; DeClerck et al., 2006; Van Ruijven and Berendse, 2010; Wang et al., 2007) with species diversity. Likewise, positive (Tilman and Downing, 1994; Van Ruijven and Berendse, 2010; Vogel et al., 2012), negative (Pfisterer and Schmid, 2002) and neutral (Carter and Blair, 2012; Isbell et al., 2015; Xu et al., 2014) diversity-ecosystem functional recovery relationships have been reported. By comparison, relatively few studies have addressed the diversity-structural stability relationships (Baert et al., 2016; Frank and McNaughton, 1991; Van Peer et al., 2004). Therefore, future studies should consider examining how species diversity relates to both functional and structural resistance/recovery for a more comprehensive understanding of ecological consequences of ongoing biodiversity loss.

Rather than species diversity, the mass ratio hypothesis suggests that the properties of an ecosystem are largely determined by its dominant species (Grime, 1998). Consistent with this hypothesis, functional resistance and/or recovery of grassland communities in response to drought were found to be closely related to the resource-use strategies (Mackie et al., 2019), traits and abundance (Stampfli et al., 2018; Volaire et al., 2014) of dominant plant species. Functional resistance of forest communities to drought has also been reported to depend upon dominant tree species (DeClerck et al., 2006). By comparison, the role of dominant species in modulating community structural resistance and recovery in response to drought has rarely been assessed. Elucidating the importance of dominant species, relative to species richness and asynchrony, for resistance and recovery at functional and structural levels would provide a more mechanistic understanding of ecosystem dynamics under ongoing anthropogenic changes.

Nitrogen enrichment has been reported to alter species richness (Suding et al., 2005; Vitousek et al., 1997), species asynchrony (Hector et al., 2010; Isbell et al., 2009), and the abundance of dominant species (Bowman et al., 2018; Xu et al., 2015), with potential consequences for community drought resistance and recovery. However, nitrogen enrichment effects on community drought resistance and recovery remain poorly understood. The few empirical studies on this topic have explored the effect of increased nitrogen availability on grassland functional resistance to drought (Bharath et al., 2020; Hofer et al., 2017; Xu et al., 2014) and functional recovery after drought (Bharath et al., 2020; Kinugasa et al., 2012; Xu et al., 2014). Few studies, to our knowledge, have explored the linkage between nitrogen input and community structural resistance/recovery (but see Jia et al., 2021). As a

common land-use practice in grasslands, mowing may also result in changes in species diversity (Maron and Jefferies, 2001; Socher et al., 2013) and the abundance of dominant species (Clark and Wilson, 2001; Galvánek et al., 2015) as well as soil water and nitrogen availability (Wang et al., 2021), which may potentially influence the response of plant communities to drought (Stampfli et al., 2018; Tilman and Downing, 1994; Xu et al., 2014). Nevertheless, we know relatively little about how mowing influences grassland stability. The few studies that examined the effect of mowing on grassland biomass temporal stability have produced mixed results that mowing either increased (Yang et al., 2012) or decreased community stability (Zhang et al., 2017) in temperate grasslands. Even less is known about how mowing affects plant community drought resistance and recovery (but see Vogel et al., 2012), especially from the structural perspective.

In this study, we experimentally simulated nitrogen addition and mowing in a temperate semiarid grassland in Erguna, Northeast China to assess their effects on grassland drought resistance and recovery from both functional and structural perspectives. The temperate semiarid grassland constitutes an important component of the Eurasian grassland biome, providing a range of necessary products and services for local human populations. Atmospheric nitrogen deposition is projected to increase in the next decades in this region (Liu et al., 2011), which, combined with mowing as a common grassland management practice (Wang et al., 2011), may impose significant impact on this important ecosystem that is also projected to experience more frequent and intense drought (Lu et al., 2021).

During the experiment, our study grassland experienced natural drought in three consecutive growing seasons (2015 to 2017), reducing aboveground plant biomass by 73.3%, 58.4% and 45.3%, respectively, compared with 2014. The arid index (defined as the ratio of annual precipitation and potential evapotranspiration; UNEP, 1997) suggested severe water deficiency in the drought years (Figure S1 in Supporting Information). Such natural drought events provide an excellent opportunity to study grassland responses to extreme climate events. We aimed to (1) explore how nitrogen enrichment and mowing influence functional and structural stability (resistance and recovery) of the temperate grassland in response to drought, and (2) elucidate the pathways through which nitrogen enrichment and mowing influence functional and structural stability.

RESULTS

Species richness and community AGB were both significantly lower (LSD tests, all $P < 0.01$ but $P = 0.243$ for richness in 2017) in the drought years (2015–2017) than the

pre-drought year (2014) (Figure 1). Nitrogen enrichment increased community AGB, even in the drought years (except for 2015), but had no effect on species richness; mowing resulted in decreased community AGB, but increased species richness (Table 1; Figure 1). Nitrogen enrichment decreased species asynchrony for both drought resistance and recovery ($P < 0.01$ & 0.001 , respectively), while mowing increased species asynchrony for both drought resistance and recovery ($P < 0.1$ & 0.05 , respectively) (Table 1).

As the most dominant species, *L. chinensis* accounted for approximately 46.5% of plant AGB, which was much greater than the contribution of any other species (none exceeded 12.3%). Nitrogen enrichment consistently increased the AGB of *L. chinensis* (all $P < 0.05$), while mowing consistently reduced the AGB of *L. chinensis*, across the five years of the experiment (all $P < 0.001$, Table S1, Figure S3 in Supporting Information). The treatment effects on the summed AGB of the five dominant species largely mirrored those for *L. chinensis* (Table S1, Figure S3 in Supporting Information).

Nitrogen enrichment showed no effect on community biomass resistance (Figure 2A) but significantly increased community biomass recovery (Figure 2B), which was rather similar to the effects of mowing (Figure 2A, B). For structural stability, nitrogen enrichment had no discernable effect on community structural resistance but reduced community structural recovery, whereas mowing significantly decreased community structural resistance but increased community structural recovery (Table 1; Figure 2C, D).

Nitrogen enrichment had no significant effects on biomass resistance or recovery of *L. chinensis* (Table 1; Figure 3A, B), while mowing showed no effect on biomass resistance of *L. chinensis* but increased its biomass recovery (Table 1; Figure 3A, B). At the functional group level, nitrogen addition and mowing both increased biomass recovery of grasses ($P < 0.1$ & 0.01 , respectively; Figure 3D); however, neither nitrogen addition nor mowing effects on grass resistance, forb resistance and forb recovery were found (all $P > 0.1$, Figure 3C, E, F). Nitrogen enrichment did not change dominant structural resistance but stimulated dominant structural recovery, while mowing had no significant effect on dominant structural resistance but reduced dominant structural recovery in response to drought (Table 1; Figure 3G, H).

Structural equation modelling (SEM) revealed that nitrogen addition had no significant effect on community biomass resistance to drought, as its negative effect through decreasing species asynchrony was largely offset by its positive effect through stimulating *L. chinensis* biomass resistance and then grass biomass resistance to drought. Mowing decreased community structural resistance by reducing dominant structural resistance, and then exerted a weak negative effect on community biomass resistance, however, this negative effect on community biomass resistance was offset by

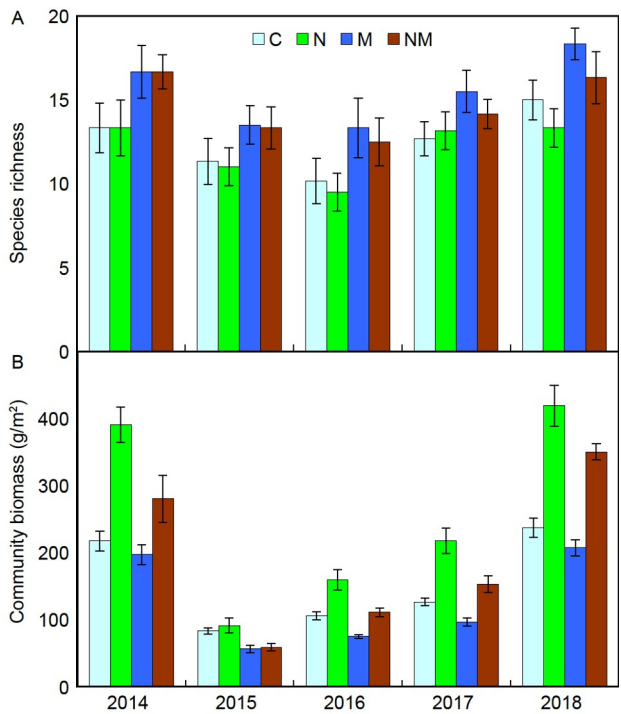


Figure 1 Effects of nitrogen addition and mowing on (A) species richness and (B) community above-ground biomass from 2014 to 2018. Bars indicate means $\pm$ SE. C: control; N: nitrogen addition; M: mowing; NM: nitrogen addition plus mowing.

its positive effect through stimulating species asynchrony (Figure 4A, Table S2 in Supporting Information). Nitrogen-

stimulated *L. chinensis* biomass resistance weakly decreased community structural resistance by decreasing dominant structural resistance (Figure 4A). Nitrogen addition promoted community biomass recovery after drought mainly by increasing biomass recovery of grasses and decreasing species asynchrony, although this positive effect was offset, to a lesser extent, by decreasing dominant structural recovery and then community structural recovery. Mowing increased community biomass recovery after drought mainly by increasing biomass recovery of *L. chinensis* and by stimulating community structural recovery through decreasing dominant structural recovery (Figure 4B, Table S2 in Supporting Information). Nitrogen addition reduced community structural recovery after drought mainly by decreasing species asynchrony and by increasing structural recovery of dominant species (Figure 4B, Table S2 in Supporting Information). The SEMs also revealed positive relationships between community biomass resistance and structural resistance and between community biomass recovery and structural recovery (Figure 4).

DISCUSSION

Many terrestrial ecosystems are increasingly experiencing drought events. However, despite much research, a general understanding of mechanisms underlying ecosystem resistance to drought and recovery after drought remains elu-

Table 1 Results (*F*-value) of linear mixed-effects models on the effects of year (*Y*), nitrogen addition (*N*), mowing (*M*) and their interactions on community aboveground biomass (AGB) and species richness, and results (*F*-value) of two-way ANOVAs on the effects of block (*B*), *N*, *M* and their interactions on biomass resistance (B_{rst}), biomass recovery (B_{rc}), structural resistance (S_{rst}), structural recovery (S_{rc}) of plant communities, B_{rst} and B_{rc} of *L. chinensis*, B_{rst} and B_{rc} of grasses and forbs, S_{rst} and S_{rc} of dominant species experienced drought in three consecutive growing seasons

Variables	<i>Y</i>	<i>N</i>	<i>M</i>	<i>N</i> × <i>M</i>
Community AGB	177.66***	104.79***	58.58***	1.06 ns
Species richness	8.69***	1.38 ns	24.70***	0.15 ns
	<i>B</i>	<i>N</i>	<i>M</i>	<i>N</i> × <i>M</i>
Asynchrony for resistance	3.91*	14.18**	3.29^	2.06 ns
Asynchrony for recovery	3.02*	27.39***	4.97*	1.06 ns
Community B_{rst}	0.81 ns	0.46 ns	0.71 ns	1.88 ns
Community B_{rc}	1.02 ns	11.73**	13.78**	0.08 ns
Community S_{rst}	3.04*	0.13 ns	8.69**	0.40 ns
Community S_{rc}	2.23 ns	7.27*	12.98**	1.89 ns
<i>L. chinensis</i> B_{rst}	0.73 ns	3.00 ns	0.24 ns	3.44^
<i>L. chinensis</i> B_{rc}	0.99 ns	0.43 ns	13.38**	0.72 ns
Grass B_{rst}	0.48 ns	0.74 ns	0.19 ns	7.78*
Forb B_{rst}	1.04 ns	1.69 ns	0.44 ns	2.58 ns
Grass B_{rc}	1.45 ns	4.22^	13.22**	0.44 ns
Forb B_{rc}	0.76 ns	0.02 ns	0.09 ns	0.93 ns
Dominant S_{rst}	1.89 ns	0.53 ns	2.25 ns	0.09 ns
Dominant S_{rc}	1.18 ns	9.25**	13.77**	0.10 ns

Note: ***: $P < 0.001$, **: $P < 0.01$, *: $P < 0.05$, ^: $P < 0.1$, ns: $P > 0.1$.

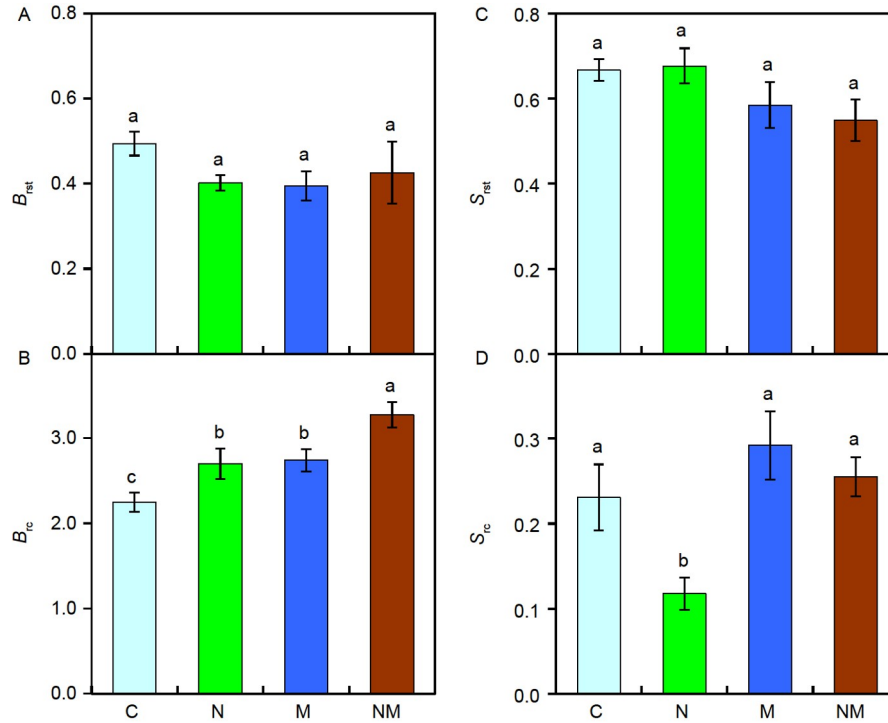


Figure 2 Effects of nitrogen addition and mowing on biomass resistance (B_{res}), biomass recovery (B_{rec}), structural resistance (S_{res}) and structural recovery (S_{rec}) of grassland communities experiencing drought in three consecutive growing seasons. Bars indicate means $\pm$ SE. Different letters above the bars indicate significant differences ($P < 0.05$) among treatments. C: control; N: nitrogen addition; M: mowing; NM: nitrogen addition plus mowing.

sive. Elucidating how ecosystems respond to drought is becoming particularly pressing when these ecosystems are simultaneously undergoing chronic environmental changes (e.g., increased N deposition), which may have the potential to alter ecosystem responses to drought (Shi et al., 2018; Xu et al., 2014).

Our study showed that nitrogen addition increased plant community biomass recovery after drought, but not biomass resistance to drought, a result partially consistent with that of Bharath et al. (2020) in the Great Plains in North America. Mechanistically, we found that decrease in species asynchrony with nitrogen enrichment contributed substantially to the increase in community biomass recovery. This relationship presumably results from the way that most species tend to reestablish their biomass following drought, especially when nitrogen (the most important limiting nutrient for this grassland) was supplied, and the summed increment in community biomass may increase with decrease of species asynchrony due to the reduced opposite responses of some species (Xu et al., 2014).

The influences of mowing on grassland drought resistance and recovery have rarely been explored. The only study on this topic, to our knowledge, examined the response of grasslands to experimentally induced drought under mowing of different frequency, reporting that grassland biomass resistance declined with increasing mowing frequency (Vogel et al., 2012). However, our study found that mowing tends to

promoted community biomass recovery but not resistance, primarily via enhancing the biomass recovery of *L. chinensis* (Figure 4B). *L. chinensis* has long strong rhizomes, relative deep root and high capacity of vegetative expansion (Luo et al., 2021; Wang et al., 2004). *L. chinensis* plants are known to allocate more of their biomass into their belowground components when experiencing drought (Xu and Zhou, 2006) and mowing (Luo et al., 2021), presumably as an adaptive strategy to maximize water and nutrients intake. This strategy may have allowed *L. chinensis* to quickly expand its clonal reproduction when more water becomes available, contributing to increased community biomass recovery in the mowing plots after drought. Furthermore, mowing relieves water stress for the community by reducing evaporation after drought, which may also lead to increased biomass recovery of grassland. The discrepancy between the results of our study and Vogel et al. (2012) may be explained by the differences in mowing frequency (once in our study vs. four times a year in Vogel et al.) and community assembly (naturally assembled grasslands in our study vs. experimentally assembled grasslands in Vogel et al.) between the two studies, since both mowing frequency and community assembly may potentially influence community drought resistance and recovery (DeClerck et al., 2006; Stampfli et al., 2018).

One of our most important results is that mowing altered grassland structural stability, resulting in reduced structural

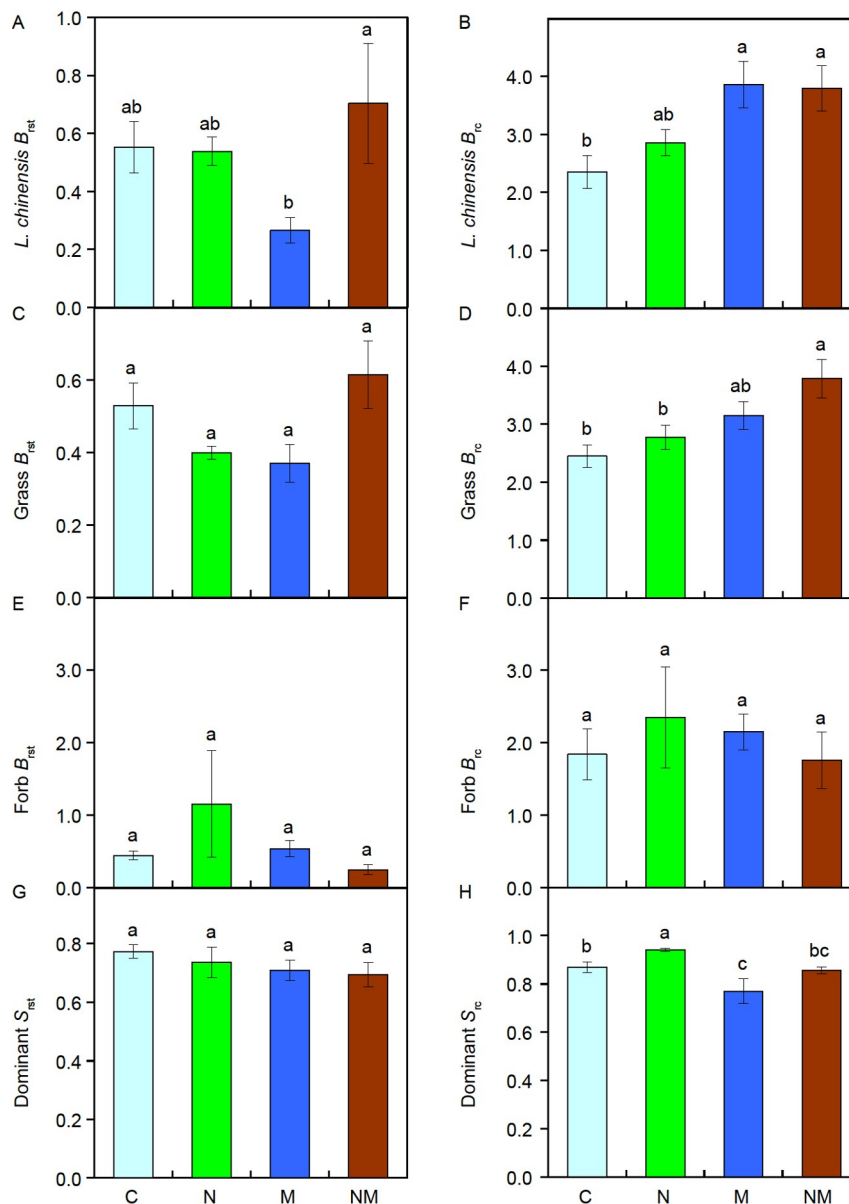


Figure 3 Effects of nitrogen addition and mowing on biomass resistance (B_{rst}) and recovery (B_{re}) of *L. chinensis* (A, B), B_{rst} and B_{re} of grasses and forbs (C–F), and structural resistance (S_{rst}) and structural recovery (S_{re}) of dominant species assemblages (G, H) experiencing drought in three consecutive growing seasons. Bars indicate means $\pm$ SE. Different letters above the bars indicate significant differences ($P < 0.05$) among treatments. C: control; N: nitrogen addition; M: mowing; NM: nitrogen addition plus mowing.

resistance and increased structural recovery of the grassland. Notably, these effects of mowing on community structural stability were largely mediated via dominant species structural stability. As the most dominant species, *L. chinensis* imposed negative effects on the other dominant species (Figure S4 in Supporting Information). Mowing may have reduced the dominance of *L. chinensis* by hampering the formation of regeneration buds and the propagation of rhizomes (Yang et al., 1995), which provided more opportunities for the survival and prosperity of other species. The increases in the number and abundance of other species (e.g., the dominant species *C. duriuscula*, *C. squarrosa* and *B.*

scorzonrifolium) under mowing increased the dissimilarity between drought and pre-drought communities and between drought and post-drought communities, resulting in decreased community structural resistance and increased structural recovery. Our results are consistent with previous studies reporting that mowing tended to reduce the abundance of dominant species, resulting in increase in grassland plant diversity (Leps, 2014). Although species richness was involved in modulating the effects of mowing on community biomass recovery, our study demonstrates that dominant species was much more important in driving the reassembly of communities experiencing drought.

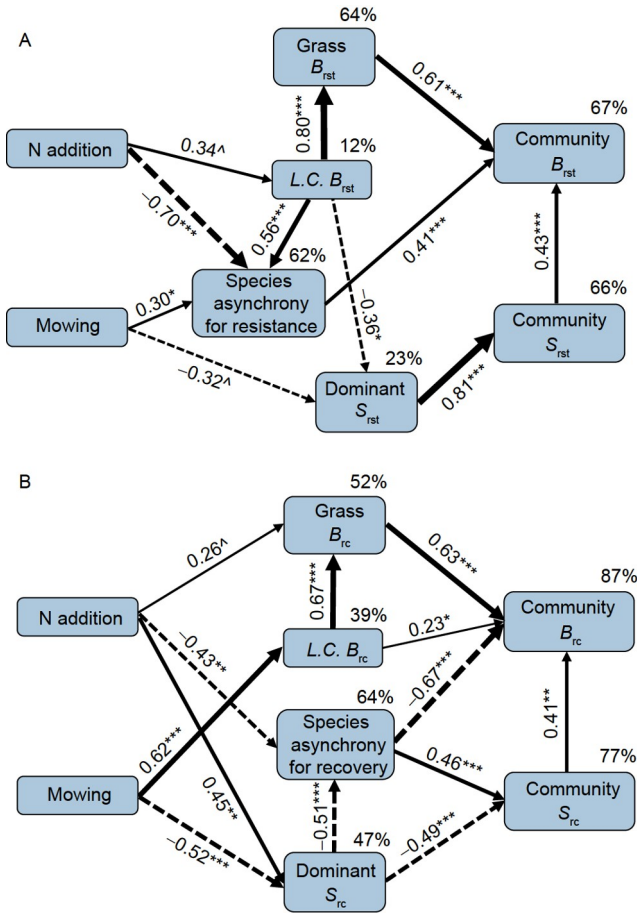


Figure 4 The final structural equation models relating nitrogen addition and mowing to (A) biomass resistance (B_{rst}) and structural resistance (S_{rst}), (B) biomass recovery (B_{rc}) and structural recovery (S_{rc}) of our study grassland in response to drought. L.C.: *L. chinensis*. The final models adequately fitted the data (A: $\chi^2=16.67$, $P=0.477$, $df=17$, RMSEA=0.000, $P=0.541$, AIC=70.67; B: $\chi^2=15.87$, $P=0.391$, $df=15$, RMSEA=0.050, $P=0.451$, AIC=73.87). Solid and dashed arrows indicate positive and negative pathways, respectively (ns: $P>0.10$, [^]: $P<0.10$, ^{*}: $P<0.05$, ^{**}: $P<0.01$, ^{***}: $P<0.001$). Arrow width is proportional to the strength of the relationship. Numbers along the arrows are standardized path coefficients indicating the effect size of the relationship. The proportion of variance explained (R^2) appears alongside the response variables in the models.

Overall, our results point to the importance of dominant species and species asynchrony for determining both biomass and structural stability of our study grassland experiencing drought. We attributed these results to the predominant role of dominant species in contributing to plant biomass production and driving plant community assembly in our study grassland. In our experiment, *L. chinensis*, accounted for almost half of grassland aboveground biomass. Its response to drought may largely drive grassland biomass stability and impose substantial influences on the responses of other species (including other dominant species, Figure S4 in Supporting Information) to drought, with subsequent influences on community structural resistance and recovery. Our results are thus consistent with the findings of several previous studies that plant community functional resistance

and recovery are modulated by the traits of dominant species (DeClerck et al., 2006; Hoover et al., 2014; MacGillivray and Grime, 1995). Together, these results provide strong support for the mass ratio hypothesis that properties of an ecosystem are largely determined by its dominant species (Grime, 1998). Moreover, our finding that the response of dominant species to disturbance also strongly influenced the reassembly of communities undergoing disturbance suggests that the mass ratio hypothesis may also be applied at the community level. We suggest that elucidating traits that regulate dominant species resistance to disturbance and recovery from disturbance are particularly important for predicting both community and ecosystem responses to increasingly frequent disturbance events. Furthermore, our study demonstrates an important contribution of biomass stability of plant functional group in modulating community biomass resistance and recovery in response to drought. This result is in line with findings in the same grassland (Xu et al., 2021) and upland grasslands (Mackie et al., 2019), although the specific plant functional groups driving community biomass stability are different among these studies presumably due to discrepant plant traits. Thus, our result suggests the importance in supporting specific plant functional groups to maintaining community stability in facing natural drought.

A recent meta-analysis (Hillebrand and Kunze, 2020) reported that functional and structural stability of ecological communities tended to be positively correlated. In line with this trend, we found that the community biomass resistance/recovery following disturbance were positively associated to the corresponding structural stability of plant communities in our study grassland (Figure 4). This pattern, indicative of a lower dimensionality of stability in our grassland, suggests that the functional stability of plant communities could be predicted, at least partially, by its compositional stability.

Similar to many other grasslands, our study grassland experienced grazing and mowing before the initiation of our experiment; these historical management certainly influenced the initial composition and function of our study grassland. Therefore, although all our experimental plots experienced similar historical disturbance, caution must be excised when extrapolating our results to other, unmanaged grassland ecosystems. Moreover, our experiment took advantage of natural drought events, and thus may not be directly comparable to drought-manipulation experiments in which a no-drought control treatment was typically included. Nevertheless, such “natural” experiments can still provide valuable insight into mechanisms underlying grassland responses to extreme climate events (Bharath et al., 2020; Kinugasa et al., 2012; Van Ruijven and Berendse, 2010). It would be interesting to directly compare the two types of experiments within the same study system to assess their relative relevance for predicting community and ecosystem

responses to drought and other climate events.

CONCLUSIONS

Our study provides novel empirical evidence that nitrogen addition and mowing, two common grassland management practices, can have substantial effects on grassland functional and structural stability. Nitrogen enrichment increased grassland biomass recovery and decreased structural recovery, whereas mowing increased grassland biomass recovery and functional recovery, but decreased structural resistance. These effects, however, were both largely driven by the response of the dominant species to drought and the degree of species asynchrony, emphasizing the importance of elucidating dominant species traits that determine their stability for understanding community and ecosystem stability properties in the face of drought or other disturbance events. Our study also suggests the importance of specific plant functional groups in modulating community biomass resistance and recovery in response to drought, and illustrates the necessity of considering stability across multiple levels of ecological organization to gain a more complete understanding of the effects of anthropogenic environmental changes on ecological ability.

MATERIALS AND METHODS

Study site and experimental design

The experiment was conducted at the Erguna Forest-Steppe Ecotone Research Station (119°22′56.4″E, 50°10′46.1″N) in Erguna of Inner Mongolia, China. Long-term mean annual precipitation at the study site is 358 mm, and mean annual temperature is -2.5°C , with mean monthly temperatures ranging from -28.0°C in January to 19.2°C in July. Soil is chernozem according to the US soil taxonomy classification.

The study site was located in a temperate semiarid grassland, and fenced in early 2010. Thereafter livestock grazers have been excluded from the study site, and mowing was conducted once annually in August to harvest hay. The grassland was dominated by four perennial grasses, *Leymus chinensis*, *Carex duriuscula*, *Cleistogenes squarrosa*, *Stipa baicalensis*, and a perennial forb, *Bupleurum scorzonnerifolium*. We defined dominant species as the species present in over 85% of the plots across treatments and years and its AGB accounting for more than 6% of the community AGB.

In early August 2013, six blocks were established using a randomized block design. Four 6 m×6 m plots within each block were randomly assigned to the following treatments: control (C, no nitrogen addition or mowing), nitrogen addition (N), mowing (M), and nitrogen addition plus mowing

(NM). Both the blocks and plots were separated by a 1-m-wide buffer zone. Plots receiving the mowing treatments were mowed at 7 cm (the same height as stubble in hay harvest in the local area) aboveground in mid-August (after the completion of plant survey) from 2013 to 2018; mowed plant materials were immediately removed from the plots. In early May from 2014 to 2018, each nitrogen addition plot received nitrogen fertilizer (in the form of urea) at the rate of $10\text{ g nitrogen m}^{-2}\text{ yr}^{-1}$. The plot was sprinkled with 10 L tap water with urea dissolved in it; each plot without nitrogen addition was sprinkled with 10 L tap water. The added water each year is equivalent to 0.28 mm precipitation. The amount of nitrogen addition is greater than the current atmospheric nitrogen deposition (approximately $1.42\text{ g m}^{-2}\text{ yr}^{-1}$) in the study area, but is comparable to the projected nitrogen deposition rate in northern China in the near future (He et al. 2007).

Plant community survey

In August 2013, a permanent quadrat of 1 m×1 m, approximately 1 m away from the edge of the plot, was established in each plot. In early August from 2014 to 2018, when vegetation reached its peak biomass, plant species within each permanent quadrat were recorded. Species were classified into two functional groups, grasses (including sedges) and forbs. Species richness was defined as the total number of species recorded within the permanent quadrat each year. In mid-August from 2014 to 2018, all living plants within three randomly selected 0.4 m×0.4 m quadrats in each of the 24 plots were clipped at the ground level and sorted by species, and oven-dried at 65°C for 48 h to determine aboveground biomass (AGB).

Data analysis

Except for the three drought years (2015–2017), precipitations in 2014 and 2018 were close to the long-term mean precipitation in our study grassland. We quantified both functional (i.e., biomass based) and structural resistance and recovery of plant communities to examine their responses to our experimental treatments. Biomass resistance (B_{rst}) was quantified as the ratio of the mean AGB of three drought years (2015–2017) to the AGB in the year before drought (2014) (MacGillivray and Grime, 1995). Biomass recovery (B_{rc}) was quantified as the ratio of the AGB in post-drought year (2018) to the mean AGB of the drought years (2015–2017) (Lloret et al., 2011). B_{rst} and B_{rc} were also calculated at species (the five dominant species) and functional group levels. Structural resistance (S_{rst}) was defined as the Bray-Curtis similarity (Bray and Curtis, 1957) between communities in the pre-drought year and the drought years, which was calculated as:

$$S_{rst} = 1 - \sum_i |AGB_{i,pre-drought} - AGB_{i,drought}| / 2,$$

where $AGB_{i,pre-drought}$ is the relative AGB of species i in the community before drought (2014) and $AGB_{i,drought}$ is the relative mean AGB of species i of the three drought years (2015–2017), respectively. S_{rst} equals 1 if there is no structural difference between drought and pre-drought communities and equals 0 when drought and pre-drought communities have no species in common. Structural recovery (S_{rc}) was measured as the Bray-Curtis dissimilarity between communities in the drought years and the post-drought year, which was calculated as:

$$S_{rc} = \sum_i |AGB_{i,post-drought} - AGB_{i,drought}| / 2,$$

where $AGB_{i,postdrought}$ is the relative AGB of species i in the community after drought (2018). Maximum recovery values approach 1 (i.e., when post-drought AGB is substantially greater than AGB during the drought), whereas values $\ll 1$ reflect low recovery. We also calculated S_{rst} and S_{rc} of dominant species (hereafter dominant structural resistance and dominant structural recovery, respectively) using the above formulas by considering only the five most common species (*L. chinensis*, *S. baicalensis*, *C. squarrosa*, *C. duriuscula* and *B. scorzonrifolium*), whose summed AGB accounted for 79.2% of community AGB across treatments and sampling years. To determine the role of species asynchrony in regulating community stability, we calculated species asynchrony (ϕ') as:

$$\phi' = \sigma_{x_c}^2 / \left(\sum_i \sigma_{x_i} \right)^2,$$

where $\sigma_{x_c}^2$ is the variance of community AGB and σ_{x_i} is the standard deviation of the AGB of the i th species in a community (Loreau and de Mazancourt, 2008). Species asynchrony was calculated separately for resistance (using data from 2014 to 2017) and recovery (using data from 2015 to 2018), respectively.

Linear mixed-effects models were used to assess the effects of year, N , mowing, and their interactions on community AGB and species richness; block was included as a random effect in the models. Two-way ANOVAs were used to test the effects of block, N , mowing, and their interactions on biomass resistance, biomass recovery, structural resistance and structural recovery. Fisher's LSD multiple range tests were used to evaluate differences among treatments. Relationships between community resistance/recovery and their potential abiotic and biotic drivers were explored with bivariate regressions. Bivariate regressions were also used to test for relationships among dominant species. Based on the bivariate relationships (Table S3 in Supporting Information), we constructed *a priori* structural equation models (SEMs) to understand the direct and indirect effects of abiotic and biotic factors on community biomass resistance, biomass recovery, structural resistance and structural recovery in re-

sponse to drought (Figure S2 in Supporting Information). Overall fit of the SEM was evaluated using the chi-square test (the model has a good fit when $0.05 < P \leq 1.00$ for χ^2 test), Akaike information criteria (AIC; lower AIC indicating a better fit) and the root mean square error of approximation (RMSEA; the model has a good fit when $0 \leq RMSEA \leq 0.10$ and $0.10 < P \leq 1.00$) (Steiger, 1990); final models were obtained by eliminating non-significant pathways and state variables based on regression weight estimates.

The data on community AGB and biomass resistance of forbs were ln-transformed and data on dominant structural recovery were arcsin-transformed to meet the assumptions of normality. SEM analyses were performed using AMOS 25.0 (Amos Development Co., Greene, USA). The remaining statistical analyses were conducted using SPSS 24.0 (SPSS, Inc., Chicago, USA).

Compliance and ethics The author(s) declare that they have no conflict of interest.

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