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The shape of the intraspecific metabolic-rate–body-size relationship affects interspecific biomass and abundance distributions of soil animals within a forest ecosystem

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It has long been known that there is an allometric relationship between metabolic rate (M) and body weight (W) of the form: $M = M_0W^b$. However, the debate remains open regarding the value of b. Only recently research turned to the ecological implications of existing differences in metabolic scaling among taxa. Using a data set on forest soil invertebrates, we evaluated the influence of differences in intraspecific metabolic rate scaling on observed species biomass and abundance distributions. We found that absolute densities and biomass were correlated with the exponents of the intraspecific metabolic scaling. Evenness of the abundance distributions and species diversity were also moderately linked to b. These results suggest that the shape of the intraspecific metabolic-rate–body-size relationship affects interspecific biomass and abundance distributions. This emphasizes the importance of intraspecific variations in allometric scaling and indicates the need to take these variations into account when proposing models to explain these relationships.

Introduction

The allometric scaling of animal and plant metabolic rates with body weight has long been known to ecology (Kleiber 1932, Hemmingsen 1960) but has gained increasing interest since the development of the metabolic theory of ecology (MTE) by Brown and co-workers (Brown *et al.* 2004) and the formulation of mechanistic hypotheses to explain metabolic scalings. These hypotheses include fractal branching supporting networks (West *et al.* 1997, 1999), cell size dependencies (Kozłowski *et al.* 2003), and biochemical metabolic constraints (Glazier 2005, 2010). They all aim at explaining the exponent value of the relationship between metabolic rate and body weight (MWR) known as:

$$M = M_0 W^b \quad (1)$$

where M is the metabolic rate, W is the body mass, M_0 is the normalizing constant, and b is the scaling exponent.

Much of the debate within the metabolic framework focused on whether the MWR scaling exponent b is universal and close to the predicted value of 0.75. (e.g. West *et al.* 1999, Farrell-Gray & Gotelli, 2005, Reich *et al.* 2006, Enquist *et al.* 2007, Isaac & Carbone 2010). Adherents of MTE treated the observed deviations from the prediction as a random variate centered around 0.75 (Allen *et al.* 2002, Brown *et al.* 2004, Savage *et al.* 2004, Gillooly & Allen 2007) or introduced correction terms to recover the predicted value (Hechinger *et al.* 2011). Opponents either proposed different universal exponents (e.g. White & Seymore 2003, Reich *et al.* 2006, McNab 2008) or argued in favor of taxon-specific variability (White *et al.* 2009, Clarke *et al.* 2010). Only recently research turened to the ecological implications of the existing differences in metabolic scaling among taxa (Glazier 2005, Isaac & Carbone 2010, Clarke *et al.* 2010).

The basic equations of MTE predict that metabolic rate M and species abundance N scale with body weight W: $M \propto W^b$ and $N \propto W^{-c}$. Thus species abundance scales with metabolic rate as follows:

$$N \propto M^{-c/b} \quad (2)$$

If scaling exponents were universal, as assumed by MTE, the metabolic scaling of abundances would be identical within and among taxa and thus observed differences in abundance distributions and population densities could not be attributed to invariance of energy use. In turn, species-specific metabolic scaling would link energy use directly to species abundances and part of the observed variability in species abundance distributions (Ulrich *et al.* 2010) could be traced back to the metabolic level.

Literature data on metabolic rates are for most taxa, particularly invertebrates, given as aggregate values without species-specific differentiation. However, Isaac and Carbone (2010) were the first to notice that the well-known proportional rescaling of the variance σ^2 with the associated arithmetic mean μ (variances $\sigma^2 \propto \mu^z$ with z often scattering around 2 according to Taylor's power law; Taylor 1961) also applies to metabolic-scaling exponents. Thus among taxa, differences in scaling exponents should be accompanied by respective within-taxa variability. According to Eq. 2, this variability should cause systematic differences in observed abundances. If we assume c to be constant, Eq. 2 predicts more pronounced abundance differences in a population of species with different body sizes when b increases with rising metabolic rate M (Fig. 1). Thus we speculate that differences in metabolic-rate scaling might have direct and measurable effects on observed species abundance distributions.

Species-specific metabolic rates have long been used to calculate population energy use and biomass (Ernest 2005, Meehan 2006) but were not directly linked to species abundances. However, abundance distributions directly influence other aggregate ecological variables like total abundance, biomass, and total energy use. Thus the influence of metabolic scaling might be twofold: direct by the link with energy use and indirect via its influence on abundance distributions.

Here we use an exceptionally large data set on soil invertebrates to test these ideas. Soil and litter systems are among the most species rich terrestrial ecological systems on Earth. Their biodiversity is often orders of magnitude higher than that of above-surface habitats (Adams & Wall 2000), and body sizes span over more than six orders of magnitude (Petersen & Luxton 1982). These features make soil animals an ideal candidate to test how metabolic scaling exponents influence soil community structures.

Material and methods

From 2009 to 2011, we studied the soil fauna of a 10 × 20 m^2 plot in a 40–50-year-old deciduous forest of the Kampinos National Park (Poland) situated on a dune terrace (Kaczmarek 1973). The tree layer covers about 70% of the plot surface and is dominated by *Quercus robur* and *Betula pendula*. The patchy shrub layer is dominated by *Frangula alnus* and covers about 50% of the surface. *Poa trivialis*, *Agrostis alba*, *Juncus effusus* and *Deschampsia caespitosa* are most abundant in the well-developed herb layer (80%–85% cover). Soil pH ranged between 4.4 and 4.9.

The samplings took place in August and October 2009, April, July and October 2010, and May 2011. Core samples for each group of organisms were collected close to each other in randomly chosen 1-m^2 quadrats. Ten replicates were collected for each studied group. Each sample was taken to a depth of 10 cm. The nematodes were sampled using a corer 1.8 cm in diameter, and were extracted using Whitehead and Hemming's modification of the Baermann method (Whitehead & Hemming 1965). The mesofauna was sampled using a corer 3.5 cm in diameter, and were extracted using the MacFadyen high gradient canister extractor (MacFadyen 1961) in the case of springtails and mites, and using the O'Connor modification of the Baermann funnel (O'Connor 1955) in the case of enchytraeids. The macrofauna was hand-sorted from 30 × 30 cm^2 quadrats. In addition, the surface layer of 50 × 50 cm^2 quadrats with 20 cm high borders thrown from a distance were hand-sorted directly in the field, enabling us to sample fast moving invertebrates that would otherwise escape from our samples. All individuals collected were identified to the species level and density per square meter was calculated for each species.

We estimated body weights either by direct weighing after 48 h at 60 °C in vacuum conditions or by standard length and/or width-to-weight regressions (Andrassy 1956, Abrahamsen 1973, Persson & Lohm 1977, Górny & Grum 1993). When necessary, fresh-weight/dry-weight ratios were adopted according to Persson and Lohm (1977), Persson *et al.* (1980), and Axelsson *et al.* (1984).

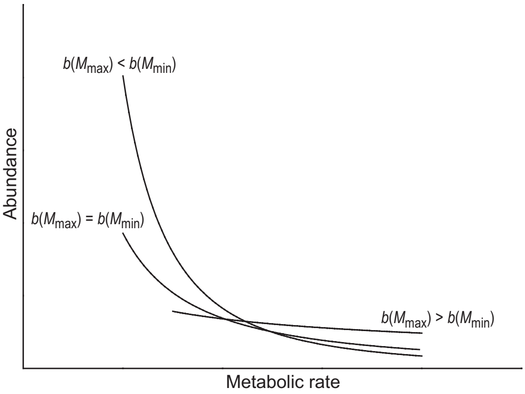

Fig. 1. The relationship between metabolic rate *M* and abundance *N* according to Eq. 2 ($N \propto M^{-c/b}$) depends on the variability of the scaling exponent *b* of the metabolic-rate–body-weight relationship. At the constant parameter *c*, an increase of *b* with $M[b(M_{max}) > b(M_{min})]$ results in a shallower decrease of *N* with respect to *M* in comparison to the decrease when *b* is independent of *M* and constant. The situation reverses when *b* decreases with increasing $M[b(M_{min}) > b(M_{max})]$.

Metabolic rates of the collected organisms were derived from allometric body weight (W) to metabolic rate relationships (M) (MWR: $M = aW^b$ with parameters a and b). The constants a and b were either directly taken from the literature or were calculated from the literature data. Metabolic rate is known to vary with temperature and adjustment to field temperature was made using the traditional Q_{10} factor (Van't Hoff 1884). The parameters a, b and Q_{10} values used in the present work are summarized in Table 1. A detailed description of their sources is given in Appendix I.

For ten taxa (Nematoda, Collembola, Mesostigmata, Enchytraeidae, Lumbricidae, Chilopoda, Gastropoda, Carabidae, Staphylinidae, Araneae), we calculated average values of MWR slopes, and square-meter-based total densities, biomass, and metabolic rates on those sample dates when more than ten species S were found (in total 40 data sets). To each data set, we fitted a log-normal distributions to observed abundance and biomass rank order distributions with parameters S and a as in Ulrich *et al.* (2010). The shape parameter a defines the variance in abundance and is a measure of evenness with lower values of a indicating a more even distribution. As a metric of the goodness of fit we used the χ^2

errors of measured and expected log-transformed densities for each species:

$$\mathrm{Fit} = \frac{1}{S}\sum_{i=1}^{s}\frac{\left(\mathrm{measured}_i - \mathrm{expected}_i\right)}{\mathrm{expected}_i} \quad (3)$$

Lower values of Fit indicate a better fit to a log-normal distribution, the most common type of community organization (Ulrich *et al.* 2010). Additionally, we calculated for each set the slopes of the respective fits of the log-series species abundance distribution, which is a widely used metric of alpha diversity (Taylor *et al*. 1976, Magurran 2004). Because the data were not normally distributed, MWR slopes were related to these measures of community structure by means of Spearman's rank order correlation (r_S). In addition, ordinary least squares multiple regression was used to estimate the slope of

Table 1. Parameters used for the calculation of individual metabolic rates (*M*, mm^3 O$_2$ indiv.$^{-1}$ h^{-1}) from fresh individual body masses (*W*, g) at 10 °C. The relationships are given in the form $M = aW^b$.

Taxon	*a*	*b*	Q_{10}	Sources
Nematoda	11.7	0.72	2.5	Klekowski *et al.* 1972
Collembola				
Isotomiella minor	47.5	0.828	2	Petersen 1981
Parisotoma notabilis	48.68	0.8	1.9	Petersen 1981
Lepidocyrtus lanuginosus	101.37	0.835	2.9	Petersen 1981
Folsomia quadrioculata	9.5	0.669	2.2	Petersen 1981
Pogonognathellus flavescens	260.64	0.963	5.2	Petersen 1981
Other collembolan	64.77	0.85	2.6	*Ehnes 2011 (*n* = 128, r^2 = 0.85)
Mesostigmata				
Gamasina	102.33	0.869	3	Wood & Lawton 1973
Uropodina	5.035	0.671	3	Wood & Lawton 1973
Enchytraeidae	18.67	0.67	1.6	Persson & Lohm 1977
Lumbricidae				
Aporrectodea caliginosa	41.8	0.91	2	Byzova 2007
Dendrobaena octaedra	63.8	0.71	2	Byzova 2007
Lumbricus rubellus	49.84	0.84	2	Byzova 2007
Diplopoda				
Polydesmus complanatus	52.28	0.79	2.5	Byzova 2007
Other diplopoda	18.4	0.69	2.5	Byzova 2007
Chilopoda	22	0.64	2.5	Byzova 2007
Isopoda	31.1	0.63	2.15	Byzova 2007
Araneae	44.8	0.68	2	*Byzova 2007, Ehnes 2011 (*n* = 395, r^2 = 0.71)
Gastropoda				
Deroceras agreste	188.8	0.85	1.95	Byzova 2007
Arion fasciatus	221.5	0.75	1.95	Byzova 2007
Punctum pygmaeum	0.3	0.65	1.69	Mason 1971
Vitrina pellucida	0.3	0.65	2.01	Mason 1971
Fruticicola fruticum	0.3	0.65	2.21	Mason 1971
Oxychilidae	0.3	0.65	2.37	Mason 1971
Coleoptera				
Larvae	77.9	0.61	2	*Byzova 2007 (*n* = 37, r^2 = 0.43)
Carabidae	93.4	0.86	2	*Byzova 2007, Makarieva *et al.* 2008, Persson & Lohm 1977, Ehnes 2011 (*n* = 1014, r^2 = 0.74)
Staphylinoidea	91	0.81	2	*Byzova 2007, Makarieva *et al.* 2008, Persson & Lohm 1977, Ehnes 2011 (*n* = 66, r^2 = 0.82)
Scarabaeoidea	74.55	0.64	2	*Makarieva *et al.* 2008 (*n* = 29, r^2 = 0.69)
Diptera larvae	135.28	0.788	2.25	*Persson & Lohm 1977, Byzova 2007 (*n* = 24, r^2 = 0.87)
Blattodea	77.76	0.87	2	*Makarieva *et al.* 2008 (*n* = 14, r^2 = 0.93)
Lygaeidae	84.5	0.62	2	*Makarieva *et al.* 2008 (*n* = 11, r^2 = 0.69)
Dermaptera	113.14	0.82	2	Makarieva *et al.* 2008

* Regressions calculated using the data from the quoted sources

the density–respiration relationship. In order to avoid the over-proportional influence of outliers, density, biomass, and respiration data were log-transformed.

Results

In total, we collected more than 77 000 individuals belonging to 11 taxa (Nematoda, Collembola, Mesostigmata, Enchytraeidae, Lumbricidae, Diplopoda, Chilopoda, Gastropoda, Isopoda, Araneae, Insecta). The average density was 4.9 ± 1.4 million indiv. m^{-2} with an average biomass of 9.44 ± 2.4 g$_{fw}$ m^{-2} (Table 2). Although the average MWR exponent for our species derived from the data available from the literature ($b = 0.76 \pm 0.003$) was close to the MTE expectation of 0.75, taxon specific exponent values differed significantly among the major taxa (ANOVA: $p < 0.001$). When calculated over all the taxa, MWR exponents did not significantly correlate with body weight ($r_S = -0.05$, $P > 0.1$), but we found taxon-specific dependencies for Myriapoda ($r_S = 0.69$, $p < 0.001$) and Arachnida ($r_S = -0.78$, $p < 0.001$), but not for insects ($r_S = 0.11$, $p > 0.1$). Exponent values did not depend on species richness ($r_S = 0.08$, $p > 0.2$).

Because of the outliers corresponding to Nematoda, densities of micro and mesofaunal taxa were weakly and negatively correlated with the MWR exponent ($r_S = -0.50$, $p = 0.02$), while for the macrofauna a positive correlation was found ($r_S = 0.52$, $p = 0.04$). Total biomass and total respiration, of all the taxa in turn, were not linked to the MWR exponent ($r_S = 0.02$, $p > 0.5$).

Irrespective of whether the fits of the log-normal distribution were done with abundance- or with biomass rank order distributions, taxa with higher average MWR slopes were more even (Fig. 2A and D) and less diverse (Fig. 2C and F), although the respective correlations were

Table 2. Average numbers of species, mean densities ± SEs, biomass ± SEs, and daily respiratory metabolism ± SEs.

	Number of species	Density (indiv. m^{-2})	Biomass (g m^{-2})	Respiratory metabolism (kJ m^{-2} d^{-1})
Microfauna	**88**	**4.8×10^6**	**0.36**	**0.21**
Nematoda	88	$(4.8 \pm 1.4) \times 10^6$	0.36 ± 0.08	0.21 ± 0.07
Mesofauna	**78**	**61×10^3**	**3.07**	**0.77**
Collembola	31	$(13 \pm 2.8) \times 10^3$	0.24 ± 0.18	0.04 ± 0.02
Mesostigmata	27	$(9 \pm 2.6) \times 10^3$	0.14 ± 0.05	0.04 ± 0.01
Enchytraeidae	20	$(39 \pm 13.3) \times 10^3$	2.65 ± 1	0.68 ± 0.24
Macrofauna	**137**	**402**	**6.07**	**0.79**
Lumbricidae	3	34 ± 11	2.13 ± 0.61	0.13 ± 0.03
Araneae	29	37 ± 8	0.24 ± 0.08	0.02 ± 0.004
Diplopoda	2	7 ± 2	0.19 ± 0.05	0.01 ± 0.005
Chilopoda	6	13 ± 4	0.04 ± 0.01	0.004 ± 0.001
Isopoda	1	1.2 ± 0.6	0.03 ± 0.01	0.002 ± 0.001
Gastropoda	7	5.2 ± 2.2	0.33 ± 0.22	0.04 ± 0.01
Insecta				
Diptera	*	97 ± 26	1.06 ± 0.3	0.19 ± 0.04
Coleoptera				
Larvae	*	114 ± 17	1.19 ± 0.29	0.30 ± 0.09
Carabidae	13	15 ± 2.9	0.28 ± 0.07	0.03 ± 0.01
Staphylinidae	62	58 ± 12	0.10 ± 0.04	0.02 ± 0.005
Others	8	4 ± 1.2	0.264 ± 0.258	0.03 ± 0.02
Dermaptera	1	7 ± 4.5	0.18 ± 0.04	0.02 ± 0.01
Blattodea	1	0.9 ± 0.5	0.007 ± 0.004	0.0005 ± 0.0003
Lygaeidae	4	9 ± 4	0.03 ± 0.006	0.01 ± 0.006
Mesofauna	**303**	**4896265**	**9.49**	**1.77**

* Not identified to the species level.

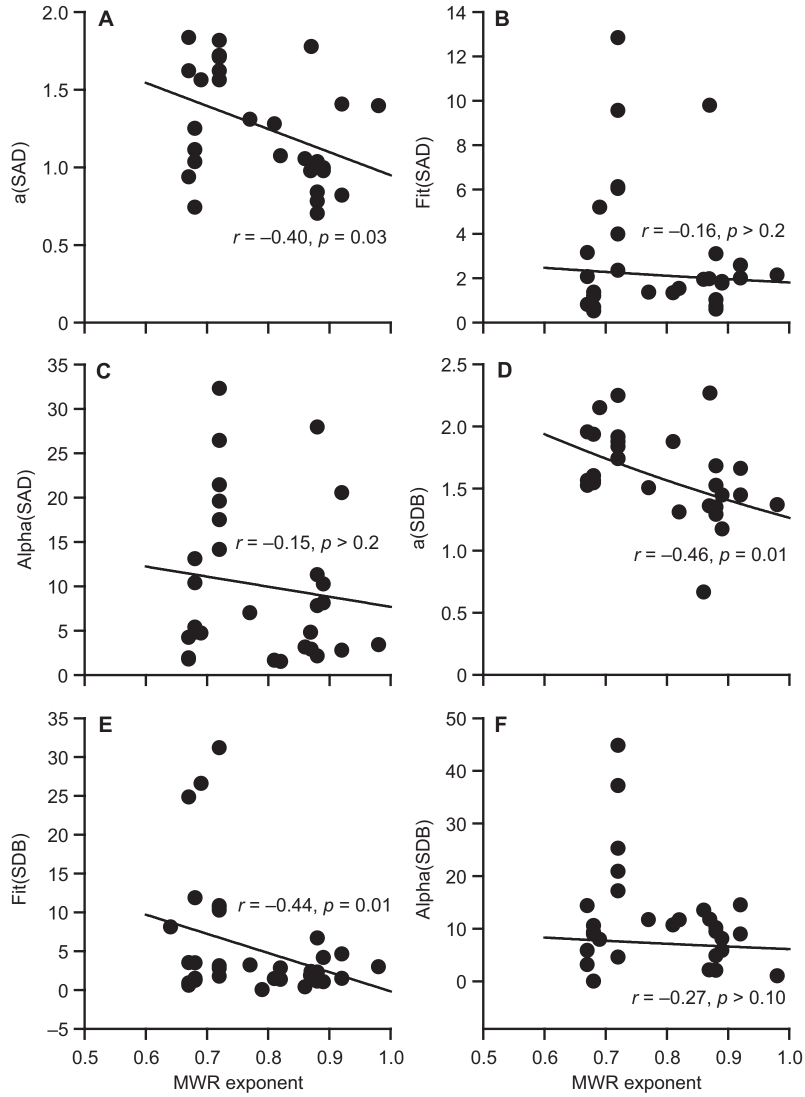

Fig. 2. Alpha diversities obtained from the fit of log-transformed abundance rank order (SAD) and biomass rank order (SBD) distributions for 32 soil communities with more than 10 species, dependent on average taxon metabolic rate slopes.

statistically significant ($p < 0.05$) only in the case of evenness. Additionally, there was a weak indication of better fits of the log-normal in taxa with higher MWR exponent (Fig. 2B and E).

Lastly, we compared the measured-density–respiration relationship for all the species with the theoretical expectation under the assumption of a constant MWR exponent of 0.75 (Fig. 3). The true exponent ($b = 0.87 \pm 0.02$) produced significantly ($p < 0.001$) less steep line than the predicted exponent (0.98 ± 0.02) (Fig. 3A). Accordingly the predicted respiration was generally higher than the true one (Fig. 3B).

Discussion

Our work indicates that observed differences in MWR exponents should not only be treated as random variation centered around a predicted value of 0.75. Even if the average value is close to expectation, the observed variance might have measurable impact on metabolism-dependent ecological distributions and aggregate variables like total density, biomass, or metabolism. For some taxa, b appeared to be correlated with average body weight. This contradicts the MTE claim of a universal exponent for all taxa. This fact has certainly been neglected in the discussion about

MTE and its predictions according to ecological scaling (Brown *et al.* 2004, Farrell-Gray & Gotelli 2005, White & Seymore 2003, Enquist *et al.* 2007, McNab 2008).

We tentatively showed that absolute densities and biomass were correlated with exponent values (Fig. 3), although these correlations were statistically not strong. Further, alpha diversity decreased moderately with increasing exponent (Fig. 4). However, more and better resolved data are necessary to unequivocally answer the question how strong MWR exponents scatter across taxa. Available compilations (cf. Makarieva *et al.* 2008, Ehnes *et al.* 2011 for reviews) indicate a lower boundary of $b_{\mathrm{min}} = 0.5$ and an upper boundary of $b_{\mathrm{max}} = 1.2$. In our data set, b_{min} was 0.64 (Heteroptera) and $b_{\mathrm{max}} = 0.98$ (several Collembola). However, for many taxa, for instance Nematoda, Acarina, or Enchytraeidae, species-specific metabolic scaling exponents are not available and any calculation must base on average taxon-level values. Although it seems reasonable to assume that these small and morphologically very similar organisms (within one taxon) have also similar metabolism, better resolved data are urgently necessary for a sound testing of metabolic theory.

Species densities and individual respiration appeared to be allometrically linked with an exponent of $b/c = -1.00$ (Fig. 4). This finding implies the equality of the MWR exponent and the exponent of the abundance–body mass relationship c, and is an equivalent to the well-known energy equivalence rule EER (Damuth 1981, Allen *et al.* 2002, Ernest 2005, White *et al.* 2007) that states independence of population energy use from body size. EER has been confirmed for a number of ecosystems (Damuth 1987, Meehan *et al.* 2006) but negative findings (Russo 2003 *et al.* Ernest 2005) still prohibit to call it a universal ecological rule.

A shortcoming of our study is the fact that many data points in our regressions are statistically not independent. First, we had to use pooled data from several sampling dates. This seems of minor importance due to the large differences in abundance and species composition among the samples. Thus they might be treated as being independent. More important is the lack of phylogenetic independence (Webb *et al.* 2002, Felsenstein 2004). There is surely a certain but unknown degree of phylogenetic autocorrelation in our data introduced by the uneven spacing of our soil taxa across the metazoan phylogenetic tree. Unfortunately, most taxa are phylogenetically very poorly resolved. This regards particularly the micro- and mesofauna but also many arthropod taxa. Therefore, any phylogenetically explicit correlation analysis would have to struggle with a large number of unresolved polytomies making the final correlation coefficients not more reliable than the raw coefficients.

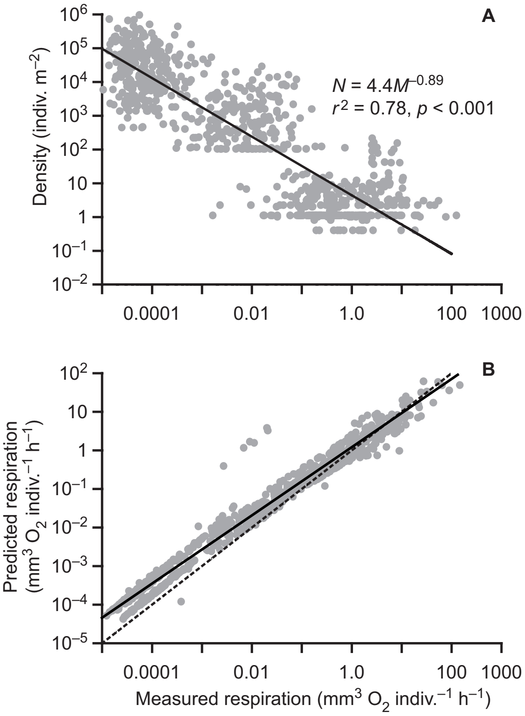

Fig. 3. (**A**) Measured-respiration–density relationship for all the species. (**B**) Predicted respiration calculated using a constant MWR with the exponent of 0.75 was generally higher than the true respiration (solid line). The dashed line shows the expected 1:1 relationship.

Thus, our work does not give straightforward answers about the impact of exponent variability on ecological processes. Although the results are consistent and in line with our theoretical predictions, statistical corroboration was at most moderate. Our findings should therefore be treated as a hypothesis generating and not a hypothesis confirming.

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Appendix

The individual metabolic rates of the present study were derived from literature. It has long been recognized that there is a relationship between body weights (W) and metabolic rates (M) such as $M = aW^b$, where a and b are constants, for specific groups of organisms (Duncan & Klekowski 1977). In the present study, these constants were either directly taken from the literature or were calculated from literature data, using reduced major axis regression.

Metabolic rate is known to vary with temperature and adjustment to field temperature was made using the traditional Q_{10} factor, which measures the change in rate of a biochemical reaction over a 10 °C rise in temperature. Field-temperature-adjusted metabolic rate relates to the original metabolic rate as follows:

$$M_T = M_{T_0} Q_{10}^{(T-T_0)/10}$$

where M_T is the metabolic rate at field temperature T, M_{T_0} is the metabolic rate at temperature T_0, i.e. the temperature for which the regression holds; and Q_{10} is the correction coefficient, which varies according to the group of organisms considered (Van't Hoff 1884).

In most cases, the regression between metabolic rate and body weight is based on fresh weight. Conversion of dry weight to fresh weight was made assuming a fresh weight/dry weight ratio specific for each group.

Nematoda

Metabolic rates (mm^3 O$_2$ indiv.$^{-1}$ h^{-1}) were calculated using the equation of Klekowski *et al.* (1972) at 20 °C: $M = 0.0014W^{0.72}$, where W is the fresh body weight (μg), and adjusted to field temperatures using $Q_{10} = 2.5$ (Uvarov *et al.* 2009).

Mesostigmata (Acari)

Metabolic rates (mm^3 O$_2$ indiv.$^{-1}$ h^{-1}) of mesostigmats were calculated using the regressions provided by Wood and Lawton (1973) at 10 °C: Gamasina: $M = 102.33W^{0.869}$, Uropodina: $M = 5.035W^{0.671}$, where W is the fresh body weight (g), and adjusted to field temperatures using $Q_{10} = 3$ (Persson & Lohm 1977).

Collembola

Metabolic rates of springtails were calculated in different ways depending on the species. Petersen (1981) estimated the relationship between metabolic rate (mm^3 O$_2$ indiv.$^{-1}$ h^{-1}) and dry body weight (μg) at 10 °C to be $M = 0.00147W^{0.828}$ for *Isotomiella minor*; $M = 0.00214W^{0.80}$ for *Isotoma notabilis*; $M = 0.00263W^{0.835}$ for *Lepidocyrtus lanuginosus*; $M = 0.00216W^{0.669}$ for *Folsomia quadrioculata*; $M = 0.00134W^{0.963}$ for *Pogonognathellus flavescens*. Temperature corrections were made with Q_{10} of 2, 1.9, 2.9, 2.2 and 5.2, respectively (Petersen 1981). Due to the lack of data for the other species of collembola encountered in the present work, a general relationship was calculated for the whole taxa from the data reported by Ehnes *et al.* (2011) on 128 individuals from 26 species. Using reduced major axis regression, this relationship between metabolic rate (mm^3 O$_2$ indiv.$^{-1}$ h^{-1}) and fresh body weight (g) was estimated to be: $M = 168.4W^{0.85}$ at 20 °C (Fig. A1). The Q_{10} value was assumed to be 2.6.

Enchytraeidae

Metabolic rates (mm^3 O$_2$ indiv.$^{-1}$ h^{-1}) were calculated using the regression provided by Persson and Lohm (1977) at 20 °C: $M = 33.6W^{0.67}$, where W is the fresh body weight (g), and adjusted to field temperatures using $Q_{10} = 1.4$ between 2.5 and 10 °C and $Q_{10} = 1.8$ between 10 and 20 °C (Phillipson *et al.* 1979).

Lumbricidae

Metabolic rates of earthworms were calculated according to Byzova (2007). She estimated the relationship between metabolic rate (mm^3 O$_2$ indiv.$^{-1}$ h^{-1}) and fresh body weight (g) of adult earthworms at 19 °C to be $M = 78W^{0.91}$ for *Aporrectodea caliginosa*, $M = 119W^{0.71}$ for *Dendrobaena octaedra* and $M = 93W^{0.84}$ for *Lumbricus rubellus*. In the present study, the equations were used for both adults and juveniles. The values obtained were adjusted to field temperatures using $Q_{10} = 2$ (Axelsson *et al.* 1984).

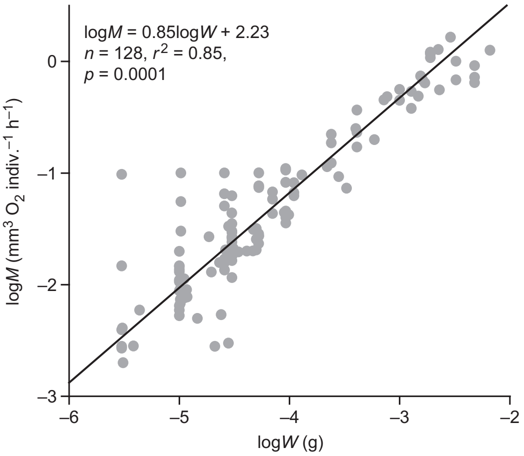

Fig. A1. Relationship between fresh body weight (W, g) and metabolic rate (M, mm^3 O$_2$ indiv.$^{-1}$ h^{-1}) at 20 °C for 26 species of springtails.

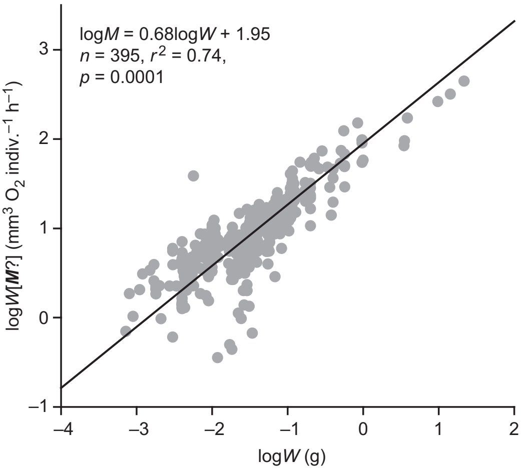

Fig. A2. Relationship between fresh body weight (W, g) and metabolic rate (M, mm^3 O$_2$ indiv.$^{-1}$ h^{-1}) at 20 °C for 65 species of spiders.

Diplopoda

Metabolic rates of millipedes were calculated according to Byzova (2007). She estimated the relationship between metabolic rate (mm^3 O$_2$ indiv.$^{-1}$ h^{-1}) and fresh body weight (g) at 22 °C to be $M = 157W^{0.79}$ for *Polydesmus complanatus* and $M = 45.96\ W^{0.69}$ for other millipedes at 20 °C. Temperature corrections were made assuming $Q_{10} = 2.5$ (Axelsson *et al*. 1984).

Chilopoda

Metabolic rates of centipedes were calculated according to Byzova (2007). She estimated the relationship between metabolic rate (mm^3 O$_2$ indiv.$^{-1}$ h^{-1}) and fresh body weight (g) at 20 °C to be $M = 54.98W^{0.64}$. Temperature corrections were made assuming $Q_{10} = 2.5$ (Axelsson *et al*. 1984).

Araneae

The relationship between metabolic rate (M, mm^3 O$_2$ indiv.$^{-1}$ h^{-1}) and fresh body weight (W, g) of spiders was derived from the data reported by Byzova (2007) and Ehnes *et al*. (2011) on 395 individuals from 65 species. Using reduced major axis regression, this relationship was estimated to be: $M = 89.13W^{0.68}$ at 20 °C (Fig. A2).

Temperature corrections were made assuming $Q_{10} = 2$ (Persson & Lohm 1977).

Isopoda

Metabolic rates of woodlice were calculated according to Byzova (2007). She estimated the relationship between metabolic rate (M, mm^3 O$_2$ indiv.$^{-1}$ h^{-1}) and fresh body weight (W, g) of 14 species of woodlice at 20 °C to be $M = 66.85W^{0.63}$. Temperature corrections were made assuming $Q_{10} = 2$ (From 1.4 to 2.9; Byzova 2007).

Gastropoda

Snails

Mason (1971) estimated the relationship between metabolic rate (M, mm^3 O$_2$ indiv.$^{-1}$ h^{-1}) and ash-free dry body weight (W, mg) at 10 °C to be $M = 0.0115W^{0.65}$ for 20 species of wooland snails. Temperature corrections were made assuming Q_{10}= 1.69 for *Punctum pygmaeum*, Q_{10}= 2.01 for *Vitrina pellucida*, Q_{10}= 2.21 for *Fruticicola fruticum* and Q_{10}= 2.37 for *Oxychilidae* (Mason 1971).

Slugs

Metabolic rate of *Doreceras agreste* was calculated according to the relationship between metabolic rate (M, mm^3 O$_2$ indiv.$^{-1}$ h^{-1}) and fresh body weight (W, g) proposed by Byzova (2007) for *Doreceras reticulatum*: $M = 333W^{0.85}$, while

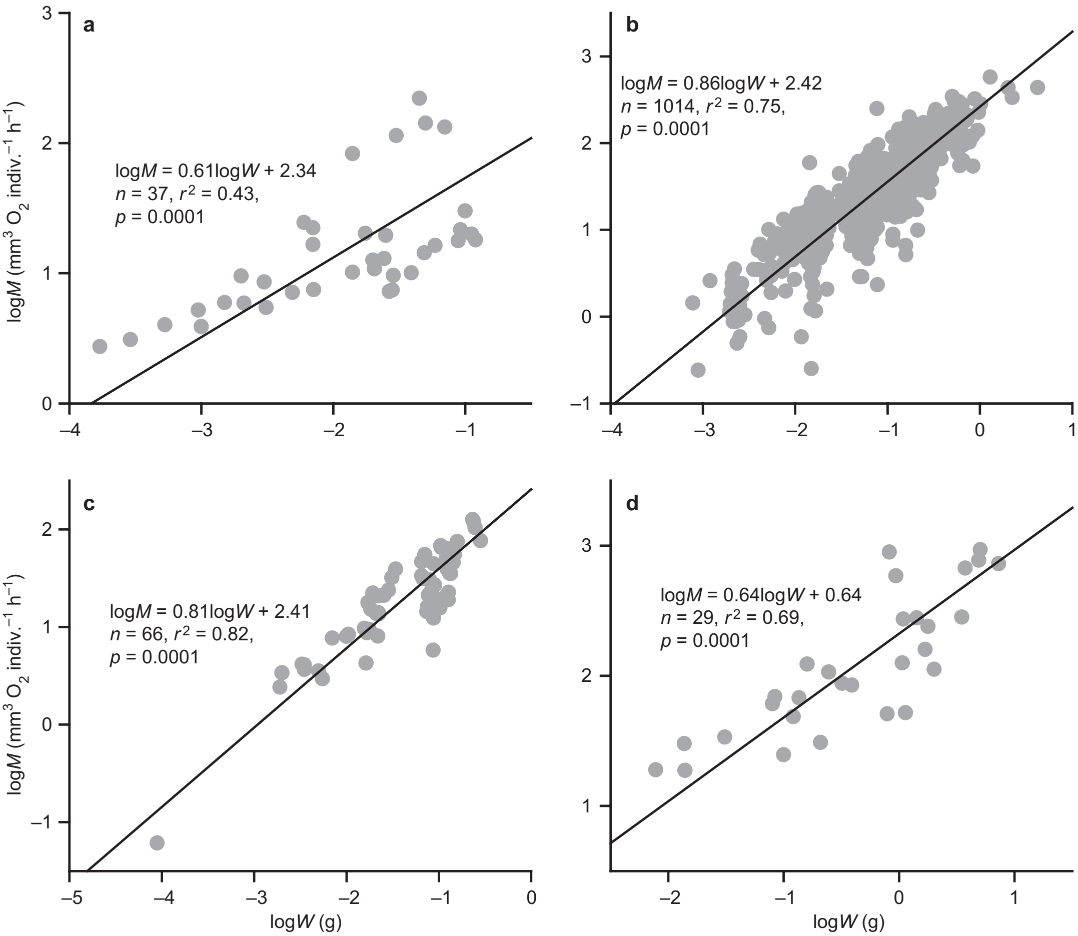

Fig. A3. Relationships between fresh body weight (*W*, g) and metabolic rate (*M*, mm^3 O$_2$ indiv.$^{-1}$ h^{-1}) at 25 °C in (**a**) beetle larvae based on 37 individuals, (**b**) carabid beetles based on 1014 individuals of 55 species, (**c**) staphylinoid beetles based on 66 individuals of 13 species, (**d**) scarabaeoid beetles based on 29 individuals of 29 species.

metabolic rate of *Arion fasciatus* was calculated according to the relationship proposed for *Arion circumscriptus*: $M = 261.8W^{0.75}$.

Coleoptera

Larvae and pupae

The relationship between metabolic rate (M, mm^3 O$_2$ indiv.$^{-1}$ h^{-1}) and fresh body weight (W, g) of coleopteran larvae was derived from the data reported by Byzova (2007) on 37 individuals. Using reduced major axis regression, this relationship was estimated to be: $M = 220.4W^{0.61108}$ at 25 °C (Fig. A3a). Due to the lack of relevant data, this equation was also used for pupae. Temperature corrections were made assuming $Q_{10} = 2$ (Persson & Lohm 1977).

Carabidae

The relationships between metabolic rate (M, mm^3 O$_2$ indiv.$^{-1}$ h^{-1}) and fresh body weight (W, g) of ground beetles were derived from the data reported by Byzova (2007), Makarieva *et al.* (2008), Persson and Lohm (1977) and Ehnes *et al.* (2011) on 1014 individuals from 55 species. Using reduced major axis regression, this relationships was estimated to be at 25 °C: $M = 264.12W^{0.86}$ (Fig. A3b).

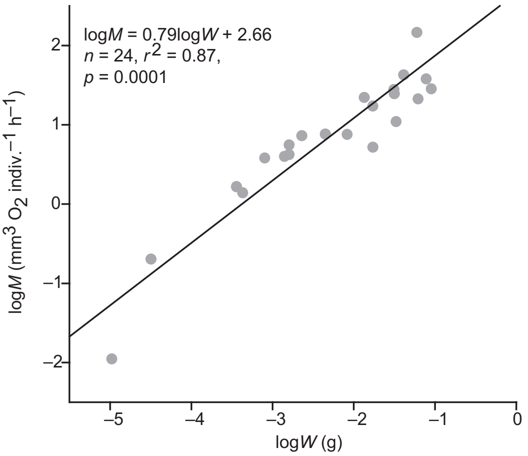

Fig. A4. Relationship between fresh body weight (W, g) and metabolic rate (M, mm^3 O$_2$ indiv.$^{-1}$ h^{-1}) at 25 °C of dipteran larvae based on 24 measurements.

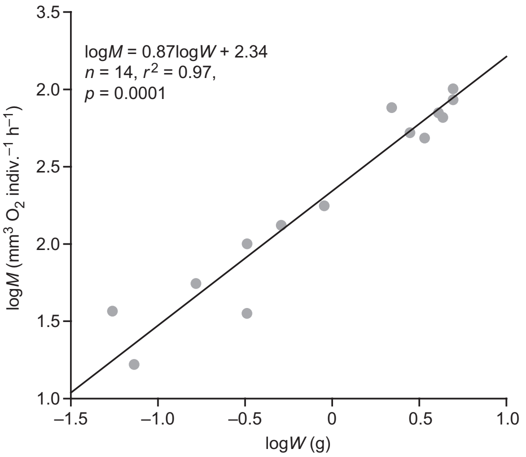

Fig. A5. Relationship between fresh body weight (W, g) and metabolic rate (M, mm^3 O$_2$ indiv.$^{-1}$ h^{-1}) at 25 °C for 14 species of cockroaches.

Staphylinoidea (Silphida, Leiodidae, Scydmaenidae, Staphylinidae)

The relationships between metabolic rate (M, mm^3 O$_2$ indiv.$^{-1}$ h^{-1}) and fresh body weight (W, g) of *Staphylinoidea* beetles were derived from the data reported by Byzova (2007), Makarieva *et al*. (2008), Persson and Lohm (1977) and Ehnes *et al*. (2011) on 66 individuals from 13 species. Using reduced major axis regression, this relationship was estimated to be at 25 °C: $M = 257.34W^{0.81}$ (Fig. A3c).

Scarabaeoidea (Geotrupidae, Aphodiidae)

The relationship between metabolic rate (M, mm^3 O$_2$ indiv.$^{-1}$ h^{-1}) and fresh body weight (W, g) of scarabaeids was derived from the data reported by Makarieva *et al*. (2008) on 29 species. Using reduced major axis regression, this relationship was estimated to be at 25 °C: $M = 210.86W^{0.64}$ (Fig. A3d). Temperature corrections were made for all adult coleopterans assuming $Q_{10} = 2$ (Persson & Lohm 1977).

Diptera (larvae)

The relationship between metabolic rate (M, mm^3 O$_2$ indiv.$^{-1}$ h^{-1}) and fresh body weight (W, g) of Diptera larvae was derived from the data reported by Persson and Lohm (1977) and Byzova (2007). Using reduced major axis regression, this relationship was estimated to be at 25 °C: $M = 456.56W^{0.788}$ (Fig. A4). Temperature corrections were made assuming $Q_{10} = 2.25$ (considering estimates of $Q_{10} = 1.37$–3.54; Byzova 2007).

Blattodea

The relationship between metabolic rate (M, mm^3 O$_2$ indiv.$^{-1}$ h^{-1}) and fresh body weight (W, g) of cockroaches was derived from the data reported by Makarieva *et al*. (2008) on 14 species. Using reduced major axis regression, this relationship was estimated to be at 25 °C: $M = 219.94W^{0.87}$ (Fig. A5). Temperature corrections were made assuming $Q_{10} = 2$ (Persson & Lohm 1977).

Heteroptera (Lygaeidae)

The relationship between metabolic rate (M, mm^3 O$_2$ indiv.$^{-1}$ h^{-1}) and fresh body weight (W, g) of ground bugs was derived from data reported by Makarieva *et al*. (2008) on 11 species. Using reduced major axis regression, this relationship was estimated to be at 25 °C: $M = 238.95W^{0.62}$ (Fig. A6). Temperature corrections were made assuming $Q_{10} = 2$.

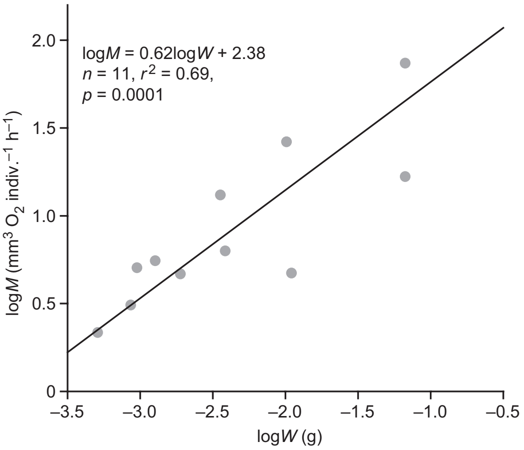

Fig. A6. Relationship between fresh body weight (*W*, g) and metabolic rate (*M*, mm^3 O$_2$ indiv.$^{-1}$ h^{-1}) at 25 °C for 11 species of bugs.

Dermaptera

The relationship between metabolic (*M*, mm^3 O$_2$ indiv.$^{-1}$ h^{-1}) and fresh body weight (*W*, g) of insects was given by Makarieva *et al*. (2008) as $M = 320W^{0.82}$. This relationship was used to calculate the metabolic rate of earwigs.