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Detritivory: stoichiometry of a neglected trophic level

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Abstract Previous syntheses have identified the key roles that phylogeny, body size, and trophic level play in determining arthropod stoichiometry. To date, however, detritivores have been largely omitted from such syntheses, despite their importance in nutrient cycling, biodiversity, and food web interactions. Here, we report on a compiled database of the allometry and nutritional stoichiometry (N and P) of detritivorous arthropods. Overall, both N and P content for detritivores varied among major phylogenetic lineages. Detritivore N content was similar to the N content of herbivores, but below that of predators. By contrast, detritivore P content was independent of trophic level. Contrary to previous reports, neither nutrient varied with body size. This analysis places detritivores in the context of related herbivores and predators, and as such, sets the stage for future investigations into the causes and consequences of elemental (mis)matches between detritivores and their detrital resources.

Keywords Detritivory · Ecological stoichiometry · Body nitrogen content · Body phosphorus content

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Introduction

Recent syntheses have yielded insight into the nature and extent of stoichiometric variation in terrestrial, marine, and freshwater autotrophs (Elser et al. 2000, 2007), and terrestrial arthropods, especially insects (Fagan et al. 2002; Denno and Fagan 2003; Woods et al. 2004). It is now clear that both herbivorous (Fagan et al. 2002; Elser et al. 2000) and predaceous arthropods (Fagan and Denno 2004) are limited by the nitrogen (N) and phosphorus (P) content of their food resources in primary producer-based food webs. Stoichiometric variation may be linked to differences in growth rates and nutritional requirements (Elser et al. 2003) or differential allocation to body resource pools (Fagan et al. 2002). To complement ecologists' growing understanding of the nutritional demands of terrestrial insects and other arthropods, we focus here on the elemental stoichiometry of detritivorous species, a group that has been excluded from prior stoichiometric syntheses (Denno and Fagan 2003; Fagan et al. 2002).

Detritivores have evolved to obtain their nutrient resources from senescent plant tissue, animal waste products, and carcasses of dead animals. Because many organisms have elaborate tactics for reabsorbing and retaining limiting nutrients before senescence (plants; Killingbeck 1996; Nooden et al. 1997) or excretion of wastes (animals; Anderson et al. 2005), detritus-based systems are widely considered to be extremely nutrient-limited, i.e., with a low N and P concentration. Such nutrient limitation may impose severe constraints on detritivores (Cross et al. 2003), thereby increasing the importance of stoichiometric imbalances in detritus-based systems compared to primary producer-based food webs (Moe et al. 2005).

In this paper, we seek to characterize the elemental stoichiometry of detritivorous arthropods, focusing on body N and P. Using databases of detritivores compiled from diverse sources, we perform phylogenetic-comparative tests for variation in the body N and P content

of detritivorous arthropods in comparison with published data for herbivores and predators.

Methods

Using 20 published and unpublished sources, we obtained data on arthropod nutrient content (N, $n = 49$; P, $n = 68$). When multiple observations were available for a single species, they were averaged prior to analysis. In all, stoichiometric data were available for representatives of 12 taxonomic orders (Acari, Chordeumatida, Amphipoda, Isopoda, Collembola, Ephemeroptera, Orthoptera, Plecoptera, Coleoptera, Hymenoptera, Trichoptera, and Diptera). We also obtained data on adult body length (mm) or body mass (mg). The complete dataset, which includes source references, is posted at <http://www.nceas.ucsb.edu/ecostoichiometry>.

For all comparative analyses, we used a modification of the method of generalized least squares (GLS; Martins and Hansen 1997), implemented in R using the package *ape* (Paradis et al. 2004). Rather than assuming that species values are drawn from independent and identical distributions, as in ordinary least squares analysis, GLS methods allow species to be drawn from distributions with different variances. However, these variances are assumed to covary according to the phylogenetic distance separating them. The shape of the decay in species correlation with phylogenetic distance can be modelled according to different assumptions about the underlying evolutionary process. We assumed that species correlations dropped off exponentially with phylogenetic distance, typical of traits under stabilizing selection (Hansen and Martins 1996). The main alternative model is linear decay of species correlations arising from the Brownian model of evolution, typical of random drift or fluctuating directional selection. This is assumed implicitly by the related method of independent contrasts (Felsenstein 1985; Garland et al. 1992). Linear decay explained less variance in the response variable than exponential decay in all our analyses, as determined by Akaike's Information Criterion (AIC; Crawley 2007, data not shown).

To describe species relationships, we built a composite phylogeny to family level, using the following published phylogenies: Wheeler et al. (2001, Hexapoda); Caterino et al. (2002), Shull et al. (2001) and Hunt et al. (2007, Coleoptera); Yeates et al. (2006, Diptera); Maddison and Schulz (2007, other taxa). Below family level, we used a multifurcating phylogeny based on taxonomic classification at the subfamily and genus levels. To reflect lack of branch lengths, two models were tested against the data: setting all lengths to 1, or scaling them according to taxonomic depth (Grafen 1989) using the `compute.brLen()` function in the *ape* package. In all cases using branch lengths of 1 explained more variance in our data, so this method was used throughout (data not shown).

We fitted GLS models fully to begin with, and used likelihood ratio tests sequentially to determine which terms and interactions to retain in the minimal model. Once the minimal model was obtained, planned contrasts were carried out between factor levels. The significance threshold for non-orthogonal contrasts was adjusted downwards using the Dunn–Sidak correction (Crawley 1993).

First, we asked whether our sample of detritivores ($n = 49$) differed in body N content from predators and herbivores, which we obtained from the dataset of Fagan et al. (2002; 34 predators, 116 herbivores). In keeping with Fagan and colleagues, we also included body length, a known correlate of body stoichiometry for some nutrients (Woods et al. 2004). Hence, the model fitted was of the form ($N \approx$ trophic level \times body length). Identical analysis for detritivore P content ($n = 68$) was carried out using the dataset of Woods et al. (2004; 55 predators, 77 herbivores). For this analysis, subfamily level taxonomy was omitted owing to lack of taxonomic resolution in the Woods et al. dataset. In keeping with Woods and colleagues, dry body mass was used as an index of body size.

Results

Within detritivores, mean (\pm SE) detritivore body N and P were 10.25 ± 0.13 and $0.81 \pm 0.03\%$, respectively. Detritivore stoichiometry was highly variable across taxa, ranging from 5.00% (Isopoda: *Armadillidium vulgare*) to 13.53% (Paleoptera: Heptageniid morpho-species) in N and 0.15% (Trichoptera: *Lepidostoma* sp.) to 1.62% (Diptera: *Drosophila hydei*) in P. Notably, crustaceans (Isopoda, Amphipoda) had relatively low %N compared to other detritivores, as did millipedes (Diplopoda), a group which also appears to be characterized by high %P. For detritivores, no general trend was evident across the phylogeny (Fig. 1).

Combining our data with the published results of Fagan et al. (2002), arthropod body N had a grand mean of $10.01 \pm 0.12\%$, but differed among trophic levels (GLS, dropping “trophic level”, likelihood ratio [LR] = 8.02, $\Delta df = 2$, $P \approx 0.01$, Fig. 2). Among trophic levels, herbivores and detritivores did not differ (detritivores, $10.13 \pm 0.33\%$; herbivores, $9.64 \pm 0.36\%$; planned contrast, $P = 0.18$, NS), but predators were higher in N than both herbivores and detritivores [predators, $10.81 \pm 0.39\%$; planned contrast, $P < 0.01$, significant after the Dunn–Sidak correction for non-orthogonality (adjusted threshold = 0.016)]. N varied neither with body length (dropping “body length,” LR = 0.41, $\Delta df = 1$, $P = 0.52$), nor its interaction with trophic level (dropping “length \times trophic level,” LR = 0.98, $P = 0.62$). Body P, combined with the Woods et al. (2004) data, had a grand mean of $0.80 \pm 0.02\%$ and did not vary with trophic level (dropping “trophic level,” LR = 2.77, $\Delta df = 2$, $P = 0.25$), body mass

Fig. 1 Mean (\pm SE) body N (light bars) and body P (dark bars) of detritivorous arthropods. Taxa are represented by their first four letters (Amphipoda, Isopoda, Diplopoda, Acari, Collembola, Paleoptera, Lower Neoptera, Coleoptera, Hymenoptera, Panorpida) and are arranged from most ancestral (left) to most derived (right); basal phylogeny is given for comparison. Panorpida includes representatives of Diptera and Trichoptera. Lower Neoptera includes representatives of Orthoptera and Plecoptera

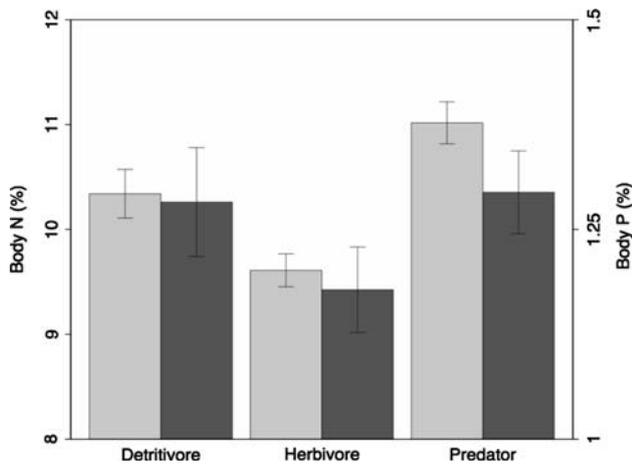
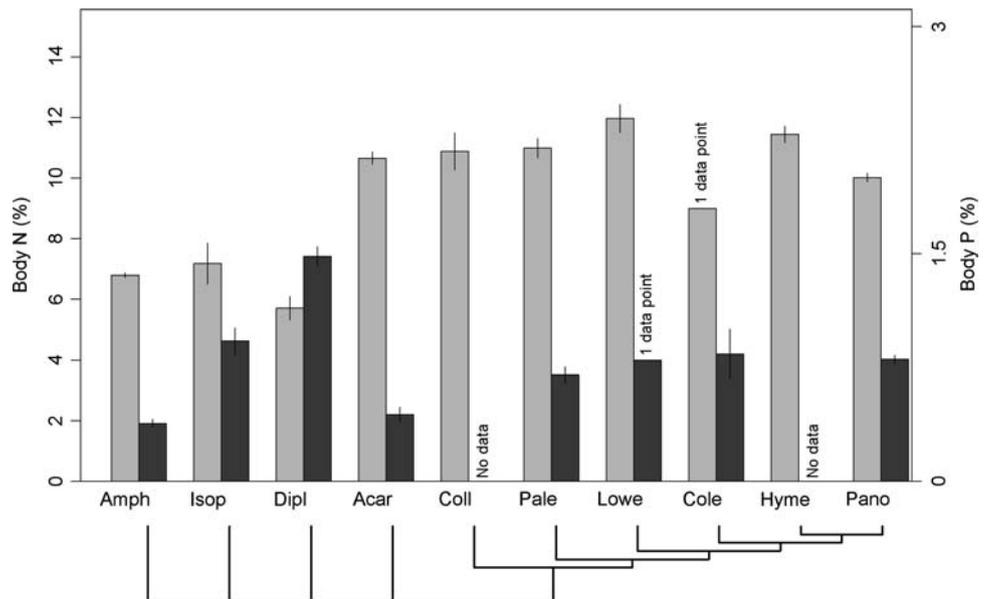


Fig. 2 Mean (\pm SE) body N (light bars) and body P (dark bars) for detritivores compared to herbivores and predators. Data for herbivores and predators are from Fagan et al. (2002, N) and from Woods et al. (2004, P)

(dropping “body mass,” $LR = 2.12$, $\Delta df = 1$, $P = 0.15$), or with their interaction (dropping “trophic level \times body mass,” $LR = 3.26$, $\Delta df = 2$, $P = 0.20$).

Discussion

Detritivory occurs across many major arthropod lineages (Fig. 1). Detritivorous Acari had high %N, consistent with previous findings that other arachnids (e.g., spiders, pseudoscorpions) have high body N content (Fagan and Denno 2004). Detritivorous Collembola had high %N, supporting the prediction (Fagan et al. 2002) that this group would have high %N because they tend to accumulate rather than excrete N over their lifetimes. On the other hand, the millipedes (Diplopoda) and crustaceans

(Isopoda, Amphipoda) had the lowest body N content of all taxa. These low %N values may be due to the damp or wet habitats in which these groups are found, which could relax the need for thick, N-rich cuticles and result in lowered overall body N (Davidson 2005; Klowden 2002; Sterner and Elser 2002). The very high %P in the Diplopoda provides a striking contrast with other detritivores (Fig. 1) and with terrestrial arthropods in general (Woods et al. 2004). The source and ecophysiological implications of this P enrichment are the subject of ongoing research focusing on the ways in which nutritional constraints can influence adaptation in limiting environments (Schneider et al., in preparation).

Detritivore body N was similar to that of herbivores, but lower than that of the predators published in Fagan et al. (2002). This mirrors what we know about the stoichiometry of the resources that these groups of consumers use (Sterner and Elser 2002; Denno and Fagan 2003), and hence supports the idea that consumer N is at least partially driven by resource quality. By contrast, detritivore body P was not different from the results for either herbivores or predators published in Woods et al. (2004), consistent with the idea that across very broad trophic groups, body P may be relatively independent of resource quality.

If arthropods in general are more N- than P-limited, as suggested by White (1993), then we might expect to see the observed difference in N, but relative constancy of P across trophic levels. If N is limiting, arthropods should conserve and retain this element, and ultimately reflect the differences in uptake potential due to variation in their resources (Boersma and Kreutzer 2002). Likewise, if P is not limiting, then an individual arthropod can take what it needs and excrete the rest. The result in this situation would be no differences across trophic levels despite differences in P intake from resources.

Body size was not a predictor of body N or P across the detritivores we considered. This is somewhat surprising because previous studies have reported such allometric relationships. For example, Cross et al. (2003) found that N and P decreased with body size among collector-gatherers and collector-filterers in detritus-based streams. Fagan et al. (2002) found that the body N of a diverse sample of insect taxa scaled positively with size in predators, but not in herbivores, whereas Davidson (2005) found that both predatory and herbivorous ant species showed allometric scaling of %N. Moreover, %P scales negatively with body size across many taxonomic orders of insects regardless of trophic group (aquatic detritivores, Cross et al. 2003; predators and herbivores, Woods et al. 2004). Our analysis also includes terrestrial detritivores, which may be sufficiently diverse in stoichiometry to obscure any allometric trend. Alternatively, the lack of allometric scaling among detritivores observed here may be related to the coarse taxonomic resolution of many of the species in our database, which limited the allometric analysis to a subset of the data. Indeed, where length data were available for many specific taxa within an ordinal group (Diptera), we do find a negative scaling of %P with body size, a pattern that will be discussed in detail elsewhere (Hambäck et al., in preparation).

A better understanding of the actual feeding ecology of detritivores will be necessary to fully interpret the variation we have documented here. In particular, given the wide variety of materials that constitute detritus (dead plant parts, animal carcasses, animal waste products), it seems necessary to explore the relative stoichiometry of detritivores and the specific detrital materials that they consume. For example, those species feeding on fungus or bacteria are likely to have higher quality food resources and thus potentially higher N and P content than those more directly feeding on leaf litter. Unfortunately, the majority of studies included in our review have not performed such fine-scale investigations into detritivore feeding ecology, making it difficult to match consumer–resource stoichiometry on a pairwise basis.

Additional research on the potential stoichiometric (mis)matches of detritivores and their resources is warranted because detritivores critically influence the efficiency of nutrient cycling in both aquatic and terrestrial environments (Cebrian 1999) and provide a critical bridge between the green and brown components of food webs (Moore et al. 2004, Shurin et al. 2006). Further progress on these issues may be most easily addressable in detritus-dominated systems (such as caves, desert islands, and phytotelmata) where the specific feeding ecology of arthropod detritivores may be more directly studied in connection with their resources.

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