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Testing Metabolic Theory of Ecology on the local scale: a preliminary study

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Abstract. Data on the density and the body mass of a single community of soil fauna were collected and metabolic rates were calculated from the literature data to test some predictions of the metabolic theory of ecology on the local scale. Part of the results are in accordance with the theory: power functions were found between the metabolic rate and the body mass, and between the density and the body mass. These two relationships have opposite exponents inducing that total population energy use is independent of the body mass. However, the exponents of the relationships were significantly different from the predicted values of |3/4|. The metabolic rate – body mass relationships yielded an exponent >0.8, while the density – body mass relationships yielded an exponent <-0.85. Our results indicate that the metabolic theory of ecology does not hold at the local level. Few studies have been carried out on the local scale and further analysis is required to validate this controversial but promising theory.

Key words: allometric scaling; soil fauna; energy equivalence.

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1. Introduction

The metabolic theory of ecology, MTE, (Brown et al. 2004) is recently one of the most controversially discussed ecological theories (Kozłowski & Konarzewski 2004; Gillooly et al. 2005; Muller-Landau et al. 2006; van der Meer 2006; Allen et al. 2007; Hawkins et al. 2007; del Rio 2008; Enquist et al. 2009; Price et al. 2012). Developed using first principles of physics, geometry, chemistry and biology, MTE consists of a series of mathematical models that describes the complexities of ecology by showing how metabolic rate controls ecological processes at all levels of organization from individuals to the biosphere (Brown et al. 2004). It is a potentially powerful tool, capable to explain many ecological – in particular macroecological – and evolutionary patterns from a small number of assumptions, such as the optimization of metabolic rates with respect to body size and temperature, or the approximate self-similarity of metabolic active networks of organisms.

The basic equation of the metabolic theory

$$M \propto W^{3/4} e^{-E/kT} \qquad (1)$$

links whole organism metabolic rate M to body weight W and body temperature T (E denotes the average activation energy of catalytic reactions and k is the Boltzmann's constant). Within this equation, the long known three quarter power scaling rule suggested by Kleiber (1932) can be recognized. The temperature term is taken from the Arrhenius equation of chemical reactions. Although equation 1 is derived from a model that strictly applies only to organisms with fractal like supply networks like vertebrates and vascular plants (West et al. 1997, 1999). Brown and co-workers (2004) have found support for this simplistic basic equation over a wide range of organisms from bacteria to invertebrates and higher plants.

Savage et al. (2004) combined equation 1 with Malthusian growth law to develop a model relating species densities N to body weight:

$$N \infty W^{-3/4} e^{E/kT} \quad (2)$$

Equation 2 therefore predicts that the scaling of population density with body mass is inversely proportional to the scaling of individual metabolic rate (Eq. 1). As a result, the total population energy use M_p, calculated as the product of individual metabolic rate and population density, is independent of body weight:

$$M_p = MN = const \quad (3)$$

This last equation is known as the energy equivalence rule (equal biomass hypothesis in the case of poikilothermic organisms) proposed by Damuth (1987).

A large number of tests was carried out to assess the validity of MTE but the results obtained were mixed (e.g. Meehan 2006; Ulrich 2006; Chown et al. 2007; Downs et al. 2007; Duncan et al. 2007; Hawkins et al. 2007; Sanders et al. 2007; Wang et al. 2009). One of the main questions is whether this theory is universal (i.e. independent of taxon, and spatial and temporal scale), as claimed by its authors. If so, MTE should also hold at the local level and, although developed on vertebrates and plants, should hold for invertebrates. So far, no test has confirmed this claim. Tilman et al. (2004) indicated that body weight data must span at least over four orders of magnitude to allow for good fittings of the MTE model. This explains why no test has been carried out so far at the local scale, where variable ranges are relatively low. The present study intends to verify MTE predictions described above at the local level for soil invertebrates (*Nematoda, Enchytraeidae, Collembola, Lumbricidae, Araneae, Diplopoda, Gastropda, Isopoda, Insecta*) from a deciduous forest in Central Poland. Working with the soil sub-system enables us to collect data ranging over a few orders of magnitude, both in term of body weight and density, allowing for a good testing of the above equations. More precisely, we hypothesize that:

1 – The natural logarithm of temperature-corrected metabolic rate (M) should be a linear function of the logarithm of body mass (W). The slope of this relationship is predicted to be 3/4:

$$\ln (M e^{E/kT}) = 3/4 \ln W + const \quad (4)$$

2 – The natural logarithm of a given species density (N), corrected for temperature, should be a linear function of the logarithm of average body mass (W). The slope of this relationship is predicted to be – 3/4:

$$\ln (N e^{-E/kT}) = -3/4 \ln W + const \quad (5)$$

3 – The total energy flux of a population per unit area (M_p) should be invariant with respect to body mass:

$$M_p = \text{constant} \quad (6)$$

2. Materials and methods

The fieldwork was conducted on a rather homogeneous 200 m^2 (10 x 20 m^2) plot located on the Eastern border of Kampinos National Park (Poland) close to the village „Dziekanów Leśny” in a 40–50 year-old deciduous forest growing on a podzolic soil. Although collecting the data from a single site introduces the problem of data non-independency, it allows to obtain data related to a single community of interacting individuals.

The soil fauna was sampled in August and October 2009. Samples for different organism groups were collected close to each other in randomly chosen 1 m^2 quadrats. Ten replicates were taken for each group. Given that most soil fauna populations are concentrated within the first 5 to 10 cm of soil (Petersen & Luxton 1982), the samples were collected to a depth of 10 cm. The nematodes were sampled using a 1.8 cm diameter corer and were extracted using the Whitehead and Hemming's modification of the Baerman method (Whitehead & Hemming 1965). The mesofauna was sampled using a 3.5 cm diameter corer and were extracted using a modified Macfadyen high gradient canister (Macfadyen 1961) in the case of springtails and using the O'Connor modification of the Baerman funnel (O'Connor 1955) in the case of enchytraeids. The macrofauna was hand-sorted from 30 x 30 cm samples to a depth of 10 cm. In addition, the surface layer of 50 x 50 cm 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.

Body mass was estimated either by direct weighing after drying for 48 h at 60°C in vacuum conditions; or by length and/or width-to-weight regressions. When necessary, fresh-weight/dry-weight ratios were adopted from Persson and Lohm (1977).

The metabolic rate of each individual was derived from the long known relationship between body weights (W) and metabolic rates (M) for specific groups of organisms such as $M=aW^b$, where a and b are constants (cf. the detailed discussion in Persson & Lohm 1977). These parameters were either directly taken from the literature or were calcu-

Table 1. Parameters used for the calculation of individual metabolic rate (*M*, mm^3 O_2 ind^{-1} h^{-1}) from fresh individual body mass (*W*, g) at 10°C. The relationships are given in the form $M=aW^b$

Taxon	**a**	**b**	Q_{10}	**Sources** *** Regression calculated on the basis of data from the quoted 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	”
Lepidocyrtus lanuginosus	101.37	0.835	2.9	”
Folsomia quadrioculata	9.5	0.669	2.2	”
Pogonognathellus flavescens	260.64	0.963	5.2	”
other collembolan	64.77	0.85	2.6	* Ehnes 2011 (n=128; r^2=0.85)
Mesostigmata				
Gamasina	102.33	0.869	3	Wood and Lawton 1973
Uropodina	5.035	0.671	3	”
Enchytraeidae	18.67	0.67	1.6	Persson and Lohm 1977
Lumbricidae				
Aporrectodea caliginosa	41.8	0.91	2	Byzova 2007
Dendrobaena octaedra	63.8	0.71	2	”
Lumbricus rubellus	49.84	0.84	2	”
Diplopoda				
Polydesmus complanatus	52.28	0.79	2.5	”
other diplopoda	18.4	0.69	2.5	”
Chilopoda	22	0.64	2.5	”
Isopoda	31.1	0.63	2.15	”
Araneae	44.57	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	”
Punctum pygmaeum	0.3	0.65	1.69	Mason 1971
Vitrina pellucida	0.3	0.65	2.01	”
Fruticicola fruticum	0.3	0.65	2.21	”
Oxychilidae	0.3	0.65	2.37	”
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 and Lohm 1977; Ehnes 2011 (n= 1014; r^2 = 0.74)
Staphylinoidea	91	0.81	2	* Byzova 2007; Makarieva et al. 2008; Persson and 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)
other coleopterans	98.39	0.84	2	* Makarieva et al. 2008 (n= 159; r^2 = 0.79)
Diptera larvae	135.28	0.788	2.25	* Persson & Lohm 1977; Byzova 2007 (n= 24; r^2 = 0.87)
Blattodae	77.76	0.87	2	* Makarieva et al. 2008 (n= 14; r^2 = 0.93)
Heteroptera	84.5	0.62	2	* Makarieva et al. 2008 (n= 11; r^2 = 0.69)
other insects	113.14	0.82	2	Makarieva et al. 2008

lated from literature data, using reduced major axis regression (RMA) (Table 1). We adjusted to field temperatures using Q_{10} values. Temperature data were collected from the closest meteorological station of Kampinos National Park (Izabelin).

In order to test the first hypothesis, regarding the relationship between metabolic rate (M), body mass (W) and temperature (T), regressions of the form ln ($Me^{E/kT}$) = δ ln $W + a$ were run on ln-transformed data. The parameter δ was expected to equal 3/4. Body weight (g FW) and whole organism metabolic rate (mm^3 O_2 ind^{-1} h^{-1}) were averaged per species. The second hypothesis, relating population density (N) to body mass, was tested by performing regressions of the type ln ($Ne^{-E/kT}$) = β ln $W + a$ on ln-transformed data. The parameter β was expected to equal -3/4. Density referred to the number of individuals per square meter. In both cases temperature values used corresponded to the 30 day average preceding the sampling date. The value of 0.65 eV was taken as the average activation energy (E) of catalytic reactions (Gillooly et al. 2001). The third hypothesis, stating that population energy use (M_p) is invariant with body mass, was evaluated in two ways. First we checked whether there was a correlation between both parameters. Second we checked whether the sum of the slopes calculated for the two first hypotheses was close to zero.

Each sampling date (August 2009 and October 2009) was considered separately. Correlation and regression analyses were performed on ln-transformed data using *Past* (Hammer et al. 2001). As advised by Griffiths (1992), regression slopes refer to reduced major axis (RMA) slopes.

3. Results

A total number of 1651 and 1680 individuals belonging to 127 and 122 species were collected in August 2009 and October 2009 respectively. The total biomass was 4.55±2.09 g FWm^{-2} in August 2009 and 2.72±1.43 g FWm^{-2} in October 2009. Body mass covered eight orders of magnitude, ranging from 5.09 x 10^{-9} g FW (*Eucephalobus* sp.1- Nematoda) to 0.28 g FW (*Aporrectodea caliginosa* – Lumbricidae) in August 2009 and from 8.6 x 10^{-9} g FW (*Aphelenchoides* sp.1- Nematoda) to 0.51 g FW (*Arion fasciatus* – Gastropoda) in October 2009. The most abundant species was the nematode *Aphelenchoides* sp.1 (1,871,642 ind. m^{-2} in August 2009 and 1,369,966 ind. m^{-2} in October 2009), while the least abundant species were carabid beetles (<1 ind. m^{-2}). The density ranged six orders of magnitude.

As expected, a strong positive correlation (Fig. 1) was found between individual metabolic rate and body mass for both data sets (r^2=0.99; p=0.0001). However, the RMA slopes significantly differed from the expected 3/4 value (95% CI: 0.82;0.85 and 0.84;0.87 respectively). Similarly, the density – body mass relationship (Fig. 2) can be described by a power function, since a strong correlation has been found for the ln-transformed data (r^2 =0.85 and 0,82; p=0.0001) but once again the RMA slopes significantly deviated from the predicted value of -3/4 (95% CI: -0.92; -0.81 and -0.95; -0.83).

Figure 3 shows that there was no significant relationship between body mass and total energy use (p=0.31 and 0.16),

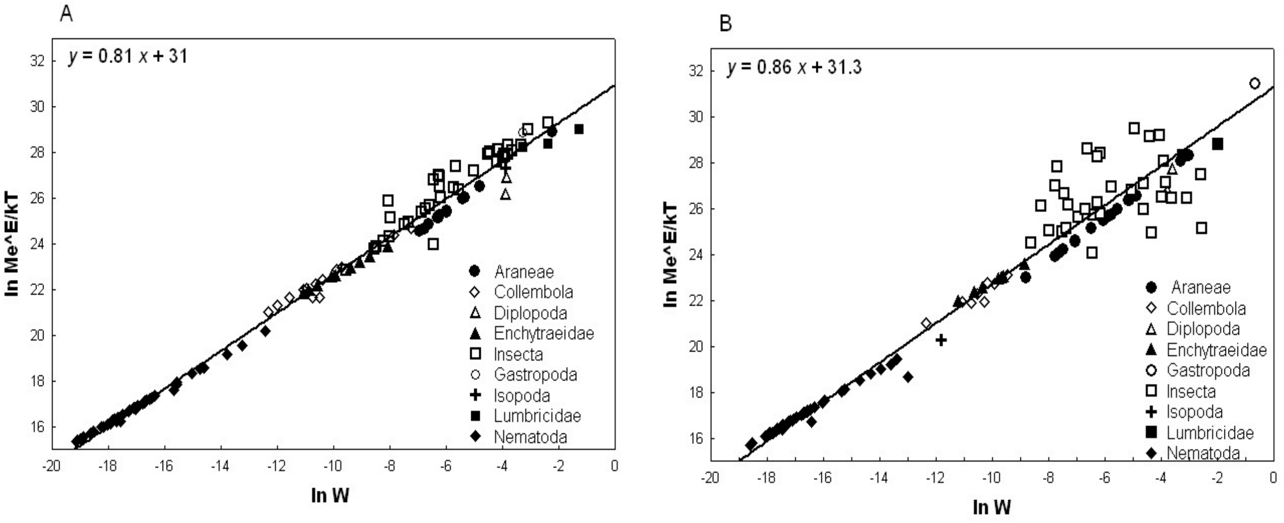

Figure 1. Relationship between temperature-corrected metabolic rate, ln(Me^E/kT) and body weight, ln W (g FW). (A) Animals collected in August 2009. r^2 = 0.99; p=0.0001; N= 127. The slope significantly differs from the predicted 3/4 (95%CI: 0.82;0.85). (B) Animals collected in October 2009. r^2 = 0.99; p=0.0001; N= 122. The slope significantly differs from the predicted 3/4 (95%CI: 0.84;0.87)

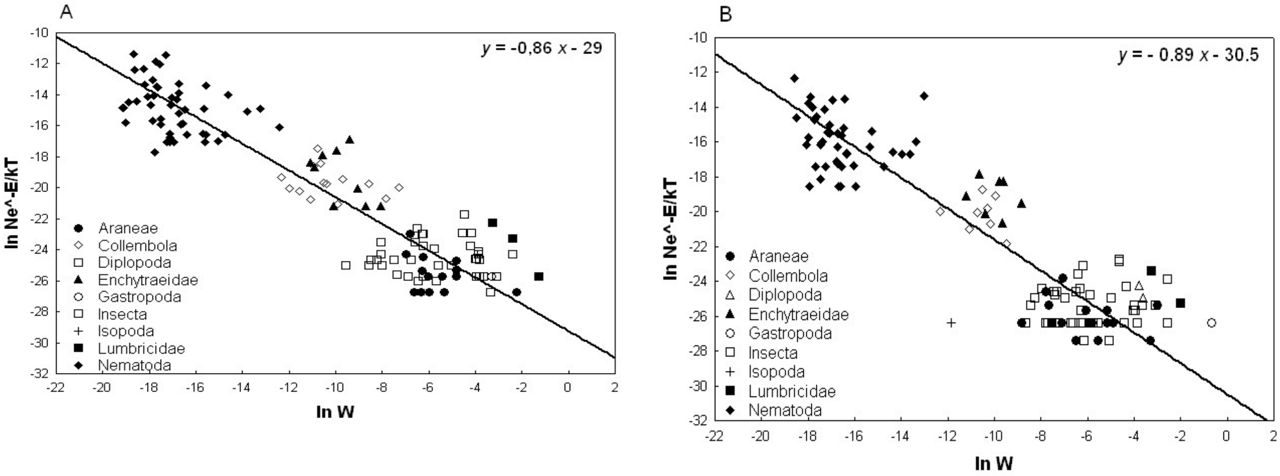

Figure 2. Relationship between temperature-corrected density, ln(Ne^-E/kT) and body weight, ln W (g FW). (A) Animals collected in August 2009. $r^2 = 0.85$; p=0.0001; N= 127. The slope significantly differs from the predicted 3/4 (95%CI: -0.92;-0.81). (B) Animals collected in October 2009. $r^2 = 0.82$; p=0.0001; N= 122. The slope significantly differs from the predicted 3/4 (95%CI: -0.95;-0.83)

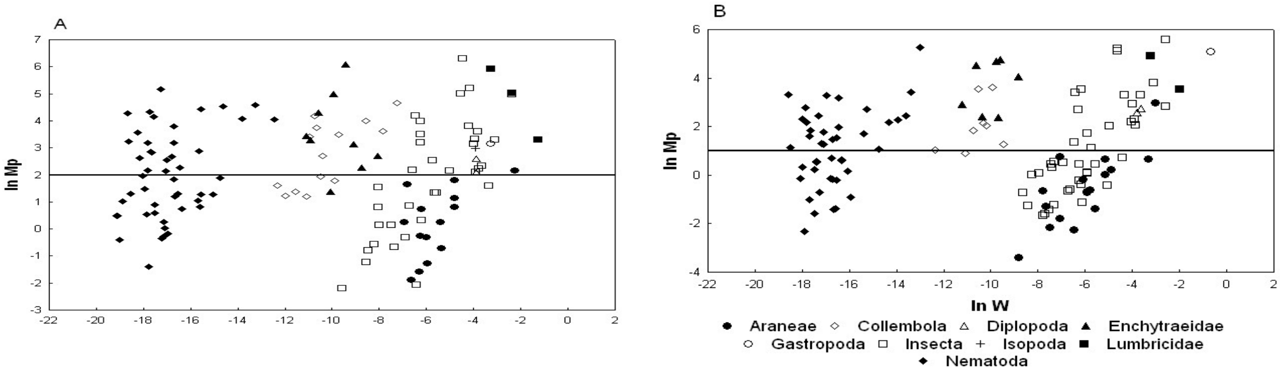

Figure 3. Relationship between total population energy use, ln Mp and body weight, ln W (g FW). (A) Animals collected in August 2009. $r^2 = 0.01$; p=0.31; N= 127. (B) Animals collected in October 2009. $r^2 = 0.02$; p=0.16; N= 122

and the sums of the slopes of equation 1 and 2 were found to be close to zero (-0.031±0.031 and -0.03028±0.035 respectively), as predicted by equation 3. These results are in agreement with the energy equivalence rule.

4. Discussion

The aim of the present study was to test some predictions of the metabolic theory of ecology (eq. 1 to 3) at the local scale on invertebrates. MTE has so far been tested mostly at wide scales, using data compiled from different studies and spanning up to 21 orders of magnitude (Brown et al 2004). One can wonder whether this theory is applicable at the local scale where variable ranges are comparatively narrow. Besides, MTE has been developed on vertebrates and vascular plants (West et al. 1997, 1999) and some doubts have been expressed on whether these models can be applied to invertebrates (Kozłowski & Konarzewski 2004, 2005).

The present study is, to some extent, is accordance with MTE. The metabolic rate and density – body weight relationships were power functions with exponents having the correct sign, and no dependence was found between total population energy use and body weight. However, at the quantitative level, the slopes differed from the predicted values. There has been some debate over the correct value of the exponent of the metabolic rate – body weight scaling (Isaac & Carbone 2010). While the MTE's authors predict 3/4, others claim it to 2/3 as predicted by classical Euclidean geometry from the consideration of surface/volume ratio (Dodds et al. 2001; White & Seymour 2003). The slopes obtained in this study were steeper than 3/4 (Fig. 1), rejecting both predictions. Brown et al. 2004 indicated that the exponent of this relationship should not necessarily equal 3/4 but exhibit a close value. In our case, the slopes obtained are almost a point higher than expected. This suggests that the scaling between metabolic rate and body weight does not take any particular value but vary among organisms. Similarly, the slopes found for the density – body weight relationship were steeper than predicted by equation 2 (Fig. 2). This came as a surprise since many studies carried out at the level of a single community found shallower slope than -3/4 (c.f. Blackburn et al 1993). However, studies carried out at a wider scale often found a slope steeper than -3/4 (c.f. Blackburn & Gaston 1997). Our results may be explained by the fact that the data ranged over many orders of magnitude, reducing the noise inherent to small data bases.

As predicted by MTE, the exponents of equations 1 and 2 were found to have opposite values. As a result, total population energy per unit area is independent of body weight (Fig. 3). It would seem that this last model holds both at the local level and for invertebrates.

The present study found some qualitative supports to the metabolic theory of ecology, yet the parameter values were found to differ from the predicted ones at the local level and for invertebrates. While the specific values are questionable, the basic scaling rules and the evolutionary optimization argument remain undisputed and provide a good starting point for further analysis (del Rio 2008). This work was a short one and more data are necessary to allow for a sound testing of MTE. If its predictions are supported by future data, theoreticians will have a better ground to improve this controversial but promising theory.

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