

The size–grain hypothesis: do macroarthropods see a fractal world?

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Abstract. 1. In the size–grain hypothesis (a) long legs allow walking organisms to step over gaps and pores in substrate but prohibit them from entering those gaps; (b) the world is more rugose for small organisms; and (c) the relative cost of long legs increases as organisms grow smaller. The hypothesis predicts a positive allometry of leg length (= mass^b where $b > 0.33$ of isometry), a pattern that robustly holds for ants.

2. Toward testing for leg length allometries in other taxa, arthropods were extracted from the Panama leaf litter and measured. Three common taxa (spiders, diplopods, Coleoptera) yielded b s that exceeded 0.33 while three others (Acarina, Pseudoscorpiones, and Collembola) did not. The exponent b tended to increase ($P = 0.06$, $n = 7$) with an arthropod taxon's average body mass.

3. Since leg length in cursorial organisms tends toward isometry in very small and very large taxa (i.e. mammals) this suggests that the size–grain hypothesis may best apply at a transition zone of intermediate body mass: the macroarthropods.

4. Body length was a robust predictor of mass in all groups despite variation in shape.

Key words. Allometry, arthropods, body size, brown food web, cursorial, detritus, scaling.

Introduction

Leaf litter is home to a diverse group of arthropods that play a key role in the structure and function of brown food webs (Coleman & Crossley, 1996; Swift *et al.*, 1979). Decomposition contributes to the structural complexity of this habitat, producing a graded series of overlapping planes interspersed with gaps, both of which tend to get smaller as one travels downwards toward the soil (Fig. 1). So while larger organisms (e.g. ecologists) experience this landscape as a two-dimensional plane, smaller organisms (e.g. macro to microarthropods) may experience a landscape that is more three-dimensional and sieve-like.

The size–grain hypothesis (Kaspari & Weiser, 1999) posits that the morphology of walking organisms reflects a trade-off in how individuals move over and through such environments. It assumes that long legs better allow an individual to step over gaps in substrate and hence increase the efficiency of lateral movement. Long legs impede, however, the ability to penetrate those gaps, which can provide food or shelter. If the world

becomes an increasingly rugose place for smaller individuals of a taxon (Fig. 1), the cost of food/refuges denied by long legs may increase relative to the benefits of rapid lateral movement. The size–grain hypothesis predicts a positive allometry of leg length (i.e. proportionately longer legs in larger individuals) in cursorial organisms that meet these assumptions.

As evidence, Kaspari and Weiser (1999) showed that while walking mammals (size range: 10^6 – 10^1 g) show leg isometry (leg length $M^{0.33}$, Prothero, 1992) treating their world as a two-dimensional plane, ants (size range: 10^1 – 10^6 g) show positive leg allometry (leg length $\propto M^{0.37}$), suggesting that smaller ants increasingly live in, not on, the interstitial world of the soil and litter (see also Schoning *et al.*, 2005). Subsequently, this allometry has been confirmed in a variety of native ant assemblages (Kaspari & Weiser, 1999; Espadaler & Gomez, 2000; Parr *et al.*, 2003; Farji-Brener, 2004; Farji-Brener *et al.*, 2004) but not an island assemblage recently assembled from invasives (Sarty *et al.*, 2006). But is this allometry robust? Here this key prediction of the size–grain hypothesis is evaluated for other cursorial arthropods of the litter.

The trophic biology of brown food webs is poorly understood (Sih *et al.*, 1985; Polis *et al.*, 1997) in part for lack of data on the mass of key litter taxa. The small size (i.e. <1 mg) of

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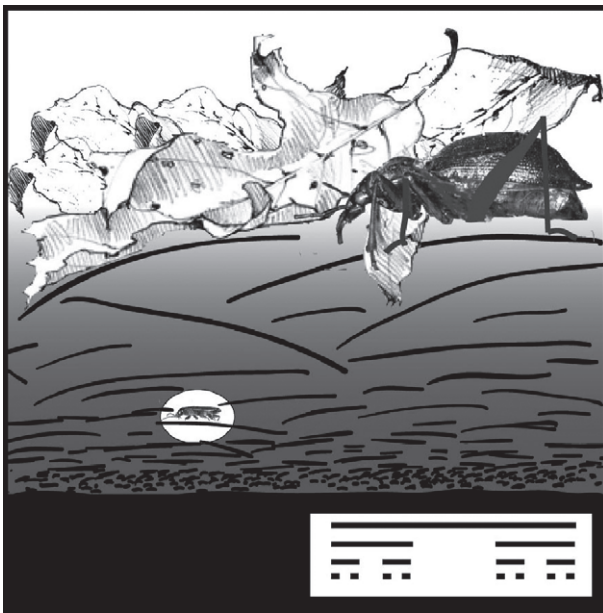


Fig. 1. The vertical structure of leaf litter consists of large, whole leaves on the surface that are increasingly fragmented and compressed as one approaches mineral soil. It thus resembles a cantor set (inset, constructed by successively removing the middle-third segment of a series of lines), an early example of a fractal surface (Hastings & Sugihara, 1993). The size–grain hypothesis assumes that long legs allow an organism to walk over these gaps in the substrate but increase the difficulty of penetrating those gaps. It predicts that as one samples from smaller and smaller individuals of a taxon (e.g. from the large carabid *Scaphinotus* to the tiny *Apristus*) these individuals transition from walking over the litter to walking through the litter, and that leg allometry should scale >0.33 (i.e. be proportionately longer in large individuals).

microarthropods like mites and Collembola makes measuring mass onerous. It is, however, relatively simple to sort, count, and size even the smallest litter arthropods. Studies of allometry can also be useful toward the more prosaic task of generating predictive regressions of mass from length.

Materials and methods

Specimens were collected in ongoing studies of the brown food web (M. Kaspari, unpublished). Leaf litter was collected from Barro Colorado National Monument (Leigh *et al.*, 1996), a lowland

moist rainforest in the Republic of Panama. Berlese funnels (Southwood, 1978) separated arthropods from leaf litter and collected them in 95% ethanol where they were processed within 1 year.

These collections were used to isolate the observed size range of six common litter taxa: two Hexapoda (Collembola, Coleoptera), the Diplopoda, and three Arachnida (Acarina, Pseudoscorpiones, and the cursorial spiders). These taxa generated 10–71 morphospecies each (given the sparse taxonomic literature on these taxa, it cannot be ruled out that in some cases different size classes/sexes of the same species were sampled). Individuals were measured with an Olympus SXH microscope equipped with an ocular micrometer for total body length (minus antenna) and front leg length. The specimen was transferred to a pre-weighed aluminium dish, dried in a convection oven at 60 °C for 36 h and then weighed to 0.1 µg with a Cahn Electrobalance or to 0.1 mg with an OHAUS electronic balance.

Variables were \log_{10} transformed and least squares linear regression was used to generate power laws (Proc Reg, SAS, 1995). To test the size–grain hypothesis for these taxa, leg length was regressed to dry mass; an *F*-test evaluated the null hypothesis of isometry (i.e. $b = 0.33$). To generate an estimate of mass, dry mass was regressed to body length. This was done for each taxon, plus all taxa measured (which included rarer taxa with $n < 10$ morphospecies).

Results

Litter taxa from three classes of the phylum Arthropoda varied in mass over five orders of magnitude, from 1.6 µg to 331 mg (Table 1, Fig. 2). Three (the Acarina, Collembola, and Pseudoscorpiones, henceforth the microarthropods) yielded a mean body mass <1 mg; three (the spiders, diplopods and Coleoptera, henceforth the macroarthropods) had a mean mass >1 mg. There was considerable variation in body mass within all the taxa, from 30-fold for Acarina to 2500-fold for the spiders. Likewise, there was 10-fold variation in proportional leg length for a given body mass from diplopods to spiders (Fig. 2).

Five of six taxa yielded $bs > 0.33$, three significantly (Table 1). The three macroarthropods yielded significant b -values ≥ 0.41 . The three microarthropods had lower exponents that did not significantly differ from isometry, with the latter two showing poorer fits (r^2 s about half those of the macroarthropods, Table 1). To explore how the scaling exponent b itself scaled, data from Kaspari and Weiser (1999) were used for the mean size of ants

Table 1. Scaling of leg length (mm) = $a \times \text{biomass (mg)}^b$ using least square regression. Six common litter taxa are sorted by average size. $\text{pWR} = \log_{10}(\text{Maximum mass/Minimum mass})$ is a measure of size range.

Taxon	<i>n</i>	$\log_{10}(\text{mean mass mg})$	pWR	$\log_{10}(a)$	<i>b</i>	r^2	$P(b \neq 0.333)$
Acarina	41	−1.77	1.5	0.086	0.290	0.39	0.4575
Collembola	34	−1.68	2.2	0.0223	0.386	0.39	0.5381
Pseudoscorpions	12	−0.76	1.8	0.190	0.405	0.75	0.3511
Spiders	66	0.12	3.3	0.466	0.470	0.61	0.0046
Diplopods	19	1.18	2.1	−0.709	0.524	0.87	0.0011
Coleoptera	71	1.18	2.4	0.261	0.411	0.77	0.0048

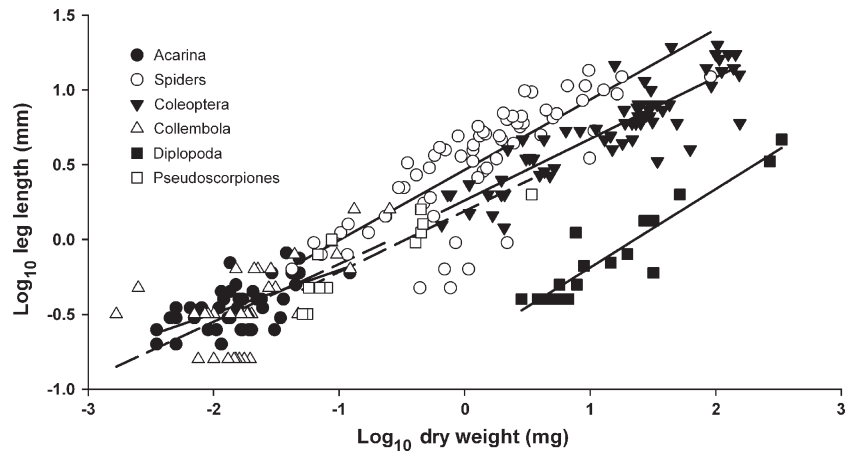


Fig. 2. The scaling of leg length for six common litter taxa. All scale positively, but dashed lines do not differ from isometry (i.e. $\text{leg size} \propto \text{Mass}^{0.33}$).

(0.99 mg) and their scaling exponent of leg size ($b = 0.374$). This resulted in seven taxa, albeit uncorrected for phylogeny. Across common litter arthropod taxa, there was a positive correlation between \log_{10} (average body mass) and the allometric exponent of leg length ($r_p = 0.73$, $P = 0.061$, $n = 7$).

Despite the range of body shapes (from the elongate diplopods to the squamate pseudoscorpions) body length was a statistically significant predictor of body mass ($ps < 0.001$). It was also an efficient predictor of body mass ($r^2s \geq 0.69$) for all taxa but the Acarina ($r^2 = 0.45$, Table 2). This occurred over considerable variation in b , from 1.49 (Acarina) to 3.24 (Millipedes). When all litter taxa were lumped together the regression yielded an r^2 of 0.89.

Discussion

The size–grain hypothesis assumes that smaller organisms experience an increasingly rugose world (Hastings & Sugihara, 1993; Kaspari & Weiser, 1999; With, 1994). Ants – the focal taxon thus far for tests of the hypothesis – occupy the middle of the size range of walking organisms, bracketed by the tiny tardigrades and the large mammals. In the present study, it is shown how a basic prediction of the size–grain hypothesis, that leg size

is positively allometric, is supported for four common litter arthropod taxa with a mean size of about 1 mg, but not for three taxa typically measured in micrograms. Furthermore, this does not appear to be a simple function of phylogeny as positive allometries are scattered incompletely across three classes of the Arthropoda–Myriapoda (diplopods), Hexapoda (Coleoptera and Formicidae, but not Collembola), and Arachnida (Spiders but not Pseudoscorpiones nor Acarina). A more formal phylogenetic treatment awaits a resolved phylogeny of the Arthropoda and a more complete sampling of its cursorial taxa. For now it can be observed that the leg size isometry of mammals (Prothero, 1992) and microarthropods (this study), combined with the positive allometry of macroarthropods, suggests a unimodal relationship between b and a taxon's average body mass. If so, then the leg allometry of the tiniest walking taxa (e.g. tardigrades) is predicted to conform to isometry while taxa intermediate in size between macroarthropods and mammals (e.g. newts and salamanders) are predicted to have leg allometries $0.33 < b < 0.45$.

Such 'kinks' in allometries indicate a changing balance in the fundamental constraints on how organisms make a living (Brown *et al.*, 1993; Kelt & Van Vuren, 2001). These results suggest that for large (> 10 g) walking taxa the litter is effectively two-dimensional; for intermediate (i.e. 1 mg to 10 g) taxa the litter reaches its maximum apparent rugosity, and as taxa grow smaller still (< 1 mg) individuals treat particles of soil and litter as interconnected planes.

Why do microarthropods show allometries closer to mammals than macroarthropods? The size–grain hypothesis assumes that as one grows smaller the opportunities for food and shelter afforded by interstitial spaces exceed the benefits of mobility afforded by long legs. One possibility, then, is that the physical rugosity of the litter environment eventually diminishes at the smallest scales; that decomposition in generating smaller particles ultimately creates a more uniform substrate. If so, the gaps between the decomposing leaves that keep *Apristis* in Fig. 1 from moving laterally would have no equivalents to the mite 1/100th its size.

A second complementary possibility is that as taxa grow smaller they become more mobile, and actively choose planar parts of the litter environment. There is some support for such

Table 2. Least square regressions for body length (mm) = $a \times \text{Mass}(\text{mg})^b$ for six common taxa of the tropical litter and for all taxa measured in this study (including some outside of the six focal taxa). All regressions significant at $P < 0.001$.

Taxon	n	r^2	$\log_{10}(a)$	b
Acarina	17	0.45	-1.49	1.947
Spiders	66	0.69	-1.33	2.284
Coleoptera	71	0.74	-1.87	2.901
Collembola	34	0.71	-2.30	2.813
Diplopoda	19	0.87	-3.24	3.380
Pseudoscorpiones	11	0.97	-1.55	2.821
All taxa	341	0.89	-1.59	2.438

an allometric kink in the mammals, with home range decreasing down to 100 g and then increasing again toward the shrews (Kelt & Van Vuren, 2001). What would cause this increasing mobility in litter microarthropods? As one goes deeper into the litter, one encounters proportionately more predators (Halaj *et al.*, 2005; Schmidt *et al.*, 2004), with, perhaps, the need to search more substrate for their high quality prey (Brown *et al.*, 1993). Many gamasid mites, for example, are speedy, long-legged predators (Coleman & Crossley, 1996). If smaller arthropods must move proportionately farther to find prey, size–grain's putative advantages to small legs may in turn decrease. Both of these scenarios go some way toward accounting for isometry in the pseudoscorpions, mites, and springtails but not the macroarthropods. Both are prone to laboratory study.

A hypothesis proves most useful when it generates a variety of predictions (Platt, 1964). Thus far, tests of the size–grain hypothesis in the field have focused on generating or comparing size distributions of ants (which have positive leg allometries) in environments of differing rugosity (Yanoviak & Kaspari, 2000; Parr *et al.*, 2003; Chown & Parr, 2004; Farji-Brener, 2004; Farji-Brener *et al.*, 2004). These tests have remained controversial, in part hinging on how environmental rugosity is manipulated and/or defined. While these are critical issues, other tests may also be useful. For example, individuals of taxa that regularly experience less rugose environments (including volant taxa) should not be under the same selection for positive allometries as those in the litter and should, *ceteris paribus*, converge on *bs* of 0.33. Moreover, a key prediction of the size–grain hypothesis is that leg length isometry should be accompanied by movement of similar fractal dimensions across a range of body mass, while positive leg allometries will generate a lower fractal dimension of movement as individual size increases. In an across-taxon comparison (Kaspari & Weiser, 1999; Wiens *et al.*, 1995) of macroarthropods this appears to be the case. Similar studies of movement across the isometric microarthropods while challenging, would be of exceptional interest.

Chown and colleagues (Parr *et al.*, 2003; Chown & Parr, 2004) are correct that alternate hypotheses for positive leg allometries are key to truly testing the size–grain hypothesis. It is hoped that these data (1) show that such allometries are not ant-specific and thus require explanations equally applicable to millipedes and spiders, and (2) attract further tests of the hypothesis by non-myrmecologists.

Finally, these data suggest that by sorting litter arthropods into size classes, a good approximation of total biomass may be achieved. Such measures are key to understanding the role of invertebrates in the functioning of these little-studied communities (Polis *et al.*, 1997).

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