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# **RESEARCH ARTICLE**



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# Species richness mediates within-species nutrient resorption: Implications for the biodiversity-productivity relationship

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# 1 | INTRODUCTION

Abstract

- Between-species variation in nutrient resorption is one of the mechanisms explaining the positive relationship between biodiversity and primary productivity. Yet, the role of within-species variations in nutrient resorption in mediating the relationship between biodiversity and productivity remains unclear.
- 2. We examined how within-species nutrient resorption, and ultimately productivity, respond to changes in species richness by using four traits related to nitrogen and phosphorus use in four dominant species from different plant functional groups in a biodiversity removal experiment in the temperate steppe.
- 3. Nitrogen and phosphorus concentrations in both green and senesced leaves in all species significantly decreased with increasing plant species richness, suggesting that plants used those limiting nutrients more efficiently with increasing biodiversity. Plants in higher diversity communities resorbed more nutrients during senescence, which may facilitate reproduction and vegetative regrowth in the next year.
- 4. *Synthesis*. Our results highlight the importance of considering within-species variation in nutrient resorption as an important underlying mechanism explaining the positive effects of biodiversity on primary productivity and ecosystem carbon accumulation.

# KEYWORDS

biodiversity loss, ecosystem functioning, intraspecific variation, litter quality, plant functional trait, plant-soil feedback, species complementarity

Nutrient resorption during the senescence of plant organs is an important nutrient conservation strategy (Aerts & Chapin, 2000). It has been estimated that, world-wide, more than 60% of N and P is resorbed from senescing leaves in perennial plants (Vergutz, Manzoni, Porporato, Novais, & Jackson, 2012). The resorbed nutrients, which can be used for further plant growth and thus make plants less dependent on soil nutrient supply, greatly contribute to the plant nutrient economy. Thus, higher nutrient resorption implies more efficient nutrient use in plants. Nutrient resorption is sensitive to the alteration of both biotic and abiotic factors, with plants in lower fertility sites generally displaying higher nutrient resorption efficiency (Brant & Chen, 2015).

Biodiversity has positive impacts on ecosystem functioning, including primary productivity, litter decomposition and nutrient cycling (Hooper et al., 2005; Tilman, Isbell, & Cowles, 2014). Given that primary productivity in most terrestrial ecosystems is largely limited by the availability of nitrogen (N) and phosphorus (P) (Fay et al., 2015; Harpole et al., 2011), understanding the role of biodiversity in structuring how plants obtain and conserve those limiting nutrients is critical to fully accounting for the effects of biodiversity on ecosystem functioning. Soil nutrient availability and plant nutrient concentrations can change in response to biodiversity changes (Borer et al., 2015; van Ruijven & Berendse, 2005), in turn leading to changes in nutrient resorption (Brant & Chen, 2015). However, the direction and magnitude of the effects of biodiversity on nutrient resorption remain largely untested.

Between-species variation in resource use within a system is one of the mechanisms explaining the positive relationship between biodiversity and primary productivity (Hooper et al., 2005). For instance, Roscher, Thein, Schmid, and Scherer-Lorenzen (2008) found that communities with higher species richness have a more complete soil nitrate uptake and a higher productivity and N yield. Moreover, plants in this system adjusted their N uptake patterns in response to species richness (Gubsch et al., 2011). More complete resource use by plants in higher diversity communities leads to lower soil nutrient concentrations across the soil profile (Roscher et al., 2008). However, between-species variation in resource use is not always sufficient to explain this relationship (Yachi & Loreau, 2007). While the role of between-species variation in plant traits in driving the positive relationship between biodiversity and productivity has been widely addressed, it remains unclear whether within-species variation (intraspecific variation) in nutrient acquisition and conservation traits (including nutrient resorption) may also contribute to this pattern.

Considering the contribution of within-species nutritional responses to biodiversity is crucial to understand the mechanisms underlying the relationship between biodiversity and ecosystem functioning. From the perspective of resource-use efficiency at the individual level, a newly developed theoretical model predicts that higher biodiversity will increase individual plant productivity (Liang, Zhou, Tobin, McGuire, & Reich, 2015). Liang et al. (2015) showed that every 1% loss of biodiversity could render a 0.23% reduction in individual tree productivity in a boreal forest, indicating that individuals living in communities with lower biodiversity have lower resource-use efficiency.

In this study, we examined nutrient concentrations and resorption in four dominant species from four different plant functional groups (PFG) using The Inner Mongolian Grassland Removal Experiment (IMGRE), a grassland biodiversity experiment manipulating PFG richness (Wu et al., 2015). We hypothesized that plants living in communities with higher richness will have lower foliar concentrations of both N and P, because of the overall lower soil nutrient availability as a consequence of the more complete resource use. As plants in resource-poor environments have higher rates of resorption (Brant & Chen, 2015), we further hypothesized that plants in species-diverse communities will have higher nutrient resorption efficiency.

# 2 | MATERIALS AND METHODS

#### 2.1 | Field site and experimental design

The removal experiment started in June 2006. The field site is located near the Inner Mongolia Grassland Research Station (116°14′E, 43°13′N, 1,250 m a.s.l.) in Inner Mongolia Autonomous Region, China. The mean annual air temperature is 0.3°C (1983–2014) and the mean annual precipitation is 350 mm, 60%–80% of which occurs during the growing season. The soil is classified as Haplocalcid and Calcic-Orthic Aridisol by the FAO and the US soil classification system respectively. Topsoil (0–10 cm depth) has a pH of ~7.5 and a bulk density of 1.3 g/cm<sup>3</sup>. The plant community is dominated by the perennials *Leymus chinensis* (Trin.) Tzvel and *Stipa grandis* P. Smirn., accounting for 65% of total above-ground biomass. Species richness in this community is 10–20 species per m<sup>2</sup>.

The removal experiment was arranged in a completely randomized block design (Wu et al., 2015). All plant species were classified into each of the following five plant functional groups: perennial rhizome (PR), perennial bunchgrass (PB), perennial forbs (PF), annual and biennials (AB) and shrubs and subshrubs (SS). All targeted PFGs in a plot were removed completely by clipping off the above-ground tissues at tilling nodes at 0-3 cm soil depth. For further details of the protocol for plant removal, see Wu et al. (2015). There were 32 treatments, representing all possible combinations of PFGs; each treatment was replicated eight times, and treatments were blocked, with one replicate per treatment in each block. As the distribution of the plant functional type SS in our experimental plots was very limited, we focused on the other four functional types. Overall, 15 treatments with 1-4 plant functional types were used in this study, including four treatments with only one functional type (PR, PB, PF, AB), six treatments with two functional types (PR + PB, PR + PF, PR + AB, PB + PF, PB + AB, PF + AB), four treatments with three functional types (PR + PB + PF, PR + PB + AB, PR + PF + AB, PB + PF + AB), and one treatment with all the four functional types (PR + PB + PF + AB). The initial soil nutritional conditions in 2005 (as measured by the concentrations of total soil C, N and P at 0-5 cm depth) were similar among different treatments, which began in 2006 (Figure S1). To maintain the diversity treatments, plots were also weeded at the beginning of the growing season in 2007 and 2008. To balance sampling feasibility and sufficient replication, we sampled six blocks in this experiment.

#### 2.2 | Field sampling and measurements

We sampled four dominant species from four different plant functional types: *Leymus chinensis* (L.c.) from PR, *Stipa grandis* (S.g.) from PB, *Allium tenuissimum* L. (A.t.) from PF, and *Salsola collina* Pall. (S.c.) from AB. Each of these species represented the dominant species in its respective functional group, and each appeared in all the plots from which the particular plant functional type was not removed. In mid-August 2008, after 3 years of removal treatments, 20 mature shoots for both L.c. and S.g., 4–8 shoots of A.t. and 10 shoots of S.c., were randomly selected from separate individuals and marked with thin red thread in each plot where they existed. The amount of tissue sampled from each individual was chosen to ensure enough sample was collected for chemical analysis (Lü & Han, 2010). For the two grasses, L.c. and S.g., and the forb A.t., two fully expanded leaves from each shoot were selected. One of those two leaves was



**FIGURE 1** The relationship between plant species richness and community above-ground primary productivity for all plots with different combinations of plant functional groups in a temperate steppe of China. \*\*\*p < 0.001

sampled immediately, and the other one (marked with ink) was sampled at the end of September or at the beginning of October 2008, depending on the senescence time for each species. Given the small size of the leaves in S.c., we sampled three mature leaves from each shoot in August and three senesced ones in mid-September 2008. All the leaves for each species from the same plot at each sampling time (summer vs. autumn) were pooled to one composite sample. All plant samples were oven-dried at 70°C for 48 hr, weighed and ground using a ball mill (Retsch MM 400; Retsch). Foliar N concentrations were analysed colorimetrically by the Kjeldahl acid-digestion method after extraction with sulphuric acid (Lü & Han, 2010). Total P concentrations were measured by persulphate oxidation followed by colorimetric analysis (Schade, Kyle, Hobbie, Fagan, & Elser, 2003).

Concurrent with leaf sampling in mid-August 2008, three soil cores (diameter 5 cm) were taken from each experimental plot at a depth of 0–10 cm of the mineral soil; these three cores were pooled into one composite sample per plot. The soil samples were thoroughly mixed and sieved through a 2-mm mesh for further analysis. Soil water content was determined by oven-drying at 105°C for 48 hr. For ammonium and nitrate measurements, 10 g of fresh soil was extracted with 50 ml 2 M KCl solution and then colorimetrically analysed using a flow injection auto-analyser (FLAstar 5000 Analyzer; Foss Tecator). Plant-available P in soil was determined by extracting soil samples (~2.5 g) with 0.5 M NaHCO<sub>3</sub> (pH = 8.5), and the inorganic P concentrations of filtered soil extract were assessed using the molybdenum blue-ascorbic acid method (Olsen, Cole, Watanabe, & Dean, 1954).

In late August 2008, when above-ground biomass peaked in this region, above-ground biomass was clipped at the soil surface and plant species richness was assessed in a  $1 \times 1$  m quadrat randomly located in each plot. All clipped vascular plants were sorted to species and oven-dried at 65°C for 48 hr and then weighed. Because the plant community is dominated by non-woody species, the dry mass

of living plants in late August approximated the above-ground net primary productivity.

### 2.3 | Calculation and statistical analysis

Nutrient resorption efficiency (RE), which is the proportion of nutrients in mature leaves that was resorbed during senescence, was calculated as:

 $RE = (1 - [Nutrient_{senesced} / Nutrient_{green}]) \times 100\%$ 

where Nutrient<sub>senesced</sub> is the N or P concentration in senesced leaves of each species from each plot collected after the growing season (October) and Nutrient<sub>green</sub> is the N or P concentration of green leaves collected in the mid-growing season (August).

Data were tested for normality using the Kolmogorov–Smirnov test and for equality of variances using the Levene's test. Results showed that all the data met the assumption of normality and equality of error variance. We used measured plant species richness as the independent variable in all analyses; the relationships between species richness and plant nutrient traits were estimated using linear regressions. We also examined the Pearson correlation between plant nutrients and soil-available nutrients. All analyses were conducted in SPSS 13.0 (SPSS Inc.).

# 3 | RESULTS

Plant community above-ground net primary productivity significantly increased with increasing species richness across all the plots (p < 0.001, Figure 1). Plant-available resources in soils, including N, P and water, significantly decreased with the increases in plant species richness across all the plots (Figure S2). Soil water content was positively correlated with the concentrations of soil inorganic N (r = 0.34, p < 0.001) and plant-available P in soils (r = 0.26, p < 0.05). Soil inorganic N concentration was positively correlated with plant-available P in soil (r = 0.50, p < 0.001). For all four species, soil moisture showed limited correlation with the changes in plant nutrient traits (Table 1). The nutrient traits of forbs seem to be more sensitive to the variation in soil nutrient concentrations than those of grasses (Table 1). Nutrient concentrations in senesced leaves of both forb species were positively correlated with plant-available soil nutrient concentrations while nutrient resorption efficiencies were negatively correlated with plant-available soil nutrient concentrations.

Plants showed within-species changes of nutrient status with changes in species richness in the communities (Figures 2 and 3). For all four species, both N and P concentrations in green and senesced leaves were negatively correlated with plant species richness (all p < 0.05, Figure 2), except for P concentration in green leaves of *Stipa grandis* (Figure 2f). Increasing plant species richness significantly increased RE<sub>N</sub> in three out of the four species

**TABLE 1** Correlation coefficients between foliar nutrient traits (Ng amd Pg, green leaf N concentrations and P concentration; Ns and Ps, senesced leaf N and P concentration; RE<sub>N</sub> and RE<sub>P</sub>, N and P resorption efficiency) and soil properties (nutrient concentrations and water content) for the four species in the biodiversity experiment in a temperate steppe of northern China

		Ng	Pg	Ns	Ps	RE <sub>N</sub>	RE <sub>P</sub>
	Leymus chinensis						
	Moisture	0.06	0.26	-0.13	0.07	0.17	0.19
	Inorganic N	0.41**	0.48***	0.13	0.27 <sup>d</sup>	0.09	0.07
	Available P	0.59***	0.20	0.48***	0.29*	-0.28*	0.22
	Stipa grandis						
	Moisture	0.07	0.11	0.23	0.25.	-0.26 <sup>d</sup>	-0.22
	Inorganic N	0.25 <sup>d</sup>	0.2	0.12	0.18	-0.05	-0.10
	Available P	0.56***	0.43**	0.04	0.05	-0.04	0.05
Allium tenuissimum							
	Moisture	0.27 <sup>d</sup>	0.44**	0.40**	0.27 <sup>d</sup>	-0.35*	0.11
	Inorganic N	0.41***	0.56***	0.56***	0.46***	-0.48***	-0.06
	Available P	0.45***	0.60***	0.66***	0.54***	-0.63***	-0.12
Salsola collina							
	Moisture	0.23	-0.20	0.35*	-0.07	-0.31	-0.11
	Inorganic N	0.56***	0.57***	0.39**	0.37*	-0.50***	-0.36*
	Available P	0.54***	0.40**	0.61***	0.45**	-0.42**	-0.18

\*\*\*p < 0.001. \*\*p < 0.01. \*p < 0.05. †0.05 .



**FIGURE 2** Nitrogen (a, b, c, d) and phosphorus (e, f, g, h) concentrations in green (green datapoints) and senesced (brown datapoints) leaves of the four dominant plant species *Leymus chinensis, Stipa grandis, Allium tenuissimum* and *Salsola collina* as a function of the plant species richness. \*\*\*p < 0.001; \*\*p < 0.05 [Colour figure can be viewed at wileyonlinelibrary.com]

(Figure 3); RE<sub>p</sub> increased with species richness only for *Stipa grandis* (Figure 3b).

# 4 | DISCUSSION

Our results show that the four dominant plant species reuse their nutrients more efficiently in species-diverse communities, demonstrating a new pathway by which higher species richness increases productivity at the ecosystem level. For all species we examined, within-species plant N and P concentrations in green leaves generally decreased with increasing species richness, indicating that plants use those nutrients more efficiently in biomass production. More importantly, nutrients were more efficiently resorbed in all species during leaf senescence in the communities with higher species richness (Figures 2 and 3). Thus, our results imply that within-species variation in nutrient-use traits in living and senescing plant organs may contribute to the positive effects of biodiversity on primary



**FIGURE 3** Nitrogen (red datapoints) and phosphorus (blue datapoints) resorption efficiency for the four dominant plant species *Leymus chinensis* (a), *Stipa grandis* (b), *Allium tenuissimum* (c) and *Salsola collina* (d) as a function of the plant species richness. \*\*\*p < 0.001; \*\*p < 0.01; \*p < 0.05;  $^{n}p < 0.1$  [Colour figure can be viewed at wileyonlinelibrary. com]

productivity found in diverse ecosystems (Hooper et al., 2005), including the temperate steppe.

While most previous studies have focused on between-species variation in nutrient concentration in plants (Carnicer et al., 2015; Weber & Deutsch, 2012), we found that within-species variation in nutrient concentration is important for mediating the effects of biodiversity on nutrient cycling. We observed substantial within-species variations in both N and P concentrations in green leaves in the four studied species across the gradient of species richness. Our results highlight the importance of species richness in explaining variations in within-species plant traits, potentially as a result of neighbouring plant traits and crowding effects (Le Bagousse-Pinguet et al., 2015).

Both N and P concentrations in senesced leaves of all species were negatively correlated with species richness (Figure 2), indicating that individuals in higher diversity communities were more proficient at nutrient resorption. While such proficient resorption may have positive consequences for reproduction and vegetative regrowth, it could also result in lower litter quality. In a separate biodiversity experiment, root decomposition rates are negatively correlated with species richness due to the variation in fine root nutrient concentration across biodiversity levels (Fornara, Tilman, & Hobbie, 2009). Our results present evidence for the negative impacts of biodiversity on the nutrient quality of leaf litter at the within-species level. The relatively lower nutrient availability in decomposing litter may negatively impact litter decomposition rates (Hobbie, 2015; Mooshammer et al., 2012). Within-species variation in litter guality in response to biodiversity may thus contribute to the positive effects of biodiversity on soil C and nutrient accumulation.

In this study, higher biodiversity increased the efficiency of plant nutrient use not only through reducing the amount of nutrients in living tissues (van Ruijven & Berendse, 2005; Selmants, Zavaleta, & Wolf, 2014) but also by increasing residence time of nutrients via resorption during senescence. For all species across all treatments,  $RE_N$  was much higher that  $RE_P$  (Figure 2), indicating that N was more limiting than P for plant growth in this semi-arid grassland. The higher nutrient resorption in higher diversity communities suggests that biodiversity facilitates more efficient nutrient use through changes in within-species plant nutrient conservation traits. Previous studies have shown that biodiversity enhances community N use efficiency through changes in morphological traits (stem: leaf ratio) or species composition (the presence of legumes) (Fornara & Tilman, 2009; van Ruijven & Berendse, 2005; Selmants et al., 2014). Here, we show that biodiversity enhances nutrient-use efficiency through higher nutrient resorption. Increased nutrient resorption in higher diversity communities extends the mean residence time of nutrients in plants, with effects on a wide variety of processes including nutrient cycling and loss pathways and the longer term efficiency of biomass production (Aerts & Chapin, 2000). Moreover, our results show that the responses of nutrient resorption in the annual species (Salsola collina) paralleled that of perennials. Higher nutrient resorption for annuals in higher diversity communities may facilitate seed production, and thus have implications for productivity in future years.

Soil moisture and plant-available N and P in soils significantly decreased with increasing species richness (Figure S2), indicating that higher biodiversity contributed to the resource depletion in soils. Such changes in soil resource availability are caused partly by changes in plant acquisition and also partly by changes in environmental conditions, for example, light availability and soil temperature. Our results agree with those of many past studies in showing that above-ground primary productivity is positively correlated with species richness (Hooper et al., 2005). Higher nutrient acquisition for primary production and thus nutrient competition often results in lower plant-available nutrient concentrations in soils (Fornara & Tilman, 2009; Oelmann et al., 2007).

Previous results from this ecosystem have shown that plants conserve nutrients through enhanced nutrient resorption under lower nutrient- and water-availability conditions in this semi-arid temperate steppe (Lü & Han, 2010). Nutrient resorption of forb species was negatively correlated with the changes in plant-available nutrient concentrations in topsoil (Table 1). In contrast, the correlations between nutrient resorption of grasses and nutrient concentrations in topsoil were generally weak. This result suggests that the pathway through which biodiversity influences plant nutrient-use traits varies among plant functional groups. The differences in sensitivity between forbs and grasses may result from their root vertical distribution. Grasses generally have deeper roots than forbs in water-limited ecosystems (Hooper & Vitousek, 1998; Schenk & Jackson, 2002), which would facilitate their use of resources in deep soils. Also, we acknowledge that our study was framed on dominant species, and call for further studies considering nutrient resorption in subordinate species to better grasp the importance of these underlying mechanisms in mediating the biodiversity-primary productivity relationship.

# 5 | CONCLUSIONS

Species richness facilitates within-species plant nutrient conservation through decreasing nutrient concentrations in green leaves and enhancing nutrient resorption in senescing tissues. Such changes in plant nutrient conservation strategy might have positive consequences on regrowth in the following seasons, allowing plants to rely more on resorbed nutrients and less on soil-available nutrients. In addition, higher nutrient resorption from senescing leaves would create lower quality litter, which has implications for decomposition rates and biogeochemical cycling.

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#### AUTHORS' CONTRIBUTIONS

X.-T.L. and X.-G.H. conceived the study; X.-T.L. performed the field experiment; X.-T.L., Y.-Y.H. and A.A.W. analysed the data and wrote

the paper. All authors contributed to manuscript revision and gave final approval for publication.

#### DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi. org/10.5061/dryad.kc4m7p2 (Lü, 2019).

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### SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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