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4
5 **Title: Does body size-abundance allometry in soil fauna vary with environment?**
6 **A field test for nematode communities in response to fertilization**
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21 **Abstract:** The “energetic equivalence rule” predicts that abundance should always
22 scale as the $-3/4$ power of body size within a trophic group, but if the body
23 size-abundance allometry (BSA) of soil fauna in fact is labile then the relationship
24 could potentially be used as a standard descriptor for shifts in community function in
25 response to environmental change. To assess the possibility that the BSA could serve
26 as an index of community function, we measured the effect of fertilization on the
27 slope and intercept of the BSA in nematode communities in a rice-wheat crop rotation
28 over three years. Fertilization increased the BSA intercept but did not affect the slope
29 in either rice or wheat phases, which highlights the stable scaling of BSA.

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31 **Keywords:** Allometric scaling; Body size spectra; Energetic equivalence rule

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35 With the recent development of trait-based soil biology, the allometric
36 relationship between body size and abundance (BSA, including mass–abundance
37 regressions and body size spectrum) in soil fauna has been proposed as a standard
38 descriptor of functional structure in communities responding to environmental change
39 (George and Lindo, 2015; Turnbull et al., 2014). The application of BSA predicts that
40 disturbance and nutrient enrichment will favor smaller over larger individuals in the
41 soil fauna with a consequent change in the allometric slope of the body
42 size-abundance relationship (George and Lindo, 2015; Turnbull et al., 2014; Wilson et
43 al., 2010; Zhao et al., 2015). This prediction, however, challenges the prediction of the
44 “energetic equivalence rule” (EER: Damuth (1981), which asserts that the allometric
45 scaling should be constant near a value of $-3/4$.

46 Studies from diverse organisms across a wide range of environments show that
47 population density scales with body size to the $-3/4$ power (Brown et al., 2004;
48 Hechinger et al., 2011; Peters, 1991; White et al., 2007), but the prediction of EER
49 has been often questioned in animals assemblages (Blackburn et al., 1994; Hechinger
50 et al., 2011), especially for free-living soil fauna in association with soil fertility
51 (Mulder and Elser, 2009), disturbance (George and Lindo, 2015) and land use change
52 (Zhao et al., 2015). A key criticism, however, is that the data used to establish the $-3/4$
53 relationship generally are derived from studies in the literature that often
54 underestimate the number of small-bodied rare species (Lawton, 1990). Besides, not
55 only abundance but also the body size of soil organisms varies with environmental
56 change (Liu et al., 2015), which may further complicate use of the BSA as a standard

57 descriptor of functional structure in the soil fauna community.

58 Accordingly, the intercept of BSA varies with total fauna biomass and the slope
59 depends on environmental selection on body size (Henderson and Magurran, 2010;
60 Mulder et al., 2011; Hoste-Danylow et al., 2013). Thus, in this paper we address two
61 working hypotheses: i) fertilization will steepen the slope and increase the intercept of
62 the BSA in nematode communities by both increasing small-bodied nematodes and
63 total fauna biomass, and ii) the BSA will differ over time under crop rotations due to
64 changing fauna biomass and energy during the growing season. We test these
65 expectations in a fertilization experiment over the course of three years in a rotation
66 system of rice (*Oryza sativa* L.) and wheat (*Triticum aestivum* L.).

67 In October 2010, we established the fertilization experiment in a subtropical
68 monsoon climate zone of China (31°39'N, 119°28'E). We randomly allocated three
69 fertilization treatments across twelve plots (each was 5m × 8 m) separated by cement
70 barriers (Liu et al., 2015). The three fertilization treatments are unfertilized control,
71 chemical fertilizer and manure + 50% chemical fertilizer (detailed in Liu et al., 2015).
72 In each plot, eight soil cores (2.5 cm in diameter) were randomly collected (0-10 cm)
73 for measurement of abundance and body size for each genus of soil nematode in the
74 wheat (May) and the rice (October) cropping phase in 2011, 2012 and 2013 (detailed
75 in Liu et al., 2015).

76 We used Standardized Major Axis (model II) regressions (Warton et al., 2006) to
77 calculate the slope and intercept of the allometric relationship between body size and
78 abundance for 72 nematode communities (3 years × 2 seasons × 3 treatments ×

79 4 replicates) each plot (community). Ten communities without a significant allometric
80 relationship ($R^2 < 0.10$ and $P > 0.05$) were omitted from further analysis. We then
81 tested whether each slope differed significantly from $-3/4$ using the *smatr* package in
82 R (Warton and Ormerod, 2007). Finally, we used ANOVA to assess the effect of
83 fertilization, season (rice, wheat) and year (2011-2012-2013) on the slope and
84 intercept of the 62 allometric relationships. Variables met the assumptions of the
85 normality and homogeneity of variance. When the year effect was significant, we
86 re-analyzed each year separately.

87 As expected, body size was negatively correlated with abundance in the 62
88 communities with the R^2 ranging from 0.10-0.35. The slopes ranged from -0.52 to
89 -1.16, but none of them differed significantly from $-3/4$ (Fig. 1A). There were no
90 significant differences among fertilization treatment or between years, but the slopes
91 in the rice phase were significantly larger than the wheat phase in 2012 and 2013,
92 irrespective of fertilization ($P < 0.05$, Table 1 and Fig. 1A). Fertilization tends to
93 increase the intercept with the effect marginally significant in the rice phase in 2011
94 and 2013 ($P < 0.05$, Table 1 and Fig. 1B). Interestingly, the intercept differed
95 significantly among years but the effect was qualitatively different in two phases ($P <$
96 0.05 , Table 1 and Fig. 1B). The intercept tends to increase from 2011 to 2012 and
97 2013 in the rice phase but decrease in the wheat phase irrespective of fertilization
98 (Table 1 and Fig. 1B). Indeed, when each year was analyzed separately, both slope
99 and intercept differed significantly between rice and wheat phase (Fig. 1A and B).

100 Contrary to expectations under BSA but consistent with EER, our results show

101 that neither fertilization nor year significantly changed the scaling relationship
102 between body size and abundance. This result may be explained by several
103 mechanisms that can stabilize the slope by increasing larger nematodes and/or
104 promoting mortality of small nematodes in fertilized treatments. Firstly, we found that
105 not only small-bodied but also large-bodied nematode abundance were increased
106 following fertilization (Liu et al., 2015). Secondly, fertilization increased the body
107 size of most genera, which resulted in a higher community-levels body size in
108 fertilized treatments compared to control (Mulder and Vonk, 2011). Additionally, there
109 are many possible mechanisms that could depress abundance of small-bodied
110 nematodes via increasing mortality in fertilized treatments. The most probable are: i)
111 increase in size- and frequency-dependent competition; ii) increase in predation due to
112 increased abundance of larger-bodied predacious and omnivorous nematodes; and iii)
113 the effects of size-dependent mortality and competition interacting to stabilize body
114 size-abundance relationships, food-webs and trophic structure (Brännström et al.,
115 2011; Taborsky et al., 2012; Troost et al., 2008). Fertilization may induce a rapid
116 increases in abundance of small-bodied nematodes, which will result in a steepening
117 slope in a transient nematode community (e.g. community soon after fertilization), but
118 then increased size- and frequency-dependent competition and predation will result in
119 higher mortality of small-bodied nematodes, returning the slope to control values
120 (Turnbull et al., 2014).

121 In conclusion, our results show that the nature of scaling relationship did not
122 vary substantially with environmental change, which supports the general prediction

123 of the EER (Damuth, 1981). Hence the body size–abundance relationship may not be
124 a reliable index for the response of functional structure in soil fauna to environmental
125 change. For example, fertilization did not change the allometric scaling, but did
126 significantly increase the mean of body size distribution. Indeed, many studies
127 successfully have used community weighted mean and functional diversity to quantify
128 the mean and variance of body size distribution as well as aspects of ecosystem
129 function (Petchey et al., 2007; Rudolf et al., 2014; Villéger et al., 2010). Such
130 weighted analyses of the nematode fauna potentially could also be used to assess the
131 effect of environmental change on the functional structure of soil fauna (Ferris et al.,
132 2001).

133

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141 **References**

142 Blackburn, T.M., Beverton, R., Clarke, K., Lawton, J.H., 1994. Population Abundance
143 and Body Size in Animal Assemblages [and Discussion]. Philosophical
144 Transactions of the Royal Society B: Biological Sciences 343, 33-39.

145 Brännström, Å., Loeuille, N., Loreau, M., Dieckmann, U., 2011. Emergence and
 146 maintenance of biodiversity in an evolutionary food-web model. *Theoretical*
 147 *Ecology* 4, 467-478.

148 Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M., West, G.B., 2004. Toward a
 149 metabolic theory of ecology. *Ecology* 85, 1771-1789.

150 Damuth, J., 1981. Population density and body size in mammals. *Nature* 290,
 151 699-700.

152 Ferris, H., Bongers, T., Goede, R.G.M.D., 2001. A framework for soil food web
 153 diagnostics: extension of the nematode faunal analysis concept. *Applied Soil*
 154 *Ecology* 18, 13-29.

155 George, P.B., Lindo, Z., 2015. Application of body size spectra to nematode
 156 trait-index analyses. *Soil Biology & Biochemistry* 84, 15-20.

157 Hechinger, R.F., Lafferty, K.D., Dobson, A.P., Brown, J.H., Kuris, A.M., 2011. A
 158 common scaling rule for abundance, energetics, and production of parasitic and
 159 free-living species. *Science* 333, 445-448.

160 Henderson, P.A., Magurran, A.E., 2010. Linking species abundance distributions in
 161 numerical abundance and biomass through simple assumptions about community
 162 structure. *Proceedings of the Royal Society of London B: Biological Sciences*
 163 277, 1561-1570.

164 Hoste-Danylow, A., Ilieva-Makulec, K., Olejniczak, I., Hajdamowicz, I., Stańska, M.,
 165 Marczak, D., Wytwer, J., Faleńczyk-Koziróg, K., Ulrich, W., 2013. The shape of
 166 the intraspecific metabolic-rate-body-size relationship affects interspecific

167 biomass and abundance distributions of soil animals within a forest ecosystem.
 168 *Annales Zoologici Fennici* 50, 289-302.

169 Lawton, J., 1990. Species richness and population dynamics of animal assemblages.
 170 Patterns in body size: abundance space. *Philosophical Transactions of the Royal*
 171 *Society B: Biological Sciences* 330, 283-291.

172 Liu, T., Guo, R., Ran, W., Whalen, J.K., Li, H., 2015. Body size is a sensitive
 173 trait-based indicator of soil nematode community response to fertilization in rice
 174 and wheat agroecosystems. *Soil Biology & Biochemistry* 88, 275-281.

175 Mulder, C., Elser, J.J., 2009. Soil acidity, ecological stoichiometry and allometric
 176 scaling in grassland food webs. *Global Change Biology* 15, 2730-2738.

177 Mulder, C., Vonk, J.A., 2011. Nematode traits and environmental constraints in 200
 178 soil systems: Scaling within the 60–6000 μm body size range. *Ecology* 92, 2004.

179 Mulder, C., Vonk, J.A., Den Hollander, H.A., Hendriks, A.J., Breure, A.M., 2011.
 180 How allometric scaling relates to soil abiotics. *Oikos* 120, 529-536.

181 Petchey, O.L., Evans, K.L., Fishburn, I.S., Gaston, K.J., 2007. Low functional
 182 diversity and no redundancy in British avian assemblages. *Journal of Animal*
 183 *Ecology* 76, 977-985.

184 Peters, R.H., 1991. A critique for ecology. Cambridge University Press, Cambridge.

185 Rudolf, V.H., Rasmussen, N.L., Dibble, C.J., Van Allen, B.G., 2014. Resolving the
 186 roles of body size and species identity in driving functional diversity.
 187 *Proceedings of the Royal Society B: Biological Sciences* 281, 20133203.

188 Taborsky, B., Heino, M., Dieckmann, U., 2012. Size-dependent mortality and

189 competition interactively shape community diversity. *Evolution* 66, 3534-3544.

190 Troost, T.A., Kooi, B.W., Dieckmann, U., 2008. Joint evolution of predator body size
191 and prey-size preference. *Evolutionary Ecology* 22, 771-799.

192 Turnbull, M.S., George, P.B., Lindo, Z., 2014. Weighing in: Size spectra as a standard
193 tool in soil community analyses. *Soil Biology & Biochemistry* 68, 366-372.

194 Villéger, S., Miranda, J.R., Hernández, D.F., Mouillot, D., 2010. Contrasting changes
195 in taxonomic vs. functional diversity of tropical fish communities after habitat
196 degradation. *Ecological Applications* 20, 1512-1522.

197 Warton, D., Ormerod, J., 2007. Smatr: (Standardised) major axis estimation and
198 testing routines. R package version 2.1.

199 Warton, D.I., Wright, I.J., Falster, D.S., Westoby, M., 2006. Bivariate line - fitting
200 methods for allometry. *Biological Reviews* 81, 259-291.

201 White, E.P., Ernest, S., Kerkhoff, A.J., Enquist, B.J., 2007. Relationships between
202 body size and abundance in ecology. *Trends in Ecology & Evolution* 22,
203 323-330.

204 Wilson, S., Fisher, R., Pratchett, M., Graham, N., Dulvy, N., Turner, R., Cakacaka, A.,
205 Polunin, N., 2010. Habitat degradation and fishing effects on the size structure of
206 coral reef fish communities. *Ecological Applications* 20, 442-451.

207 Zhao, J., Xun, R., He, X., Zhang, W., Fu, W., Wang, K., 2015. Size spectra of soil
208 nematode assemblages under different land use types. *Soil Biology &
209 Biochemistry* 85, 130-136.

210

211 **Table 1** Summary of ANOVA for effect of year, season and fertilization on the slope
 212 and intercept of the body size–abundance allometric relationship. Df: degrees of
 213 freedom; SS%: the percentage of sum of squares.

	Df	Slope			Intercept		
		SS%	F	<i>P</i>	SS%	F	<i>P</i>
Year	1	3.31	2.340	0.132	10.53	7.639	0.008
Season ^a	1	13.51	9.482	0.003	1.69	1.224	0.273
Treatment	4	6.27	1.104	0.364	13.34	2.419	0.060
Residuals	54	76.91			74.44		

214 ^a The intercept differed significantly between rice phase and wheat phase when each
 215 year was analyzed separately.

216

217 **Figure caption**

218 **Fig. 1** The effect of season and fertilization (nested in season) on the slope (A) and
219 intercept (B) in the body size–abundance allometric relationship over three years. NS:
220 no significant difference among fertilization treatments.

221

222 **Figure 1**

223