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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 $\delta X = (\mathrm{Rsample}/\mathrm{Rstandard} - 1) \times 1000(‰)$, $X = {}^{13}C$ 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).