



Review paper

Weighing in: Size spectra as a standard tool in soil community analyses



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ABSTRACT

The variety and abundance of organism sizes in a community allows valuable conclusions to be drawn concerning trophic transfer efficiency, process rate dynamics, and ecological stability. Body size spectrum analyses have been applied to great effect in aquatic systems, but have only relatively recently gained interest for the description of soil communities. This approach should be added to existing sorting protocols and adopted as a standard tool of soil fauna analysis because of its ease of use, universal applicability regardless of taxonomy, and value as a predictor of both soil fauna function and response. This paper reviews the available methods for calculating soil fauna mass, constructing of body size spectra, and relating these spectra to existing fauna analysis frameworks such as the nematode maturity index. We also detail several of the functional conclusions that can be drawn from shifts in body size spectra and how this methodology can be further improved to supplement existing soil ecology methods.

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1. Introduction

There is an overall need to develop, test, and refine general principles of ecology to describe and predict the status of ecosystems under current anthropogenic global environmental change regimes. This need is particularly strong in soil ecology, where there are still many unknowns with respect to basic species biology and mechanistic understanding of soil function. Furthermore, many accepted ecological paradigms are currently inept when applied to soil systems because of this general lack of information on soil inhabitants, and the complexity of soil food webs. It is thought that these challenges have become prohibitive for attempts to use models, hypothesis testing from first principles, or the development of unifying theories in soil biology (Lavelle, 2009). Although there are many studies describing soil biodiversity and function on local, regional, or even global scales, most of these studies are correlative; advancement for understanding generalized patterns, particularly for soil biodiversity and community structure, could benefit from a standardized and harmonized approach. We need comprehensive models that are interdisciplinary, that model

relationships across scales, and that simulate scenarios for soil function (Lavelle, 2009).

In a recent paper Sutherland et al. (2013) outline 100 fundamental questions in ecology today, which embodies many of the challenges faced in soil ecology research. In particular, #39: “How well can community properties and responses to environmental change be predicted from the distribution of simple synoptic traits, e.g. body size?” And #72: “Can we predict the response of ecosystems to environmental change based on the traits of species?” Here the general idea is to use traits to predict community compositional changes and the rates of ecosystem functions those traits produce, where traits of species are a measure of functional diversity (*sensu* Tilman, 2001). Traits such as body size are easily measured characteristics that we can use to explore community level dynamics by looking at shifts in body size distributions (i.e., size spectra). Because body size is correlated with many other traits (e.g. desiccation resistance, vagility, trophic position), and has a strong allometric relationship with metabolism (Brown et al., 2004), we propose that body size can be used as a measure of functional diversity to relate community structure with ecosystem function in soil systems.

Correlates of body size, as mentioned above, pertain to individual organisms and the link to their population-scale counterparts (e.g. nutrient flow, environmental mortality, population growth, foraging efficiency) is not explicit. In order to link organism size to

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ecological interactions, we can describe the variety and abundance of body sizes in the community using body size spectra (Petchev and Belgrano, 2010). This approach has already been successfully applied to aquatic communities, most notably planktonic populations (Sprules and Munawar, 1986), where it has been shown to be a strong predictor of trophic transfer efficiency and stability (Jennings and Mackinson, 2003). The use of body size spectra could be especially valuable to study soil fauna communities due to the high degree of undiscovered diversity, high density of certain soil fauna populations, and difficulty isolating species for individual study, which impedes quantification of the contribution of individuals and populations to process rates and soil dynamics. Body size analyses can be applied to whole communities, do not require extensive taxonomic knowledge, and allow inference of ecological roles and relations without separate study of each possible species combination. Several recent studies have demonstrated the efficacy of this approach in a soil context as both a response and predictor to environmental change (Hocking et al., 2013; Mulder and Elser, 2009; Mulder et al., 2008). Body size differences between soil fauna have also been investigated as a measure of trophic linkage and resource dependence (Mulder et al., 2009, 2011a). However, body size is still not considered a standard descriptor of soil communities.

Here we argue that body size analysis should become a standard component of soil fauna community description because of its universality, ease of application, and value as a predictor of soil function. We describe the various methods by which body size can be measured, calculated, or estimated for various groups of key soil fauna, and how the distribution of body sizes should be plotted to generate a body size spectrum. We also indicate ecosystem processes and characteristics that are linked to the shape of the body size spectrum, demonstrating the functional link between this descriptor and soil function. This includes factors which are known to affect the slope of body size spectra, thus simultaneously demonstrating the appropriateness of this approach as a descriptor of response to disturbance or change.

2. Methods for determining size of different taxonomic groups

Several methods exist to describe the size of different soil fauna. Although “size” may simply entail the dimensions or volume of an

organism, it can be argued the most important metric of size for soil fauna is body mass. We also argue that body mass is the size descriptor most closely related to functional impact at both the individual and population level – that is to say, body mass explains a greater proportion of an organism’s metabolism and a species’ resource usage than length or volume (Brown et al., 2004). Here we outline how body mass measurements can be made across macro-, meso- and microfaunal soil groups.

For soil macrofauna, including Coleoptera larvae and adults, Diptera larvae, Formicidae, Oligochaeta, Araneae, and Myriapoda, direct measurement of body dimensions and/or mass are easily obtained. Calculations for mass based on body length/width measurements exist for various groups (see Table 1), but research is needed to derive standardized dry weight proportions or calculations for most macro- and mesofauna groups. Power functions most accurately describe the size–weight relationship of many macrofaunal groups using the equation

$$M = b_0 + (\text{length})^{b_1}$$

where M is mass and b_0 and b_1 are experimentally determined parameters (Ganihar, 1997). Isopods and coleopteran larvae are more accurately described by the linear function

$$M = b_0 + b_i(\text{length})$$

due to their uniform body shape (Ganihar, 1997). Parameters can be determined by measuring the length and width of individuals from the group of interest and desiccating them for 48h or more, then obtaining a final weight; however, it should be noted that these equations were derived for tropical arthropods and others equation forms may prove more accurate for temperate soil fauna as body geometry may vary (Gowing and Recher, 1985; Ganihar, 1997).

The size of mesofauna, including Acari, Collembola, and Enchytraeidae, can also be measured directly, where dimensions of length and width are measured using an ocular micrometer attached to a microscope during analysis of specimen slides, but more problematic are direct measurements of mass which require microbalance measurements due to the small size of these fauna. When dealing with small organisms and high densities, such as mesofauna, it is possible to weigh batches of individuals from each

Table 1
Body size equations to calculate the mass of various soil invertebrates as a function of length.

Taxon	Typical body length	Body mass calculation	Reference	
Rotifera	150–700 μm^{A}	Not determined		
Tardigrata	0.1–0.5 mm^{B}	Not determined		
Nematoda	0.3–3 mm^{A}	$530 \times L \times W^2$	Tita et al. (1999)	
Annelida	Oligochaeta	0.6–3000 $\text{mm}^{\text{A,B}}$	Direct measurement	Mulder et al. (2008)
Chelicerata	Acari	0.1–2 mm^{A}	$\log c + a \log(L + W)$	Caruso and Migliorini (2009)
	Pseudoscorpiones	2–8 mm^{A}	$a + b \ln(\text{length})$	Höfer and Ott (2009)
	Opiliones	2–10 mm^{B}	$b_{0a} + b_1 \ln(\text{length})$	Ganihar (1997)
	Araneae	2–4 mm^{C}	$b_0 + (e)^{b_1(\text{length})}$	Ganihar (1997)
Crustacea	Isopoda	2–30 mm^{B}	$b_0 + b_i(\text{length})$	Ganihar (1997)
	Paurapoda	0.5–1.5 mm^{B}	Not determined ^d	
Myriapoda	Symphyla	0.2–1.5 cm^{B}	Not determined ^d	
	Chilopoda	0.05–30 cm^{B}	$b_0 + (e)^{b_1(\text{length})}$	Ganihar (1997)
	Diplopoda	5–30 cm^{3C}	Not determined ^d	
	Collembola	0.1–2 cm^{A}	$b_0 + (e)^{b_1(\text{length})}$	Ganihar (1997)
Apterogota	Protura	1–2 mm^{A}	Not determined ^d	
	Diplura	2–5 mm^{A}	Not determined ^d	
	Coleoptera (larvae)	0.5–25 mm^{B}	$b_0 + b_i(\text{length})$	Ganihar (1997)
Insecta	Coleoptera (adult), Hymenoptera, Homoptera,	0.3–38 mm^{B}	$b_0 + (e)^{b_1(\text{length})}$	Ganihar (1997)
	Hemiptera, Thysanoptera			
	Diptera (larvae), Pscoptera, Isoptera	8–23 mm^{B}	Not determined ^d	
	Lepidoptera (larvae), Dermaptera	5–20 mm^{E}	$b_0 + (\text{length})^{b_1}$	Ganihar (1997)

Measurements come from ^AWhalen and Sampedro (2010), ^BDindal (1990), ^CM. Buddle (personal communication), ^DColeman et al. (2004), ^EMarshall (2006).

^a Indicates no determined model; probable application of Ganihar (1997).

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