

Nitrogen deposition and mowing differentially alter the resistance and recovery of grassland communities

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Abstract

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Running head: Grassland resistance and recovery

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Abstract

Nitrogen deposition and land use are known to influence various ecosystems, but how these anthropogenic activities influence community and ecosystem responses to disturbance remains poorly understood. Here we investigated the effects of increased nitrogen deposition and mowing on the resistance and recovery of a temperate semiarid grassland experiencing a three-year drought. Nitrogen addition reduced grassland biomass resistance and increased biomass recovery, whereas annual mowing reduced grassland structural resistance and increased structural recovery. The treatment effects on community biomass resistance and recovery were largely modulated by the stability of the most dominant species, whereas the treatment effects on community structural resistance and recovery were largely modulated by the structural stability of dominant species assemblages. The discrepancy in the response of biomass and structural stability emphasizes the need to study changes across levels of ecological organization for a more complete understanding of ecosystem responses to disturbances under widespread environmental changes.

KEYWORDS

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

INTRODUCTION

Human activities have resulted in substantial increases in the frequency and intensity of extreme climate events worldwide (Meehl et al., 2000; IPCC, 2014). 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 following naturally occurring precipitation extremes (Buckland et al., 1997; Breshears et al., 2005; Ciais et al., 2005; Peñuelas et al., 2007; Knapp et al., 2015) and in studies experimentally imposing precipitation deficits (Heitschmidt et al., 2005; da Costa et al., 2010; De Boeck et al., 2011; Dreesen et al., 2014). Considerable efforts have been directed towards assessing the stability of ecological communities experiencing extreme climate events (e.g., Tilman & Downing, 1994; Wardle et al., 2000; Jasper & Frank, 2010; Hoover et al., 2014). 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 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 (Allison & Martiny, 2008; Baert et al., 2016; Guelzow et al., 2017; Hillebrand et al., 2018; Polazzo & Rico, 2021). On the other hand, functional response of a community to disturbance may not necessarily parallel its structural response. In particular, ecosystem functions are expected to be generally 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 (Yachi & Loreau, 1999; Allison & Martiny, 2008). Within this context, accumulating theoretical and empirical evidence suggests asynchronous population dynamics among species as a potentially important mechanism stabilizing ecosystem functions (Ives et al., 1999; Yachi & Loreau, 1999; Loreau & de Mazancourt, 2008; Hector et al., 2010; Hautier et al., 2014; Xu et al., 2021). 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.

Species diversity is often thought as an important factor influencing plant community resistance (Caldeira et al., 2005; Anja et al., 2012; Baert et al., 2016) and recovery (Jasper & Frank, 2010; Kreyling et al., 2017; Wagg et al., 2017). More diverse communities may better withstand disturbance, and recover more quickly

from disturbance, due to the greater probability of containing species resistant to disturbance and species resilient after disturbance in more diverse communities, as well as increased asynchronous species responses to environmental changes in more diverse communities (Yachi & Loreau, 1999). On the other hand, theory suggests that more diverse communities may take more time to return to their steady states after disturbance (May, 1973; Ives & Carpenter, 2007), potentially resulting in lower structural and functional recovery with increasing diversity. Moreover, more diverse communities may be more likely to contain species vulnerable to disturbance, making it more difficult to maintain stable structure and function after disturbance. In apparent accordance with these opposing predictions, empirical studies of the diversity-resistance/recovery relationships have reported mixed results. For instance, ecosystem functional resistance has been found to increase (Tilman & Downing, 1994; Kahmen et al., 2005; Isbell et al., 2015), decrease (Pfisterer & Schmid, 2002; Allison, 2004; De Boeck et al., 2008), or remain unchanged (DeClerck et al., 2006; Wang et al., 2007; Van Ruijven & Berendse, 2010; Carter & Blair, 2012) with species diversity. Likewise, positive (Tilman & Downing, 1994; Van Ruijven & Berendse, 2010; Vogel et al., 2012), negative (Pfisterer & Schmid, 2002) and neutral (Carter & Blair, 2012; Xu et al., 2014; Isbell et al., 2015) diversity-ecosystem functional recovery relationships have been reported. By comparison, few studies have addressed the diversity-structural stability relationships, showing that species diversity may increase (Frank & McNaughton, 1991; Baert et al., 2016) or decrease (Van Peer et al., 2004) structural resistance, or shows varied relationship with structural resistance (Shurin et al., 2007); we know of only one study that examined diversity effect on community structural recovery (Baert et al., 2016). 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), life history (Ruppert et al., 2015), traits and abundance (Macgillivray et al., 1995; Florence et al., 2014; Stampfli et al., 2018) 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 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.

Increase in atmospheric nitrogen deposition has been reported to alter species richness (Vitousek et al., 1997; Suding et al., 2005), species asynchrony (Isbell et al., 2009; Hector et al., 2010), and the abundance of dominant species (Xu et al., 2015a; Bowman et al., 2018), with potential consequences for community resistance and recovery. However, nitrogen enrichment effects on community resistance and recovery remain understudied. The few empirical studies on this topic reported that increased nitrogen availability could increase grassland functional recovery after drought (Kinugasa et al., 2012; Xu et al., 2014), and increase (Hofer et al., 2017) or have little effect (Xu et al., 2014) on grassland functional resistance to drought. No studies, to our knowledge, have explored the linkage between nitrogen input and community structural resistance/recovery. As a common land-use practice in grasslands, mowing may also result in changes in species diversity (Maron & Jefferies, 2001; Williams et al., 2010; Socher et al., 2013) and the abundance of dominant species (Clark & Wilson, 2001; Galvanek et al., 2015). Nevertheless, we also know little about how mowing affects plant community resistance and recovery (but see Vogel et al., 2012), especially from the structural perspective.

In this study, we experimentally simulated nitrogen deposition and mowing in a temperate semiarid grassland in Erguna, Northeast China to assess their effects on grassland resistance and resilience 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, Fig. S1), reducing aboveground plant biomass by 73.3%, 58.4% and 45.3%, respectively. This natural drought event provides us an excellent opportunity to assess the response of our study grassland to drought under nitrogen deposition and mowing scenarios. 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.

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, which was used for livestock grazing for more than 50 years before being 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 until 2012. At the beginning of the experiment in 2013, the grassland was dominated by four perennial grasses, *Leymus chinensis*, *Carex duriuscula*, *Cleistogenes squarrosa*, *Stipa baicalensis*, and a perennial forb, *Bupleurum scorzonrifolium*.

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 aboveground in mid-August (after plant survey) from 2013 to 2018; mowed plant materials were 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 g nitrogen m⁻²yr⁻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 (about 1.42 g m⁻² 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; Zhang et al. 2011).

Plant community survey and soil nutrient measurement

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 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). Since nitrogen amendment-induced soil acidification (Tian et al., 2016) and increase in soil inorganic nitrogen (Xu et al., 2015b) may affect species diversity and asynchrony, we measured soil pH and inorganic nitrogen concentration in each plot. In mid-August each year, soil cores (10 cm in depth) were taken from five randomly selected locations in each plot and mixed as a composite sample. Soil pH was measured in a 1:2.5 (soil: water) suspension; soil inorganic nitrogen concentration was determined using a flow-injection autoanalyser (FIAstar 5000 Analyzer, Foss Tecator, Denmark), following extraction with solutions of 2 M KCl (Kaye & Hart, 1998).

Data analysis

We quantified both functional (i.e., biomass based) and structural resistance and recovery of plant communities to examine their responses to our experimental treatments. We focused on absolute biomass changes as

measures of functional resistance and recovery because they are directly relevant for agriculture and animal husbandry. Biomass resistance (B_{rst}) was determined as the difference in AGB between each of the drought years (2015-2017) and the year before the drought (2014) (Pfisterer & Schmid, 2002). Biomass recovery (B_{rc}) was determined as the difference in AGB between the post-drought year (2018) and each of the drought years (2015-2017) (Jasper & Frank, 2010). Structural resistance (S_{rst}) was defined as the Bray-Curtis similarity (Bray & Curtis, 1957) between communities in the pre-drought year and each of the drought years, which was calculated as: $S_{rst} = 2\sum_i \min(AGB_{i,pre-drought}, AGB_{i,drought}) / (\sum_i AGB_{i,pre-drought} + \sum_i AGB_{i,drought})$, where $AGB_{i,pre-drought}$ and $AGB_{i,drought}$ are the AGB of species i in the community before and during drought, 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 (Bray & Curtis, 1957) between communities in each of the drought years and the post-drought year, which was calculated as: $S_{rc} = 1 - 2\sum_i \min(AGB_{i,post-drought}, AGB_{i,drought}) / (\sum_i AGB_{i,post-drought} + \sum_i AGB_{i,drought})$, where $AGB_{i,postdrought}$ is the AGB of species i in the community after drought. Maximum recovery values approach 1 (i.e., when post-drought AGB is substantially greater than AGB during the drought), whereas values < 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 as σ^2 , where σ^2 is the variance of community AGB and σ is the standard deviation of the AGB of the i th species in a community (Loreau & de Mazancourt, 2008). Species asynchrony was calculated separately for resistance and recovery by using data from the years relevant to the calculation of resistance and recovery, respectively.

Linear mixed-effects models were used to assess the effects of block, N, mowing, and their interactions on soil pH, inorganic nitrogen concentration, community AGB, species richness, biomass resistance, biomass recovery, structural resistance, and structural recovery; year was included as a random effect in the models. Two-way ANOVA was used to test the effects of block, N and mowing on species asynchrony. One-way ANOVAs with Duncan's 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 potential trade-offs among stability properties. Based on the bivariate relationships, 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 resistant and structural recovery (Fig. S2). Overall fit of the SEM was evaluated using the chi-square test (the model has a good fit when $0.05 < P[?] 1.00$ for χ^2 test) and Akaike information criteria (AIC; lower AIC indicating a better fit); final models were obtained by eliminating non-significant pathways and state variables based on regression weight estimates.

The data on community AGB and biomass recovery were ln-transformed to meet the assumptions of normality. SEM analyses were performed using AMOS 18.0 (Amos Development Co., Greene, Maine, USA). The remaining statistical analyses were conducted using SPSS 13.0 (SPSS, Inc., Chicago, IL, USA).

RESULTS

Nitrogen addition reduced soil pH and increased inorganic nitrogen concentration, while mowing had no significant effects on these two variables (Table 1, Fig. S3). The three-year (2015-2017) drought significantly reduced species richness and community AGB (all $P < 0.01$) across treatments when compared to 2014, the year before the drought (Fig. S4). Nitrogen enrichment increased community AGB, but had no effect on species richness; mowing resulted in decreased community AGB, but increased species richness (Table 1; Fig. S4).

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; Fig. S5). The treatment effects on the summed AGB of the five dominant species mirrored those for *L. chinensis* (Table S1; Fig. S5).

Nitrogen enrichment significantly reduced community biomass resistance (Fig. 1a), but increased community biomass recovery (Fig. 1b). Mowing marginally significantly increased community biomass resistance, but did not affect community biomass recovery (Fig. 1a,b). Mowing, however, mitigated the negative effect of nitrogen enrichment on biomass resistance (significant nitrogen $\times$ mowing term; Table 1; Fig. 1a). For structural stability, nitrogen enrichment had no discernable effect on community structural resistance or recovery, whereas mowing significantly decreased community structural resistance, and increased community structural recovery (Table 1; Fig. 1c,d). Nitrogen enrichment, but not mowing, decreased species asynchrony for both resistance and recovery (Table 1).

Nitrogen enrichment decreased biomass resistance of *L. chinensis* but increased its biomass recovery (Table 1; Fig. 2a,b), paralleling its effect on community-level biomass resistance and recovery. By contrast, mowing increased biomass resistance of *L. chinensis* but decreased its biomass recovery (Table 1; Fig. 2a,b). Mowing, but not nitrogen addition, reduced dominant structural resistance; both nitrogen addition and mowing had a positive effect on dominant structural recovery (Table 1; Fig. 2c,d).

Structural equation modelling (SEM) revealed that nitrogen deposition decreased community biomass resistance by reducing biomass resistance of the most dominant species *L. chinensis* and, in turn, its positive effect on species asynchrony (Fig. 3a). Mowing promoted community biomass resistance by increasing biomass resistance of *L. chinensis* and resultant species asynchrony (Fig. 3a). Nitrogen deposition had no detectable effect on community structural resistance, as its positive effect through decreasing *L. chinensis* biomass resistance was offset by its negative effect through decreasing species asynchrony and dominant structural resistance (Fig. 3a). Mowing decreased community structural resistance mainly through reducing dominant structural resistance, and this negative effect was partially offset by increased *L. chinensis* biomass resistance which increased dominant structural resistance (Fig. 3a).

Nitrogen addition promoted community biomass recovery by increasing biomass recovery of *L. chinensis* and a host of other less dominant species (the latter captured as decreasing species asynchrony in the SEM; Fig. 3b). However, mowing showed no significant effect on community biomass recovery, as its negative effect through decreasing biomass recovery of *L. chinensis* was largely offset by its positive effect through increased dominant structural recovery (Fig. 3b). Whereas nitrogen deposition had little effect on community structural recovery, mowing promoted community structural recovery mainly by increasing dominant structural recovery (Fig. 3b).

Bivariate regressions revealed that community biomass resistance and recovery were significantly positively associated with their structural resistance and recovery, respectively (Fig. S6a, b). SEMs also revealed a positive effect of community structural recovery on biomass recovery, but no significant relationship between community biomass and structural resistance (Fig. 3).

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 elusive. This is at least, in part, due to the focus on the functional resistance and recovery in previous studies of ecological stability, which have paid relatively little attention to structural resistance and recovery. 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 (Xu et al., 2014; Shi et al., 2018). Using a manipulative field experiment conducted in a temperate semiarid grassland, our study showed that N enrichment and mowing had strikingly different effects on grassland biomass and structural resistance/recovery. Specifically, nitrogen addition resulted in reduced biomass resistance and increased biomass recovery, whereas annual mowing resulted in reduced structural resistance and increased structural recovery. Importantly, our study

demonstrated that dominant species resistance/recovery, rather than species diversity, largely modulated the effects of nitrogen enrichment and mowing on both functional and structural resistance/recovery of our study grassland.

An appreciable number of studies have shown that nitrogen enrichment often reduces grassland biomass temporal stability (Yang et al., 2012; Hautier et al., 2014; Hautier et al., 2015; Song & Yu, 2015; Xu et al., 2015b; Zhang et al., 2016; Zhang et al., 2019; Hautier et al., 2020; but see Grman et al., 2010). Much less, however, is known about how nitrogen enrichment influences grassland biomass resistance to disturbance (Xu et al., 2014; Shi et al., 2018) and recovery after disturbance (Kinugasa et al., 2012; Xu et al., 2014). Our study showed that nitrogen addition decreased plant community biomass resistance to drought, but increased biomass recovery after drought. As nitrogen addition resulted in increased plant community biomass, indicating nitrogen limitation in our study grassland, this opposite effect of nutrient addition on biomass resistance and recovery also means that more productive communities lost more biomass during drought but recovered more biomass after drought (Fig. S7). The strong negative relationship between biomass resistance and pre-drought community biomass ($r^2 = 0.918, P < 0.001$) lends strong support to the hypothesis that drought-induced plant biomass reduction is sensitive to pre-drought community biomass (the biomass-dependent resistance hypothesis; Wang et al., 2007). This result is also consistent with the idea that more fertile grasslands should be more responsive to climate change (Grime et al., 2000). This result arose presumably because of increasing water shortage associated with communities that attained greater biomass, and therefore, increased evapotranspiration, following N addition (Friedrich et al., 2012; Valliere et al., 2017; Shi et al., 2018). More mechanistically, we found that nitrogen enrichment reduced community biomass resistance mainly by exacerbating the biomass loss of *L. chinensis* during drought. *L. chinensis* is a perennial rhizomatous grass with relatively high foliar nitrogen content (Cui et al., 2010), and nitrogen enrichment tends to increase its abundance, stature and root biomass (Pan et al., 2005; Bai et al., 2009). As the most dominant species in our study grassland, *L. chinensis* plants are known to show reduced stomatal conductance and photosynthesis, and in turn, reduced biomass production when experiencing drought (Xu & Zhou, 2006), especially under nitrogen enrichment (Shi et al., 2018). *L. chinensis* plants are also known to allocate more of their biomass into their belowground components when experiencing drought (Xu & Zhou, 2006), particularly under nitrogen enrichment (Shi et al., 2018), presumably as an adaptive strategy to maximize water 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 nitrogen addition plots after drought.

Compared with nitrogen deposition, 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 (Yang et al., 2012; Zhang et al., 2017). Even less is known about how mowing influences grassland resistance and recovery. The only study on this topic, to our knowledge, examined the response of experimental 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 promoted community biomass resistance, primarily via enhancing the biomass resistance of *L. chinensis* (Fig. 3a). The fact that mowing reduced community and dominant species biomass and made our study grassland less vulnerable to drought is again consistent with the biomass-dependent resistance hypothesis (Wang et al., 2007). The apparent discrepancy between the results of our study and Vogel et al. (2012) may be explained by the difference in mowing frequency between the two studies. Whereas mowing was implemented once per year in our experiment, it was implemented two or four times a year in the experiment of Vogel et al. (2012), with only the more frequent mowing treatment diminishing biomass accumulation and reducing community biomass resistance to drought in the latter study. Note that increased species asynchrony under mowing (manifested in the SEM as an indirect effect of mowing via *L. chinensis* biomass resistance) also contributed to community biomass resistance (Fig. 3a). Mechanistically, mowing reduced the abundance of dominant, drought-sensitive species (i.e., *L. chinensis*), which offered greater opportunities for species that were less abundant but more tolerant of drought (e.g., *C. duriuscula*, *S. baicalensis*, *Thermoposis lanceolata*) to compensate for its biomass loss under drought, leading to greater

asynchrony.

One of our most important results is that only mowing altered grassland structural stability, resulting in reduced grassland structural resistance and increased grassland structural recovery. Notably, these effects of mowing on community structural stability were largely mediated via dominant species structural stability, which was strongly associated with community structural stability (Fig. 3). Importantly, mowing had opposite effects on *L. chinensis* biomass stability and dominant species structural stability. Mowing reduced dominant structural resistance despite its positive effect on *L. chinensis* biomass resistance, as three of the other four dominant species exhibited the trend of declining resistance to drought under mowing (Fig. S8a-d). On the other hand, mowing increased dominant structural recovery despite its negative effect on *L. chinensis* biomass recovery, as all the other four dominant species exhibited the trend of increased recovery from drought under mowing (all $P < 0.001$; Fig. S8e-h). These results correspond to the fact that *L. chinensis*, as the most dominant species, imposed negative effects on the other dominant species (Fig. S9) but suffered substantial biomass loss from mowing (Fig. S5), with ensuing consequences for the abundance of other species and the structural stability of our study communities. Previous work has shown that mowing reduces the dominance of *L. chinensis* by hampering the formation of regeneration buds and the propagation of rhizomes (Yang et al., 1995). Our results are consistent with previous studies reporting that mowing tended to reduce the abundance of dominant species, resulting in increased light availability (Molina et al., 2021) and, in turn, increases in grassland plant diversity (Leps, 2014; Yang et al., 2019; Molina et al., 2021). Our study, however, focused on examining the effects of mowing on community resistance and recovery, demonstrating the importance of dominant species for driving the reassembly of communities experiencing drought.

Overall, our results point to the importance of dominant species for determining both biomass and structural stability of our study grassland experiencing drought. Species richness was not identified as a significant predictor of grassland biomass or structural stability (Fig. 3). 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, the most dominant species, *L. chinensis*, accounted for almost half of grassland aboveground biomass. Its response to drought not only largely drove grassland biomass resistance and recovery, but also imposed substantial influences on the responses of other species (including other dominant species) 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 (Macgillivray et al., 1995; DeClerck et al., 2006; Hoover et al., 2014). Together, these results provide strong support for the mass ratio hypothesis that properties of an ecosystem are largely determined by its dominant species, rather than species diversity (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, such as the pre-drought biomass as identified here, are particularly important for predicting both community and ecosystem responses to increasingly frequent disturbance events.

A recent meta-analysis (Hillebrand & Kunze, 2020) reported that functional and structural stability of ecological communities tended to be positively correlated, such that functional recovery of communities following disturbance is more complete with greater structural recovery. In line with this trend, we found that the recovery of the structure of our study grassland promoted its biomass recovery (Fig. 3b; Fig. S6b). This pattern emerged as the recovery in the biomass of other species complemented that of *L. chinensis* in contributing to community biomass recovery, particularly under mowing that inhibited *L. chinensis* biomass accumulation. The meta-analysis of Hillebrand and Kunze (2020) also found that for some communities, functional recovery was possible in the absence of structural recovery, a pattern attributable to the functional redundancy among species (Yachi & Loreau, 1999; Allison & Martiny, 2008). Likewise, we found that the biomass resistance of our study communities was decoupled from their structural resistance (Fig. 3a). This pattern arose as drought substantially altered grassland community structure, but *L. chinensis* remained a

predominant contributor to community biomass and drought-tolerant species partially compensated for the loss of biomass of drought-intolerant species.

CONCLUSIONS

Our study provides novel empirical evidence that nitrogen deposition and mowing, two common grassland management practices, can have vastly different effects on grassland biomass and structural stability. Nitrogen deposition mainly influenced grassland biomass stability, decreasing grassland biomass resistance and increasing biomass recovery. By contrast, mowing mainly influenced grassland structural stability, decreasing structural resistance and increasing structural recovery. These different effects, however, were both largely driven by the response of the most dominant species, *L. chinensis*, to drought, 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 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.

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AUTHOR CONTRIBUTIONS

Z.X., Y.J. and L.J. designed the study; Z.X., H.L., Y.M., J.Y. and S.Y. performed the field experiment; Z.X. performed statistical analyses; Z.X. and L.J. wrote the manuscript with input from H.R., M.H.L, and S.T.

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Table 1 Results (F -value) of linear mixed-effects models on the effects of block (B), nitrogen addition (N), mowing (M) and their interactions on soil pH, soil inorganic nitrogen concentration (soil IN), community aboveground biomass (AGB), species richness, asynchrony, 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*, S_{rst} and S_{rc} of dominant species experienced drought in three consecutive growing seasons. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, ^ $p < 0.1$, ns $p > 0.1$.

	B	N	M	N × M
soil pH	1.50ns	29.24***	2.56ns	0.11ns
soil IN	0.03ns	65.72***	0.00ns	0.22ns
community AGB	0.08ns	93.71***	45.35***	1.52ns
species richness	0.68ns	1.21ns	21.59***	0.13ns
asynchrony for resistance	1.06ns	9.58**	1.06ns	3.77ns
asynchrony for recovery	3.04*	18.34***	0.15ns	2.16ns
community B_{rst}	1.23ns	37.51***	3.42^	6.24*
community B_{rc}	1.31ns	186.88***	186.88***	0.65ns
community S_{rst}	0.78ns	0.57ns	14.70***	0.08ns
community S_{rc}	0.07ns	2.08ns	13.52***	0.30ns
<i>L. chinensis</i> B_{rst}	2.68*	7.24**	19.37***	6.38*

	B	N	M	N × M
<i>L. chinensis</i> Brc	5.46**	99.96***	31.86***	1.14ns
dominant Srst	0.53ns	0.20ns	7.50**	2.02ns
dominant Src	0.18ns	4.12*	17.27***	0.38ns

Fig. 1. Effects of nitrogen addition and mowing on biomass resistance (*B* rst), biomass recovery (*B* rc), structural resistance (*S* rst) and structural recovery (*S* rc) of grassland communities experiencing drought in three consecutive growing seasons. Bars indicate means ± SE. Different letters above or below the bars indicate significant differences ($P < 0.05$) among treatments. C: control; N: nitrogen addition; M: mowing; NM: nitrogen addition plus mowing.

Fig. 2. Effects of nitrogen addition and mowing on biomass resistance (*B* rst) and recovery (*B* rc) of *L. chinensis*, and structural resistance (*S* rst) and structural recovery (*S* rc) of dominant species assemblages experiencing drought in three consecutive growing seasons. Bars indicate means ± SE. Different letters above or below the bars indicate significant differences ($P < 0.05$) among treatments. C: control; N: nitrogen addition; M: mowing; NM: nitrogen addition plus mowing.

Fig. 3. The final structural equation model relating nitrogen deposition and mowing to **a**) biomass resistance (*B* rst) and structural resistance (*S* st), **b**) biomass recovery (*B* rc) and structural recovery (*S* rc) of our study grassland. *L. C* : *L. chinensis*. The final models adequately fitted the data (**a** : $\chi^2 = 16.65, P = 0.082$, $df = 10$, $AIC = 66.65$; **b** : $\chi^2 = 20.78, P = 0.054$, $df = 12$, $AIC = 66.78$). Solid and dashed arrows indicate positive and negative pathways, respectively (ns $P > 0.10$, $^{\wedge}P < 0.10$, $*P < 0.05$, $**P < 0.01$, $***P < 0.001$). 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.

Figure 1

Figure 2

Figure 3

a)

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b)

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SUPPORTING INFORMATION

Table S1 Results (F -value) of two-way ANOVAs on the effects of block (B), nitrogen addition (N), mowing (M), and N×M interactions on the above-ground biomass of *L. chinensis* and five dominant species in each year from 2014 to 2018. $***p < 0.001$, $**p < 0.01$, $*p < 0.05$, $^{\wedge}p < 0.1$, ns $p > 0.1$.

Species	Source	2014	2015	2016	2017	2018
<i>L. chinensis</i>	B	2.54 $^{\wedge}$	0.27ns	0.77ns	0.77ns	1.50ns

Species	Source	2014	2015	2016	2017	2018
Five dominant species	N	23.89***	5.43*	28.82***	25.83***	42.19***
	M	44.42***	42.65***	49.02***	19.54***	24.86***
	N × M	8.22*	0.06ns	6.26*	3.47^	3.11^
	B	2.01ns	0.19ns	2.14ns	1.20ns	2.69^
	N	24.47***	1.82ns	26.90***	32.65***	62.93***
	M	15.69**	27.47***	25.81***	9.75**	5.29*
	N × M	8.55*	0.00ns	2.02ns	1.55ns	1.59ns

Figure S1 The annual and growing season (May-Aug) precipitation during the study period (2014-2018), as well as the long-term mean precipitation (over the last 57 years) at our study site.

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Figure S2 The *a priori* models relating experimental treatments to community biomass resistance (*B* rst), biomass recovery (*B* rc), structural resistance (*S* rst), structural recovery (*S* rc) through their impacts on soil pH, inorganic nitrogen concentration (soil IN), species asynchrony, species richness and the corresponding stability of dominant species.

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Figure S3 Effects of nitrogen addition and mowing on a) soil pH and b) inorganic N concentration. Bars indicate means ± 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.

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Figure S4 Effects of nitrogen addition and mowing on a) species richness and b) community above-ground biomass from 2014 to 2018. Bars indicate means ± SE. C: control; N: nitrogen addition; M: mowing; NM: nitrogen addition plus mowing.

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Fig. S5 Above-ground biomass of a) *L. chinensis* and b) five dominant species in response to nitrogen addition and mowing from 2014 to 2018. Bars indicate means ± SE. C: control; N: nitrogen addition; M: mowing; NM: nitrogen addition plus mowing.

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Fig. S6 The relationships between community biomass resistance (panel a)/recovery (panel b) and pre-drought community aboveground biomass (AGB).

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Fig. S6 . Relationships a) between biomass resistance and structural resistance, and b) between biomass recovery and structural recovery of our study grassland communities.

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Fig. S8 . Effects of nitrogen addition and mowing on the biomass resistance (B_{rst}) and recovery (B_{rc}) of four other dominant species (*C. duriuscula*, *C. squarrosa*, *B. scorzonrifolium* and *S.baicalensis*) experiencing drought in three consecutive growing seasons. Bars indicate means $\pm$ SE. Different letters above or below the bars indicate significant differences ($P < 0.05$) among treatments. C: control; N: nitrogen addition; M: mowing; NM: nitrogen addition plus mowing.

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Fig. S9 . Relationships between the aboveground biomass (AGB) of *L. chinensis* (*L.C.*) and that of the other four dominant species (*C.S.* : *C. squarrosa*, *B.S.* : *B. scorzonrifolium*, *C.D.* : *C. duriuscula* and *S.B.* : *S. baicalensis*) in the three drought years (2015-2017) (a-d) and the post-drought year (2018) (e-h).

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