



Changes of community composition strengthen the positive effects of nitrogen deposition on litter N:P stoichiometry in a semi-arid grassland

Shuang-Li Hou · Jun-Jie Yang · Jiang-Xia Yin ·
Hai-Wei Wei · Yan-Yu Hu · Zhi-Wei Zhang · Guo-Jiao
Yang · Xiao-Tao Lü

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Abstract

Aims The stoichiometric traits of litter play an important role in driving litter decomposition and ecosystem nutrient cycling. While the impacts of nitrogen (N) deposition on the species-level litter stoichiometric traits have been well addressed, we know little about that at community-level, which is supposed to be driven by both intra-specific variation and changes in community composition.

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S.-L. Hou · H.-W. Wei · Y.-Y. Hu · Z.-W. Zhang ·
G.-J. Yang · X.-T. Lü (✉)

Erguna Forest-Steppe Ecotone Research Station, CAS Key Laboratory of Forest Ecology and Management, Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang 110016, China
e-mail: lvxiaotao@iae.ac.cn

J.-J. Yang
State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, Beijing 100093, China

J.-X. Yin
School of Life Sciences, Liaoning University, Shenyang 110036, China

Z.-W. Zhang
University of Chinese Academy of Sciences, Beijing 100049, China

Methods We examined the effects of N deposition on litter phosphorus (P) concentration and N:P ratio at both species- and community-level in a semi-arid grassland of northern China. We further decomposed the community-level variations of litter nutritional traits into intra- and inter-specific variation.

Results Nitrogen addition, especially at high rates, substantially changed community composition. Litter P concentrations and N:P ratios significantly varied among different species. Litter P concentrations and N:P ratios at both species- and community-level were positively correlated with N addition rates. Biomass-weighted community-level N:P ratios were more sensitive to N addition than the non-weighted ones, indicating that community composition strengthened the positive impacts of N addition on litter N:P ratios. There was positive co-variation between intra- and inter-specific variation for litter N:P ratio, indicating the consistency of community composition and intra-specific variation in their effects on litter N:P ratio.

Conclusions Our results indicated that the imbalance of N and P following N enrichment would be much larger than the expectation based on the findings from species-level, and thus highlight the importance of changes in community composition in driving the responses of community-level litter N:P stoichiometry to N deposition in the semi-arid grassland.

Keywords Global changes · Intra-specific variation · Litter quality · Nutrient cycling · Nutrient stoichiometry · Semi-arid grassland · Species rank · Species turnover

Introduction

Increasing nitrogen (N) deposition is one of strong impacts humans ever had on global ecosystems, as a result of extensive fertilizer application and industrial emissions (Gruber and Galloway 2008; Liu et al. 2013). The anthropogenic N inputs to terrestrial ecosystems increased by $\sim 8 \text{ kg N ha}^{-1}$ between 1980s and 2010s in China (Liu et al. 2013). The effects of N deposition on ecosystem processes are largely dependent on its impacts on the stoichiometric traits of nutrients in plants (Sardans and Penuelas 2012). The responses of nutrient concentrations and stoichiometry in living plants to N deposition are well documented (Li et al. 2015; Li et al. 2016). The responses of stoichiometric ratios in plant litters would not mirror that in living plants due to the occurrence of nutrient resorption during plant senescence (Billings et al. 2003; Lü et al. 2012). However, limited literature is available on the responses of litter nutrient stoichiometry to global changes.

Stoichiometric traits of litter are vital determinants of litter quality (Yuan and Chen 2009) and the rates of litter decomposition (Parton et al. 2007; Mooshammer et al. 2012), because both the compensatory feeding of invertebrates (Jochum et al. 2017) and the activities of microbial decomposers are fundamentally associated with stoichiometry (Manzoni et al. 2008). A review study across 256 reports of litter decomposition reported that plant detritus with higher N and phosphorus (P) concentration decomposed faster, as higher N and P status was positively related to the activities of bacteria and saprophytic fungi (Enríquez et al. 1993). The nutrient limitation status of litter decomposition is closely dependent on N:P supply ratio (Aerts 1997; Güsewell and Verhoeven 2006). Nitrogen deposition could increase green foliar N and P concentrations and decrease N and P resorption during plant senescence, consequently enhance N and P concentrations in the litter (Lü et al. 2013). However, the responses of litter N and P concentrations to N enrichment are imbalanced, with stronger enhancement of litter N concentration than P concentration, which leads to higher N:P stoichiometric ratios in litter (Lü et al. 2013). The changes of litter N:P ratios under global changes would potentially alter litter decomposition and nutrient cycling, which would in turn affect plant growth.

Nutrient stoichiometry of plant litter as well as their responses to N deposition have substantial inter-specific variation (Morecroft et al. 1994; Lü et al. 2012). Both

intra-specific variation of litter stoichiometry (Hou et al. 2018) and plant community composition are sensitive to N deposition (Wedin and Tilman 1996; Duprã et al. 2010). Therefore, community-level changes of litter N:P stoichiometry following N deposition would be caused simultaneously by both intra-specific variation of N:P stoichiometry and plant community composition. In a recent study, we reported that both the intra-specific variation of litter N concentration and community composition contributed to the positive effects of N addition on litter N concentration at community-level in a semi-arid grassland of northern China (Hou et al. 2018), partly because the dominance of *Leymus chinensis*, a species with higher N concentration than others, was strongly stimulated by high rates of N deposition (Zhang et al. 2015). Stoichiometric traits at species-level could not be simply scaled up to that at community-level (Sistla and Schimel 2012), because of the differences in their inherent components (Violle et al. 2007). Given that ecosystem properties are highly correlated with plant functional traits at community-level (Garnier et al. 2004), the changes in litter quality at community-level are significant for ecosystem nutrient cycling and plant-soil interactions. The responses of litter P status to N enrichment are generally insensitive than that of litter N status at species-level (Lü et al. 2013; Vitousek and Porder 2010). However, the responses of community-level P status and N:P stoichiometry to N enrichment is not well known.

To understand the impacts of N deposition on litter N:P stoichiometry, we conducted an experiment of N addition in a semi-arid grassland in northern China, with six addition rates of 0, 2, 5, 10, 20, and $50 \text{ g N m}^{-2} \text{ yr}^{-1}$. We examined the effects of N addition on litter P concentrations and N:P ratio at species- and community-level. Through the comparison of biomass-weighted and non-weighted community-level stoichiometry, we could understand the role of dominant species in driving the responses of community-level stoichiometry to N addition (Violle et al. 2012). The relative contributions of intra- and inter-specific variation to shifts in community-level litter N:P ratios were also quantified. As we have reported the changes of litter N concentration in a previous study (Hou et al. 2018), here we focused on the changes of litter P concentrations and N:P ratios, two factors also important for litter decomposition (Enríquez et al. 1993; Güsewell and Verhoeven 2006). We hypothesized that (1) N addition would decrease litter P concentrations and increase N:P ratio at

species- and community-level in the semi-arid grassland, as the dilution effects of N addition on P concentration by stimulating plant growth (Perring et al. 2008); (2) The biomass-weighted values of litter N:P ratio would be more sensitive to N addition than the non-weighted values, as the growth of species with higher N:P ratios is facilitated by N enrichment (Han et al. 2014).

Materials and methods

Study site

This study was performed in a semi-arid grassland that located in Xilin River Basin, Inner Mongolia in northern China (116°14'E, 43°13'N), which is dominated by grasses of *L. chinensis* and *Stipa grandis*. The mean annual temperature is about 0.9 °C. The mean annual precipitation is approximately 355 mm, with about 70% falling during the growing season from May to September. The soil is classified as Calcic-Orthic Aridisol according to US soil taxonomy classification system. The ambient N deposition in this area is 1~2 g N m⁻² yr⁻¹ for recent two decades (Jia et al. 2014).

Experimental design

This field experiment followed a randomized block design began in September 2008, with six rates of N addition (0, 2, 5, 10, 20, and 50 g N m⁻² yr⁻¹). Each treatment with six replicates separated by 1 m buffer and each plot was 8 m × 8 m in size. Purified NH₄NO₃ (>99%) was added twice each year. In June of each year, fertilizer was dissolved in purified water and sprinkled evenly to each plot to simulate wet N deposition. In November, fertilizer was mixed with sand (sand was sieved to 1 mm size, dipped by hydrochloric acid, washed by purified water and heated at 120 °C for 24 h) and spread evenly by hand to each plot to simulate dry N deposition in winter.

Sampling and chemical analysis

In mid-August 2015, aboveground biomass of living plants in 1 m × 1 m quadrat from each plot was collected using scissors. The quadrat was randomly placed in each plot but at least 50 cm away from the edge. All living vascular plants in the plots were classified into

species, and then weighed after oven-drying at 70 °C for 48 h.

In October 2015, we collected standing litter of all species in each plot, as that had been recorded in the corresponding plot during the field survey in August 2015. Litter of each species were randomly sampled above the soil surface in the whole plot. Plants were considered ready to abscise when they were completely dry and with a brown color (Wright and Westoby 2003). Litter samples were oven-dried for 48 h at 70 °C and then ground with a ball mill (Retsch MM 400, Retsch GmbH & Co KG, Haan, Germany).

Total N concentration in litter samples was analyzed by an Alpkem autoanalyzer (Vario Micro cube, Germany). For total P detecting, litter samples were digested in H₂SO₄-H₂O₂ and measured colorimetrically at 880 nm after reaction with molybdenum blue. The stoichiometric N:P ratio is reported as mass ratio.

Data calculation and statistical analysis

For the species-level P concentration and N:P ratio, we examined that in dominant species, *L. chinensis* (L.c.) and *S. grandis* (S.g.), and subdominant species, *Achnatherum sibiricum* (A.s.), *Agropyron cristatum* (A.c.), *Carex korshinskii* (C.k.), *Potentilla bifurca* (P.b.) and *Allium ramosum* (A.r.). Together, they contributed >85% of total aboveground biomass averaged across all the treatments.

Community litter P concentrations and N:P ratios were calculated with biomass-weighted and non-weighted for each plot. The non-weighted traits were calculated as arithmetic means of all the species presented in the plot. The community biomass-weighted means (CWM) of each trait were calculated as:

$$CWM = \sum p_i x_i$$

where p_i is the ratio of i th species biomass to community total biomass, and x_i is the trait value of i th species.

The impacts of intra- and inter-specific variation with N deposition on community nutrient (both biomass-weighted and non-weighted values) changes were quantified following Lepš et al. (2011). In brief, we decomposed the total sum of squares (SS_{specific}) of community variance to N addition gradient into 'fixed' (SS_{fixed}), 'intraspecific' (SS_{intra}) and 'covariation' (SS_{cov}) effects, thus SS_{specific} = SS_{fixed} + SS_{intra} + SS_{cov}. We calculated 'specific' community nutrient values

using species trait values as detected in that plot, which includes both intra- and inter-specific impacts. The ‘fixed’ community nutrient values using species trait values averaged across all the plots across different treatments, and thus only includes inter-specific impact. The ‘intra-specific’ community values were calculated as the difference between ‘specific’ and ‘fixed’ community nutrient values. The SS_{cov} component represents the effect of covariation between intra- and inter-specific variation and was calculated by subtracting SS_{fixed} and SS_{intra} from $SS_{specific}$.

The equality of error variance was examined for all data by Levene’s test, and data normality was detected by Kolmogorov-Smirnov test. The effects of species identity, N addition, and their possible interactions for litter P concentration and N:P ratio were determined using two-way ANOVAs. One-way analysis of covariance (ANCOVA) was used to distinguish the two slopes between the biomass-weighted and non-weighted litter nutrient values at community-level. All data analyses were performed with SPSS version 17.0 (SPSS, Chicago, IL, USA).

Results

Nitrogen addition altered plant community composition as indicated by the changes of rank orders of plant species (Fig. 1a–f). Biomass of *L. chinensis* was significantly enhanced by N addition, and it became the mono-dominant species at high rates of N addition (20 and 50 g N m⁻² yr⁻¹). Biomass of *S. grandis* and *A. cristatum* slightly increased at rates of 5 and 10 g N m⁻² yr⁻¹ but greatly decreased at rates of 20 and 50 g N m⁻² yr⁻¹. Biomass of *A. sibiricum* was slightly increased at N addition rates of 2, 5, and 10 g N m⁻² year⁻¹, but slightly decreased at rates of 20 and 50 g N m⁻² year⁻¹. Nitrogen addition did not alter the species rank of *C. korshinskii*, *P. bifurca*, and *A. ramosum* (Fig. 1).

Nitrogen addition increased litter P concentration and N:P ratio in all the examined species ($P < 0.001$; Table S1; Fig. 2). Litter P concentrations and N:P ratio varied significantly across different species ($P < 0.01$; Fig. 2a,b). Averaged across all the treatments, litter P concentration was the highest in *L. chinensis* (0.80 mg g⁻¹) and the lowest in *C. korshinskii* (0.62 mg g⁻¹; Fig. 2a). Litter N:P ratio in *L. chinensis* was higher than that of other six species (Fig. 2b). The

effects of N addition on litter P concentrations and N:P ratio depended on species identity, as indicated by the significant interaction between N addition and species identity ($P < 0.05$; Fig. 2a,b).

Community-level litter P concentrations and N:P ratios increased with the increasing N addition rates ($P < 0.001$; Fig. 3). The increases of biomass-weighted values of community-level nutrition were faster than that of the non-weighted values along the N addition gradient, as indicated by the significant differences between slopes of biomass-weighted and non-weighted regression lines (Fig. 3a,b).

Intra-specific variation accounted for 34% and 24% of the total variation in biomass-weighted litter P concentration and N:P, respectively, and the contribution of inter-specific variation was 17% and 16% ($P < 0.05$; Fig. 4a). For the non-weighted community traits, intra-specific variation explained the total variation of P concentration for 32% and N:P for 25%, whereas inter-specific variation accounted for 11% variation of P concentration and 10% variation of N:P ($P < 0.05$; Fig. 4b). Positive covariations between intra- and inter-specific variability drove the variability of community-level P concentration and N:P ratio (Fig. 4a,b).

Discussion

By examining the paralleled changes of community composition and nutritional changes of litter at species-level, we found that N addition could exacerbate litter N:P imbalance at community-level through changing community composition. The actual enhancement of litter N:P ratios at community-level following N enrichment would be much larger than our previous expectation that based on the mean values from species-level. While the importance of intra-specific variation in driving community-level nutritional responses to N deposition has been widely accepted, we presented evidence for the role of inter-specific variation and its co-variation with intra-specific variation.

Partly inconsistent with our first hypothesis, increasing N addition rates significantly enhanced litter P concentrations and N:P ratios for all the examined species. Our results did not support the dilution hypothesis which predicts that increasing N addition would reduce litter P concentrations due to the strong stimulation effects of increasing N availability on primary productivity (Perring et al. 2008). In a previous study, we

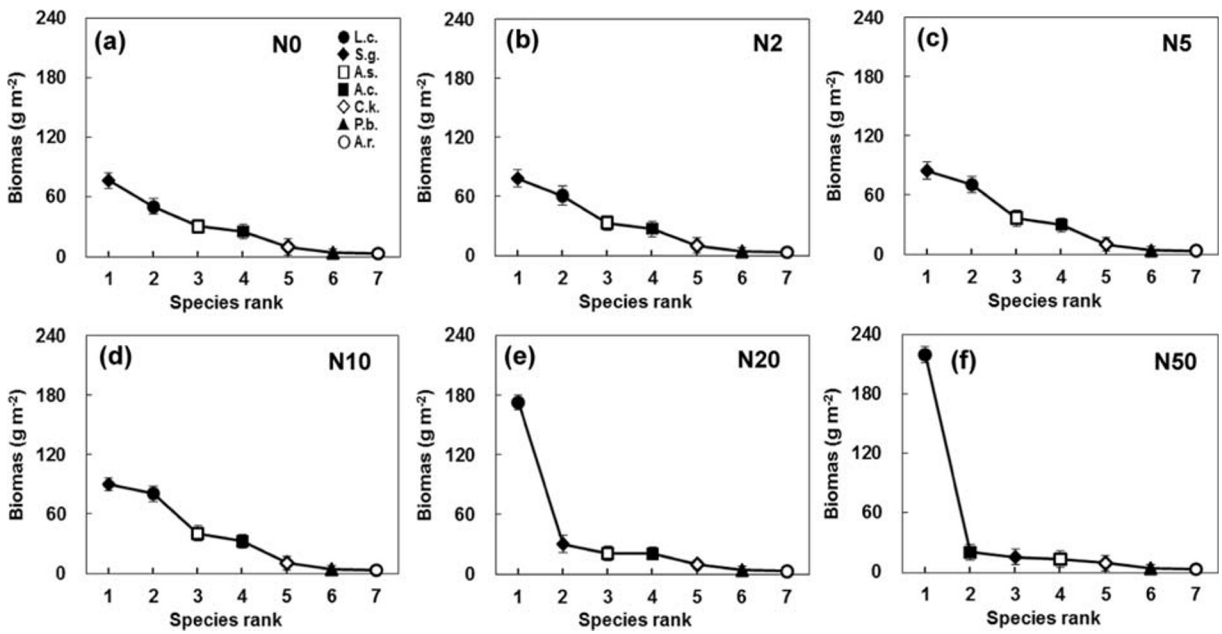


Fig. 1 Effects of nitrogen addition rate (0, 2, 5, 10, 20, and 50 g N m⁻² yr⁻¹) on species rank of the seven dominant and subdominant species in the semi-arid grassland. Data are shown as means ±1 SE

reported that litter N concentrations of most species in this ecosystem were positively correlated with increasing N addition rates, which contributed to the lower lignin:N ratios in litter (Hou et al. 2018). Concentrations of N and P in plants are generally positively related as they are closely associated in biochemical functioning in plants (Reich et al. 1998; Wright et al. 2004). Similarly, along another gradient of N addition rates in a nearby ecosystem, Lü et al. (2013) reported that N addition increased P concentrations in both living and senesced

leaves of two dominant species *L. chinensis* and *S. grandis*. Furthermore, Ren et al. (2015) found positive responses of litter P concentrations in five dominant species to N addition in another grassland. Soil P availability could be stimulated by N addition due to biotic (Marklein and Houlton 2012) and abiotic pathways (Wang et al. 2016), which may facilitate plant P uptake. Averaged across all the examined species, the enhancement of litter N concentration was 28% along this N addition gradient (Hou et al. 2018), which were much

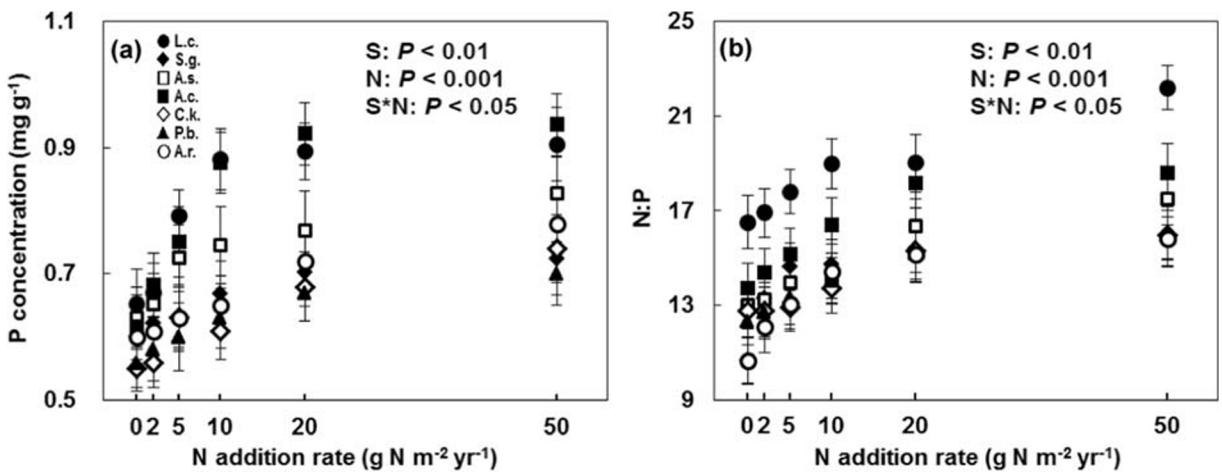


Fig. 2 Effects of nitrogen addition rate (0, 2, 5, 10, 20, and 50 g N m⁻² yr⁻¹; N), species identity (S), and their interactions on litter P concentration and N:P ratio in the seven dominant and subdominant species. Data are shown as means ±1 SE

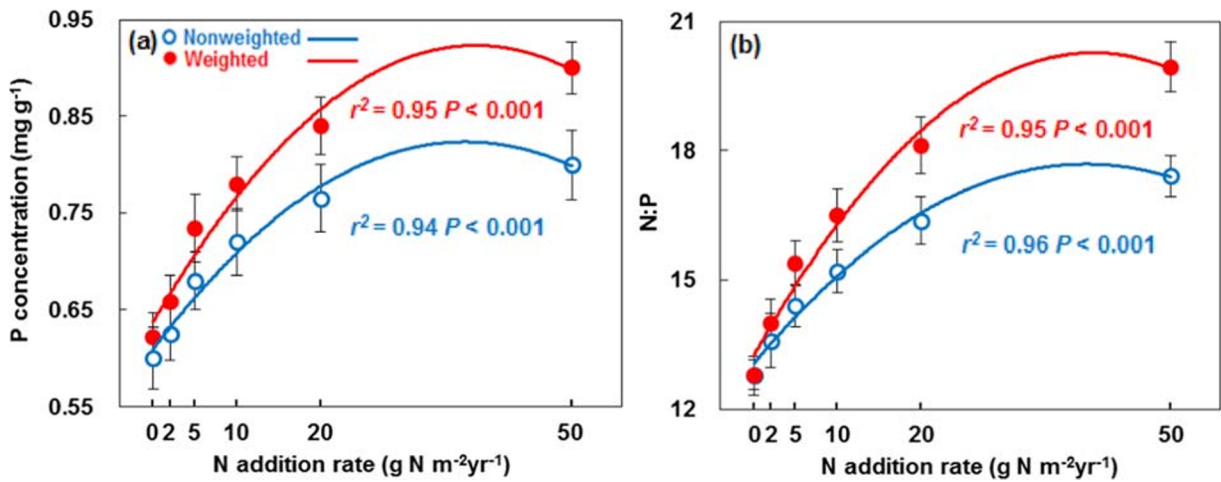


Fig. 3 Effects of nitrogen addition rate (0, 2, 5, 10, 20, and 50 g N m⁻² yr⁻¹) on litter P concentration and N:P ratio of plant community with biomass-weighted and non-weighted. Data are shown as means \pm 1 SE

higher than that of P concentration (16%). Such imbalanced responses of litter N and P concentrations to N addition led to higher litter N:P ratios.

The increases of N addition rates enhanced litter P concentrations and N:P ratios at community-level, indicating the convergent responses of dominant and sub-dominant species to N enrichment, a phenomenon supported by the results at species-level. By considering the responses at both species and community levels, our results indicate that the responses of litter N:P stoichiometry to increasing N addition are consistent across different biological organization levels in this semiarid grassland. The higher litter P concentrations would lead to more rapid P release and thus affect soil P cycling.

However, the higher litter N:P ratios could lead to a higher abundance of fungi that with lower P requirements and lower metabolic activity than bacteria, which would have negative impacts on litter decomposition (Güsewell and Gessner 2009). Therefore, although N deposition often accelerates litter decomposition and ecosystem nutrient cycling (Norby 1998; Hobbie 2000), the higher litter N:P as found here would potentially retard such positive effects of N deposition on litter decomposition. Empirical evidence showed that litter decomposition would be limited by lower P concentration in litter with higher N:P ratios (Güsewell and Verhoeven 2006).

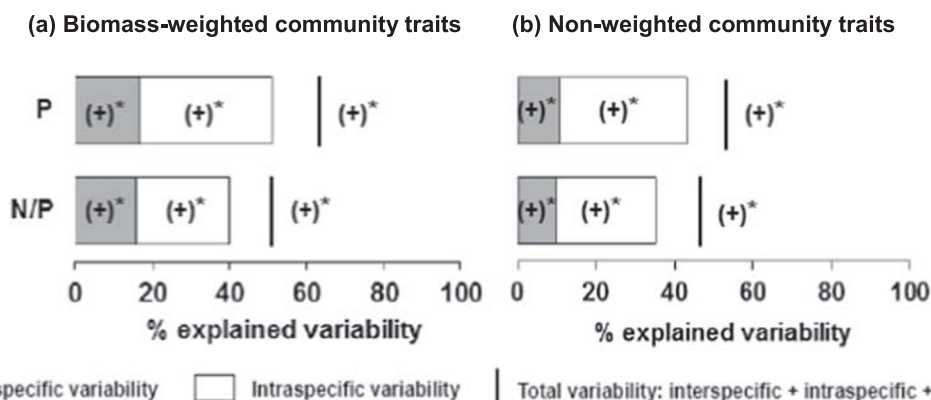


Fig. 4 Decomposition of changes in community trait values with increasing N deposition into inter-specific, intra-specific and co-variation effects for litter P concentration and N:P ratio. Black bars denote total variation. The signs (\pm) and statistical significance ($*$ $P < 0.05$) of inter-specific, intra-specific and total variability

effects are represented on the graph when significant. A value of total variability that is lower than the sum of inter- and intra-specific variability effects indicates negative covariation, and a value of total variability that is higher than the sum of inter- and intra-specific variability indicates positive co-variation

The second hypothesis was supported by the result that the biomass-weighted community-level P concentrations and N:P ratios increased faster than the non-weighted values along this N addition gradient. The biomass-weighted traits are more driven by dominant species, whereas the non-weighted traits are driven by the presence and absence of species (Violle et al. 2007). Consistent with previous finding during 2008 to 2013 in this ecosystem (Zhang et al. 2015), our results showed that increasing N deposition greatly enhanced the biomass of *L. chinensis* after seven years of annual treatment in 2015. Further, our results showed that *L. chinensis* had higher litter P concentration and N:P ratio than other species. The responses of biomass of *S. grandis*, *A. sibiricum* and *A. cristatum* were highly dependent on the rate of N addition, in that their biomass increased under moderate N addition rates (5 and 10 g N m⁻² yr⁻¹) but decreased under high N addition rates (20 and 50 g N m⁻² yr⁻¹). Those changes of species composition thus strengthened the positive impacts of N deposition on litter P concentrations and N:P ratios at community-level. The higher sensitivity of biomass-weighted community-level litter N:P ratios to increasing N addition rates than that of non-weighted values indicates the changes of community composition would exacerbate litter N and P imbalance as the traditional prediction based simply on physiological changes of species-level following N enrichment. Similarly, in a recent study, Hu et al. (2020) found that the changes in plant community composition following historical N addition had positive effects on the changes of living plant N:P ratio at community-level in a semi-arid grassland. Our results highlight the difference of stoichiometric flexibility at community-level and add new evidence for the prediction that stoichiometric flexibility at community-level would be higher than that at species-level due to the changes of community composition (Sistla and Schimel 2012).

Following the methods of Lepš et al. (2011), we quantified the contribution of both intra- and inter-specific variation to the changes of community-level litter P concentrations and N:P ratios across the N addition gradient and found that the contribution of intra-specific variation was higher than that of inter-specific variation. Even the dominant status of different species was completely changed (Fig. 1) and some species were lost following N enrichment in this ecosystem (Zhang et al. 2014), our results indicated that plant physiological changes following N enrichment was more important

than community composition in driving the community-level changes of litter N:P stoichiometry. Besides the direct contribution of intra- and inter-specific variation, the covariation between them also had positive effects on litter nutritional changes along the N addition gradient. Previous study also showed a positive co-variation between intra- and inter-specific variability impacts on community functional traits such as leaf dry matter content and leaf N content along a N addition gradient (Pérez-Ramos et al. 2012). The positive co-variation impacts in this study represented that N enrichment increased the predominance of fast-growing species characterized by a rapid resource capture (e.g. *L. chinensis*) rather than species with a conservative resource-use strategy such as *S. grandis*. Those results indicate that changes of species composition play an important role in driving the responses of community-level trait values to environmental changes.

Conclusion

Our results showed that N addition significantly increased litter P concentrations and N:P ratios at community-level by changing nutritional traits at species-level, altering plant community composition, and a positive covariation between intra- and inter-specific variation. While the direct contribution of inter-specific variation was lower than that of intra-specific changes, we provided evidence that litter nutritional traits at community-level were more sensitive to increasing N addition when considering the changes of plant community composition, which increased the imbalance of litter N:P stoichiometry following N enrichment. The enhancement of litter N:P ratios following N addition indicates that litter decomposition tends to be P-limiting in this ecosystem under the scenarios of increasing atmospheric N deposition. Given the importance of community composition in determining the changes of community nutrient stoichiometry and the role of litter stoichiometry in nutrient cycling, our results suggest that community composition would be an unnegligible pathway in plant-mediated biogeochemical cycling.

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