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Nitrogen Enrichment Reduces Nitrogen and Phosphorus Resorption Through Changes to Species Resorption and Plant Community Composition

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ABSTRACT

Anthropogenic nitrogen (N) deposition has affected plant community composition and nutrient cycling in terrestrial ecosystems worldwide. This includes changes to the way plants use and recycle nutrients, including effects on nutrient resorption, which is a key process through which plants recover nutrients from tissue during senescence. Nutrient resorption has considerable adaptive and functional significance for plants and helps regulate core ecosystem processes such as decomposition. However, our understanding of how N deposition affects nutrient resorption and, in particular, of how N inputs alter ecosystem resorption via changes to existing species' resorption compared with changes to community composition remains poor. To disentangle the role of species *versus* community composition controls driving variation in nutrient resorption responses to N inputs, we carried out an experiment with six different N addition rates in a temperate steppe. We found that species-scale nutrient resorption responses to N enrichment were variable; for example, only half of the measured species reduced both N and P resorption efficiency in response to increased N inputs. In contrast, community-scale responses consistently resulted in reduced N and P resorption. Still, N-induced changes in community composition were a weaker control on overall resorption responses than were the effects on individual species; however, it was the synergistic interaction between the two that resulted in the large total reductions of nutrient resorption in the face of increased N. Taken together, our results highlight that understanding and predicting nutrient resorption responses will be most accurately scaled

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Authors Contributions XTL, SLH and XGH designed the study. SLH, YYH, HWW, ZWZ, ZYL and GJY collected the data. XTL, SCR, JXY and SLH analyzed the data. XTL, JXY and SCR wrote the first draft of the manuscript. All authors discussed the results and substantially contributed to manuscript revisions.

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by accounting not only for species' reductions in resorption but also for changes in community composition.

Key words: community-weighted means; intraspecific variation; nitrogen deposition; nutrient translocation; plant functional traits; species composition.

HIGHLIGHTS

- Increased nitrogen inputs reduced the nitrogen and phosphorus resorption of some species and dramatically changed plant community composition.
- Interactions between changes to species-level resorption and plant community composition together determined overall changes in nutrient resorption.
- Nitrogen enrichment reduced community-scale nitrogen and phosphorus resorption.

INTRODUCTION

One of the most globally widespread environmental changes is the increase in reactive nitrogen (N) deposition due to heightened human activities (Galloway and others 2004). Increased inputs of N can alter internal plant biogeochemistry; for example, affecting plant growth, carbon allocation, and foliar chemistry (Baer and others 2003; McNeil and others 2007; Farrer and others 2013). Nitrogen deposition also can drive dramatic changes to plant community composition, with implications for the maintenance of diversity, rare species, and community-level function (Wassen and others 2005; Bobbink and others 2010; Simkin and others 2016). For example, increased N availability has been shown to facilitate the growth of nitrophilic plants to the disadvantage of species with a conservative N use strategy (Suding and others 2005; Bobbink and others 2010). Yet, although changes to both individual plants and to community composition will determine the overall ecosystem effects of increased N deposition, our understanding of how these controls interact to govern ecosystem-level responses remains poor.

Nutrient resorption is a fundamental process through which plants withdraw nutrients from tissue during senescence and prior to abscission. Resorbed nutrients are available for subsequent plant use and thus reduce a plant's dependence on nutrient uptake from the environment (Aerts and Chapin 2000; Killingbeck 2004; Brant and Chen 2015). Nutrient resorption is most commonly assessed in one of two ways. Nutrient resorption efficiency is the difference between the amount of a given nutrient in green versus fully senesced tissue relative to the amount in the green tissue, and nutrient resorption proficiency is the absolute level of nutrients found in senesced leaves (Killingbeck 1996). Nutrient efficiency and proficiency are different components of the same process, and both are ecologically important. Because they offer different insights into the evolution and functioning of resorption, these two measures of resorption are most powerfully used in concert (Killingbeck 1996).

Resorption plays a key role in regulating plant processes as diverse as competition, productivity, and nutrient uptake (Vitousek 1982; Killingbeck 1996). Because resorption also controls the chemistry, nutrient concentration, and stoichiometry of litterfall, which represents the largest source of nutrients to most terrestrial ecosystems (Moore and Braswell 1994; Cleveland and others 2013), resorption likely plays a role in regulating a wide range of ecosystem processes, including soil respiration, soil carbon storage, and N_2 fixation, among others (Davidson and others 1993; Cleveland and Townsend 2006; Reed and others 2011). Indeed, it is critical to understand the consequences of intraspecific responses *versus* community-level responses for overall nutrient resorption, as community-level litter chemical quality is highly correlated with litter decomposition and nutrient cycling at the ecosystem scale (Garnier and others 2005; Garcia-Palacios and others 2016), even under N-enriched conditions (Pichon and others 2020). Despite the importance of this process, our understanding of the ways in which plant communities tune resorption to varying environmental conditions remains far from complete (Richardson and others 2005; Hayes and others 2014).

Although results from a global meta-analysis showed negative impacts of N enrichment on plant N resorption (Yuan and Chen 2015), empirical evidence at the species-level is highly variable, with negative, neutral, and positive effects reported (van Heerwaarden and others 2003; Lü and others 2013). Moreover, enhanced N availability can affect the resorption of other elements (Brant and Chen 2015; See and others 2015). For example, it could be expected that N enrichment would lead to increased phosphorus (P) resorption, as plants increase P conservation during a transition from N limitation to P limitation (Vitousek and others 2010; Reed and others 2012). However, N enrichment could also enhance soil P availability through stimulation of extracellular phosphatase enzyme activity (Marklein and Houlton 2012). There is evidence of N enrichment lowering P resorption, at least for some species (van Heerwaarden and others 2003; Lü and others 2013). Species-specific variability in nutrient resorption responses to N enrichment makes it difficult to give a clear projection of changes in nutrient resorption at the community-scale.

Given species-specific variation in nutrient resorption even in a single ecosystem, changes to plant community composition would also drive changes in community-scale nutrient resorption. For example, Richardson and others (2005) found a reduction in community-scale nutrient resorption along a soil chronosequence in a temperate rain forest that was caused by both community compositional changes and intra-specific plant responses. Similarly, changes to plant community composition contributed to variations in community-scale nutrient resorption along a 2-million-year dune chronosequence (Hayes and others 2014). Plant species resorption is related to a plant's overall nutrient strategy, and plants with strategies aimed at acquisition are inherently less efficient in nutrient resorption than those with conservative strategies (Aerts and Chapin 2000). Thus, changes to plant community composition could occur in predictable ways (for example, nitrophiles overtaking conservative N users).

Most previous studies separately address intra-specific responses of nutrient resorption (van Heerwaarden and others 2003; Lü and others 2013; Gilliam and others 2018) and changes in plant community composition under N enrichment (Bobbink and others 2010; Zhang and others 2014; Gilliam and others 2016), regardless of the fact that both responses to increased N inputs have strong potential to affect overall resorption patterns. Opposing responses of inter- and intra-specific nutrient resorption to N enrichment, as indicated by a negative covariation, would result in a moderate or even neutral response at the community-scale (Figure 1). In contrast, consistent responses of inter- and intra-specific variability would reinforce one another and thus strengthen the community-level response. The role of inter- and intra-specific co-variation in driving community-scale responses to environmental change has been addressed for many traits (Auger and Shipley 2013; Volf and others 2016). For instance, Kinchenin and others (2013) found stable foliar N and P concentrations at the community-scale across an elevation gradient due to the strong but opposite changes at intra- and inter-specific responses. However, responses of chemical quality of living tissues do not fully reflect that of senesced tissue or plant litter, due to the sensitivity of nutrient resorption to the alteration of soil resources (Lü and others 2012a, b). Thus, there

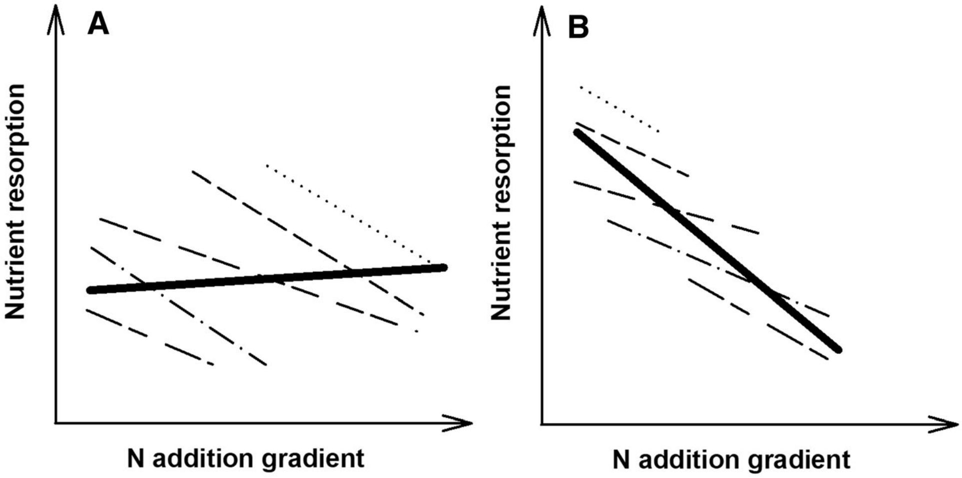

Figure 1. Conceptual diagram of how intra- and inter-specific variations could drive community-level nutrient resorption responses (*solid line*) across a N addition gradient. Each dashed line represents the nutrient resorption responses of a different plant species. **A** If the intra-specific responses of nutrient resorption to N addition do not favor a community shift to species with lowered resorption, then the responses of community-level nutrient resorption could be neutral even if individual species reduce their resorption. **B** However, if N inputs facilitate an increased dominance of species with less efficient nutrient resorption, negative community-level resorption responses to increased N are strengthened.

is a large knowledge gap regarding the relative roles of intra- and inter-specific variation in driving the variation of community-level nutrient resorption and litter quality.

Here, we examined the changes of species- and community-scale N and P resorption efficiency and proficiency from senescing shoots in response to N enrichment in a temperate steppe after 7 years of N addition. We focused on nutrient resorption from whole shoots instead of individual leaves because of the substantial amount of nutrients resorbed in culms and stems (Freschet and others 2010; Lü and others 2012a, b). We hypothesized that N enrichment would reduce nutrient (N and P) resorption at the community-level through both (1) intraspecific decreases of nutrient resorption for individual plant species and (2) changing species dominance, such that species more efficient in nutrient resorption would decline and the dominance of species less efficient in resorption would increase.

Materials and Methods

Study Site

The study site is a temperate semi-arid grassland in Xilinhot, Inner Mongolia, China (43° 38′ N, 116° 42′ E, 1255 m.a.s.l.). The mean annual temperature is 0.9°C, and mean annual precipitation is 337 mm (1980–2015). Vegetation is typical of temperate steppes, with dominance by *Stipa grandis*, *Achnatherum sibiricum*, *Agropyron cristatum*, *Leymus chinensis*, and *Cleistogenes squarrosa*. Traditional grassland management at the site has been livestock grazing in the growing season, lasting from April to September; however, the site has been fenced to exclude livestock grazing since 1999. The soil is classified as a Haplic Calcisol by the FAO system and as a Calcic-Orthic Aridisol in the US soil classification system. The rate of ambient total N deposition in this region was estimated to be about 1.5 g N m^{-2} y^{-1} for the last two decades (Zhao and others 2017).

Experimental Design and Plant Sampling

The N addition experiment was started in 2008, and detailed information about the experimental design can be found in Zhang and others (2018). Briefly, there were nine rates of N enrichment ranging from 0 to 50 g N m^{-2} y^{-1}, with each treatment replicated ten times across ten blocks under a completely randomized block design. Such a broad and multi-level gradient of N addition rates was used to find the thresholds for the responses of biodiversity and ecosystem functioning to N enrichment. The area of each plot was 8 m × 8 m. Blocks were separated by 2 m buffers, and plots within each block were separated by 1 m buffers. Nitrogen (NH_4NO_3) was added twice each year: once in June (growing season) in a dissolved form and once in November (non-growing season) in a dry form. In the beginning of June, half of the NH_4NO_3 was mixed with distilled water (9 l for each plot) and sprinkled with a sprayer to simulate wet N deposition. In the beginning of November, another half of the NH_4NO_3 was mixed with sand (0.5 kg sand for each plot) and broadcasted evenly by hand. We added N in both wet and dry forms to better mimic expected N deposition at the site. To maintain a study design feasible for the resorption work described here, we chose six different N addition rates and used six randomly selected blocks from the ten N addition rates and ten blocks of the larger experiment. We used six blocks each of 0, 2, 5, 10, 20, and 50 g N m^{-2} y^{-1}, for a total of 36 plots.

This study was carried out in 2015, 7 years after the establishment of this long-term experiment. In mid-August, community aboveground biomass and species composition were assessed in each of the 36 plots using a 1 m × 1 m quadrat. For each plot, the quadrat was randomly placed inside the plot avoiding spatial overlap with sampling quadrats from previous years. Moreover, the quadrats were placed no less than 50 cm inside of the borders of each plot. Aboveground biomass was sampled by clipping all vascular plants at the soil surface. The timing of plant clipping was concurrent with peak biomass, a point after which plant nutrient uptake would be limited. Thus, clipping was unlikely to significantly affect the nutrient status of plants living at the border of clipped quadrats. All plants were sorted by species and oven-dried at 65°C for 48 h. The dry mass of each species was then weighed. Shoot samples from those quadrats were used as green tissue for nutrient analyses.

The senesced shoots were sampled after the growing season in October 2015 when they were fully senesced for all species in this area. All species represented in the August biomass quadrat were sampled. For each species, 10–30 senesced shoots were clipped near the August quadrat in each plot. All samples were oven-dried at 65°C for 48 h. Shoot samples from those quadrats were used as senesced tissue for nutrient analyses.

Dry samples of both green (August samples) and senesced shoots (October samples) were ground using a ball mill (Retsch MM 400; Retsch, Haan, Germany). Total N concentrations of plant samples were analyzed by an Alpkem autoanalyzer (Kjektec System 1026 Distilling Unit, Sweden) (Gallaher and others 1976). For assessing total P concentrations, the ground samples were digested with H_2SO_4–H_2O_2 and measured colorimetrically at 880 nm after reaction with molybdenum blue (Kuo 1996).

Data Analysis

The species-level nutrient resorption efficiency (RE) was quantified by the proportional changes of nutrient concentrations between green and senesced shoots following the equation:

$$\mathrm{RE} = \left(1 - \mathrm{Nutrient}_{\mathrm{senesced}}/\mathrm{Nutrient}_{\mathrm{green}}\right) \times 100\%.$$

In which $\mathrm{Nutrient}_{\mathrm{senesced}}$ and $\mathrm{Nutrient}_{\mathrm{green}}$ is the N or P concentration in the October (senesced) and August (green) shoots, respectively. Here, we did not account for the mass loss of shoots during senescence due to the difficulty of accurately measuring shoot-level mass loss in the field, which would underestimate the actual values of nutrient resorption. Nutrient resorption proficiency was quantified as $\mathrm{Nutrient}_{\mathrm{senesced}}$ (Killingbeck 1996), and we used the reciprocal of this value so that, as with nutrient resorption efficiency, a higher value would signify higher efficiency. The community biomass-weighed mean values (CWM) of nutrient resorption efficiency in each plot were calculated based on the relative biomass and resorption efficiency of each species present. The relative biomass for each species in each plot was calculated based on the aboveground biomass data of the August sampling.

Data were tested for normality using the Shapiro–Wilk test and for equality of variance using Levene's test. The relationships between N addition rates and changes in species- and community-level nutrient concentrations and resorption efficiency were tested by linear and nonlinear regression; results of the best-fitting curve are given. The relative contributions of inter- and intra-specific trait variation effects on community-level nutrient concentration and resorption efficiency along the N addition experimental gradient were assessed following Lepš and others (2011), which is based on the division of total sum of squares (SS_{specific}) of the community-level trait variance related to an environmental factor (the N addition gradient here) into three different effects: 'fixed' (SS_{fixed}), 'intra-specific' (SS_{intra}), and 'covariation' (SS_{cov}). The 'specific' community-average trait values in each community were calculated using species trait values as measured in the particular community, which includes both inter- and intra-specific effects. The 'fixed' community-average trait values were calculated with a fixed trait value (averaged across all plots along the N addition gradient), which thus only included the inter-specific variation effect. The 'intra-specific' community-average trait values were calculated as the difference between 'specific' and 'fixed' community-average trait values. For each of the traits examined here (N and P concentrations in green and senesced shoots, N resorption efficiency, and P resorption efficiency), we ran three generalized linear model regressions for the 'specific,' 'fixed,' and 'intra-specific' community averages with N addition rate as an explanatory variable. From such regressions, we extracted the sums of squares for each of the three community-average measures (SS_{specific}, SS_{fixed}, and SS_{intra}) explained by N addition. Then, we calculated the SS_{cov} by subtracting SS_{fixed} and SS_{intra} from SS_{specific}. All analyses were conducted with SPSS 13.0 (SPSS Inc., Chicago, IL, USA).

Table 1. Mean Values of Relative Biomass (%) for Seven Dominant Plant Species in a Temperate Steppe Across All Treatments of the N Addition Gradient (0–50 g N m^{-2} y^{-1}) in 2015

	0	2	5	10	20	50
Agropyron cristatum	23.6 (8.5)	7.8 (2.5)	3.0 (2.3)	11.6 (2.5)	17.8 (10.2)	10.1 (8.7)
Achnatherum sibiricum	13.7 (7.1)	10.8 (3.3)	16.1 (4.9)	15.8 (4.2)	3.7 (1.9)	0.7 (0.7)
Chenopodium glaucum	0.4 (0.2)	2.9 (2.9)	9.1 (3.6)	20.3 (10.5)	26.8 (8.5)	19.6 (9.4)
Carex korshinskyi	1.3 (0.3)	3.7 (1.9)	1.9 (0.6)	3.3 (2.4)	5.0 (4.5)	0.0 (0.0)
Cleistogenes squarrosa	1.4 (0.4)	1.2 (0.6)	1.0 (0.8)	0.1 (0.1)	0.9 (0.9)	0.0 (0.0)
Leymus chinensis	15.1 (6.0)	17.8 (12.2)	27.8 (13.8)	15.1 (6.8)	36.5 (13.3)	69.3 (9.9)
Stipa grandis	43.2 (5.0)	54.0 (10.8)	39.7 (8.4)	32.0 (10.4)	5.5 (3.0)	0.2 (0.2)

SE values are given in parentheses.

Table 2. The *r*-Value of Pearson Correlation Between N Addition Rates (Nrate) and Resorption Efficiency of N and P (NRE and PRE, respectively) and Resorption Proficiency of N and P (NRP and PRP, respectively) for Seven Plant Species in a Temperate Steppe

	n	**NRE − Nrate**	**PRE − Nrate**	**NRP − Nrate**	**PRP − Nrate**
Agropyron cristatum	30	− 0.76***	− 0.47**	− 0.76***	− 0.58**
Achnatherum sibiricum	28	− 0.33^	− 0.33^	− 0.65**	− 0.26
Chenopodium glaucum	30	− 0.07	− 0.04	− 0.86***	− 0.36*
Carex korshinskyi	27	0.04	− 0.51**	− 0.50**	− 0.63**
Cleistogenes squarrosa	17	0.28	− 0.72***	− 0.78***	− 0.70***
Leymus chinensis	31	− 0.57**	− 0.50**	− 0.75***	− 0.61***
Stipa grandis	33	− 0.35*	− 0.21	− 0.72***	− 0.39*

****$P < 0.001$; **$P < 0.01$; *$P < 0.05$; ^$0.05 < P < 0.1$.*

RESULTS

Changes of Species Dominance in Response to N Addition

The dominance of plant species varied greatly in treatments with different N addition rates (Table 1). Among the seven dominant plant species, which together contributed more than 98% of the total biomass averaged across the gradient, *S. grandis* was the most dominant in the control plots and in plots with N addition rates less than 10 g N m^{-2} y^{-1}, contributing about 40% of the total community biomass in those plots. In contrast, *S. grandis* contributed less than 10% of total biomass in plots with addition rates of 20 and 50 g N m^{-2} y^{-1}. Nitrogen addition increased the contribution of a perennial rhizome grass, *L. chinensis*, and an annual forb, *C. glaucum* (Table 1). *L. chinensis* was the third most dominant species in the control plots, but was the most dominant plant in plots with the highest N addition rate (contributing 70% of total community biomass). *C. glaucum* was the least dominant species in the control plots, but was the second most dominant species in plots with N addition rates higher than 10 g N m^{-2} y^{-1}.

Species-Scale Nutrient Resorption

Nitrogen resorption efficiency (NRE) was negatively correlated with N addition rates for three out of the seven species (Table 2). The correlation between N addition rate and NRE was marginally significant for *A. sibiricum* and not significant for *C. glaucum*, *C. korshinskyi*, and *C. squarrosa*. Nitrogen addition rates were negatively correlated with P resorption efficiency (PRE) for five species (marginally significant for *A. sibiricum*) and were not significantly correlated with PRE for *C. glaucum* and *S. grandis* (Table 2). Averaged across all the treatments, *L. chinensis* and *C. glaucum* had the lowest NRE values, whereas *A. sibiricum*, *C. squarrosa*, and *S. grandis* had the highest NRE values (Figure S1a). For P resorption, *S. grandis* was the most efficient, *C. squarrosa* was the least efficient, and *L. chinensis* had an intermediate value (Figure S1b). For all species, resorption proficiencies of both N and P were negatively correlated with N addition rates, except P resorption proficiency in *A. sibiricum* (Table 2; Figure S2).

Community-Scale Nutrient Concentrations and Nutrient Resorption

Nitrogen addition significantly increased community-scale biomass-weighted N and P concentrations in both green and senesced shoots (Figure 2A, B) but decreased both NRE and PRE (Figure 2C). N/P resorption efficiency ratios significantly decreased with increased N addition rates (Figure 2D).

The contributions of species- and community-level variability were each statistically significant in explaining the response of nutrient concentrations and resorption efficiencies to N addition rates (Figure 3). Further, there were positive covariations between the effects of species- and community-level variability on changes to the concentration and resorption efficiency of both N and P (Figure 3C). The relative contribution of intra-specific variability in explaining total variation was the highest for both nutrient concentration and resorption. However, the relative contribution of covariation in explaining total variation was much higher than that of inter-specific variability alone for both NRE and PRE (NRE: 36% vs. 7%; PRE: 39% vs. 11%, respectively).

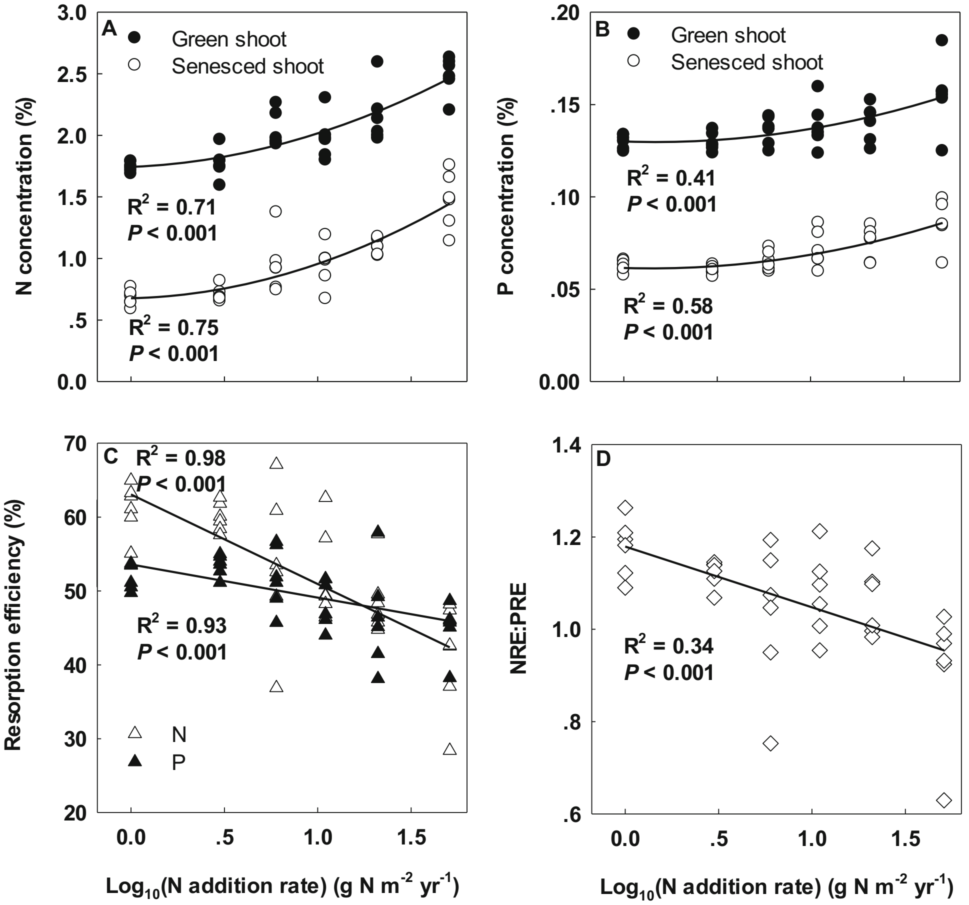

Figure 2. Changes in biomass-weighted community-level means for N (**A**) and P concentrations in green and senesced shoots (**B**), as well as nutrient resorption efficiency for N and P (**C**) and the N resorption efficiency/P resorption efficiency ratio (**D**) across the N addition gradient (0–50 g N m^{-2} y^{-1}) shown on a $\log_{10}$ scale. The *P*- and R^2 values for the best fit regressions of the relationships between N addition rate and each measured factor are shown.

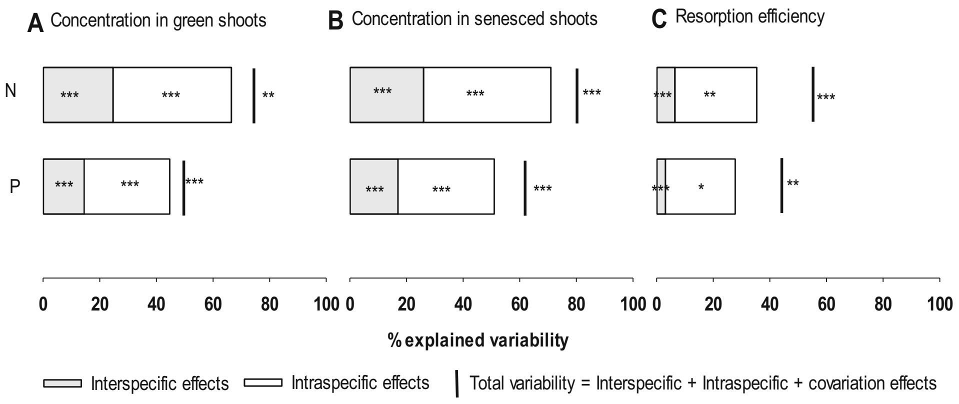

Figure 3. Separation of the total variation in community N and P concentrations in green shoots (**A**) and senesced shoots (**B**) and the resorption efficiency (**C**) explained by N addition rates, with explanatory values parsed into inter-specific, intra-specific and covariation effects. Co-variation strength is indexed by the interval between the 'total variability' and the sum of inter- and intra-specific variability effects. The statistical significance (***$P < 0.001$; **$P < 0.01$; *$P < 0.05$) of inter-specific, intra-specific, and total variability effects is indicated on the graph when significant.

DISCUSSION

Our results showed negative effects of N enrichment on community-level resorption efficiency for both N and P in the temperate steppe. Such changes were the result of reductions of species-level nutrient resorption efficiency (intra-specific variability), changes in community composition (inter-specific variability), and the positive covariation between intra- and inter-specific variability (Figure 3). Although previous studies have found that both inter- and intra-specific variability contributed to changes in community-scale nutrient resorption across natural soil nutrient availability gradients (Richardson and others 2005; Hayes and others 2014), this study disentangled their relative contributions to the responses of community-scale N and P resorption with N enrichment. More nutrients (both N and P) remained in plant litter with reduced resorption efficiency and proficiency following increasing additions of N, suggesting important changes to plant-driven nutrient inputs into soil in conjunction with the changes to inputs via anthropogenic N deposition. Given the well-established positive relationship between substrate nutrient concentrations and litter decomposition (Melillo and others 1982) and the importance of internal nutrient recycling in driving primary production (Cleveland and others 2013), the reduction in community-level nutrient resorption could have important consequences for ecosystem nutrient cycling.

We observed marked community shifts with different N addition rates, with higher dominance of *L. chinensis* and lower dominance of *S. grandis* in treatments with higher rates of N addition (Table 1). For example, *S. grandis* made up more than 40% of the biomass in plots receiving 5 g N m^{-2} y^{-1} or less, but the species represented less than 1% of the biomass in plots receiving 50 g N m^{-2} y^{-1}. Given the substantial inter-specific variation in nutrient resorption (Figure S1), such shifts in species assemblage have important consequences for community-level nutrient resorption. Indeed, it was shifts in community composition and species-specific responses to increased N *together* that determined the community-level changes observed (Figure 3). Although some work has highlighted the role of community composition in controlling responses of ecosystem function to environmental change (Wedin and Tilman 1996; Austin and Zanne 2015), our findings present an additional pathway through which species composition can alter ecosystem biogeochemical cycles in the face of anthropogenic change: nutrient resorption. Assessing the changes of community-level functional traits across environmental gradients facilitates our understanding of the subsequent changes to ecosystem processes, as indicated by the stronger relationship between community-level functional traits and fundamental ecosystem properties relative to the relationships with species-level traits alone (Garnier and others 2005; Castro-Díez 2012).

Another important aspect of species composition changes driving community-scale nutrient resorption was reflected by the positive covariation between species- and community-level effects, the relative contribution of which was much greater than the direct contribution of species composition alone (Figure 3). This positive covariation resulted from a consistency in the direction of inter- and intra-specific selection by environmental factors (Figure 1B; Cornwell and Ackerly 2009; Lepš and others 2011; Siefert and others 2014). At the community-scale, N enrichment facilitated the growth of *L. chinensis*, the species with the lowest NRE. Meanwhile, N enrichment reduced the dominance of *S. grandis*, the species with highest nutrient resorption (Figure S1). Thus, in addition to its direct effects on how different species resorb nutrients, overall, N deposition shifted the community from a species that had traits associated with high N resorption to one with low N resorption. Our findings show that changes in community composition had a strong effect via a strengthening of the negative effects of N enrichment on individual plant species' nutrient resorption.

Our hypothesis that N addition would lead to reduced nutrient resorption at the species-scale was supported; however, there was significant variability among species and among resorption methods. Resorption proficiency of both N and P (NRP and PRP) in all the examined species was negatively correlated with N addition rates, and thus this measure suggested strong, consistent reductions in N and P resorption proficiency following 7 years of N addition. Previous studies have suggested resorption proficiency may be more sensitive to nutrient addition relative to nutrient resorption efficiency (for example, Ratnam and others 2008; Rejmánková 2005) and less variable across time (Killingbeck 1996). In comparison with resorption proficiency, three out of seven species showed significant reduction in NRE and six of seven species showed reduction in PRE. Our simultaneous assessment of resorption efficiency and proficiency at the community-level highlights the importance of intra- and inter-specific variation in modulating community-level changes of nutrient conservation during plant senescence, as well as that of litter quality following plant senescence.

In particular, the NRE of four perennial grasses with tall stature were highly sensitive to N enrichment. In contrast, three species with low stature showed neutral responses of NRE to N enrichment. These results are in line with findings that tall perennial grasses are generally facilitated by N enrichment in diverse herbaceous ecosystems due to their competitive advantage for light (Gough and others 2012). There are at least two factors that could account for the neutral response of NRE in the three species with low stature. First, competition for soil available N is intense due to the rapid increases of biomass of perennial tall grasses (Zhang and others 2015) and thus the added N could be less available for less competitive species. Second, the reduction in light availability in the sub-canopy following N enrichment could mediate the effects of N enrichment on nutrient resorption in understory species through changing the composition and degradation of leaf proteins (Yasumura and others 2007).

Our results further underscore the capacity for plant nutrient resorption to vary among species even within a single site (Figure S1), which adds emphasis to the role of community composition in dictating overall ecosystem responses. Negative responses of PRE and PRP to N enrichment seem to conflict with predictions that increased N inputs could result in increased likelihood of P limitation and thus greater resorption of P. Greater soil P availability following N enrichment due to increased phosphatase enzyme activity (Marklein and Houlton 2012; Lü and others 2013) could account for the negative effects of N enrichment on PRE and PRP. Alternatively, P availability may not be limiting enough in this ecosystem to overcome N's control over the species- and community-level responses of N addition, or nutrients other than P could be playing an interactive role (Crowley and others 2012).

It should be noted that, while the plants were experiencing treatments for 7 years, we measured nutrient resorption in a single year and thus nutrient resorption and the role of species *versus* community effects could vary among years (Drenovsky and others 2019). Although we would expect these interannual fluctuations to be low relative to the overall effects of the N deposition treatments, further work should examine to what extent the relative contributions of inter-specific variability, intra-specific variability, and their co-variation to community-scale nutrient resorption change across years. Moreover, N deposition is declining or is predicted to decline for some developed countries (Stevens 2016; Gilliam and others 2019); thus, it is important to understand the recovery process for N-enriched ecosystems. The importance of plant community composition in driving the responses of ecosystem-scale nutrient resorption to N enrichment, as found here, implies that there may be a long way to go for restoring N-enriched ecosystems because plant community composition recovers more slowly than soil nutrient status after the cessation of N inputs (Stevens 2016).

In conclusion, results from this study have important implications for understanding the effects of species-specific and community composition controls over ecosystem function. Changes to nutrient resorption have myriad consequences for carbon and nutrient cycling and these findings suggest community composition and species responses together dictate nutrient resorption patterns with increasing anthropogenic N inputs. Further, the community-level changes to nutrient resorption in response to N enrichment could not have been deduced from the arithmetic means of the community's composing species. In turn, in the absence of plant community information, species-specific responses of nutrient resorption to N enrichment would not be enough to find the overall, quantitative effect. Given the co-existence of diverse species in natural ecosystems, results from this community perspective facilitate the construction of conceptual and numerical models of how species and communities function and respond to change. Further, while the direct role of species composition in driving ecosystem functioning is well recognized (Wedin and Tilman 1996), our results join others in highlighting their indirect role through the positive covariation between inter- and intra-specific effects. The functional identity of species and their sensitivity to environmental change together determine the impacts of N deposition on ecosystem functioning.

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Compliance with Ethical Standards

Conflict of interest Authors declare no conflict of interests.

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