

## RESEARCH ARTICLE

# Multidimensional stoichiometric mismatch explains differences in detritivore biomass across three forest types

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**Handling Editor:** Jonathan Zvi Shik**Abstract**

1. The ecological stoichiometry theory provides a framework to understand organism fitness and population dynamics based on stoichiometric mismatch between organisms and their resources. Recent studies have revealed that different soil animals occupy distinct multidimensional stoichiometric niches (MSNs), which likely determine their specific stoichiometric mismatches and population responses facing resource changes. The goals of the present study are to examine how long-term forest plantations affect multidimensional elemental contents of litter and detritivores and the population size of detritivores that occupy distinct MSNs.
2. We evaluated the contents of 10 elements of two detritivore taxa (lumbricid earthworms and julid millipedes) and their litter resources, quantified their MSNs and the multidimensional stoichiometric mismatches, and examined how such mismatch patterns influence the density and total biomass of detritivores across three forest types spanning from natural forests (oak forest) to plantations (pine and larch forests).
3. Sixty-year pine plantations changed the multidimensional elemental contents of litter, but did not influence the elemental contents of the two detritivore taxa. Earthworms and millipedes exhibited distinct patterns of MSNs and stoichiometric mismatches, but they both experienced severer stoichiometric mismatches in pine plantations than in oak forests and larch plantations. Such stoichiometric mismatches led to lower density and biomass of both earthworms and millipedes in pine plantations. In other words, under conditions of low litter quality and severe stoichiometric mismatches in pine plantations, detritivores maintained their body elemental contents but decreased their population biomass.
4. Our study illustrates the success in using the multidimensional stoichiometric framework to understand the impact of forest plantations on animal population

dynamics, which may serve as a useful tool in addressing ecosystem responses to global environmental changes.

#### KEYWORDS

biogeochemical, earthworm, ecological stoichiometry, elemental content, land-use change, millipede, soil animal, stoichiometric niche

## 1 | INTRODUCTION

Understanding the factors influencing individual fitness and population maintenance is a primary goal of fundamental ecology and the prerequisite to predict species responses to anthropogenic environmental changes. Whereas the effects of physical environmental conditions have been extensively documented, the ecological stoichiometry theory proposes to understand the fitness of organisms by studying the composition and balance of chemical elements in organisms and the environment (Sturner & Elser, 2002). Body elemental composition is a fundamental trait of organisms, which determines how an individual interacts with the environment and other individuals within local communities and thereby affects population growth in natural habitats (Frausto da Silva & Williams, 2001). Compared with autotrophs, heterotrophs usually have higher nutrient contents and more confined elemental composition (i.e. stoichiometric homeostasis; Elser et al., 2000; Small & Pringle, 2010). The mismatch between elemental demands of heterotrophs and elemental composition of their food resources constrains the strength of trophic interactions and nutrient flows (Hillebrand et al., 2009).

The stoichiometric mismatch between food resources and consumers can be quantified by the trophic stoichiometric ratio (TSR), that is,  $C:X_{\text{resource}}/C:X_{\text{consumer}}$ , where C and X represent concentration of carbon and another nutritional element respectively (Filipiak & Filipiak, 2022). This index is useful for identifying the elements that are relatively scarce in food resources but important to consumer growth and development. In stoichiometric studies on heterotrophs, the nutritional elements nitrogen (N) and phosphorus (P) have received most attention (Andrieux et al., 2021; González et al., 2017), which display much higher concentration in consumer body tissue compared to their resource (Lemoine et al., 2014; Sturner & Elser, 2002). However, higher nutrient concentrations or lower C:X ratios in consumers have also been reported in several other necessary elements, for example, sodium (Na), sulphur (S), copper (Cu) and zinc (Zn) (Filipiak & Weiner, 2017a; Sobczyk et al., 2020). Such differences in the C:X ratios result in high TSR values between resources and consumers, especially between herbivores and plants or between detritivores and litters, which have been shown to limit the growth, development and feeding strategies of various invertebrate taxa, as well as the decomposition rates and primary productivity of ecosystems (Filipiak et al., 2017; Filipiak & Weiner, 2017a, 2017b; Kaspari & Powers, 2016; Sobczyk et al., 2020). Recently, the framework of multidimensional stoichiometric niche (MSN) has been proposed to characterize species niches based on the multiple elements composing animals (González et al., 2017; Zhang, Chen, Deng, Li,

González, et al., 2022). Revealing the MSN may therefore help to depict trophic niche differentiations across taxa and clarify which elements in food resources represent the major restriction on consumer populations.

Soils are detritus-based terrestrial ecosystems that are generally lacking sufficient nutrients for most animal consumers. In particular, below-ground detritivores are faced with even stronger stoichiometric mismatch due to the high carbon-to-nutrient ratio of senescent plant tissues, compared to above-ground fresh-leaf consumers (Elser et al., 2000; McGroddy et al., 2004). Such stoichiometric mismatches may constrain the development of detritivores and influence their survival and population dynamics (Cross et al., 2003; Lemoine et al., 2014; Moe et al., 2005; Pokarzhevskii et al., 2003). Two hypotheses can be laid out to predict the responses of detritivores to stoichiometric mismatches. First, faced with lower food quality, detritivores may be able to change their body elemental concentration or their realized MSN (Small & Pringle, 2010). Such adjustments have been documented in laboratory experiments across broad food quality gradients (Danger et al., 2013; Halvorson et al., 2018, 2019), but it is unclear whether detritivores in the field can similarly adapt their elemental contents across narrower food quality gradients. Second, as resource quality declines (i.e. C:X ratios increase), detritivores may maintain their stoichiometric compositions by compensatory feeding, selective feeding or assimilation of nutrition-rich micro-organisms when various food resources are available, for example, in natural ecosystems (González et al., 2018; Pokarzhevskii et al., 2003; Scheu & Setälä, 2002; Sobczyk et al., 2020). In this latter case, the biomass or population size of detritivores are likely to decrease because of the lower amount of alternative high-quality food (Jochum, Barnes, Ott, et al., 2017; Ott et al., 2012, 2014).

Forest plantations are an important means to restore degraded ecosystems and provide nature-based solutions to climate change (Feng et al., 2022; Paquette et al., 2018). That said, it has been debated whether plantations can achieve similar ecosystem functioning and services as primary or secondary natural forests (Hua et al., 2022; Wang et al., 2022). A recent global meta-analysis showed that plantations delivered significantly less benefits in terms of multiple ecosystem services and biodiversity (Hua et al., 2022). In particular, conversion of natural forest to plantations has been documented to influence below-ground processes, for example, the quantity and quality of litter and populations of soil organisms that rely on litter as basal resource (Mueller et al., 2016; Rozen et al., 2010; Wardle, 2002). Such changes in soil organisms, particularly detritivores, can feedback to ecosystem processes by influencing the decomposition and cycling of

nutrients. In the face of litter changes induced by forest plantations, detritivores may adjust or retain their stoichiometric properties and maintain similar or lower population sizes. However, these hypotheses have yet to be tested.

Here, we studied how forest type (secondary oak forests, pine plantations and larch plantations) affect the elemental composition of two major soil detritivore taxa, that is, epigeic earthworms (Lumbricidae) and julid millipedes (Julida) and their litter resources. Specifically, we quantified the elemental contents of C, N, Na, magnesium (Mg), P, potassium (K), calcium (Ca), Zn, manganese (Mn) and Cu of the litter and the two detritivore taxa among the three forest types, calculated the trophic stoichiometric mismatch (represented by overall TSR values) between litter and detritivores, and examined how such mismatch might affect detritivore population size. Recent studies revealed that earthworms and millipedes occupy distinct MSNs (Zhang, Chen, Deng, Li, González, et al., 2022), and their population sizes were constrained by different elements (see also Ott et al., 2014). Therefore, we hypothesized that (1) forest plantations generated different stoichiometric mismatch patterns (TSR values) for earthworms and millipedes due to their distinct MSNs, (2) earthworms and millipedes retained their stoichiometric compositions in the face of stoichiometric mismatch and had smaller population sizes in forest types with lower litter quality.

## 2 | MATERIALS AND METHODS

### 2.1 | Ethics statement

No specific permissions were required for all study locations, for these forests were not private and the study did not involve endangered or protected species.

### 2.2 | Study area and sample collecting

This study was conducted between August and September 2020 on the Dongling mountain (115°29'48.2"E; 40°01'48.5"N), located in the west of Beijing City, China. The region is characterized by temperate semihumid climate, with a mean annual temperature of 6.3°C and a mean annual precipitation of 612 mm, mostly between June and August. The original oak forests in the region have been removed and the current trees recovered naturally or were replanted since the 1960s. We established five sampling plots (50 m × 50 m) in different valleys for each of three forest types: one secondary deciduous and broad-leaved forest dominated by *Quercus liaotungensis* Koidz. (oak); two ~60-year-old artificial plantations that are dominated, respectively, by deciduous coniferous species *Larix principis rupprechtii* Mayr. (larch) and evergreen coniferous species *Pinus tabulaeformis* Carr. (pine).

To measure the total dry biomass and density of detritivores, in each plot we collected three subsamples (30 cm in diameter) comprising litter (L layer), organic matter (F and H layer) and top 10 cm

soil (Ah layer). These three subsamples were pooled into one aggregate sample for each plot ( $n = 15$  in total) and taken to the laboratory to extract earthworms and millipedes by sieving and hand picking. Then, the samples were heated for 24 h in a Tullgren apparatus equipped with a 40 W bulb to collect smaller earthworms and millipedes. Earthworms were kept in tap water for 3 days to void their gut and then transferred to  $-20^{\circ}\text{C}$  for storage until further analyses. From each plot, we further took another five leaf litter subsamples (0.5 m × 0.5 m, in total  $n = 75$ ) for litter biomass and elemental content analysis. Earthworms and millipedes encountered in these leaf litter samples were also collected to complement elemental analyses (for plots without sufficient individuals), but they were not included for estimating population densities.

### 2.3 | Sample preparation and element determination

Animals were freeze-dried for 72 h and individual body mass (dry weight) was measured using an electronic microbalance (MYA 5.4Y, RADWAG Wagi Elektroniczne, Poland) to the nearest microgram ( $\pm 0.1 \mu\text{g}$ ). Adult individuals of earthworms and millipedes (body mass higher than 5 mg and 2 mg respectively) were selected for elemental analysis. Specimens larger than 10 mg were ground individually to a homogenous powder using a bead mill homogenizer (Bead Ruptor 12, Omni International). Approximately 2 mg powder of each ground sample was used to quantify C and N contents using a vario EL cube CHNOS Elemental Analyzer (Elementar Analysensysteme GmbH). Another ~2 mg powder of the ground sample was digested with nitric acid (2 ml and 70% by weight) for quantifying the contents of Ca, Cu, K, Mg, Mn, Na, P and Zn using an iCAP 6301 ICP-OES Spectrometer (Thermo Fisher). For specimens smaller than 10 mg, we used their whole body to quantify C/N or the other eight elements, except for six large individuals of earthworms and eight large individuals of millipedes, which we cut into two halves prior to quantifying C/N and the other elements (Zhang, Chen, Deng, Li, González et al., 2022). We use the term 'C (or other element) content' to describe elemental concentrations as the percentage of dry body mass. In total, we obtained elemental contents from 51 individuals of earthworms and 78 individuals of millipedes; in 40 individuals of earthworms and 36 of millipedes we obtained all 10 elements. Table S1 in Appendix S1 provides the number of detritivore individuals that are measured for a subset of or all 10 elements within each plot.

We also measured the 10 elemental contents of the five litter samples from each plot (except one lost sample, in total  $n = 74$ , Appendix S1, Table S1). For each litter sample, after freeze-dried for 72 h, we ground ~5 g leaf litters (included microbes living on them) and then used ~8 mg and ~50 mg powders to measure C and N and the other eight elements, respectively. The data of the elemental contents and biomass of litters, as well as individual elemental contents and plot-summed biomass and density of detritivores, are provided in Dryad Digital Repository (Zhang, Chen, Deng, Li, Chen, et al., 2022).

TABLE 1 The content (mean  $\pm$  stand error) of 10 elements of two detritivore taxa, that is, earthworms and millipedes, and leaf litters. Only individuals with all 10 elements available (see Appendix S1, Table S1) are included. Different letters indicate significant differences (one-way ANOVA,  $p \leq 0.05$ )

Taxo14n	C (%)	N (%)	Ca (%)	K (%)	Mg (%)	P (%)	Na (mg/kg)	Mn (mg/kg)	Zn (mg/kg)	Cu (mg/kg)
Earthworms	43.5 $\pm$ 0.98 <sup>a</sup>	9.9 $\pm$ 0.33 <sup>a</sup>	0.73 $\pm$ 0.07 <sup>a</sup>	0.91 $\pm$ 0.043 <sup>a</sup>	0.19 $\pm$ 0.02 <sup>a</sup>	0.86 $\pm$ 0.028 <sup>a</sup>	4626 $\pm$ 341.5 <sup>a</sup>	126 $\pm$ 36.9 <sup>a</sup>	113 $\pm$ 9.4 <sup>a</sup>	11 $\pm$ 0.9 <sup>a</sup>
Millipedes	29.3 $\pm$ 0.46 <sup>b</sup>	4.9 $\pm$ 0.11 <sup>b</sup>	16.79 $\pm$ 0.279 <sup>b</sup>	0.39 $\pm$ 0.016 <sup>b</sup>	0.58 $\pm$ 0.015 <sup>b</sup>	1.95 $\pm$ 0.087 <sup>b</sup>	1419 $\pm$ 101.7 <sup>b</sup>	144 $\pm$ 25.5 <sup>a</sup>	154 $\pm$ 7.8 <sup>b</sup>	202 $\pm$ 14.5 <sup>b</sup>
Litter	41.8 $\pm$ 0.94 <sup>a</sup>	1.5 $\pm$ 0.05 <sup>c</sup>	2.04 $\pm$ 0.075 <sup>c</sup>	0.27 $\pm$ 0.012 <sup>c</sup>	0.36 $\pm$ 0.014 <sup>c</sup>	0.08 $\pm$ 0.003 <sup>c</sup>	82 $\pm$ 4.7 <sup>c</sup>	403 $\pm$ 26.9 <sup>b</sup>	77 $\pm$ 4.1 <sup>c</sup>	12 $\pm$ 0.6 <sup>a</sup>

## 2.4 | Trophic stoichiometric ratio index calculation

To quantify stoichiometric mismatches between leaf litter and detritivores, we used the trophic stoichiometric ratio (TSR) index (Filipiak & Weiner, 2014, 2017b):

$$TSR_X = (C:X)_{\text{litter}} / (C:X)_{\text{detritivore}}$$

This index, calculated for different elements ( $X = N, P, Ca, Cu, K, Mg, Mn, Na$  and  $Zn$ ), provides an indicator for the (co-)limiting effect by food (i.e. litter) nutritional scarcity in the elements for which consumer (i.e. detritivore) demand is higher than supply. A higher  $TSR_X$  value indicates severe mismatches and high probability that the element  $X$  is limiting. Recent studies suggested that the maximum assimilation efficiency of C (25%) was much lower than that of nutritional elements (up to 100%) and proposed to use  $TSR_X \geq 4$  ( $TSR_X \geq 1/0.25$ ) as an indicator that the element  $X$  imposes a constraint on the growth and development of consumers (Filipiak et al., 2017; Filipiak & Weiner, 2017a). It is worth noting that the TSR is adapted from the concept of threshold elemental ratio (TER, Fagan & Denno, 2004; Sterner & Elser, 2002; Urabe & Watanabe, 1992), namely the elemental ratio at which consumers shift from a primarily C or energy limitation into nutrient limitation:  $TER_X = GGE_X / GGE_C \times (C:X)_{\text{consumer}}$  where  $GGE_X$  and  $GGE_C$  represent gross growth efficiencies of element  $X$  and C respectively. While TER provides a more straightforward indicator of potential stoichiometric mismatch, it could only be applied for commonly studied organisms (e.g. *Daphnia magna*, DeMott et al., 1998) for which  $GGE_X$  and  $GGE_C$  were experimentally measured through laboratory feeding trials using growing animals. As this is not the case for our focal organisms (i.e. earthworms and millipedes), we used TSR as a practically possible indicator for potentially limiting elements. For more detailed explanations on using the TSR index please refer to Filipiak and Filipiak (2022).

## 2.5 | Statistical analysis

All elemental contents were arcsine-square root transformed to improve normality and homoscedasticity. We first ran analysis of variance (ANOVA, R package *STATS*) to examine differences in elemental contents among earthworms, millipedes and litters; only samples with all 10 elemental contents available were included ( $n = 40, 36$  and  $74$  for earthworms, millipedes and litters respectively, see Appendix S1, Table S1). We then ran a principal component analysis (PCA, R package *STATS*) on the elemental contents of earthworms, millipedes and litters from three forest types (using the same data as above with all 10 elements available). We extracted the first three PC axes (Blonder et al., 2018) to calculate the hypervolume (R package *HYPERVOLUME*) of the litter and two detritivore taxa from the three forest types. To quantify the MSN distance and overlap among the three groups in multivariate space, we calculated the distance among hypervolume centroids and the degree of similarity/overlap using the Jaccard similarity index (Jaccard, 1901).

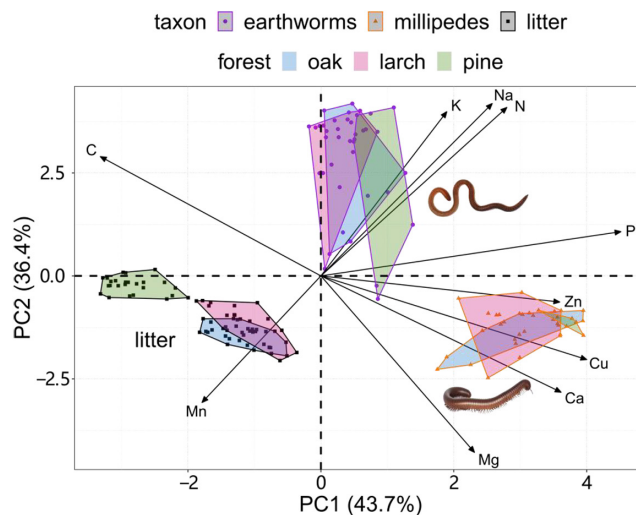
For subsequent analyses, we calculated the plot-averaged elemental contents of each detritivore taxon and litter, by taking the average across all measured detritivore individuals and litter samples within each plot ( $n = 15$ ; see Appendix S1, Table S1). For each detritivore taxon, we used ANOVA to examine the effects of forest type on TSR values of the nine noncarbon elements, as well as their plot-summed biomass and density ( $n = 15$ ). For the ANOVA on TSR, because the biomass of earthworm in one oak plot and one pine plot and that of millipedes in two oak plots and three pine plots were too low to analyse their elemental contents (Appendix S1, Table S1), we used the mean elemental contents of that taxon from other plots of the same forest type to calculate the TSR.

To test whether detritivores adjust their elemental contents following litter changes, we used simple regression models to examine the relationships between plot-averaged litter elemental contents and plot-averaged elemental contents in detritivores ( $n = 13$  and  $n = 9$ – $10$  for earthworms and millipedes respectively; plots with missing detritivore elemental data were excluded; Appendix S1, Table S1). We used simple regression models to examine the relationship between plot-level biomass (or density) of each detritivore taxon and plot-level litter quantity (i.e. summed litter biomass within the plot;  $n = 15$ ). We then used generalized linear models (GLMs) to examine the relationships between plot-level detritivore biomass (or density) and the plot-averaged litter quality represented by C:X ratios of litters ( $n = 15$ ). For the biomass or density of each detritivore taxon, we initialized a GLM by including C:X ratios of all nine noncarbon elements of litter as explanatory variables and then applied an automated backward selection algorithm to obtain the best model using the Akaike information criterion (AIC; Venables & Ripley, 2002). Models with difference in AIC smaller than 2 ( $\Delta\text{AIC} \leq 2$ ) were considered as not distinguishable.

### 3 | RESULTS

The two detritivore taxa differed significantly in the contents of all elements except Mn (Table 1). On average, earthworms had higher contents of C, N, K and Na and lower contents of Ca, Mg, P, Zn and Cu, compared with millipedes (Table 1). For both earthworms and millipedes, the contents of most elements showed no significant difference among the three forest types (exceptions were Mg, Mn and Zn in earthworms and Mg and P in millipedes; Appendix S1, Table S2). Litters contained lower contents of N, K, P, Na and Zn and higher content of Mn than both detritivore taxa, while the contents of Ca and Mg in litter were significantly lower than millipedes but higher than earthworms (Table 1). Across different forest types, the litters of pine plantations had a higher content of C but lower contents of all other nine elements than litters of oak forests and larch plantations (Appendix S1, Table S2).

The first two PCA components (PC1 and PC2) explained 80% of the total variation in the 10 elemental contents across the two detritivore taxa and litter from the three forest types (Figure 1). PC1 had the largest loadings on P, Cu and Ca contents, whereas PC2

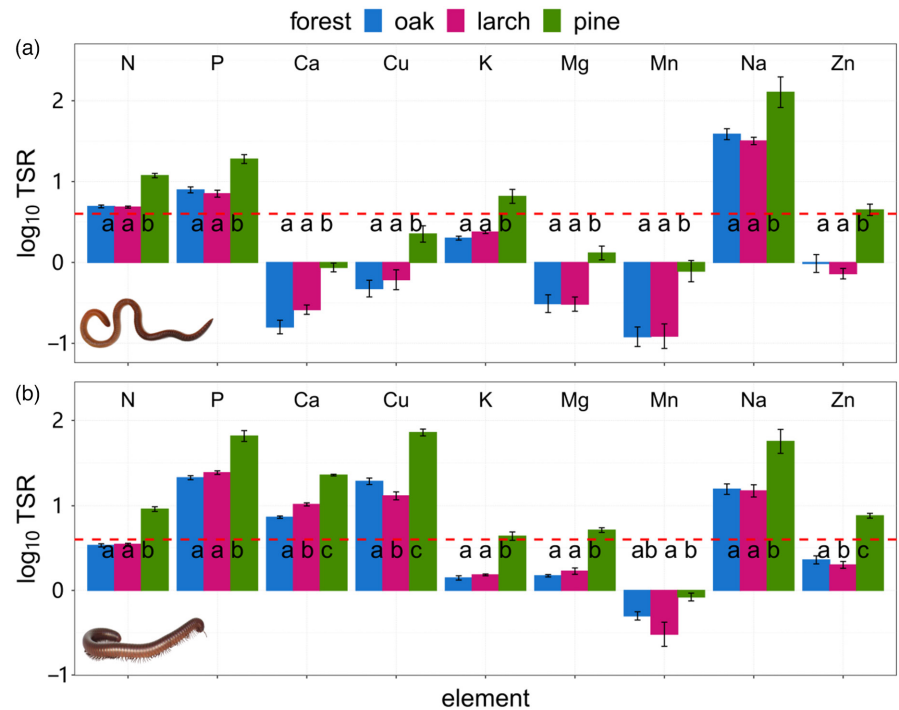


**FIGURE 1** Principal component analysis on overall contents of 10 elements (arcsine-square root transformed, percent of C, N, P, Ca, Cu, K, Mg, Mn, Na and Zn) of earthworms ( $n = 40$ , pink circles), millipedes ( $n = 36$ , orange triangles) and litter ( $n = 74$ , black squares) samples from three forest types. Arrows represent the raw loadings of 10 elemental variables on the first two axes (for loading results see Appendix S1, Table S3). Larch (purple) and pine (green) plantations were converted from oak forests (blue) approximately 60 years ago.

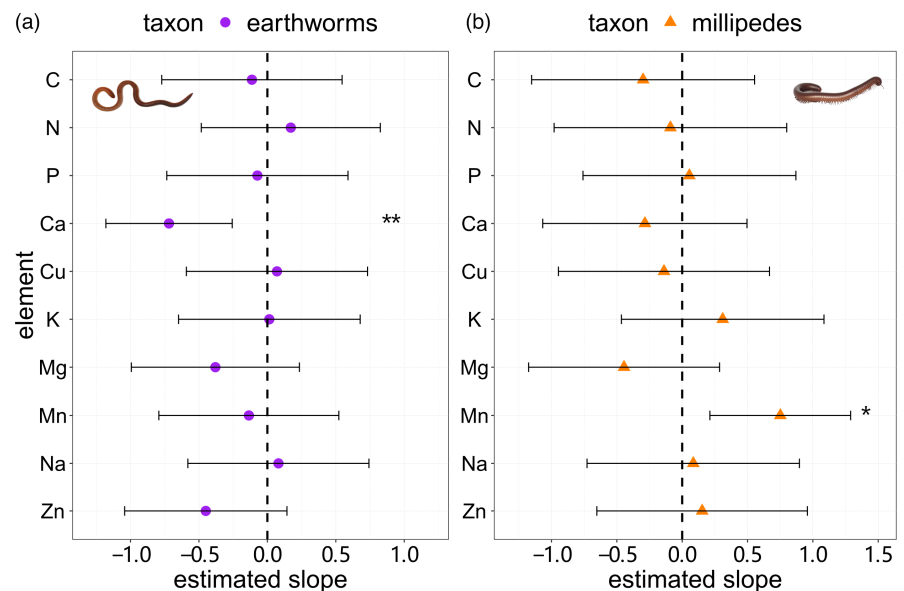
had the largest loadings on Mg, Na and N contents (Appendix S1, Table S3). Along these two PCA axes, litter, earthworms and millipedes were clearly separated from each other, and the litter of pine plantations was also separated from those of oak forests and larch plantations along the axis of PC1 (Figure 1). However, for both earthworms and millipedes, individuals from different forest types largely overlapped in the PCA plot (Figure 1). Along the first three PCA axes which explained 91% of the total variation in the 10 elemental contents, no overlap in MSN was found between litter, millipedes and earthworms across the three forest types, and longer MSN centroid distances were found between litter and detritivores in pine plantations than in oak forests and larch plantations (Appendix S1, Table S4).

The significant difference in elemental composition between litter and detritivores indicated potential stoichiometric mismatch. TSR values for both detritivore taxa were high in several elements (Figure 2). For earthworms, the elements with the highest mean TSR values were Na (33–169), P (7.2–20) and N (4.8–12) across the three forest types. The mean TSR values of K and Zn were slightly higher than 4.0 in pine plantations (7.1 and 4.7 respectively), but not in the other two types of forests. For millipedes, the elements with highest mean TSR values were Cu (13–73), followed by P (22–68), Na (16–67) and Ca (7.3–23). The mean TSR values of N, Zn, Mg and K were higher than 4.0 in pine plantations (9.2, 7.7, 5.2, and 4.5 respectively), but not in the other two types of forests. Overall, TSRs for both detritivore taxa were significantly higher in pine plantations than in oak forests and larch plantations ( $p < 0.05$  for all elements and both taxa, except for Mn of millipedes; Figure 2).

**FIGURE 2** Effects of forest type on plot-averaged TSR values [ $\text{means} \pm \text{standard error of } (C:X)_{\text{litter}} / (C:X)_{\text{detritivore}}$ ] of nine noncarbon elements for earthworms (a) and millipedes (b). C:X ratios are derived from plot-averaged elemental contents of detritivores and litters. Different letters above the bars indicate significant differences according to one-way analysis of variance ( $p \leq 0.05$ ). The red lines indicate the threshold value of TSR = 4.



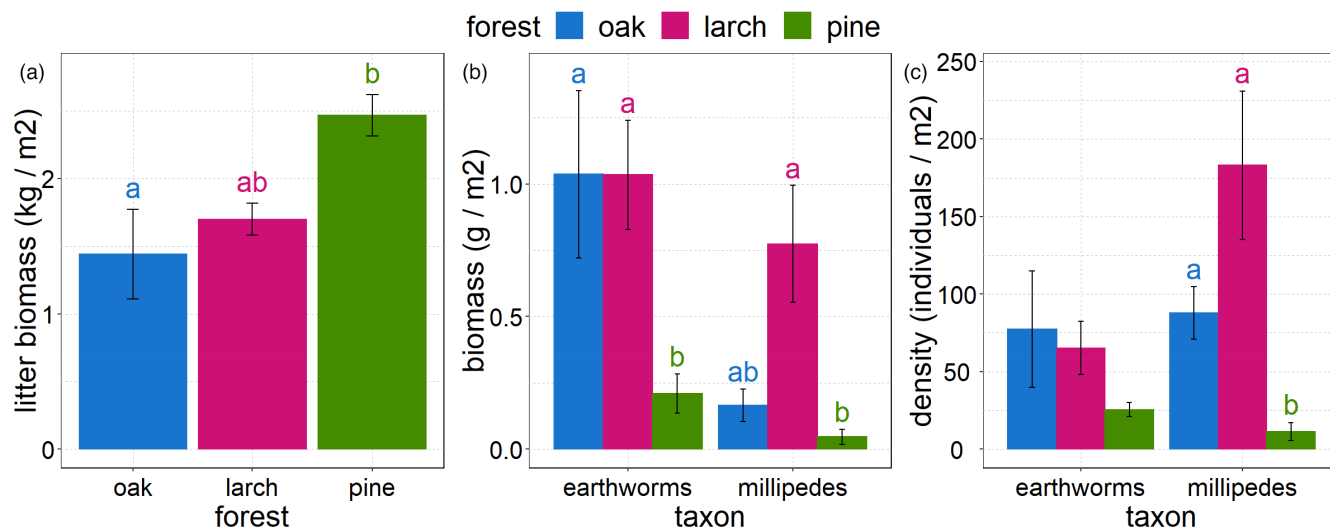
**FIGURE 3** Regression slopes estimated for plot-averaged elemental contents of litter versus plot-averaged elemental contents of earthworms (a,  $n = 13$ ) and millipedes (b,  $n = 9-10$ ) across oak forests and larch and pine plantations. Bars indicate 95% prediction intervals for the estimated slope.  $p$  values of each regressions were presented at right side of each bars: \* $0.01 < p \leq 0.05$ , \*\* $0.001 < p \leq 0.01$ , \*\*\* $p \leq 0.001$ .



Across the 15 plots, while both detritivores and litter exhibited high variations in elemental contents (Appendix S1, Table S2), their variations were largely independent. For most elements, their contents in detritivores had no relationship with those in litters across plots (Figure 3). That said, the content of Mn in millipedes was positively related to that in litter, whereas the content of Ca in earthworms was even negatively related to that in litter. In other words, we found no evidence that detritivores changed their elemental contents in face of different litter quality among forest types.

Forest plantation affected not only the quality of litters (i.e. elemental contents), but also their quantity. Across the three types of

forests, pine plantations had the highest litter biomass ( $p < 0.001$ , Figure 4a), albeit their lowest litter quality represented by the highest content of C and lowest contents of the other nine elements (Appendix S1, Table S2). Moreover, forest plantations affected the population size of millipedes and earthworms differently. For earthworms, compared to oak forests, larch plantations had weak effects on their biomass and density, but pine plantations decreased their biomass by 80% and density by 67% ( $p = 0.03$  and  $0.73$  respectively, Figure 4b,c). For millipedes, compared to oak forests, larch plantations increased their biomass by 367% and density by 109% ( $p = 0.12$  and  $0.36$  respectively, Figure 4b,c), whereas pine



**FIGURE 4** Effects of the forest type on litter biomass (a) and the total dry biomass (b) and density (c) of earthworms and millipedes (means  $\pm$  stand error,  $n = 15$ ). Different letters above the bars indicate significant differences (one-way ANOVA,  $p \leq 0.05$ ).

**TABLE 2** Top ranking models explaining detritivore biomass and density using C:X ratios of litter (log-10 transformed, X represents N, P, Ca, Cu, K, Mg, Mn, Na and Zn) across 15 plots. For simplicity, C:X ratios were represented by the element X in all models. The full model is 'biomass/density ~ N + Ca + Cu + K + Mg + Mn + Na + P + Zn'. Models were ranked using Akaike information criterion (AIC), and  $\Delta$ AIC showed the differences from the optimal model (i.e. the one with the lowest AIC values). The optimal model and suboptimal ones with  $\Delta$ AIC smaller than 2 are shown, whereas models with  $p > 0.1$  are omitted

Taxon	Model	R <sup>2</sup>	Adjusted R <sup>2</sup>	F value	p value	AIC	$\Delta$ AIC
Earthworms	biomass ~ Na	0.51	0.47	13.38	0.003	229.4	0.0
	biomass ~ Na + N	0.55	0.48	7.35	0.008	230.0	0.6
	biomass ~ Na + N + P	0.58	0.46	4.98	0.02	231.1	1.7
Millipedes	density ~ Na	0.21	0.15	3.45	0.086	164.0	0.0
	biomass ~ N + Cu + Na + Zn	0.57	0.40	3.30	0.057	222.8	0.0
	biomass ~ N + Cu + Na + Zn + Mn	0.62	0.41	2.91	0.078	223.0	0.2
	density ~ N + Ca	0.53	0.45	6.73	0.011	174.9	0.0
	density ~ N + Ca + Na	0.59	0.47	5.21	0.018	174.9	0.0
	density ~ N + Ca + Na + Cu	0.62	0.46	4.03	0.034	175.7	0.9

plantations decreased their biomass by 72% and density by 87% ( $p = 0.27$  and  $0.003$  respectively, Figure 4b,c).

Our analyses showed that variations in the biomass and density of detritivores among forest types were explained by litter quality rather than litter quantity. The biomass and density of each detritivore taxon exhibited no relationship with litter biomass ( $p > 0.3$  for all, Appendix S1, Figure S1), but were related to the C:X ratios in litters. For earthworms, the optimal models for predicting the biomass and density included the C:Na ratio in litters, and suboptimal models with  $\Delta$ AIC  $\leq 2$  also included C:N and C:P ratios in litters for earthworm biomass (Table 2). For millipedes, the optimal model for predicting their biomass included C:N, C:Cu, C:Na and C:Zn ratios in litters, and the suboptimal model also included the C:Mn ratio; the optimal model for predicting millipedes density included C:N and C:Ca ratios in litters, and suboptimal models also included C:Na and C:Cu ratios (Table 2).

## 4 | DISCUSSION

### 4.1 | Multidimensional stoichiometric mismatch between detritivores and litters

Our results revealed significant stoichiometric mismatch in both earthworms and millipedes and their variation among forest types, thus supporting our first hypothesis. In line with the study of Filipiak (2016) showing high TSR values (10–100) of N, P, S, K and Cu across different taxa of soil-dwelling detritivores, our analyses identified Na, P and N as the most potentially limiting elements for earthworms, and Na, P, Ca and Cu for millipedes. Compared to oak forests, larch plantations showed minor effects on litter (included microbes living on them) and detritivore elemental contents, as well as stoichiometric mismatch patterns. In contrast, pine plantations significantly increased C:X ratios for all elements in litter, causing all nutritional

elements increasingly limited for both earthworms and millipedes. This highlights the importance of food stoichiometry in driving the overall TSR pattern of consumers (Filipiak & Filipiak, 2022).

Plantation-induced changes in litter C:X ratios have been reported to affect soil animal species richness, but these effects were taxon dependent (Jochum, Barnes, Weigelt, et al., 2017; Mueller et al., 2016). Different soil animal taxa have recently been shown to occupy distinct MSNs, that is, multiple body elemental compositions (Zhang, Chen, Deng, Li, González, et al., 2022). Our analyses support our first hypothesis by showing that the two detritivore taxa differed in their MSNs and thus experience different stoichiometric mismatches (TSR values). For instance, millipedes have higher demand for P, Ca and Cu, whereas earthworms have higher demand for N and Na. This suggests that litter stoichiometry changes differentially affect soil animal taxa according to their MSNs. In particular, stoichiometric mismatches may decrease the fitness of certain taxa more severely than the others, thus re-shaping species interactions and altering community composition. Moreover, in a given taxon, stoichiometric mismatches may differ among ontogenetic stages. For instance, older beetle larvae experience weaker stoichiometric mismatches due to the relatively high nutritional concentrations of their food (e.g. decayed wood) compared to younger larvae (Filipiak, 2018; Filipiak & Weiner, 2017a). Our results call for future studies quantifying MSNs of soil organisms across life stages, which may provide further insight into their responses to environmental changes, such as forest plantations.

## 4.2 | Maintenance of stoichiometric niches of detritivores despite litter changes

Our analyses revealed weak associations between litter and detritivore elemental contents across plots, suggesting that detritivores can maintain their stoichiometric characteristics even if the quality of their food decreases. In pine plantations with litter containing remarkably low P and N contents (mean of 0.06% and 1.1% respectively), the contents of P in millipedes and N in earthworms remained high (mean of 2% and 10.5% respectively). This supports our second hypothesis and agrees with previous consensus that consumers maintain body stoichiometry as resource stoichiometry varies (Sterner & Elser, 2002). Similar results have been reported for earthworms, which exhibited strong homeostasis in C, N and P contents along a broad gradient of soil and litter stoichiometry (Abail & Whalen, 2018; Marichal et al., 2011). Combined, these results refute the argument that invertebrates at lower trophic levels contain low N and/or P contents due to low quality of detritus food resources (Fagan et al., 2002; González et al., 2011; Woods et al., 2004). The stable stoichiometric niches revealed here provides additional justifications for the framework of MSN in soil fauna (González et al., 2017; Zhang, Chen, Deng, Li, González, et al., 2022), which regards the elemental contents of soil organisms as taxon-specific characteristics and confined mainly by taxonomy and phylogeny. We note, however, that individuals within each detritivore

taxon do vary considerably in their body elemental contents (see Appendix S1, Table S2), possibly accounted for by different species and sexes. Resolving the influences of these biological characteristics is a promising direction for future research.

Faced with significant elemental mismatches with their resources, consumers must adjust feeding, assimilation and excretion to release excess and retain limiting elements to maintain their stoichiometric balance (Frost et al., 2005; Liess, 2014). Earthworms perform complex feeding strategies (Curry & Schmidt, 2007) and selective ingestion process, which likely enable them to maintain consistent body C:N ratio (Abail & Whalen, 2018). Millipedes were found to preferentially feed on N-rich litter and dead leaves with high microbial activity (Coq et al., 2020; Frainer et al., 2016; Loranger-Merciris et al., 2008). The high TSR values of N and P indicate that detritivores may alleviate their N and/or P deficit by compensatory feeding on micro-organisms with generally lower C:P and C:N ratios than leaf litter (Danger & Chauvet, 2013; Makino et al., 2003). Beyond N and P, the two studied detritivore taxa also experienced high TSR values of Ca, Cu and Na, suggesting that they may also consume fungi which were likely to provide Ca and Na and other elements for saprophagous consumers (Cromack et al., 1975, 1977, Crowther et al., 2011). Importantly, seasonal foraging on nutrient-rich pollen that is delivered to the forest floor (Filipiak, 2016) and consumption of decomposed organic matter with rich nutritional elements transported by fungi (Filipiak, 2018) may also mitigate stoichiometric mismatches for a broad range of detritivores including earthworms and millipedes. Revealing the detailed strategies, for example, preingestive food selection or postingestive nutritional regulation that each detritivore taxon adopts to overcome multidimensional stoichiometric mismatches under natural conditions in the field, needs further investigations.

## 4.3 | Forest plantations affect detritivore populations due to lifted stoichiometric mismatches

Sixty-year forest plantations caused significant changes in biomass and density of detritivores without affecting their stoichiometry, supporting our second hypothesis and corroborating previous findings that invertebrates adapt to environmental conditions by changing community composition rather than their body stoichiometry (González et al., 2018; Jochum, Barnes, Ott, et al., 2017). The present study revealed large variations in the population size of detritivores across three forest types (from fewer than a dozen to >300 individuals per square meter), which is partially accounted for by stoichiometric mismatch and litter quality, but not litter quantity. In particular, pine plantations provided the lowest quality of litter, causing the severest mismatches in almost all nutritional elements for both earthworms and millipedes. Although pine plantations had a larger litter biomass than oak forests and larch plantations, the higher litter quantity did not compensate its lower quality in supplying resources for detritivores. It is worth noting that our analyses were based on observational data and correlation analyses. Experiments



are needed to test the causal relationship between stoichiometric mismatch and detritivore biomass.

Our results agree with previous studies that reported the multidimensional stoichiometric limitation of litter on soil animal abundance (Jochum, Barnes, Weigelt, et al., 2017; Kaspari & Yanoviak, 2009; Ott et al., 2014). These studies interpreted the stoichiometric limitations based on different hypotheses, for example, limitation by N and Ca from the structural elements hypothesis, and limitation by P and Na from the secondary productivity and sodium shortage hypotheses. However, due to the lack of stoichiometric data of soil animals, these conclusions remain speculative and may have underestimated the explanatory power of the structural element hypothesis (González et al., 2017; Zhang, Chen, Deng, Li, González, et al., 2022). By revealing the elemental contents of two detritivore taxa and their litter resources, we found that P and Na—even though low in absolute body contents—might also influence detritivore biomass and density due to high TSR values. Thus, a single element may affect the same consumer through multiple processes (Kaspari & Yanoviak, 2009). Moreover, we found that elements showing the highest TSR values were largely consistent with those elements in litters (represented as C:X ratios) that best explained detritivore biomass and/or density, for example, Na, N and P for earthworms, and N, Ca, Cu, Mn, Na and Zn for millipedes. Even though the contents of Ca and K were higher than Na in earthworms and the contents of Mg and K were higher than Cu, Mn, Na and Zn in millipedes, they contributed less in explaining the biomass or density of the respective taxon. This suggests that the framework of multidimensional stoichiometric mismatch, which accounts for both resources and consumers, provides a useful tool to understand variation in consumer population size.

Importantly, our study suggests that forest plantations had different impacts on the biomass of earthworms and millipedes, due to their different degrees of stoichiometric mismatch. In our study sites, millipedes experienced overall higher TSR values in most elements (except N, Na and K) than earthworms, and thus larger changes in biomass and density after forest plantations. Earthworms and millipedes are 'trophic whales' in soil food webs, hampering energy transfer to higher trophic levels due to large body sizes or calcified cuticles (Potapov et al., 2019; Schwarzmüller et al., 2015). Our study further reveals their specific functions in storing different amounts and combinations of essential elements within the detritivore level (e.g. ~8%–13% N in earthworms and ~2%–3% P and ~17% Ca in millipedes), and in hampering element transfer to soil food webs due to contrasting TSR values of different elements. Integrating multidimensional stoichiometric characteristics and population biomass of detritivores thus advances understanding of the storing and cycling of elements across soil food webs under environmental changes.

## 5 | CONCLUSIONS

Our study demonstrates significant impacts of forest plantations on the population sizes of two major detritivore groups (i.e. earthworms

and millipedes) by driving trophic stoichiometric mismatch between detritivores and their litter resources. Conversion of natural forests into plantations alters litter quality and leads to different patterns of stoichiometric mismatch. In particular, pine plantations had lower litter quality and thus severer stoichiometric mismatches compared to oak forests and larch plantations. Despite the decreased litter quality, detritivores retained their body elemental contents, but experienced decreasing population sizes in pine forests. In line with the multidimensional stoichiometric niche framework, our study showed that in addition to N and P, other elements such as Ca, Cu, Mn, Na and Zn may also affect the growth and population size of detritivores. Our study illustrates the application of the framework of multidimensional stoichiometric niche for understanding the impacts of human activities such as forest plantations on animal population dynamics. We thus advocate the multidimensional stoichiometry framework as a useful tool for predicting the response of population dynamics and ecosystem elemental cycling to anthropogenic environmental changes.

## AUTHOR CONTRIBUTIONS

Bing Zhang and Shaopeng Wang conceived the idea and designed methodology; Bing Zhang, Haozhen Chen, Mingqin Deng and Xin Li collected the data; Bing Zhang analysed the data; Bing Zhang, Ting-Wen Chen and Shaopeng Wang led the writing of the manuscript. Lingli Liu and Stefan Scheu contributed critically to the revision.

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## CONFLICT OF INTEREST

The authors declare no competing interests.

## DATA AVAILABILITY STATEMENT

The data associated with this paper are available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.8w9ghx3r1> (Zhang, Chen, Deng, Li, Chen, et al., 2022).

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## SUPPORTING INFORMATION

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

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