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# Mowing weakens the positive effects of nitrogen deposition on fundamental ecosystem service of grassland

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## Abstract

Forage yield is the fundamental ecosystem service of grasslands. While the quantitative responses of forage yield to nitrogen (N) enrichment are well known, its qualitative responses remain unclear. Even less known is the relative contribution of changes in community composition to the quality of the yield at the community level. We examined the quantitative and qualitative responses of forage yield at both plant functional group and community levels with factorial treatments of N addition and mowing in a temperate steppe. Nitrogen addition significantly enhanced the community-level yield by favoring the growth of rhizomatous grass. Mowing tended to mediate the impacts of N addition on the yield. Nitrogen addition increased the concentrations of crude protein and crude fat in forage at the community level. Neither the main effects of mowing nor its interactive effects with N addition affected forage quality. The N-induced shifts in plant species composition significantly contributed to the effects of N addition on forage quality at the community level. Our results suggest that mowing would weaken the positive effects of N deposition on the quantity but not the quality of forage yield. Changes in plant community composition are important in driving the qualitative responses of yield to N deposition.

**Keywords:** Nitrogen enrichment, Primary productivity, Forage quality, Forage yield, Semi-arid grassland

## Introduction

Grasslands play a key role in animal husbandry (O'Mara 2012; Luescher et al. 2014), which are essential for meat and milk production (Sanderson et al. 2004; Vetter 2005). Forage yield, which determines the amount of livestock supplied, is a vital index to assess fundamental ecosystem services of grasslands (Macdonald et al. 2008; Nardone et al. 2010; Lemaire et al. 2014). Forage yield, which is closely associated with plant species composition, could be assessed quantitatively (forage weight) and qualitatively (nutrient concentrations) (Tilman et al. 1996; Bruinenberg et al. 2002). Compared with the influence of abiotic

factors including climate and soil nutrient availability (Shi et al. 2013; Deleglise et al. 2015), the biotic controls on the quantity and quality of forage yield remain largely unknown (but see Michaud et al. 2015). Previous studies show that the forage of different plant species and functional groups substantially differ both in quality and quantity (Licitra et al. 1997; Aerts and Chapin 2000; Duru et al. 2008).

Forage yield is sensitive to soil nutrient availability. Nutrient fertilization is therefore widely used to improve forage yield (Schellberg et al. 1999; Aydin and Uzun 2005; Balabanli et al. 2010). Increasing atmospheric nitrogen (N) deposition, an important global change driver, would have important consequences on forage yield through its impacts on soil nutrient availability (Vitousek et al. 1997; Song et al. 2011). For instance, N deposition is associated with a 30% enhancement of quantitative forage yield in different types

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of sub-alpine grassland in Central Alps (Bassin et al. 2012). Globally, N inputs could increase forage yield by 30–50% in diverse grasslands (Yandjian et al. 2011; DeMalach et al. 2017). Such quantitative enhancements of forage yield at the community level in response to N deposition are accompanied by specific responses of different plant functional groups due to their large variation in functional traits (Suding et al. 2005; Clark et al. 2019). For example, the growth of grasses with rhizome and high stature is always favored by N inputs (Dickson et al. 2014; DeMalach et al. 2017; Yang et al. 2019), while both legume and non-legume forbs are usually inhibited (Song et al. 2011; Midolo et al. 2019). Given the substantial variation of forage quality among different plant functional groups (Licitra et al. 1997; Duru et al. 2008), it is reasonable to expect that N deposition would result in qualitative changes of forage yield by altering plant community composition. It remains an open question, however, for the relative importance of the intra-group variation (through enhancing forage quality at individual plant functional group level) and the inter-group variation (through changing the community composition) in driving the responses of community-level qualitative changes of forage yield to N deposition.

The relative contributions of intra-group trait variability and inter-group trait variability to the total variation of traits at the community level could be quantified by the variance partitioning method developed by Lepš et al. (2011), the usefulness of which have been evidenced by many studies focusing on diverse functional traits (Kichenin et al. 2013; Volf et al. 2016; Hu et al. 2020). Beyond both intra- and inter-group trait variability, the co-variation between them also contributes to the variation of community-level trait, with both positive and negative co-variation being reported (Kichenin et al. 2013; Volf et al. 2016; Lü et al. 2018). Positive and negative co-variations indicate convergence and divergence in the direction of the effects of environmental change on intra- and inter-group trait variability, respectively (Lepš et al. 2011). At the intra-group level, N deposition generally increases the forage quality of each plant functional group (Knops et al. 2007; Waramit et al. 2012; Dufek et al. 2014), which has a positive contribution to the community-level forage quality. In contrast, N-induced inter-group variation would have a negative contribution to the community-level forage quality, because the growth of functional group with higher forage quality (e.g., forbs) are usually inhibited but that with lower forage quality (e.g., grasses) are promoted (DeMalach et al. 2017; Midolo et al. 2019). There would be consequently negative co-variation between intra- and inter-group trait variation in affecting the qualitative responses of forage yield to N deposition, empirical evidences are yet rather scarce.

Mowing is the dominant way for forage harvest in global grasslands (Maron and Jeffries 2001; Talle et al. 2016), which could affect the quantity and quality of

forage yield (Mikhailova et al. 2000; Yang et al. 2020). While mowing could increase forage yield in the short term (Milchunas et al. 2005; Dickson 2019), long-term mowing with high frequency could reduce the quantity and quality of forage yield either by directly declining soil nutrient availability (Venterink et al. 2009) or indirectly by changing plant community composition (Maron and Jeffries 2001). Furthermore, mowing would potentially mediate the impacts of N deposition on forage production, given that the effects of N deposition on soil nutrient availability, plant species diversity, and plant community composition differ in mown and unmown conditions (Collins et al. 1998; Yang et al. 2019). All those factors are important drivers for the quantitative and qualitative variation of forage yield (French 2017; Schaub et al. 2020). The growth of plant species living under N enriched conditions would be more negatively affected by mowing than those under ambient N conditions (Ferraro and Oesterheld 2002). It is thus important to reveal the interactive effects of mowing and N deposition on the quantity and quality of forage yield for a full mechanistic understanding of the responses of forage production under the scenarios of increasing N deposition.

To understand the role of mowing in mediating the impacts of N deposition on the quantity and quality of forage yield and the relative importance of intra- and inter-group variation in driving the community-level changes, we carried out a field experiment in a temperate steppe of northern China by examining forage production and forage quality at both plant functional group and community levels. We hypothesized that (1) intra- instead of inter-group variation would play a stronger role in driving the community-level qualitative responses of forage yield to N deposition, because N enrichment generally has positive effects on forage quality of most plant species (Buxton 1996; Shi et al. 2013; Niu et al. 2016) and that inter-group variation due to changes in plant community composition following N deposition would be a long-term process (Smith et al. 2009; Bai et al. 2010); (2) mowing would mediate such positive effects of N addition on the quantity and quality of forage yield, with stronger effects of N addition under the unmown condition.

## Materials and methods

### Study area

The field experiment was carried out near the Erguna Forest-Steppe Ecotone Research Station (50° 10' 28.8" N, 119° 23' 34.5" E, 527 m a.s.l.). Long-term mean annual precipitation (1957–2016) is 363 mm, with over 80% of which occurring in the growing season from May to September. Mean annual temperature is -2.45 °C, with -27.7 °C in January and 19.0 °C in July (Fig. S1).

The soil of this site is chernozem according to the US soil taxonomy classification. The concentration of soil organic matter and soil pH of the top layer (0–10 cm) is 2–4% and 6.8–7.0, respectively (Table S1, S2). Rhizomatous grass and bunchgrass are the dominant plant functional groups.

### Experimental design

The experiment platform was set up in the spring of 2015, with four treatments (control, N addition, mowing, combined N addition, and mowing) and following a completely random design (Fig. S2). There were six replicates for each treatment, resulting in a total of 24 plots (each measuring 6 m × 6 m). The plots were separated by 1-m walkways. Urea as N fertilizer was annually applied in mid-May with a rate of 5 g N m<sup>-2</sup> year<sup>-1</sup> since 2015. Urea was dissolved into pure water (2 L each plot) and then sprinkled with a sprayer to the N addition plots. To avoid the effects of water addition, the same amount of pure water (2 L) was added to plots without N addition. Mowing was carried out in late-August of each year (that is after aboveground biomass sampling) with a stubble height of 10 cm, with the harvested biomass being removed from the plots to simulate hay harvest.

### Sampling and nutrient analysis

In mid-August of 2016, the aboveground biomass of all living vascular plant was sampled by a 0.5 m × 1 m quadrat, which were randomly placed in each plot. Living plants within each quadrat were sorted to four different plant functional groups (bunchgrass, rhizomatous grass, forb, and sedge; Table S3) and clipped with scissors. All plant samples were oven-dried at 65 °C for 48 h before weighing.

The crude protein concentration of different plant functional groups was analyzed following the Kjeldahl method, while the crude fat concentration was determined using Soxhlet extraction method (AOAC 1990). The crude fiber concentration including neutral detergent fiber (NDF) and acid detergent fiber (ADF) was determined following the method of Van Soest et al. (1991).

### Data analysis

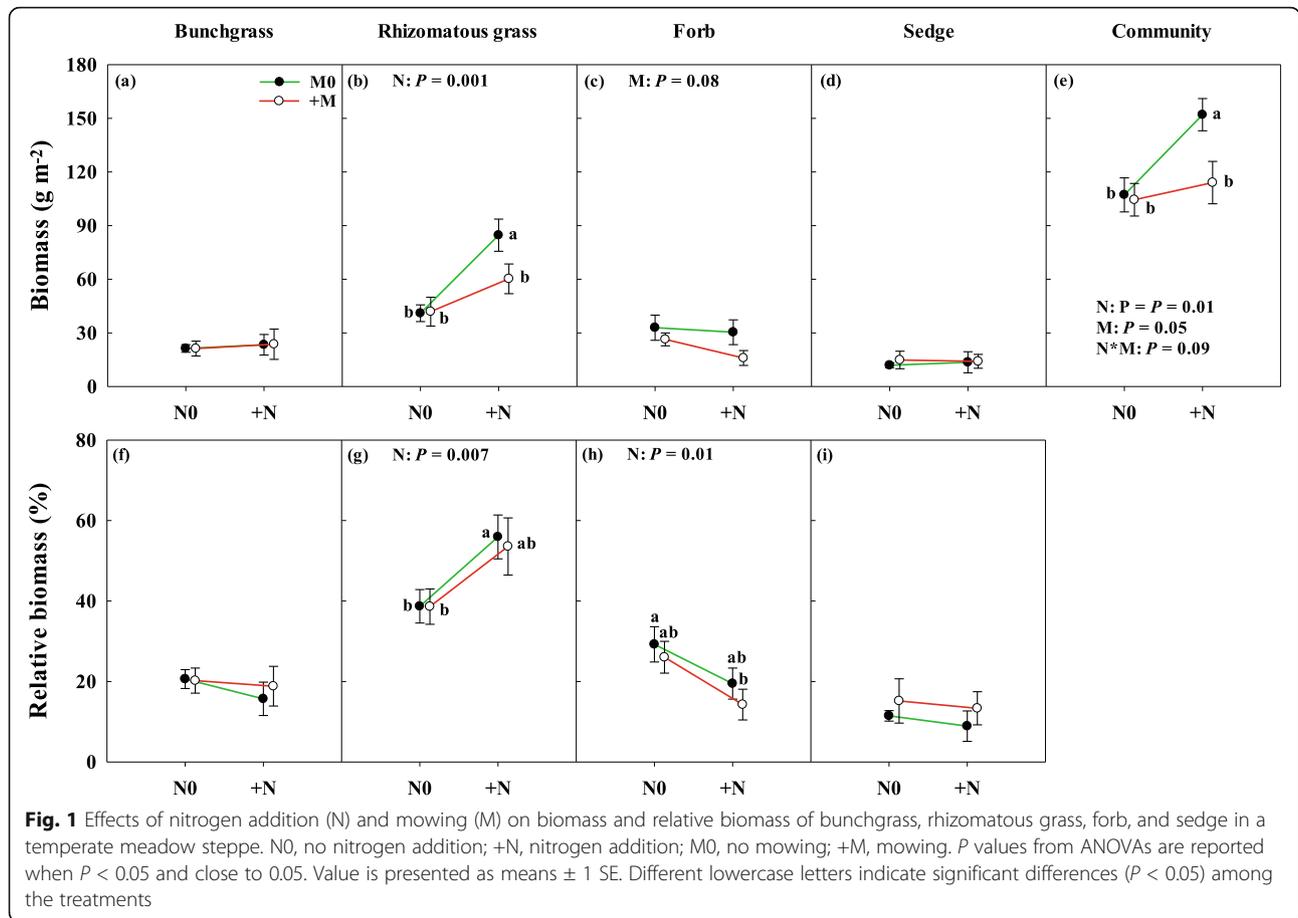
Aboveground biomass at plant functional group level and community level was used as an indicator for the quantitative changes of forage production, while the concentrations of crude protein, crude fat, and crude fiber were considered as indicators for the qualitative changes of forage production. Nutrient stocks of each plant functional group (crude protein, crude fat, and crude fiber) in each plot were calculated based on its biomass and the concentration of respective

characteristics, while that at the community level was calculated as the sum of all functional groups presented in each plot. The relative aboveground biomass of each plant functional group in each plot was used as a weighting factor to calculate the community-level forage quality characteristics. The relative contributions of intra- and inter-group variability on community functional changes were disentangled with repeated measures ANOVA analyses (Lepš et al. 2011), which requires the calculation of “fixed” and “specific” community trait mean. While the “fixed” trait mean assumes each species in all the plots of the whole experiment with a “fixed” trait value, the “specific” trait mean follows the actual value of each species in each plot. The “fixed” community trait values were calculated with the mean trait values of each functional group across all plots, and thus differences of “fixed” values across treatments only considering inter-group effects. The “specific” community trait values were calculated using plot-specific trait values of each functional group, and thus differences of “specific” values across treatments were caused by the effects of both intra- and inter-group variability. The intra-group contribution was calculated as the difference between “specific” and “fixed” trait value for each plot. Then, the total sum of squares ( $SS_{\text{specific}}$ ) of community-level trait variance related to treatments (here N addition and mowing) could be partitioned into “fixed” ( $SS_{\text{fixed}}$ ), “intra-group” ( $SS_{\text{intragroup}}$ ), and “covariation” ( $SS_{\text{covariation}}$ ) effects, with  $SS_{\text{specific}} = SS_{\text{fixed}} + SS_{\text{intra-group}} + SS_{\text{covariation}}$ .

Data was detected for normality by Kolmogorov-Smirnov test and for variance homogeneity by Levene’s test. Three-way analysis of variances (ANOVAs) was used to test the differences of the quantity and quality of forage yield at the functional group level between the treatments of N addition and mowing and among different functional groups. Two-way analysis of variances (ANOVAs) was used to test the differences of the quantity and quality of forage yield at the community level between the treatments of N addition and mowing followed by Duncan’s multiple comparison post hoc test. All data analyses were performed using SPSS version 21.0 (SPSS, Inc., Chicago, IL, USA).

### Results

Nitrogen addition significantly increased the quantity of community-level forage yield (Fig. 1), mainly due to its positive effects on rhizomatous grass (Fig. 1b). Mowing reduced the community-level biomass (Fig. 1e) but had no impacts on functional group level (Fig. 1a–d). Nitrogen addition significantly increased the relative biomass of rhizomatous grass and reduced that of forb, while mowing did not affect the relative biomass of any functional group (Fig. 1f–i).



Plant functional groups varied greatly with respect to the three examined quality indices (all *P* < 0.001; Table 1). Across all the treatments, forb had the highest concentration of crude protein, while rhizomatous grass had the highest concentrations of crude fat and crude fiber (Fig. 2; Fig. S3). At the functional group level, N addition significantly increased crude protein concentration in

bunchgrass, rhizomatous grass, and sedge (Fig. 2a, b, d), whereas mowing had no impact. Nitrogen addition and mowing did not affect the crude fat concentration in all functional groups, except that N addition significantly increased and mowing reduced that in rhizomatous grass (Fig. 2f–i). Nitrogen addition tended to decrease the crude fat concentration in forb under non-mown condition but

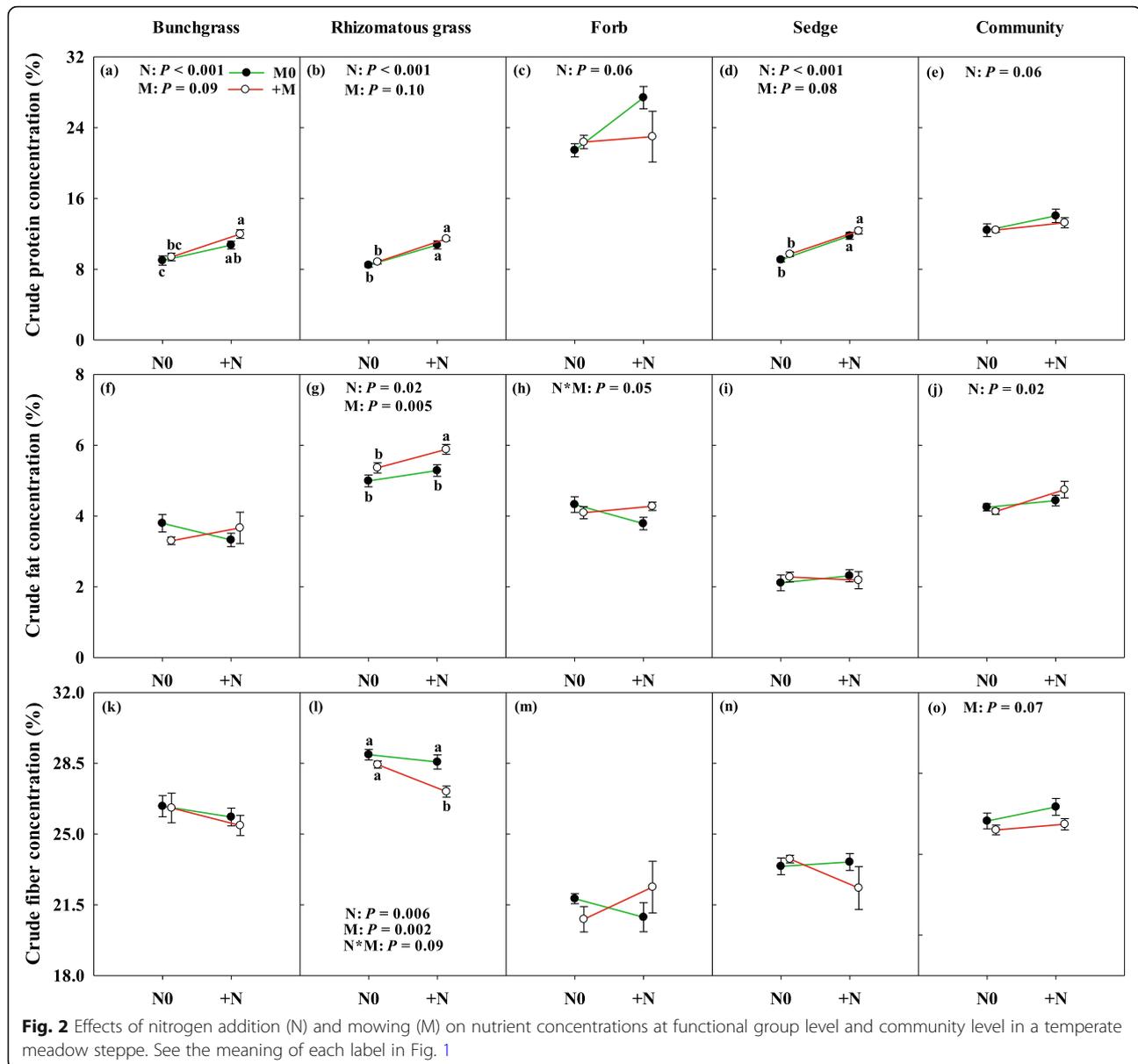
**Table 1** Results (*F* value) of three-way ANOVAs with the main and interactive effects of nitrogen deposition (N), mowing (M), and functional group identity (G) on the concentrations (%) and stocks (g m<sup>-2</sup>) of crude protein, crude fat, and crude fiber in forage of a temperate meadow steppe

Source	Concentrations			Stocks		
	[Crude protein]	[Crude fat]	[Crude fiber]	Crude protein	Crude fat	Crude fiber
N	35.38***	0.31	2.34	8.61**	8.89**	6.11*
M	0.01	1.82	1.50	3.72	2.37	3.77
G	224.24***	162.49***	100.88***	30.80***	82.70***	55.21***
N × M	1.44	3.29	0.03	2.70	1.22	2.57
N × G	0.29	1.49	0.82	6.07**	14.11**	8.12***
M × G	1.83	1.42	0.72	2.90*	0.92	1.66
N × M × G	2.62	1.56	2.36	0.94	1.21	1.37

\**P* < 0.05

\*\**P* < 0.01

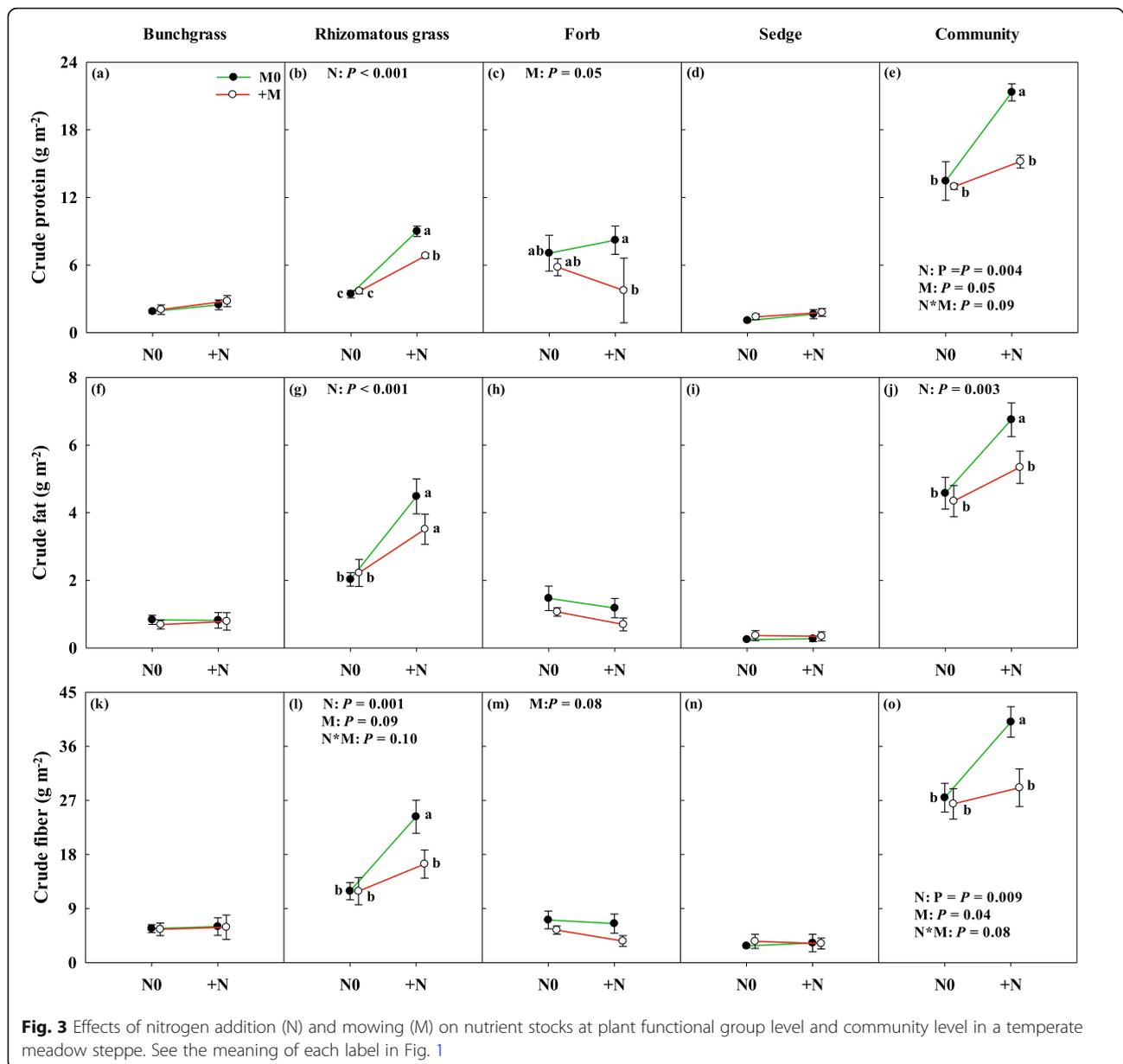
\*\*\**P* < 0.001



tended to increase it under mown condition, resulting a significant interactive effect (Fig. 2h). Both N addition and mowing reduced the crude fiber concentration in rhizomatous grass, but did not affect that in other functional groups (Fig. 2k–n).

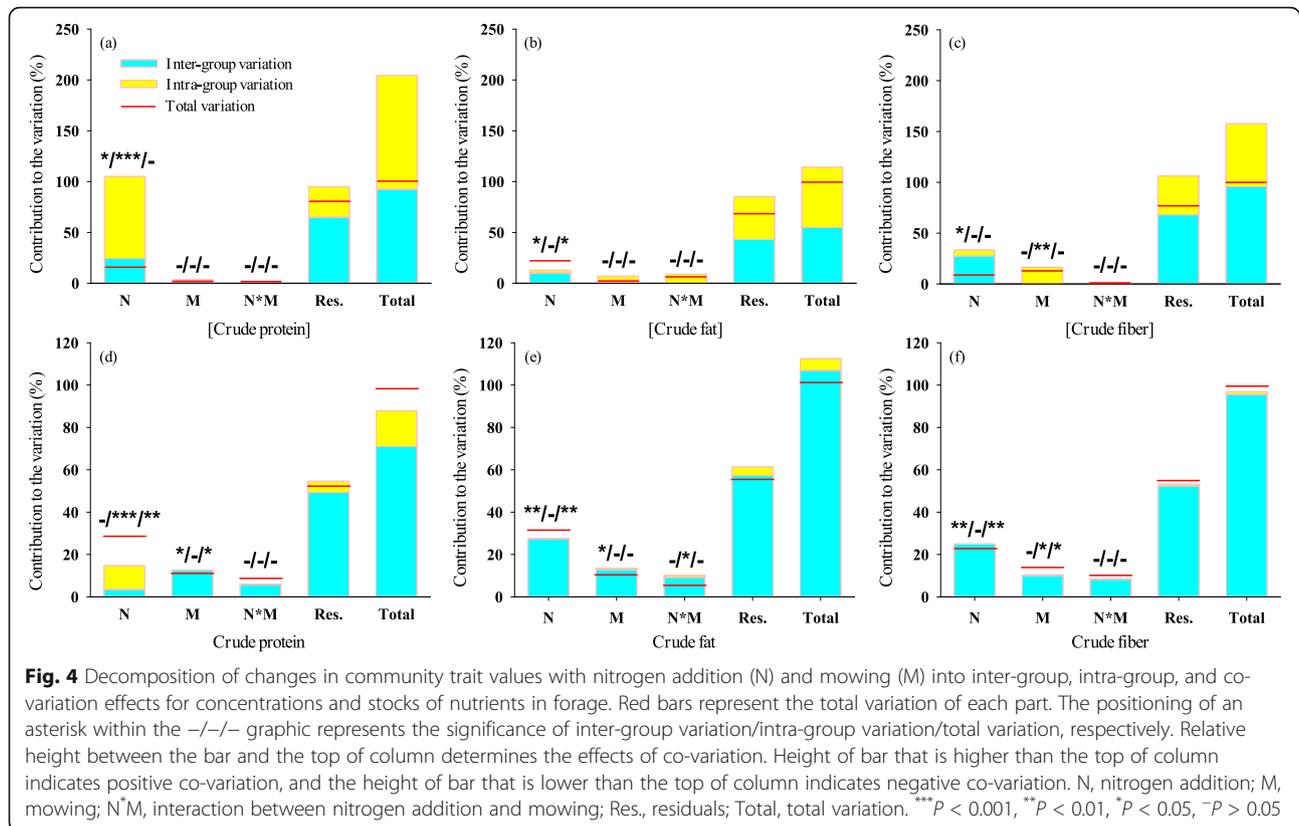
At the community level, N addition significantly enhanced the crude fat concentration ( $P < 0.05$ ; Fig. 2e), but did not affect the crude fiber concentration (Fig. 2o). Mowing did not affect the community-level concentrations of three indices of forage quality (Fig. 2e, j, o). There was no interactive effect between N addition and mowing in affecting the quality of community forage yield.

Across all functional groups, N addition significantly increased the stocks of protein, fat, and fiber in forage, whereas mowing had no significant impact (Table 1). Nitrogen addition significantly enhanced the quality-adjusted forage yield at the community level, as indicated by the changes of stocks of crude protein, crude fat, and crude fiber (all  $P < 0.01$ ; Fig. 3). Mowing significantly decreased the community-level stocks of crude protein and crude fiber (both  $P \leq 0.05$ ), but did not affect that of crude fat. Furthermore, mowing tended to mediate the effects of N addition on quality-adjusted yield, with the presence of positive effects of N addition only under unmown condition (Fig. 3e, j, o).



Across all the treatments, intra- and inter-group variability contributed almost equally to the total variation of each quality index at the community level (Fig. 4a–c). There were negative co-variations between intra- and inter-group variability in driving community-level nutrient concentrations (Fig. 4a–c). Inter-group variability had a significant contribution to the N-induced variation of each of the three quality indices at the community level (Fig. 4a–c). Intra-group variability significantly contributed to the variation of community-level crude protein concentration in response to N addition (Fig. 4a), but did not contribute to that of crude fat and crude fiber concentrations (Fig. 4b, c).

Inter- instead of intra-group variability had the dominant contribution to the total variation of quality-adjusted yield across all treatments (Fig. 4d–f). There were positive co-variations between intra- and inter-group variability in driving the community-level variation of crude protein and crude fiber stocks (Fig. 4d, f), but negative co-variation for that of crude fat (Fig. 4e). While intra-group variability contributed the most to N-induced variation of community-level crude protein stock, inter-group variability contributed the most to the variations of crude fat and crude fiber. Most of the mowing-induced community-level variations of nutrition stocks were contributed by inter-group variation, with minor contribution of intra-group variability (Fig. 4d–f).



## Discussion

We found that N addition significantly increased quantitative forage yield and the concentrations of crude fat at the community level. The positive impacts of N addition on the quantity of forage production were almost wholly contributed by rhizomatous grass. In contrast, there was no positive effect of N addition on other functional groups. Yang et al. (2019) reported that the dominance of *Leymus chinensis*, a rhizomatous grass, increased along a N addition gradient with rates ranging from 0 to 50 g N m<sup>-2</sup> year<sup>-1</sup> in a nearby ecosystem. While the traits of clone and rhizome would facilitate N uptake of rhizomatous grass, such as *Leymus chinensis*, high stature assures their advantage in the intensified light competition under N enrichment (Dickson et al. 2014; Yang et al. 2019). While numerous studies have reported the positive impacts of N enrichment on the quantity of forage yield in grasslands (Aydin and Uzun 2005; Avolio et al. 2014; Xu et al. 2018), our results shed new light on its compositional changes at plant functional group level by clarifying the unbalanced responses of different plant functional groups to N enrichment.

The role of such changes in community composition would be much stronger in driving the qualitative than quantitative changes of community forage yield, because

functional groups differed significantly in forage quality. For instance, forb had the highest crude protein concentration and rhizomatous grass had the highest concentrations of crude fat and fiber (Fig. 2). Our first hypothesis was supported by the results of crude protein concentration but not by those of crude fat and crude fiber. Due to the positive responses of all functional groups, the increases of community-level crude protein concentration following N addition were caused by the intra-group variability (Fig. 4a). It should be noted that the contribution of inter-group variability to the responses of community-level crude protein concentration to N addition was also statistically significant, though lower in magnitude than that of intra-group variability. In contrast, inter-group variability had a greater contribution than intra-group variability in driving responses of community-level crude fat and fiber concentrations to N addition, because the increases of dominance of rhizomatous grass that with the highest concentration of crude fat and fiber. Our results indicate that the relative role of intra- and inter-specific variability to community-level responses of forage quality traits to N addition is trait-dependent, and thus highlight that changes at both intra-group and inter-group levels should be given full consideration when we evaluate the

qualitative changes of forage yield under a scenario of increasing N deposition.

The co-variation between intra- and inter-group components contributed to the total variation of community-level concentrations and stocks of nutrients, but the direction of such contribution differing among quality indices and also between concentrations and stocks of a particular nutrition. For instance, negative co-variation was found for intra- and inter-group components in driving the responses of community-level crude protein concentration to N addition, which was caused by inconsistency of N effects between intra- and inter-group level. While N addition increased the crude protein concentration in all functional groups at the intra-group level, it reduced the dominance of forb, the functional group with the highest protein concentration, at the inter-group level. In contrast, the strong effect of N addition on community-level protein stocks was largely driven by substantial positive co-variation. While both positive and negative co-variations between intra- and inter-group components have been widely reported to drive the responses of community-level functional traits to environmental factors (Kichenin et al. 2013; Hu et al. 2020) or management strategy (Siefert and Ritchie 2016; Volf et al. 2016), our results suggest that the directions of this co-variation effect likely depend on whether quantitative (stocks) or qualitative aspect (concentration) is considered.

Our second hypothesis that mowing would mediate the impacts of N addition on forage production was supported by the results of quantitative changes but not by the qualitative changes of forage yield. We found an averaged 42% increase of forage production in response to N addition under unmown condition, but non-significant response under mown condition (Fig. 1e). Mowing does not facilitate the growth of species with high stature but favors species with low stature (Semmartin et al. 2007; Valko et al. 2012). In our ecosystem, the rhizomatous grass suffered a lot from mowing, which decreased its dominance, especially under N enriched condition. Mowing could reduce the positive effects of N enrichment on forage production through other pathways. For instance, the removal of biomass would move nutrient out of the ecosystem and thus offset the positive effects of N enrichment on soil N availability (Venterink et al. 2009; Song et al. 2011). Furthermore, by increasing light availability and consequently soil temperature, mowing could reduce soil water availability, which is an important factor driving nutrient cycling in semi-arid ecosystems (Wang et al. 2006). Our finding that mowing weakened the positive effects of N enrichment on the quantity of forage yield reminds us that we should reconsider the potential roles of N enrichment in driving forage production grasslands under intensified utilization.

With respect to another facet of forage quality, mowing did not mediate the N-induced effect at the community level. Only one out of the total 12 cases examined here (3 indices  $\times$  4 functional groups) showed significant interactive effects between N addition and mowing (Fig. 2h), indicating that N addition and mowing were generally independent in their impacts on forage quality at the functional group level. Furthermore, N addition and mowing did not interact to affect the relative biomass of each plant functional group. Both processes contribute to the no interaction between N addition and mowing in affecting the community-level forage quality. Our results suggest that increasing N deposition would improve forage quality in temperate steppe, even under intensified utilization. Moreover, N fertilization would be an appropriate management strategy to enhance the crude protein and crude fat concentrations in forage.

Mowing mediated the responses of quality-adjusted forage yield to N enrichment, which were mainly caused by their impacts on the biomass production instead of nutrient concentrations. Similar to the pattern of biomass, N addition significantly increased the stocks of crude protein, crude fat, and crude fiber in forage under non-mown condition, but had no impact under mown condition. Rhizomatous grass, the dominant functional group in this ecosystem, drove the responses of community-level crude fiber stocks to the interaction between N addition and mowing, supporting the mass ratio hypothesis that the effects of species on ecosystem properties would be proportionally related to their abundance (Grime 1998). But that was not the case for the stocks of crude protein and crude fat. Nitrogen addition enhanced their stocks in rhizomatous grass in both unmown and mown conditions, but increased their stocks in the whole community only under unmown condition. Such divergence of relationships between the dominant functional group and community with respect to different quality indices highlight the importance of considering community composition beyond the dominant functional group or species. Although the positive effects of N enrichment on forage quality were not mowing-dependent as mentioned above, mowing did diminish the positive effects of N enrichment on the quantity of nutrition provided in grasslands. While mass ratio effect is important in driving the quantitative responses of forage production to N addition (Smith et al. 2020), our results indicate that it might not be the case for quality-adjusted yield, at least for the stocks of crude protein and crude fat examined here.

## Conclusions

In all, we found that mowing did not alter the positive impacts of N enrichment on qualitative changes of forage yield in a meadow steppe, but diminished that on

quantitative changes, including forage mass and nutrition stocks. While N addition positively affected the quantity and quality of forage yield by stimulating the dominance of rhizomatous grass, mowing did not favor its growth and consequently mediate the positive effects of N enrichment. Our results suggest that the effects of N enrichment via either atmospheric deposition or anthropogenic fertilization on forage yield in grasslands would be moderate in grasslands under intensified utilization. Moreover, our results highlight the role of inter-group variability in driving the quantitative and qualitative changes of community-level forage yield either directly or indirectly by substantial positive or negative co-variation with intra-group variability. Given the high sensitivity of plant community composition to global change drivers (Wardle et al. 2011; Pereira et al. 2012), including N deposition (Suding et al. 2005; Clark et al. 2019), changes in plant community composition should be given full considerations when we examine or predict the changes of ecosystem function and service. Given the importance of water availability in driving the impacts of N enrichment on forage production in temperate steppe (Lü et al. 2018) and the fact that this study was based only on 1-year data, the generality of our findings should be examined in future studies under a long-term perspective.

## Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s13717-020-00273-2>.

**Additional file 1: Figure S1** Monthly mean temperature (°C) and total precipitation (mm) in Erguna in the growing season of 2016. **Figure S2** The experimental platform of nitrogen addition and mowing. **Figure S3** Differences of forage quality among bunchgrass, rhizomatous grass, forb, and sedge across all treatments in a temperate meadow steppe. Values within columns with different lowercase letters indicate significant differences ( $P < 0.05$ ) among the functional groups. **Table S1** Physical properties in 0–40 cm, 40–70 cm, 70–100 cm of soils before conducting the experiment. **Table S2** Chemical properties in 0–40 cm, 40–70 cm, 70–100 cm of soils before conducting the experiment. **Table S3** Common plant species for sampled fields classed by life form, family, genus, species.

## Abbreviations

CAS: Chinese Academy of Sciences; AOAC: Association of Official Analytical Chemists; NDF: Neutral detergent fiber; ADF: Acid detergent fiber; ANOVA: Analysis of variance

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## Authors' contributions

XTL designed the experiment and conceived the study. GJY, XGW, ZJZ, YYH, and ZWZ collected the data. CD, YYH, SLH, and XTL analyzed the data. CD wrote the draft and all co-authors revised the manuscript. The author(s) read and approved the final manuscript.

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## Availability of data and materials

Please contact the author for data requests.

## Ethics approval and consent to participate

Not applicable.

## Consent for publication

Not applicable.

## Competing interests

The authors declare that they have no known competing financial interests or personal relationships on this work.

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