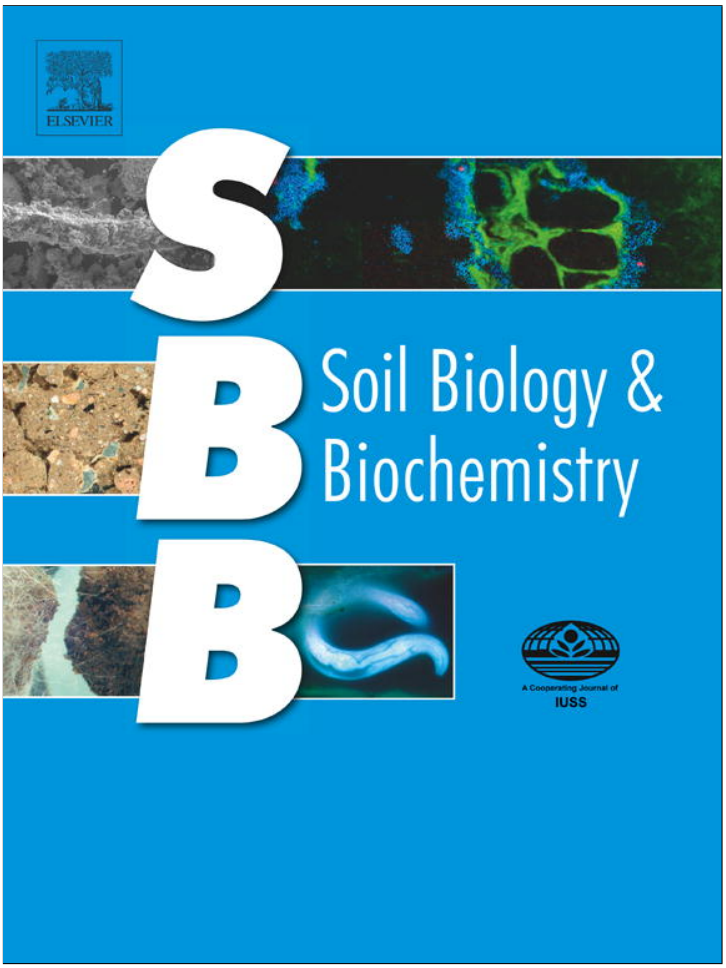

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Mouthpart morphology and trophic position of microarthropods from soils and mosses are strongly correlated

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ABSTRACT

Mosses provide habitat for microarthropod communities that are dominated in abundance and richness by mites. Although these systems are used as experimental models to address questions of relevance to general ecology, and despite the fact that they are also of relevance to key, ecosystem-wide functions such as nutrient cycling rates, the trophic relationships that underpin these functions are poorly resolved. The complexity of the moss habitat matrix and the small size of its residents have hampered progress in the determination of diets. We use stable isotope analysis of moss communities and present tools that allow for more in-depth studies of food web structure in mosses and soils than are currently available. We test in mites for the first time the association between mouthpart morphology and isotope signatures. Isotopes capture the diet of mites under field conditions and over a longer time-span than traditional, snapshot measures of diet such as gut contents analyses. Our data suggest that cheliceral morphology can be used as a first inexpensive and quick filter for estimation of dietary preference in mites, with ambiguous trophic relationships resolved through isotope analyses. This work provides new information and tools for the study of mite-dominated food webs.

1. Introduction

Mosses provide habitat for microarthropod communities that are dominated by mites, and in particular oribatid mites (Lindo and Gonzalez, 2010). Mosses have been shown to be of relevance to key, ecosystem-wide functions such as nutrient cycling rates (Turetsky, 2003), and these systems have been used as experimental models to address questions of relevance to general ecology (Gonzalez et al., 1998; Staddon et al., 2010; Starzomski and Srivastava, 2007). Despite this importance and these applications, the trophic relationships that may underpin such functions are still poorly resolved. This lack of detailed knowledge restricts our understanding of how these systems operate and limits our predictive capacity with regards to the effects of disturbances and of major environmental stressors such as climate change. Developing tools to estimate measures of food web structure in these systems, such as species richness per guild and total biomass, is of clear importance.

Many techniques have been applied to the study of dietary preferences in mites, each with notable strengths and weaknesses. Determination of diet has traditionally been hampered by mites' small size and the difficulty of carrying out field observations. Researchers attempting to determine mite diets through gut content analysis can report a large proportion of "indeterminate material" (Fashing, 1998). Where contents of the gut are identifiable, it can be unclear if the ingested items would eventually have been assimilated into biomass or excreted undigested. It is also doubtful that the snapshot nature of gut content surveys reflects longer-term dietary preferences. Although laboratory experiments of food choice have provided insights into dietary preferences of certain mite species, they are fraught with difficulty in supplying the appropriate choices and quantifying food consumption (e.g. Schneider and Maraun, 2005), and they may not reflect feeding preferences in the field.

Stable isotope techniques have recently enabled useful, time-integrated measurements of field diet in mites (Pollierer et al., 2009; Schneider et al., 2004), and have allowed the assignment of oribatid mites to feeding guilds. However, the minimum mass of mites required to perform these studies, as well as their cost, limit the number of species that can be subjected to such analyses. Most

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studies using the moss–microarthropod system as a model encounter more than 100 mite morphospecies, and family or even genus are equivocal proxies for diet where the diet of species of the same family or genus is actually known (Schneider et al., 2004). While an association between mite mouthpart morphology and diet has been suggested (Krantz and Lindquist, 1979) and studied (Buryn and Brandl, 1992; Kaneko, 1988), the data with which to compare the morphology has suffered from the pre-isotope limitations described above. Additionally, a detailed understanding of cheliceral functional morphology has only recently become available through synchrotron technologies (Heethoff and Norton, 2009). Here we integrate the information that has become available through these new techniques in order to assess whether cheliceral morphology is associated with long-term, field preferences in diet as indicated by isotope signatures. We carry out stable isotope analysis of moss communities in concert with analysis of mite chelicerae, and present tools that allow for more in-depth studies of food web structure in mosses and soils than are currently available.

2. Methodology

Two sample sets were used to study (a) isotope signatures of moss faunal communities, and (b) the association in mites between position on the food web and cheliceral morphology. Specifications of the samples used can be found in Table 1.

2.1. Stable isotope analysis

Moss (*Dicranoloma billiardieri*) samples were collected in July 2009 in the Yarra Ranges National Park, Victoria, Australia (37°29′ S 145°49′ E, 800 m, permit number 10004595 of the Department of Sustainability and Environment, State Government of Victoria, Australia). This site is a cool temperate rainforest dominated by Mountain Ash (*Eucalyptus regnans*) and Myrtle Beech (*Nothofagus cunninghamii*) trees. Fauna was extracted into 70% ethanol using Tullgren funnels and stored. Preservation in ethanol can affect carbon signatures; however these effects can be expected to be minor, directionally uniform and consistent across taxa within the timeframe considered here (Hobson et al., 1997; Sarakinos et al., 2002). The fauna included velvet worms, pseudoscorpions, slaters, spiders, springtails and mites (Table 1). Samples were sorted to morphospecies and oven-dried for 24–48 h at 60 °C. In order to obtain the minimum mass required for analysis (0.01 mg), 10 to 41 individuals per mite morphospecies were necessary. Samples were weighed after drying and sent for isotope analysis by Griffith University. Isotope content was analysed using a continuous flow-isotope ratio mass spectrometer (Europa Tracermass and Roboprep, Crewe, England). Ratios of $^{13}C/^{12}C$ and $^{15}N/^{14}N$ were expressed as the relative per mill (‰) difference between the sample and conventional standards (PeeDee Belemnite carbonate and N_2 in air), where $\delta X = (R_{sample}/R_{standard} - 1) \times 1000(‰)$, $X = {}^{13}C$ or ^{15}N and $R = {}^{13}C/{}^{12}C$ or $^{15}N/^{14}N$. Potential basal resources for the food web (fern fronds, Mountain Ash leaves, Myrtle Beech leaves and bark in different stages of decomposition, moss, lichen, fungus) were analysed in the same facility after being washed with distilled water, oven-dried and pulverized with a Retsch Mixer Mill MM301.

Estimation of the proportion of the sampled food sources that were likely to account for the isotope signature of non-predatory species was carried out by fitting Bayesian mixing models to the signatures using the package SIAR (Parnell et al., 2010) in R Statistical Package (RDCT, 2009). Models were run 30,000 times, without priors for the proportion of food sources and with no isotope concentration dependence. Mean and standard deviation of the isotope signatures for moss, bark, litter (all species pooled) and lichen were used for modelling. Due to the lack of replication of the fungal signature, the standard deviation of the litter signatures was assigned to this resource. Two sets of trophic enrichment factors (TEFs) were fitted separately in order to determine the effect of changing these on the estimation of proportions of food sources in the diets. TEFs indicate the difference in the isotope value of a consumer relative to its food source. The first set of TEFs considered in this study (Fig. 1, left) was based on the enrichment factors considered applicable for other food webs (Post, 2002). The second set of TEFs used (Fig. 1, right) takes into consideration observations by Pollierer et al. (2009), who found that the cellulose component of litter was highly enriched in ^{13}C relative to other components. The authors proposed that the large differences observed in ^{13}C signatures between bulk litter samples and all the soil fauna sampled could possibly be accounted for by selective digestion and assimilation of carbon from cellulose. Low ^{15}N enrichment was also reported in that study.

2.2. Cheliceral measurements

The following oribatid mite species were collected from the study site where Schneider et al. (2004) carried out their isotope determination (Göttinger Wald, Germany): *Paradamaeus clavipes*, *Hypodamaeus riparius*, *Nothrus palustris*, *Chamobates voigtsi*,

Table 1
Summary of invertebrate material examined and the analyses performed on it.

Country of origin	Habitat type	Taxon	Number of morphospecies	Analyses performed	
				Cheliceral shape	Stable isotopes
Australia	Moss	Arachnida			
		Acari – Oribatida	11	✓	✓
		Acari – Mesostigmata	2	✓	✓
		Acari – Prostigmata	1		✓
		Pseudoscorpiones	1		✓
		Aranae	1		✓
		Insecta			
		Coleoptera	3		✓
		Homoptera	1		✓
		Collembola	9		✓
		Crustacea			
		Isopoda	1		✓
		Onychophora	1		✓
Germany	Litter	Arachnida			
		Acari – Oribatida	12	✓	✓[a]

[a] The stable isotope analysis on German mites was carried out by Schneider et al. (2004).

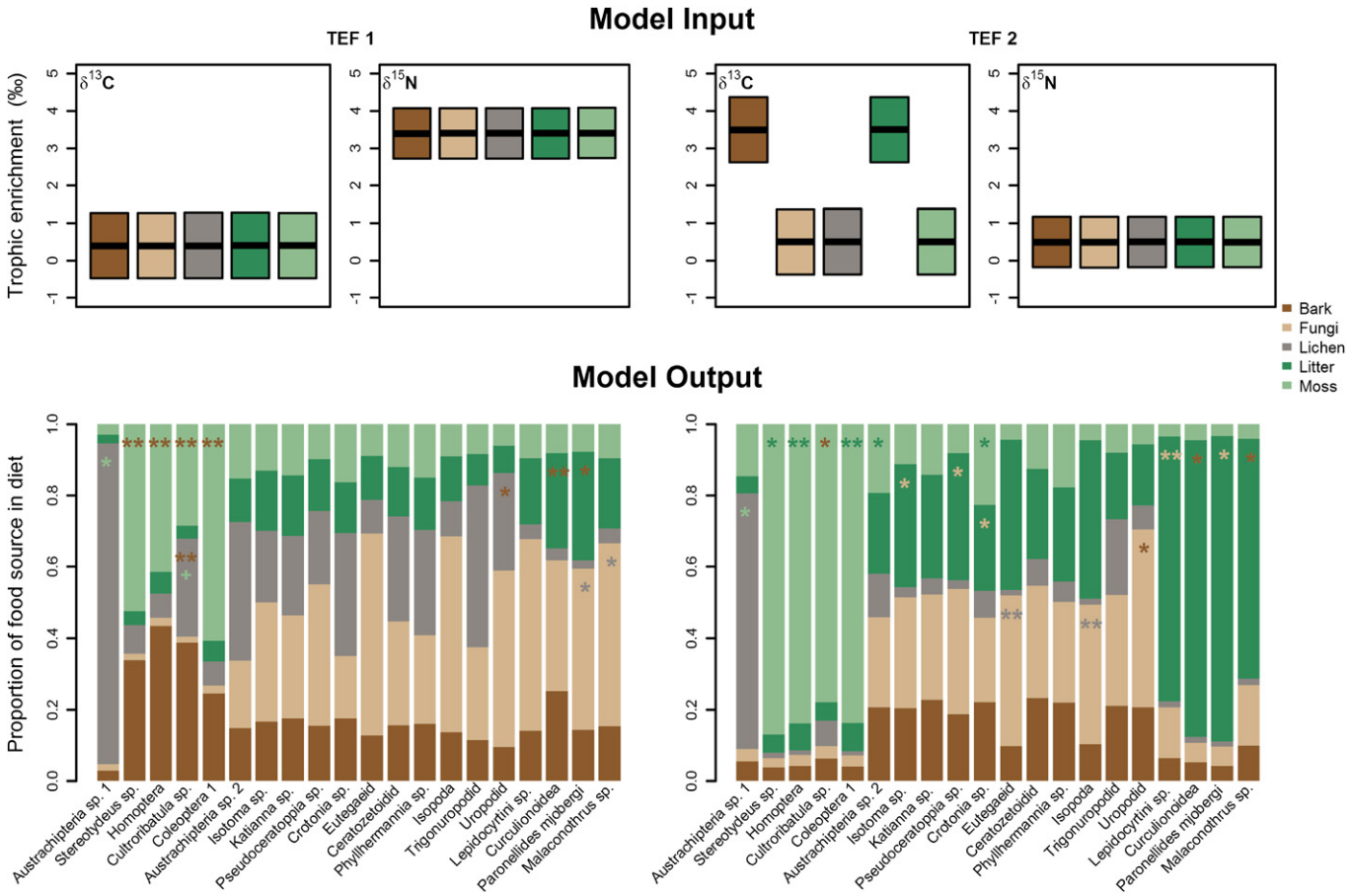

Fig. 1. Two sets of trophic enrichment factors (TEF1 and TEF2) used in Bayesian modeling, and resulting estimated proportion of food sources in non-predatory species' diets (Australian samples only). Symbols inside the bars indicate correlation between the estimated proportions of food sources. Positive correlation: "+". Negative correlation with index smaller than −0.7: "**". Negative correlation with index between −0.5 and −0.69: "*".

Chamobates cuspidatus, *Chamobates borealis*, *Oribatula tibialis*, *Hypochthonius rufulus*, *Platynothrus peltifer*, *Tectocepheus velatus*, *Amerus troisii*, *Achipteria coleoptrata* and a phthiracarid species. The feeding guilds reported in that paper via stable isotope analysis of basal resources and fauna were used to compare with cheliceral dimensions. Their guilds were: secondary decomposer (predominantly feeding on fungi and partly on litter), primary decomposer (predominantly feeding on litter little colonized by fungi and bacteria), and carnivores/scavengers/omnivores. An additional eleven oribatid morphospecies were used for this analysis from the Australian samples collected for this study as described above; feeding guilds were ascribed on the basis of the isotopic signature determined here.

Mites were dehydrated and placed on a microscope slide with double-sided tape to facilitate extraction of chelicerae under a stereoscopic microscope using fine tweezers. Dehydration was achieved by washing the specimens in 90% ethanol for 5 min, 95% for 5 min, 100% for 15 min twice, and dry 100% ethanol for 15 min. Extracted chelicerae from one to five specimens were placed on microscope slides and cleared of internal tissue by adding 80% lactic acid and heating at ~60 °C for 15 min. Cleared chelicerae were photographed at 40× with a compound microscope and measurements were taken from the images using Motic Images Plus (Motic China Group Co. LTD).

Cheliceral dimensions taken are outlined in Fig. 2. Potential of the first-class lever formed by the movable digit to crush food items against the principal segment (Heethoff and Norton, 2009) was estimated as the ratio between maximum height of the movable digit (MH) and its length (ML) (Fig. 2), under the assumption that taller digits (per unit length) were likely to have a longer distance from the fulcrum to the levator tendon attachment (effort arm) than sleeker digits. The bouquet shape of the levator muscle that lifts the movable digit and occupies most of the principal segment (Heethoff and Norton, 2009) complicates the estimation of the cross-sectional area of this muscle and therefore of its capacity, especially where only a two-dimensional image is available (as in Fig. 2). We estimated this cross-sectional area as the square of the maximum height of the principal segment (PH^2). Statistical analyses were performed in the software package R (RDCT, 2009). Principal components analysis (PCA) was carried out on all five cheliceral measurements. Species' scores along principal component axes two and three (PC2 and PC3) were used to perform single factor analyses of variance with feeding guild as a predictor variable (the lichenivorous guild was not included as it was represented by a singlemorphospecies). Tukey's post-hoc tests were performed to compare scores among feeding guilds. PC1 scores were not used as the axis was constructed with negative loadings of similar magnitude for all measurements, suggesting scores would be highly influenced by variability in size rather than shape.

3. Results

3.1. Stable isotope analysis

Groups of potential food sources for the faunal communities in moss differ in their isotope signatures, with lichens being severely

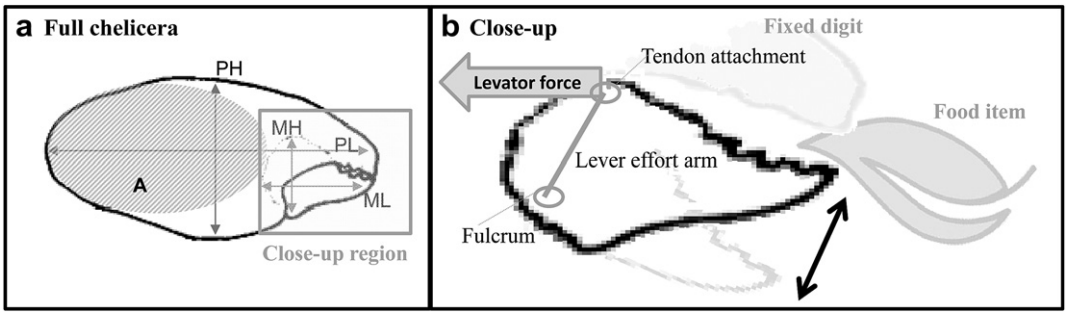

Fig. 2. a) Cheliceral measurements used in this study. PL: principal segment length. PH: principal segment height. ML: Movable digit length. MH: Movable digit height. A: shaded area, area available for the levator muscle of the movable digit. b) Schematic representation of cheliceral functional morphology (based on Heethoff and Norton, 2009).

depleted in ^{15}N and enriched in ^{13}C, moss, litter and bark being relatively high in ^{15}N and low on ^{13}C, and the fungus being relatively high for both isotopes (Fig. 3). Moss signatures were lower in ^{15}N than those of litter. The fauna spans 14.4‰ $\delta^{15}N$ and 9.5‰ of $\delta^{13}C$, with most taxa presenting ^{13}C signatures more than 3.5‰ higher than those of plants. The nitrogen signatures of one mesostigmatid (*Gamasellus* sp.) and one oribatid mite (*Lanceoppia* sp.) were as high as that of assumed top predators in the system (velvet worms, pseudoscorpions, spiders). Carbon and nitrogen signatures of *Austrachipteria congenerics* differed markedly, with one species presenting a signature intermediate between lichen and litter/bark/moss, and another similar to that of fungi. The carbon and nitrogen signatures of the prostigmatid mite (*Stereotydeus* sp.) were similar to that of moss.

Diet estimations were affected by the choice of trophic enrichment factors. The estimated proportion of litter in non-predatory mite species' diets was higher when trophic enrichment of carbon from this source was fitted as having a mean of 3.5 rather than of 0.5 (TEF set 2 vs 1, Fig. 1). Conversely, the estimated proportion of lichen and fungi in the diet was higher with TEF set 1 than 2. Overall differences in diet among four groups of species were found, and these were maintained regardless of change in trophic enrichment factors (Fig. 1, group 1 *Austrachipteria* sp. 1, group 2: from *Stereotydeus* sp. to Coleoptera, group 3: from *Austrachipteria* sp. 2 to Uropodid, group 4: *Lepidocyrtini* sp. to *Malaconothrus* sp.).

The diet estimations of *Stereotydeus* sp., *Cultroribatula* sp., Coleoptera 1 and Homoptera changed considerably depending on the trophic enrichment factors used. The TEF set with a mean 3.4‰ enrichment of nitrogen (Fig. 1, TEF1 compared to 0.5‰ in TEF2) resulted in lower estimated proportions of moss in their diets, and higher proportions of bark (around 40% bark, a source with a less-enriched nitrogen signature). There was evidence of a strong negative correlation between the estimated proportion of bark and moss in the diets using TEF1; bimodal distributions in the estimated proportions for the sources were found (data not shown).

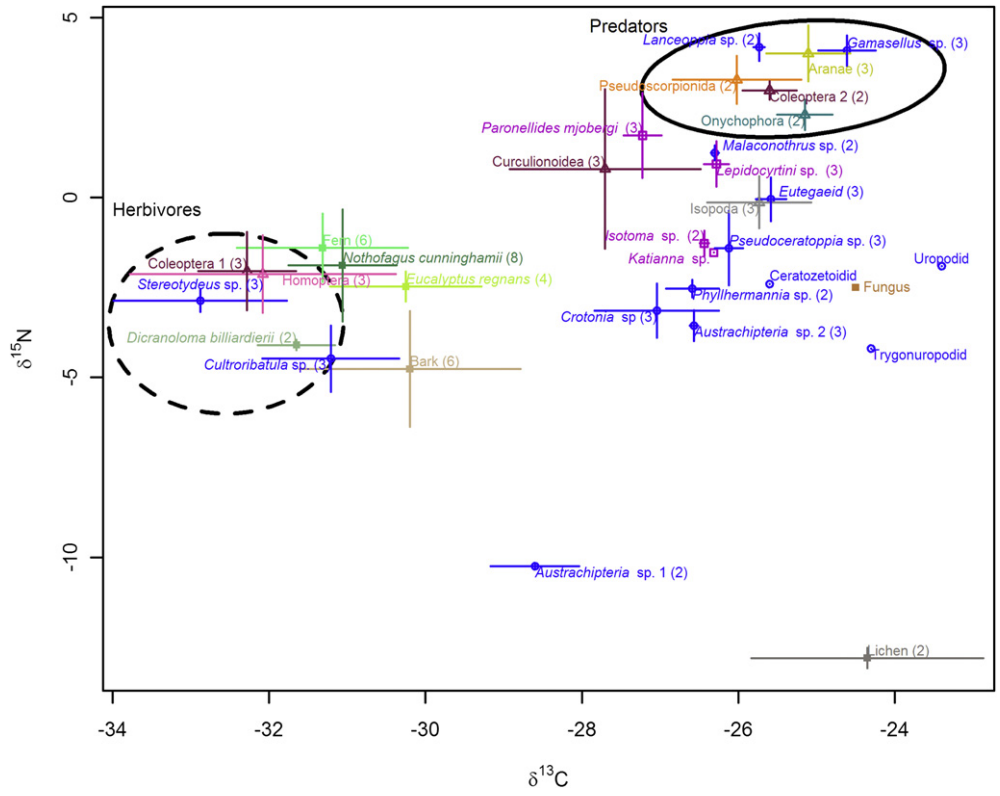

Fig. 3. $\delta^{13}C$ and $\delta^{15}N$ values of moss-dwelling fauna and its potential basal food sources (Australian samples). Blue: mites. Violet: collembolans. Other colours indicate other animal taxa and food sources. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

These negative correlations indicate that diet estimation iterations that included one food source (e.g. moss) tended to exclude the other (e.g. bark) in order to account for the species' isotope signature, i.e. the sources were found to be interchangeable. Strong negative correlations were also found between litter and moss for known herbivorous taxa (Homoptera, Coleoptera) using TEF2.

3.2. Association between mouthpart morphology and isotope signatures in oribatids

A large proportion of the variability in cheliceral shape (85%) was accounted for along a single axis (PC1) constructed through transformations of all the measurements taken (negative loadings for all variables in the PCA), implying a high degree of correlation between the variables that is likely attributable to overall differences in size of the chelicerae. PC2 and PC3 captured 10 and 5% of the variability respectively. Feeding guild is associated with cheliceral morphology (ANOVA on PC2 scores, $F_{2,19} = 11.715$, $p < 0.001$; Tukey's post-hoc $p < 0.05$ except between primary and secondary decomposers; ANOVA on PC3, $F_{2,19} = 9.22$, $p < 0.05$; Tukey's post-hoc $p < 0.05$ except between carnivores and secondary decomposers). Removal of mesostigmatid mites from the analysis (reduction of the sample size in the carnivorous guild to three) reduced the variability explained by PC2 and PC3 to 5 and 2% respectively. Significance of comparisons using PC2 scores was unaltered. PC3 scores were not significantly different across guilds without mesostigmatids in the analysis.

Leverage and estimated cross-sectional area of the levator can be used in conjunction to differentiate between guilds with higher accuracy than each measure would provide independently (Fig. 4). Carnivorous/omnivorous/scavenger mites have chelicerae that have a low leverage index and little space for levator muscles. Primary decomposers generally have chelicerae with a high leverage index, and an estimated cross-sectional area smaller than 2000 μm^2. The pthiracarid mite is an exception to this general pattern, with its chelicerae showing the second largest area of all species. Chelicerae of secondary decomposers (feeding mostly on fungi) generally have a large cross-sectional area (higher than 2000 μm^2) and a leverage index between 0.5 and 0.7. A correlation between the estimated levator cross-sectional area and mite body size was found (Appendix 1, Fig. 1, $p < 0.05$, $R^2 = 0.3752$). Leverage did not show an association with logarithm of body size (Appendix 1, Fig. 2, $p = 0.67$).

4. Discussion

Bryophytes can play important roles in key, ecosystem-wide functions such as nutrient cycling rates (Turetsky, 2003). Despite some functional understanding of moss ecosystems (Lindo and Gonzalez, 2010), and the use of moss microarthropod food webs as ecological models (Gonzalez et al., 1998; Staddon et al., 2010; Starzomski and Srivastava, 2007), food web structure has not been described in detail. This is also largely true for soil food webs, which are characterized by similar fauna (but see Berg et al., 2001 for a highly resolved soil food web). The lack of more detailed information on these food webs is in large part due to the many challenges associated with determination of the diet of the diverse and understudied community of microarthropods that inhabit these

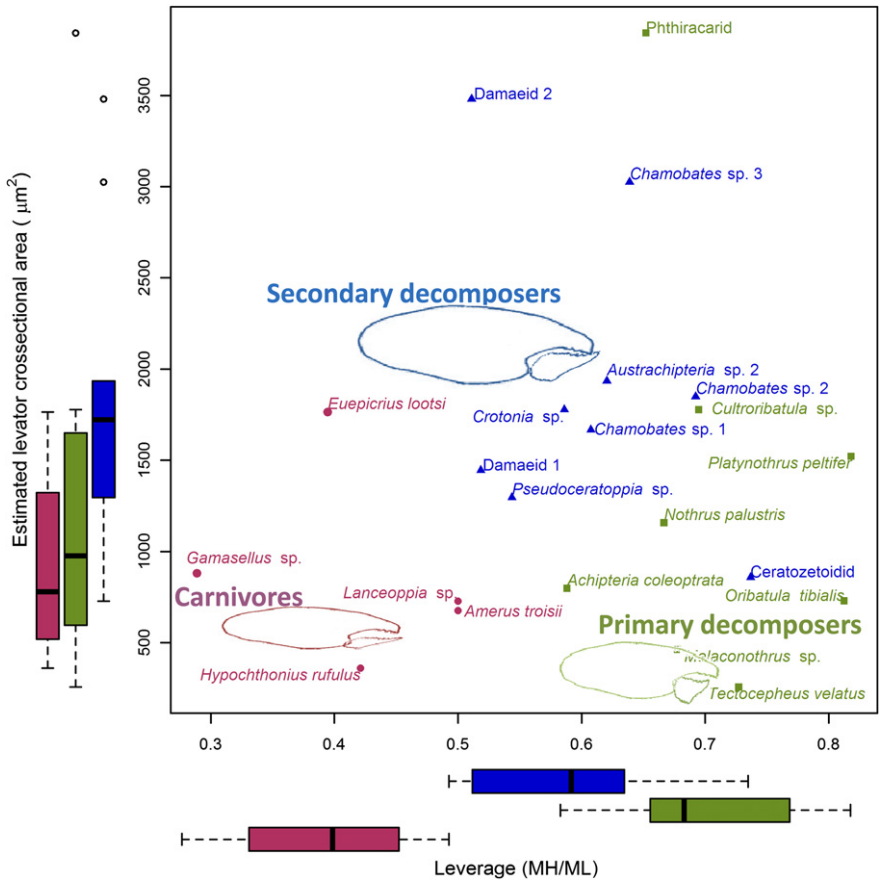

Fig. 4. Relationship between feeding guilds and cheliceral measurements. Boxplots represent median, 25th and 75th percentiles, range and outliers of values in each axis. Primary decomposers: feed predominantly on litter. Secondary decomposers: feed predominantly on fungi.

systems. Here we expand the state of knowledge of moss food webs by providing estimations of diet of a broad range of taxa, via techniques capable of capturing time-integrated measures of diet under field conditions. We also enhance the tools available to assess diets in oribatid mites, an abundant and diverse taxon present in mosses as well as soils, the diet of which has traditionally been difficult to estimate.

4.1. Trophic levels in moss communities

The most current description of the moss food web is modelled after that of a shortgrass prairie (Lindo and Gonzalez, 2010). The lack of data from moss microarthropod communities has to date precluded a system-specific understanding of these communities, as well as cross-system comparisons which could shed light on whether the moss food web resembles the complex, larger-scale food webs experimenters wish to understand. Our use of stable isotopes to trace the flow of both carbon and nitrogen in the moss system suggests that most of the fauna sampled does not feed directly on moss. The range of carbon and nitrogen signatures in this study is similar to that found in soil communities (Pollierer et al., 2009; Schneider et al., 2004), and suggests a speciose food web with more than one basal resource and trophic level. This confirms what had been assumed to be the case in mosses (Lindo and Gonzalez, 2010). The data also indicate that the basal resources pool in the moss food web should be expanded to include an additional source: lichens. The presence of oribatid mites across the range of isotope signatures confirms results of previous work in soils (Schneider et al., 2004) indicating that these mites should not be pooled into just one detritivorous guild. Oribatids can be carnivores, lichenivores, primary and secondary decomposers.

Detailed studies of trophic enrichment of ^{13}C and ^{15}N are not available for most moss-dwelling organisms and this can hamper further interpretation of the ranges. We have shown that use of different trophic enrichment factors can change estimations of diet generated by mixing models, and that the adoption of enrichment levels often applied to non-soil food webs (TEF1) can result in estimations that are not consistent with what is known about the basic biology of some taxa present in moss (e.g. the diet of Homoptera, a herbivore with sucking mouthparts, was found to consist of more than 40% bark with TEF1). In contrast, the adoption of high enrichment values of carbon from litter and bark, combined with low enrichment of nitrogen from all sources, produced results which were more consistent with the known natural history of the consumers (e.g. the diet of Homoptera was found to consist of >80% moss). This provides support for Pollierer et al. (2009) suggestion that cellulose in litter may be selectively assimilated, and suggests that trophic enrichment in moss systems may be more similar to that in soils than other systems. We propose that TEF2 is more likely to allow accurate estimation of food webs in moss systems than TEF1. In order to gain additional insight into the proportion of food sources in the diets of soil- and moss-dwelling taxa via the isotope techniques presented here, further work assessing enrichment levels for different sources and taxa is recommended.

Although the use of mixing models to estimate proportion of food sources in the diet is common, they have not to our knowledge been applied in studies of soil or moss food webs to date. One of the advantages of their use is the transformation of raw isotope signatures (represented in δ-space, ordinations that are potentially specific to particular locations) into more biologically relevant estimations of the proportion of food sources in the diet (occurring in p-space and thus potentially generalisable across locations). Here, we applied mixing models techniques in the analysis of stable isotope signatures of moss fauna, thereby providing estimations of the proportions of food sources in their diets. This type of information contrasts with that generated without mixing models, where isotope signatures are used to assign a guild to a species, with the description of the guild simply stating the likely major food sources (e.g. Schneider et al., 2004).

Mixing models are powerful tools for the analysis of stable isotope signatures. However, this technique necessitates comprehensive sampling of potential food sources in order to produce reliable results. The large negative correlation indices found in this study between litter and moss for known herbivorous taxa (Homoptera, Coleoptera) using TEF2 indicate that diet estimation iterations that included one food source tended to exclude the other. This reflects that the model could not determine with precision which of the sources was most likely to account for the signature of the fauna. It is likely that the absence of signatures of live plants other than moss in our study accounts for this. Nonetheless, results indicating that a live plant source is the major component of the diet of herbivorous mesofauna provide support for our estimations ofherbivory in the microfauna for which little information was previously available (e.g. *Stereotydeus* sp., *Cultroribatula* sp.).

We did not determine isotope composition of bacterial films in this study or perform extensive sampling of fungal hyphae. Variability around the fungal signature was however fitted into the mixing models, and fungal feeding has been reported and extensively studied in mites (Maraun et al., 2003; Schneider and Maraun, 2005; Schneider et al., 2004). It is therefore likely that the ^{13}C and ^{15}N enriched signatures we observed correspond at least in part to feeding on this resource. Additionally, the shape of the chelicerae of ^{13}C enriched mites from moss coincides well with those of the secondary decomposer (i.e. fungivorous) guild from the study by Schneider et al. (2004), further suggesting that our isotopically-enriched mites do in fact rely on fungi as a food source.

4.2. Assembling food webs in mite-dominated communities

Assembling food webs requires the determination of the roles of members of a community in terms both of their feeding preference and of the amount of mass that each member species contributes to its respective guild. In moss food webs, the most abundant and diverse arthropod taxon is oribatid mites. The biomass contributed by each species to the food web can be readily estimated via simple measures of body size (Appendix 2), but the assignment of a species to a particular feeding guild is more complex. Here we provide evidence that cheliceral morphology of oribatids is associated with the time-integrated measures of diet that can be obtained through stable isotope analyses. Furthermore, we provide a plausible mechanism explaining this association by assessing the morphological data in light of information that has recently become available about the way in which cheliceral muscles operate.

Two morphological characteristics of oribatid chelicerae can be used in conjunction to distinguish between carnivores, primary decomposers and secondary decomposers. These are leverage (i.e. height of the moveable digit relative to its length) and the estimated cross-sectional area of the muscle that lifts the moveable digit (i.e. the square of the height of the fixed digit). With regards to leverage, we propose that chelicerae showing high values in this trait represent levers with longer effort arms than chelicerae with low values (Fig. 2). The longer the effort arm, the more force can be applied at the tip of the chelicera. In accordance with this, our data show that species that rely on litter (primary decomposers) have relatively tall digits (higher leverage) as compared to carnivorous

species and those relying on fungi (secondary decomposers). Conversely, where leverage is lower, lever speed is higher and hence chelicerae would be able to close more quickly. This would be advantageous for catching fast-moving prey. As expected, a low leverage is found in carnivorous species. Species relying on fungi (secondary decomposers) show leverage values in between those of predators and primary decomposers. Similar observations were made by Kaneko (1988), who found that species classified via gut content analysis as macrophytophagous (i.e. feeding predominantly on higher plant matter) generally had leverage higher than 0.6, and microphytophagous species (i.e. feeding on predominantly on fungal hyphae and spores) had values lower than 0.6. Our work expands on this original observation by considering stable isotope signatures, incorporating species classified as carnivorous and estimating cross-sectional area of the levator muscle to further differentiate between guilds. We note however that the positive correlation found between body size and estimated levator cross-sectional area suggests that differences in body size among species could at least in part drive the patterns shown here for the levator muscle. Conversely, the lack of such a correlation for leverage confirms the expectation that this index is not affected by the size of the species.

Previous studies have suggested that one limitation of the application of stable isotopes in the study of mite-dominated communities is that enrichment of ^{15}N could possibly occur through the preferential consumption of fungi that grow on decomposing animals, rather than from direct consumption of the animals themselves (Schneider et al., 2004). We show here that the morphology of chelicerae of ^{15}N enriched oribatid mites studied is different from that of fungivorous ones and more similar to that of predatory mesostigmatid mites. This suggests not only that these oribatids are likely to be carnivorous but also highlights that cheliceral shape can provide additional insights into the dietary preferences of these organisms. Type one levers with long effort arms can be expected to be slower than those with shorter effort arms. The finding that ^{15}N enriched species have the slimmest (i.e. likely fastest) chelicerae suggests carnivory in these species may occur through predation rather than scavenging. Furthermore, the difference found in cheliceral morphology between species that had been assigned to different guilds via isotope analysis provides strength to the arguments that isotopic composition accurately distinguishes between groups of species that preferentially feed on different food sources in the field.

Although the association between morphology and isotope signature did not apply to all of the species studied, the observed discrepancies between guilds attributed via isotope analysis and the expectations of feeding preference based on mouthpart morphology are interesting and can provide focus for further work. For example, the phthiracarid mite studied had a cross-sectional area uncharacteristic of other primary decomposers, and its estimated leverage is intermediate between these two groups. The isotopic signature for this species (from Schneider et al., 2004) was also intermediate between decomposer groups. One possible explanation for these intermediate values is that the species relies on both resources, but this requires further investigation. The power to detect these discrepancies is valuable for focussing efforts of dietary preference determination on controversial species. Considering the abundance and diversity of oribatid mites in mosses and the considerable value of understanding food web dynamics in this model ecological system, we propose that where economic resources are limited, cheliceral morphology can be used as a good measure for separation of oribatid mites into three feeding guilds: carnivore, primary decomposer and secondary decomposer, and that species displaying morphological borderline values can be targeted for isotope analysis. Although some species may be allocated to guilds that would not correspond to the guilds assigned by isotopic signature, here we have shown that these techniques are in large part in accordance with each other.

The study of food web dynamics can significantly enhance our understanding of nutrient cycling and energy fluxes in ecosystems (DeAngelis, 1992). Biomass and species richness per guild are fundamental attributes of food webs, and have major impacts on properties such as stability in the face of disturbance (Ings et al., 2009; Rooney and McCann, 2012). Owing to difficulties in estimating diets of a speciose component of soil and moss food webs (oribatid mites), describing food web structure has remained difficult. Here we have developed tools that can help estimate oribatid diets, thereby making in-depth studies of soil and moss food webs more feasible.

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Appendix A. Supplementary material

Supplementary data related to this article can be found online at doi:10.1016/j.soilbio.2012.05.002.

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