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Linking changes of forage production and digestibility with grassland community assembly under nitrogen enrichment

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Abstract

Background: Forage production is the fundamental ecosystem service of grasslands. Although forage consumption occurs at community level, most studies focused on species-level changes of forage quality. The quantitative and qualitative changes of forage production are driven by species-specific trait, intra-specific plasticity, and species turnover. We examined the changes in forage production and digestibility after 5-year factorial treatments of nitrogen (N) addition and mowing in a temperate steppe and linked such changes to community assembly under the Price equation framework.

Results: Nitrogen addition significantly reduced species richness, increased forage production, but did not change forage digestibility (indicated by the total Ca+Mg concentrations). Mowing did not affect forage production and digestibility. The positive effects of N addition on forage production were driven by the enhancement of abundance of the remaining species following N enrichment, rather than by species loss or species gain. The species identity effects could offset the effects of species richness loss or gain on forage production and digestibility.

Conclusions: Our results highlight the importance of a community perspective in addressing the quantitative and qualitative changes of forage production under global change pressure of N enrichment. Species identity is important in determining the contribution of different processes of community assembly to ecosystem services.

Keywords: Community composition, Nitrogen deposition, Species turnover, Price equation, Primary productivity

Introduction

Grasslands, the largest terrestrial biome on earth, provide important goods and services (Gibson 2009). Forage production ranks among a fundamental grassland ecosystem service, with the productivity and quality of forage largely depending upon species diversity and community composition. While positive relationships between plant species diversity and primary production are widely reported (Hooper et al. 2005; Tilman et al.

2014), the relationship between community composition and primary production remains largely unknown (Bannar-Martin et al. 2018). Further, compared with our knowledge about the quantitative changes of primary production in response to the changes of biodiversity and community composition, much less is understood about its qualitative changes, such as the forage digestibility. Such knowledge gaps hinder our ability to predict the responses of grassland fundamental services to global change drivers, because both plant diversity and community composition in grasslands are sensitive to global changes (Zavaleta et al. 2003).

Increased atmospheric nitrogen (N) deposition is one of the most widespread global change drivers, which

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threatens biodiversity and alters community composition in grasslands (Bobbink et al. 2010). Nitrogen enrichment facilitates the growth of perennial grasses with high stature but inhibits forbs due to light limitation (Hautier et al. 2009), resource competition (Dickson and Foster 2011), and ammonia or metal toxicity (Tian et al. 2016). These factors consequently alter native grassland plant community composition (Dupre et al. 2010; Zhang et al. 2015). Although positive effects of N enrichment on primary productivity in grasslands are widely reported (LeBauer and Treseder 2008), the losses of species richness could substantially diminish such positive effects of N enrichment in the long-term (Isbell et al. 2013). Beyond species richness, species identity is another important determinant of primary productivity, as plant species differ in their responses to N enrichment due to their variation in evolutionary history and functional traits (Wooliver et al. 2017). In a tallgrass prairie, Avolio et al. (2014) found that the shifts of community composition from C_4 grasses to forbs (rather than change in species richness) drove temporal variation of primary productivity in response to long-term N addition. Moreover, mowing for forage in grasslands plays an important role in mediating the impacts of N addition on community composition (Yang et al. 2019). Species richness and community composition are closely related with community assembly processes. While the role of community assembly in driving ecosystem functioning including primary productivity is theoretically highlighted (Leibold et al. 2017), empirical evidence is rather scarce.

Forage digestibility is as important as the amount of forage production, because it represents the amount of energy available for livestock (Bruinenberg et al. 2002). Due to substantial inter-specific variation in forage digestibility and intra-specific responses to environmental changes, the community-level forage digestibility is sensitive to factors that can alter plant community composition, including nutrient availability, disturbance regime, and climatic factors (Pontes et al. 2007; Gardarin et al. 2014). Summing plant calcium (Ca) and magnesium (Mg) concentrations is a meaningful indicator of forage digestibility (Mladkova et al. 2018), because both elements are important for the production of soft tissues and easily digestible vegetative material (Hawkesford et al. 2012; Maathuis 2009). Forbs generally have higher Ca and Mg concentrations than grasses (Han et al. 2011), and thus have higher digestibility (Duru 1997; Mladkova et al. 2018). Consequently, reduced forb biomass and the paralleled increases of grass biomass following N enrichment as observed in diverse grasslands may lead to lower forage digestibility. In contrast, mowing would results in higher forage digestibility at community level by facilitating the growth of forbs but decreasing that of grasses. Further, the stimulation of

plant growth by N enrichment has carbon:nutrient dilution effects in plant tissue (Tian et al. 2019), including Ca and Mg, which might negatively affect forage digestibility.

Identifying how N enrichment affects the relative contribution of intra-specific (due to physiological alterations) and inter-specific changes (due to species loss and gain) would improve our mechanistic understanding of the responses of community-level forage digestibility. However, to date, there are few attempts to assess the relative importance of intra- and inter-specific changes in driving community-level alteration of the total amount and digestibility of forage production. Empirical evidence shows that the ecological version of Price equation developed by Fox (2006) could successfully partition the contributions of species loss, species gain, and intra-specific physiological changes to ecosystem function and properties (Teurlincx et al. 2017; Bannar-Martin et al. 2018). By comparing the differences in function between a baseline community and a comparison community, the extended Price equation could partition such differences into five components: (1) species richness effect of losses (SRE.L) which represents the extent by which the function has changes as a result of random loss of species with perfectly average function from the baseline community, (2) species identity effect of losses (SIE.L) which represents the effects of losing species with higher or lower function than average functioning species in the baseline community, (3) species richness effect of gains (SRE.G) which reflects the contribution of random gaining species with perfectly average function in the comparison community, (4) species identity effect of gains (SIE.G) which reflects the contribution of gaining species with higher or lower function than the average functioning species in the comparison community, and (5) context-dependent effect of resident species (CDE) which reflects the contribution of intra-specific physiological changes of shared species by baseline community and comparison community (Winfree et al. 2015; Bannar-Martin et al. 2018). Consequently, the Price equation framework could provide a quantitative link between community assembly and ecosystem function.

Here, we examined the impacts of N enrichment on forage production and digestibility with a factorial field experiment with N addition and mowing in a temperate meadow steppe, and further quantitatively linked such changes with different processes of community assembly. We hypothesized that (1) CDE would be the main contributor to the enhancement of forage production following N addition, as evidenced in literature that grasses are always facilitated by N enrichment (Dupre et al. 2010; Zhang et al. 2015), (2) N addition would reduce forage digestibility (indicated by lower total concentrations of Ca and Mg) due to the losses of forbs and

the intra-specific variation of resident species, but (3) such impacts of N addition would be less strong under mowing conditions, as mowing can mitigate the effects of N addition on species richness and the growth of dominant grass in this ecosystem (Yang et al. 2019).

Materials and methods

Study site

The experimental site—a natural meadow steppe near the Erguna Forest-Steppe Ecotone Research Station (50° 10′ 46.1′′N, 119° 22′ 56.4′′E, 650 m a.s.l.)—has been fenced since 2013 to prevent livestock grazing. Prior to 2013, the site had been annually mown for hay-harvesting. The mean annual precipitation from 1957 to 2018 is 360 mm and the mean annual temperature is −2.4 °C. The soil is classified as chernozem in the Chinese Soil Taxonomy. The pH of surface soil (0–10 cm) is 6.8–7.0. The concentration of soil organic carbon, total N, and total phosphorus in the surface layer is 25 g C kg^{-1}, 2.4 g N kg^{-1}, and 0.7 g P kg^{-1}, respectively. The dominant plant species are *Leymus chinensis*, *Stipa baicalensis*, *Cleistogenes squarrosa*, *Thermopsis lanceolate*, *Cymbaria dahurica*, and *Carex duriuscula*. Mowing for forage harvest is a common management practice in this area.

Experimental design

The experiment was established in 2014 following a factorial design with two factors: N addition and mowing, resulting in four treatments (control, N addition, mowing, combined N addition and mowing). Five replicates (n = 5) of each treatment were distributed in five blocks, with twenty 10 m × 10 m plots in total. Plots were separated by 1 m walkways. Annual N addition occurred from 2014–2018; powdered NH_4NO_3 was added at a rate of 10 g N m^{-2} year^{-1} in mid-May of each year. We chose such a N addition rate for the convenience of results comparison among different studies. Plots under the mowing treatments were mown with a mower about 10 cm above the soil surface at the end of August each year. All the plant tissue was removed to the edge of each plot after mowing.

In mid-August of 2018, during the annual peak in aboveground biomass, living shoots were sampled by clipping all vascular plants in a 1 m × 1 m quadrat randomly placed in each plot (50 cm inside each plot to avoid edge effect). Plants in each quadrat were sorted to species, oven-dried at 65 °C for 48 h, and then weighed and ground. Plant samples were acid digested with a mixture of acids (HNO_3:$HClO_4$ = 5:1) in a microwave oven. The concentrations of Ca and Mg in the solution were measured using inductively coupled plasma mass spectrometry (Perkin Elmer, ELAN-6000).

To clarify the roles of different Price components to the N-induced variation of forage production under unmowed and mown (M) conditions, we calculated the contribution of SRE.L, SIE.L, SRE.G, SIE.G, and CDE to the difference of forage production between control plot (as baseline community) and +N plot (as comparison community) in each block and between mown plot (as baseline community) and +NM plot (as comparison community) in each block, separately. Following the method developed by Fox and Kerr (2012) and Bannar-Martin et al. (2018), the contribution of each of the five components was calculated as:

$$SRE.L = (S_c - S)\bar{z} \quad (1)$$
$$SIE.L = S_c(\bar{z}_c - \bar{z}) \quad (2)$$
$$SRE.G = (S' - S_c)\bar{z}' \quad (3)$$
$$SIE.G = -S_c(\bar{z}'_c - \bar{z}') \quad (4)$$
$$CDE = S_c(\bar{z}'_c - \bar{z}_c) \quad (5)$$

in which, S, S', and S_c is the number of species in the baseline community, the comparison community, and that shared by baseline community and comparison community, respectively; $\bar{z}$, $\bar{z}'$, $\bar{z}_c$, and $\bar{z}'_c$ is the averaged biomass at species-level for all the species in the baseline community, the comparison community, and that for shared species in the baseline community and the comparison community.

Because the partitions of element concentration could not be directly summed, we evaluated the relative contribution of each Price component (pj) on the N-induced variation of community-level summing of Ca and Mg concentrations (CM) following the method of Teurlincx et al. (2017), which based on the contribution of each component to the changes of nutrient content (NC) and biomass (B) in the comparison community:

$$\Delta CM_{pj} = ((NC_{base} + \Delta NC_{pj})/(B_{base} + \Delta B_{pj})) - (NC_{base}/B_{base}) \quad (9)$$

in which, NC_{base} refers to the summing content of Ca and Mg in base community, B_{base} refers to the biomass of base community, ΔNC_{pj} refers to changes of Ca and Mg content due to the component pj, and ΔB_{pj} refers to changes of biomass due to the component pj. The contribution of SRE.L to the changes of community-level summing of Ca and Mg concentrations is zero, because random loss of species with average nutrient concentration would not affect the community-level nutrient concentration.

Statistical analysis

Normal distribution and homogeneity of variances of all data were checked with Kolmogorov-Smirnov test and Levene's test, respectively. Results showed all the data met such assumptions. With all the four treatments being combined, the differences of summed Ca and Mg concentration between forbs and grasses were detected using t tests. To detect the main and interactive effects of N addition and mowing on species richness, forage

production, and concentration of Ca and Mg, three-way ANOVAs were performed with N addition and mowing as the fixed factors and block as random factor. The *t* tests were used to test the differences of the contribution of each component from 0. All data analyses were performed with SPSS version 20.0 (SPSS, Chicago, IL, USA).

Results

Nitrogen addition significantly reduced total species richness (Fig. 1a) and forb species richness (Fig. 1b), but did not affect the species richness of grasses (Fig. 1c). The losses of species richness were due to higher species loss than species gain, with both being significantly higher than 0, indicating the occurrence of species turnover following N addition (Fig. S1). In most cases, more forb species than grass species being lost or gained during the species turnover induced by N addition under both mown and unmown conditions (Table S1). Mowing did not affect species richness of the whole community, forbs, and grasses (Fig. 1).

Nitrogen addition significantly enhanced forage production at community level and for grasses, with no effect on forbs (Fig. 2). Nitrogen addition increased community-level forage production by 120 g m^{-2} under unmown conditions, and by 180 g m^{-2} under mown conditions (Fig. 2a). Nitrogen addition did not affect the summed concentrations of Ca+Mg in forage at either the community or functional group level (Fig. 3). Across all the treatments, the biomass-weighted concentration of Ca+Mg in forbs was three times higher than that in grasses (1.47% vs 0.43%; Fig. 3). Mowing had no impact on forage production and the summed concentrations of Ca+Mg at all examined levels (Figs. 1, 2, 3).

Under both unmown and mown conditions, almost all the Price components significantly contributed to the N-induced changes of community-level forage production
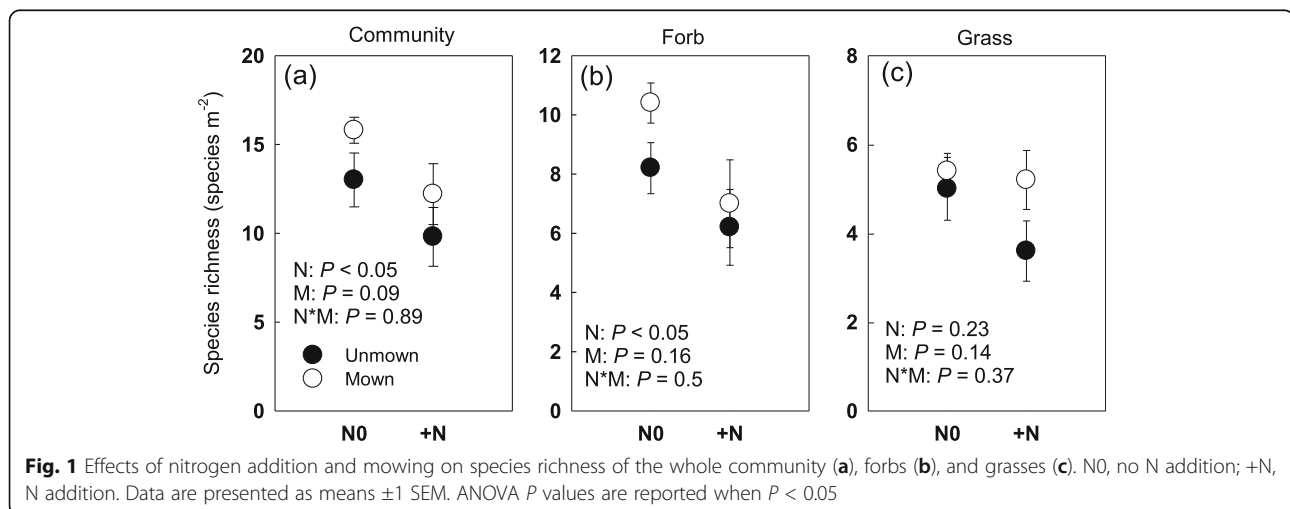
(Fig. 4a). Random species richness loss contributed negatively and the identity of species loss contributed positively to the changes of forage production (Fig. 4a). Random species gain contributed positively but the identity of gained species contributed negatively to the changes of forage production (Fig. 4a). The growth of species shared between the baseline and comparison communities was stimulated by N addition as indicated by the positive CDE values (Fig. 4a).
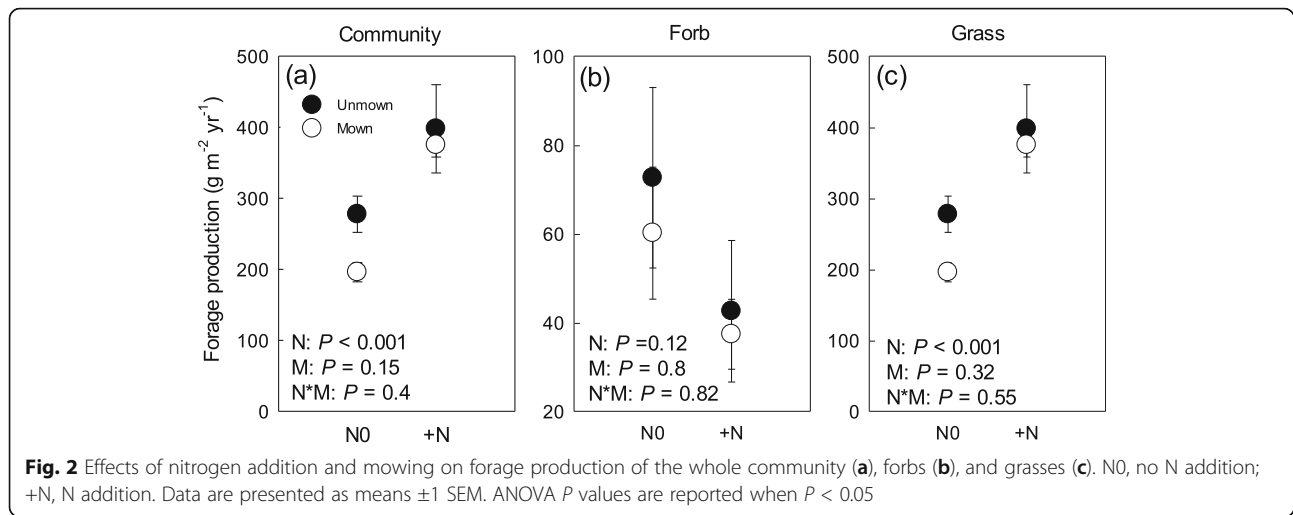
Nearly all Price components did not significantly contribute to the N-induced changes of Ca+Mg concentration at community level (Fig. 4b). One exception was the identity of species loss when N was added under unmown conditions, which negatively contributed to changes of Ca+Mg concentration (Fig. 4b).

Discussion

Our results showed that N enrichment significantly enhanced forage production under both mown and unmown conditions, but did not affect forage digestibility as indicated by its neutral impact on the summed Ca+Mg concentrations in forage. Under the framework of the extended Price equation, we quantified the contribution of species loss, species gain, and intra-specific variation to the changes of forage production and digestibility in response to N enrichment. The increases of forage production following N enrichment were contributed by the positive CDE that is the enhancement of intra-specific growth of shared species between communities with and without N addition. Although there were substantial forb species losses following N enrichment and the digestibility of forbs is greater than that of grasses, forage digestibility was not affected by N enrichment due to the offset among different community assembly processes.

Consistent with our first hypothesis, species shared by control and N-enriched communities (CDE component)

Fig. 1 Effects of nitrogen addition and mowing on species richness of the whole community (**a**), forbs (**b**), and grasses (**c**). N0, no N addition; +N, N addition. Data are presented as means ±1 SEM. ANOVA *P* values are reported when *P* < 0.05

Fig. 2 Effects of nitrogen addition and mowing on forage production of the whole community (**a**), forbs (**b**), and grasses (**c**). N0, no N addition; +N, N addition. Data are presented as means ±1 SEM. ANOVA P values are reported when P < 0.05
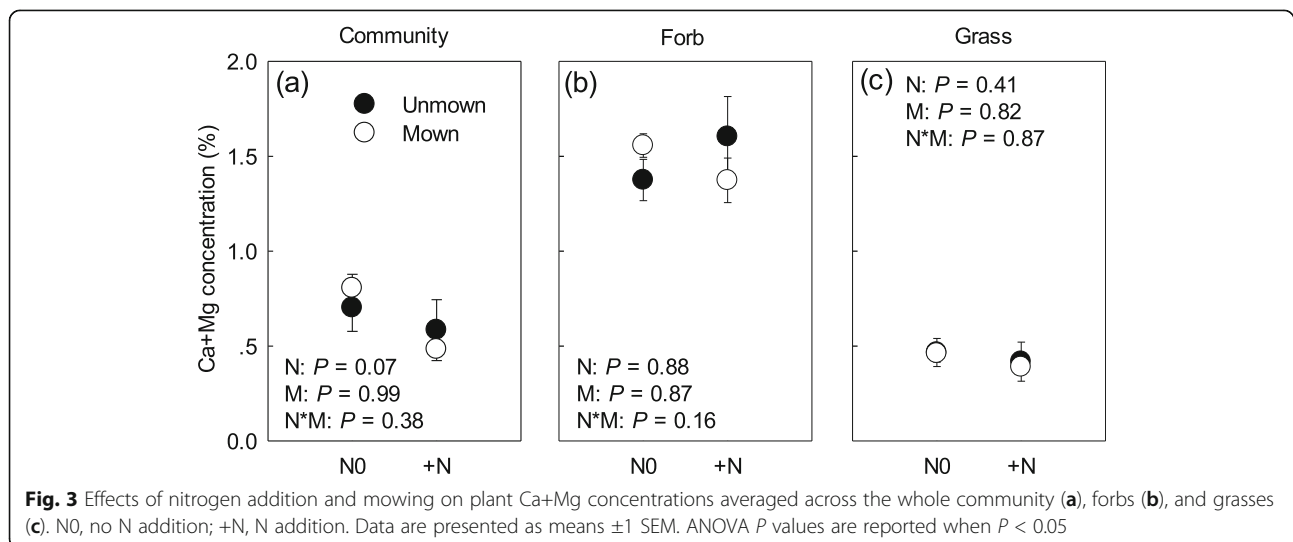
had a positive contribution to the N-induced increases of forage production. While it is widely known that N fertilization enhances primary productivity in diverse grasslands (Elser et al. 2007; Zhang et al. 2015), our study is among the first to link such changes of production with community assembly processes (Fox and Kerr 2012). Nitrogen enrichment reduces species richness in diverse grasslands and consequently alters ecosystem functioning (Isbell et al. 2013; Zhang et al. 2014). The reduction of species richness following N enrichment reflects species turnover with both species loss and species gain. Unfortunately, few studies have examined the relative contribution of species loss and species gain to changes of ecosystem functioning and services (Bannar-Martin et al. 2018).

There are several novel findings from our study. Species richness losses following N enrichment negatively influenced forage production, as indicated by the negative contribution of SRE.L. Many studies report lower primary productivity associated with species loss (Isbell et al. 2013; Tilman et al. 2014). However, species losses following N enrichment are often non-random due to functional- and abundance-based mechanisms (Suding et al. 2005). In our ecosystem, forb species richness was much more sensitive to N addition than would be expected by chance, with a significant reduction of forb richness following N addition. As their contribution to forage production was lower than that of grasses (Fig. 2b, c), the losses of forbs drove a lower reduction of forage production than expected due to species random losses. Consequently, we found significant positive contribution of SIE.L component to changes of forage production, which offset the negative effects of SRE.L. These findings highlight the importance of species identity in modulating the impacts of species losses on forage production under N enrichment.
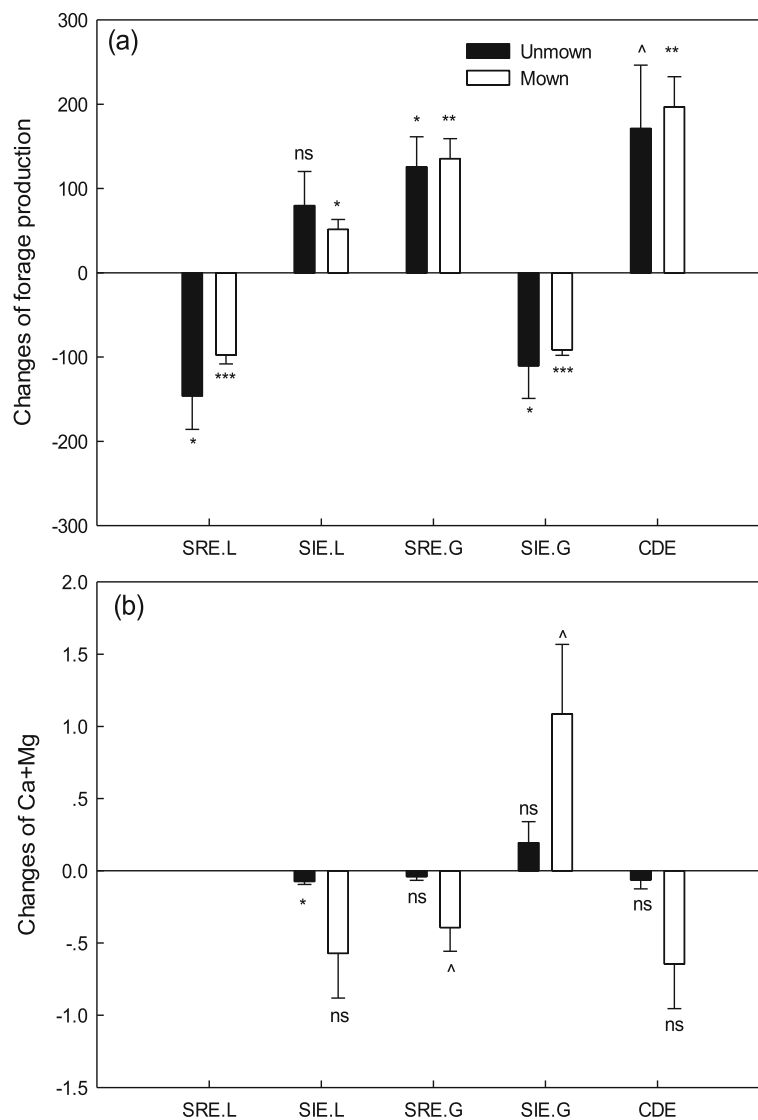

Fig. 3 Effects of nitrogen addition and mowing on plant Ca+Mg concentrations averaged across the whole community (**a**), forbs (**b**), and grasses (**c**). N0, no N addition; +N, N addition. Data are presented as means ±1 SEM. ANOVA P values are reported when P < 0.05

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Fig. 4 Price partitions of changes in forage production (**a**) and Ca+Mg concentrations (**b**) between the treatments with and without N addition under unmown and mown conditions. SRE.L, species richness effect of species loss; SIE.L, species identity effect of species loss; SRE.G, species richness effect of species gain; SIE.G, species identity effect of species gain; CDE, context dependent effect. Significance levels of the changes different from 0 were assessed using *t* tests. ns, $P > 0.1$; ^, $0.05 < P < 0.1$; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$

Species identity was important in determining the impacts of species gain on the changes of forage production. We observed that both species richness effect of gains (SRE.G) and species identity effect of gains (SIE.G) significantly contributed to the changes in forage production observed following N enrichment, with positive contribution of SRE.G and negative contribution of SIE.G. All species presented in the comparison community (N enriched) has positive contribution to forage production, and consequently a positive effects of SRE.G being found. The negative contribution of SIE.G implies that the production of gained species following N enrichment was generally lower than that averaged across all the species, which consequently offset the positive effects of SRE.G.

In contrast to our hypothesis, N addition did not significantly affect forage digestibility. The SRE.L component, which was quantified by the mean values of nutrient concentrations average across all species in the baseline community (no N addition or mowing), did not contribute to the changes of community level nutrient concentrations (Teurlincx et al. 2017). Forb species had higher Ca+Mg concentrations than grasses, indicating higher forage digestibility, which is consistent with results from previous studies (Duru 1997; Gardarin et al. 2014). We found that N addition significantly decreased

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species richness of forbs, negatively impacting forage digestibility as indicated by the contribution of SIE.L component (Fig. 4b). Notably, the negative contribution of SIE.L to changes of forage digestibility was statistically significant only under the unmown conditions. In a previous study, we found that mowing could mediate the negative effects of N deposition on plant species diversity by suppressing the competitive advantage of dominant grass species across a N addition gradient ranging from $0-50$ g N m^{-2} year^{-1} (Yang et al. 2019). In this study, however, we found no interactive effect between N addition and mowing. Such contrasting results indicate that the mediating role of mowing on the negative effects of N addition on species diversity would depend on the rates of N addition and may vary among different years. The negative impacts of SIE.L did not lead to changes of Ca+Mg concentration at community level, because its effect was offset by SIE.G.

There were substantial species gains following N enrichment, though the number of species gained was less than that of species loss. However, both the richness and identity of species gained after N enrichment did not significantly impact forage Ca+Mg concentrations, indicating the species gain process did not affect forage digestibility in this ecosystem. Together with the finding that both SRE.G and SIE.G significantly affected forage production, our results indicate that the species gain process had divergent effects on the quantity and quality of forage production. Similarly, we found that CDE did not contribute to the changes of forage digestibility, indicating that the summed concentrations of Ca+Mg in the plant species shared by communities with and without N addition were not changed by N addition. However, the biomass Ca+Mg storage in forage must be increased by N addition because the significant enhancement of forage production. Such increases of plant Ca+Mg uptake following N addition may reduce soil extractable Ca and Mg concentrations under N enrichment as reported in the temperate steppe (Wang et al. 2018). While cation leaching induced by soil acidification following N enrichment has been widely reported (Lucas et al. 2011; Wang et al. 2018), the potential decreases of soil exchangeable base cation due to plant uptake after N enrichment should receive more attention, especially in the grassland being used for forage harvest.

Conclusions

Nitrogen addition with a rate of 10 g m^{-2} year^{-1} significantly increased forage production but did not alter forage digestibility in a meadow steppe. Following the Price equation framework, we linked such responses of forage production and forage digestibility to community assembly processes. While the effects of both species richness loss and gain significantly affected forage production, as predicted by previous studies, our results showed that the identities of species being lost and gained could offset the effects of random species richness loss and gain. Our results highlight the importance of species identity in driving the contribution of community assembly processes to forage production following N enrichment. Because N addition significantly enhanced the quantity of forage production but did not change forage quality, N fertilization should be an important management strategy to enhance ecosystem services in the meadow steppe.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s13717-021-00308-2.

Additional file 1 Table S1. The number and identities of species being lost and gained in response to nitrogen addition under both unmown (control vs N) and mown (M vs NM) conditions in a temperate grassland. **Figure S1.** The N-induced changes of species loss and gain under unmown (**a**) and mown (**b**) conditions. Significance levels of the changes different from 0 were assessed using t-tests . *, $P < 0.05$; **, $P < 0.01$.

Authors' contributions

XTL conceived the ideas. ZYL, GJY, YYH, ZWZ, SLH, and CD collected the data. ZYL, SS, and XTL analyzed the data. XTL and SS led the writing of the manuscript. All authors contributed critically to the drafts. The authors read and approved the final manuscript.

Availability of data and materials

The datasets used during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate

Not applicable

Consent for publication

Not applicable

Competing interests

The authors declare that they have no competing interests.

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