Phylogenetic grouping, curvature and metabolic scaling in terrestrial invertebrates

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Abstract
For more than a century, the scaling of animal metabolic rates with individual body masses and environmental temperature has predominantly been described by power-law and exponential relationships respectively. Many theories have been proposed to explain these scaling relationships, but were challenged by empirically documented curvatures on double-logarithmic relationships. In the present study, we present a novel data set comprising 3661 terrestrial (mainly soil) invertebrate respiration rates from 192 independent sources across a wide range in body masses, environmental temperatures and phylogenetic groups. Although our analyses documented power-law and exponential scaling with body masses and temperature, respectively, polynomial models identified curved deviations. Interestingly, complex scaling models accounting for phylogenetic groups were able to remove curvatures except for a negative curvature at the highest temperatures (>30 °C) indicating metabolic down regulation. This might indicate that the tremendous differences in invertebrate body architectures, ecology and physiology may cause severely different metabolic scaling processes.

Keywords
Body mass, curvature, invertebrate, metabolic rate, MTE, phylogenetic group, polynomial, respiration, temperature.

INTRODUCTION
For more than a century, the reasons for the allometric scaling of metabolism with organism body mass and the value of the power-law exponent of this relationship have been debated extensively (White 2010). Although early concepts employed a surface-area-to-volume argument to advocate a general power exponent of $1/3$, also known as Rubner’s surface law (Rubner 1883), subsequent data analyses suggested the broad generality of a $2/3$ power law or Kleiber’s law (Kleiber 1947; Peters 1983; Savage et al. 2004). The empirically dominating $2/3$ exponent was explained by the optimised, fractal transport networks within organisms such as the cardiovascular system of vertebrates (West et al. 1997). This fractal model together with the universal temperature dependence of metabolism that is, as any thermodynamic process, determined by specific activation energies (i.e. the exponents of the exponential scaling terms, Gillooly et al. 2001) served as a basis for the metabolic theory of ecology (hereafter: MTE, Brown et al. 2004). Hence, the MTE predicts that metabolism follows a $2/3$ power-law scaling with individual body masses (West et al. 1997; Brown et al. 2004; Savage et al. 2004) and an exponential scaling with environmental temperature with an exponent (hereafter: activation energy) ranging between 0.6 and 0.7 eV (Gillooly et al. 2001, 2006; Allen & Gillooly 2007). The generality of this MTE paradigm was challenged by (1) alternative metabolic scaling models predicting different ranges of exponents, (2) lacking universality of the exponents across different groups of species and (3) curved deviations from the predicted relationships.

Alternative metabolic scaling models relax the assumption of universal scaling exponents and predict allometric exponents varying between $1/2$ and $2/3$ (e.g. explosion and quantum metabolism models) or $2/3$ and 1 [metabolic level boundaries (MLB) hypothesis and cell-size model; for detailed descriptions see Darveau et al. 2002; Kozłowski et al. 2003; Glazier 2005, 2010; Demetrius 2006; Banavar et al. 2010 or overview by Glazier 2005 and references therein]. This lack of a universal exponent is consistent with recent data analyses, which was partly explained by variance in factors such as phylogenetic groups, lifestyles, activity state or developmental stage (Dodds et al. 2001; White & Seymour 2003; Glazier 2005, 2009; Makarieva et al. 2005a,b; Niven & Scharlemann 2005; White et al. 2007; McNab 2008; Isaac & Carbone 2010). One of the central assumptions of the MTE is that the fractal nature of the metabolic transport network is invariant across organisms and body sizes (West et al. 1997; Brown et al. 2004). Although this assumption might appear adequate for vertebrates with cardiovascular systems, it is certainly violated for comparisons amongst invertebrates that are much more diverse in the size and shape of their bodies and the structure, openness or presence of tracheal and body-fluid transport systems across phylogenetic groups. In consequence, the few studies comprising metabolic data of invertebrates found substantial variation in their metabolic scaling across phylogenetic groups and deviations from linear scaling (Zeuthen 1953; Niven & Scharlemann 2005; Meehan 2006; Chown et al. 2007; White et al. 2007; Isaac & Carbone 2010). Similarly, empirical studies have also cast doubt on the narrow distribution of average activation energies predicted by the MTE (Meehan 2006; Terblanche et al. 2007; Irlich et al. 2009), and suggested a wider range between 0.46 and 0.96 eV (Downs et al. 2008). Some prior studies tried to explain differences in scaling exponents documented across studies by their focus on different body-mass ranges (according to the phylogenetic groups chosen) across a curved metabolism–mass relationship on a log–log scale (Zeuthen 1953; Haysen & Lacy 1985; Glazier 2005; Savage et al. 2008; Kolokotrones et al. 2010 and references therein).

In this study, we use the largest data set on invertebrate standard metabolic rates compiled so far to examine power-law and exponential
scaling of the metabolic rates with organism body mass and temperature respectively. The fitted exponents are tested for deviations from the MTE and alternative models. Subsequently, we test for curvatures in these scaling relationships. Finally, we address variability in these exponents across phylogenetic groups to analyse whether accounting for phylogenetic differences removes these curvatures.

**METHODS**

To address the interspecific scaling of standard metabolic rates of terrestrial invertebrates (with an emphasis on soil invertebrates) with individual body masses (wet weight) and environmental temperature, we combined data from different sources: (1) the data set of Meehan (2006), (2) the data set of Chown et al. (2007), (3) additional data from miscellaneous prior publications and (4) our own measurements [see Appendix S1(a)].

The data-selection criteria of the first two data sets are described in the materials and methods in Meehan (2006) and Chown et al. (2007). In addition, published literature on the standard metabolic rates of soil invertebrates dating back as far as 1910 with a major emphasis on the past 50 years (ending in 2010), was examined. Data were included if they contained measurements of standard metabolic rates (oxygen consumption per unit mass or per individual), individual body masses and the environmental temperature. Measurements of stressed animals or animals that were cultivated or reared in the laboratory, feeding trials, fluctuating temperature regimes, thermal acclimation or conditions that were not standardised across weight classes and temperature levels were not included into the data set. Furthermore, we excluded measurements of starving animals to avoid effects of increased searching behaviour or down regulation of respiration. Data were transformed into units of joule per hour (J h⁻¹) for metabolism, Kelvin (K) for temperature and milligram (mg) for wet weight [see Appendix S1(a) for data].

To ensure that our data cover the natural range of body masses and a similar temperature range for each phylogenetic group (see Table 1 for an overview), we added our own respiration measurements to the database. Oxygen consumption by individuals was quantified using an automated electrolytic microrespirometer (Scheu 1992). Animals for the measurements were either collected by pitfall traps or caught by hand on different field sites (i.e. field plots of the Biodiversity Exploratories, Germany). The animals were stored in climatic chambers (constant 15 °C), and they were fed adequately, but fasted for some time prior to the respiration measurement to avoid down regulation of metabolism due to starvation. Using fasted (not fed directly before the experiment) but not starved (not deprived of food over a longer period of time) animals seemed an adequate compromise, but we cannot entirely exclude a possible effect of digestion on metabolism such as specific dynamic action. Each individual was weighed with a precision scale prior to the measurement. Our measurements of oxygen consumption lasted for 12 h at each of six temperatures (5, 10, 15, 20, 25 and 30 °C) and were conducted in a closed system with oxygen supply to avoid oxygen depletion. The respiration between the 8th and 12th hour was averaged to obtain the standard metabolic rate per hour ([J h⁻¹]), 1 mL O₂ = 20.1 J, Peters 1983] as respiration had usually saturated at constantly low respiration levels indicative of standard metabolic rates. Details on the respiration measurement are provided in Appendix S1(b).

Our analyses focus on effects of body masses (wet weight) and temperature while not accounting for differences between species, which favours generality in the scaling relationships for phylogenetic groups at the cost of ignoring differences between species-specific scaling relationships within phylogenetic groups. We applied three models to the data set to test their ability of predicting standard metabolic rates of invertebrates. We started with the linear model (Downs et al. 2008), which is similar to the MTE but without fixed values for the allometric exponent a or the activation energy E:

\[
I = \exp(M^aT^{\frac{1}{a}})
\]  

(1a)

where I is the metabolic rate, a is the allometric exponent, E the activation energy (eV), k is Boltzmann’s constant (8.62 × 10⁻⁵ eV K⁻¹), T temperature in Kelvin and \(\dot{i}_0\) a normalisation factor. Natural-logarithm transformation yields:

\[
\ln I = \ln \dot{i}_0 + a \ln M - E \left( \frac{1}{kT} \right)
\]  

(1b)

We added polynomial terms to the mass and temperature terms of this linear model. An nth order polynomial form would be represented by:

<table>
<thead>
<tr>
<th>Phylogenetic group</th>
<th>Body mass (mg)</th>
<th>Temperature (°C)</th>
<th>Minimum no. species</th>
<th>Lower taxonomic groups included</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Min</td>
<td>Max</td>
<td>Min</td>
<td>Max</td>
</tr>
<tr>
<td>Arachnida</td>
<td>0.72</td>
<td>1000</td>
<td>3</td>
<td>40</td>
</tr>
<tr>
<td>Chilopoda</td>
<td>0.75</td>
<td>187.46</td>
<td>4</td>
<td>30</td>
</tr>
<tr>
<td>Clitellata</td>
<td>0.02</td>
<td>10500</td>
<td>5</td>
<td>36</td>
</tr>
<tr>
<td>Insecta*</td>
<td>0.00279</td>
<td>7285</td>
<td>−2</td>
<td>30</td>
</tr>
<tr>
<td>Isopoda</td>
<td>1.11</td>
<td>108.04</td>
<td>5</td>
<td>35</td>
</tr>
<tr>
<td>Mesostigmata</td>
<td>0.0044</td>
<td>580.2</td>
<td>0</td>
<td>25</td>
</tr>
<tr>
<td>Orbitala</td>
<td>0.0017</td>
<td>0.781</td>
<td>0</td>
<td>29</td>
</tr>
<tr>
<td>Progonatea</td>
<td>4.4425</td>
<td>293.49</td>
<td>5</td>
<td>30</td>
</tr>
<tr>
<td>Prostigmata</td>
<td>0.000035</td>
<td>0.0302</td>
<td>0</td>
<td>25</td>
</tr>
</tbody>
</table>

*Insecta also includes Archaeognatha, Dermoptera, Megaloptera, Mantodea, Mantophasmatodea, Siphonaptera with single and Thysanura with three data points.

†In some taxonomic groups, individuals were not identified to the species’ level; minimum number of species assumes that all these individuals are from identical species.
\[\ln I = \ln a + \sum_{j=1}^{i=9} a_j \ln M^j - \sum_{j=1}^{i=9} E_j \left( \frac{1}{kT} \right)^j \] (2)

Subsequently, the polynomial model with the lowest AIC was chosen. In a third approach, we accounted for the different phylogenetic groups included in the data set. As no appropriate phylogenetic tree is available for these phylogenetic groups we refrained from using phylogenetic contrasts. As surrogates, genera of invertebrates were merged into broader groups in accordance with a current phylogeny (Westheide & Rieger 2003). These phylogenetic groups represent relatively homogeneous body architectures (see Table 1). The phylogenetic model included direct effects of body mass, temperature and phylogenetic group and two-way interaction terms between phylogenetic group on the one side and body mass or temperature on the other side, which yielded group-specific intercepts \(a_{\text{PG}}\), allometric exponents, \(a_{\text{PC}}\) and activation energies, \(E_{\text{PG}}\):

\[\ln I = \ln a_{\text{PG}} + a_{\text{PC}} \ln M - E_{\text{PG}} \left( \frac{1}{kT} \right) \] (3)

We fitted the three models (eqns 1b, 2 and 3) to our data employing linear mixed effects models with maximum likelihood [function ‘lme’ with ‘method = ML’ in the nlme package (Pinheiro et al. 2009) of the statistics program R (R Development Core Team 2010)]. To account for systematic differences among studies, the study identity was entered as a random effect in these models.

We compared the goodness of fit of the three models by their AIC values. We tested for curvatures in these relationships by analysing the distribution of the residuals against the independent variables, the natural logarithms of body mass and temperature (inverse of temperature multiplied with Boltzmann’s constant; \(1/(kT)\)), utilising the function ‘loess’ in the stats package of R. Loess is a locally weighted polynomial regression method that uses weighted least squares, giving more weight to points near the point whose response value is being estimated and less weight to points further away and is plotted against the independent variable. We calculated the model confidence bands for the linear model. In this two-parameter model, confidence calculations yield planes across the dimensions of body mass and temperature. Compression of these planes in two-dimensional figures results in confidence bands. Loess fits outside these confidence bands were interpreted as indicators of curvatures. For the sake of simplicity, we refrained from calculating similar confidence bands for the higher dimensional polynomial and phylogenetic models (e.g. the phylogenetic model would yield independent confidence limits for each combination of phylogenetic group with body mass or temperature).

Instead, we compared the deviation of the residual loess fits from the zero line of the model prediction.

RESULTS

The data set compiled for this analysis includes 3661 metabolic rate measurements of 580 taxa (mostly species and some higher taxa) and 192 independent published sources [see Appendix S1(a)]. The body masses of the invertebrate species ranged over almost nine orders of magnitude from the smallest mites of 0.000035 mg body weight (Prostigmata) to the largest earthworms of 10 500 mg body weight (Clitellata), and our data base covered temperatures between −2 and 40 °C (Table 1). Across these ranges covered by our data, the standard metabolic rates increase with increasing body mass and temperature (Fig. 1). Fitting of the linear model (eqn 1b) resulted in an allometric exponent, \(a\), of 0.695 (SE ± 0.007, Table 2, Fig. 1a) differing significantly from the \(1/a\) exponent predicted by the MTE (\(t\)-test, \(P < 0.001\)); whereas, the activation energy, \(E\), of 0.686 eV (SE ± 0.011, Table 2, Fig. 1b) was within the predicted range (0.6–0.7 eV). Some phylogenetic groups such as mites (Oribatida, Mesostigmata), isopods and earthworms exhibited metabolic rates systematically lower than the prediction of the linear model (Fig. 1a,b). In contrast, Chilopoda and Arachnida had higher metabolic rates than predicted (Fig. 1a,b). Interestingly, the groups with respiration rates higher than the linear model’s prediction represent active hunters, whereas the groups with lower respiration rates mostly consist of detritivores.

To assess curvatures in the relationships, we analysed the dependence of the linear model residuals on the natural logarithms of body mass and temperature \([1/(kT)]\) and tested for deviation from linearity by ‘loess fits’ (see Methods). The closer the loess fit is to the zero (optimum) line the higher is the quality of the model. Note that positive residuals and a positive loess fit indicate underestimation of the standard metabolic rate by the model, whereas negative residuals and a negative loess fit suggest overestimation. Our residual analyses indicate significant deviations from the model (i.e. loess line outside the 95% confidence bands) at low and intermediate body masses (Fig. 1c) and strong negative deviations at high temperatures (over 30 °C, Fig. 1d). Together, these patterns clearly suggest nonlinear deviations from the linear model (eqn 1b). We repeated these analyses with nine subsets of the data that each excluded one of the phylogenetic groups. In all analyses, the residuals of the model fit against the natural logarithm of body mass and temperature exhibited similar curvatures. This suggests that the curvature was not driven by a single phylogenetic group and characterised the compound data set.

We accounted for these non-linearities by fitting polynomial models (eqn 2). The polynomial model we used here contained polynomials of second, fourth and fifth degree for the body-mass term (Table 2). While removing any of these polynomials decreased the quality of the model (i.e. yielding higher AIC values), the third order polynomial could be omitted. Comparisons of the ‘loess fits’ between the linear model (Fig. 1c,d) and the polynomial model (Fig. 2a,b) show that polynomials removed most of the curvature. The polynomial model (AIC: 6975) was much more parsimonious than the linear model (AIC: 7069). Together, the significance of the polynomial terms and the lower AIC of the polynomial model suggest that the curvatures in the metabolic scaling should be considered.

Subsequently, we replicated these analyses with a model including nine phylogenetic groups (eqn 3, Table 1). We fitted an overall linear model to the data accounting for differences in allometric exponents, activation energies and normalisation constants among these groups (see Table 2 and Fig. 3 for parameter estimates). Overall, this model including phylogenetic groups yielded the lowest AIC value (AIC: 6112) of all three models, which suggests that it has substantially superior support compared to the simpler linear and polynomial models (Burnham & Anderson 2001). Interestingly, this superior fit of the phylogenetic model was accompanied by removing most of the curvatures in the relationships as indicated by smaller deviations of the loess fits from the zero-optimum line (Fig. 2c,d vs. Fig. 1c,d). However, the overestimation of metabolic rates at the highest temperatures (indicated by the negative loess fits in Fig. 2d) remained, which suggests that they cannot be explained by phylogenetic effects. To ensure that our results are not driven by the statistical methodology chosen, we repeated the analyses with linear least
groups were significantly lower than the predicted Clitellata (Table 2, Fig. 3b). The exponents of four phylogenetic substantially in a range between 0.554 for Isopoda and 0.801 for phylogenetic model removed most of the curvatures in all subsamples. suggesting the phylogenetic as the preferred model and (3) the AICs of the linear and the polynomial model in all subsamples (2) the AICs of the phylogenetic model were much lower than the P < 0.05) indicating curvatures in the metabolic scaling relationships; versus body mass and (d) temperature characterised by deviations of the loess fit (brown curves) from the 95% confidence bands (dotted black bands). See Table 2 for parameters of the fitted linear model (eqn 1b). Note that statistical fits employed inverse temperature terms (eqns 1b, 2 and 3), whereas figure axes were labelled with temperature.

To disentangle intra and interspecific metabolic scaling, we replicated our analyses for 100 random subsamples of the data set including only one data point per species (excluding data of higher taxonomic levels) per temperature. These interspecific scaling analyses supported our prior results: (1) we found significant polynomial terms for allometric exponents (a2 and a4, P < 0.05, with four subsamples having higher P-values for a4) and activation energies (E2 and E4, P < 0.05) indicating curvatures in the metabolic scaling relationships; (2) the AIGs of the phylogenetic model were much lower than the AIGs of the linear and the polynomial model in all subsamples suggesting the phylogenetic as the preferred model and (3) the phylogenetic model removed most of the curvatures in all subsamples.

The allometric exponents (a) of the nine phylogenetic groups varied substantially in a range between 0.554 for Isopoda and 0.801 for Clitellata (Table 2, Fig. 3b). The exponents of four phylogenetic groups were significantly lower than the predicted 3/4 exponent of the MTE (95% confidence intervals do not include the dashed line in Fig. 3b). Interestingly, the exponents of Arachnida and Chilopoda were even lower than the lower boundary (3/4) of the exponent range predicted by alternative models (see Discussion below for comparison with higher exponents in prior studies). The activation energies [E (eV)] of the different groups display a wide range from 0.379 for Mesostigmata to 0.803 for Chilopoda (Table 2, Fig. 3c). Despite this substantial variation in mean activation energies, our results suggest that the range between 0.6 and 0.7 predicted by the MTE is within all 95% confidence limits.

**DISCUSSION**

We examined three models in their ability to predict standard metabolic rates of terrestrial invertebrates: a power-law model deduced from the metabolic theory of ecology that was linearised by natural logarithms (linear model), a model with additional polynomial terms added to the linear model (polynomial model) and a model allowing specific intercepts, allometric slopes and activation energies for each of nine phylogenetic groups (phylogenetic model).

Overall, we found that all three models fit the data significantly. The fitted linear model estimated an allometric exponent of 0.695 (± 0.007 SE) that is significantly different from the 3/4 exponent predicted by the MTE (West et al. 1997; Brown et al. 2004), and an activation energy (E) of 0.686 eV (± 0.011) that is in the predicted range of 0.6–0.7 eV (Gillooly et al. 2001, 2006; Allen & Gillooly 2007). Together, these results support the universal thermodynamic temperature dependence of metabolism while rejecting the universal power-law scaling with body mass (West et al. 1997). Consistent with prior studies on the metabolic rates of mammals (Haysen & Lacy 1985; Kolokotrones et al. 2010), residual analyses revealed curvatures in the relationship of the linear model that could be removed by the...
polynomial and the phylogenetic model. Overall, the phylogenetic model has the highest statistical quality (i.e., the lowest AIC), because it removes most of the curvature found for the linear model and—in contrast to the polynomial model—it allows for mechanistic interpretation of the fitted parameters. Together, these results suggest that the phylogenetic model should be preferred over the linear and polynomial models and that the assumptions of the MTE are not appropriate for invertebrates. Similarly, Kozlowski & Konarzewski (2005) found variance in scaling exponents across various mammalian groups suggesting a broader generality of the phylogenetic signatures in metabolic scaling. Alternative metabolic scaling models such as the explosion model (Banavar et al. 2010), the allometric cascade model (Darveau et al. 2002), quantum metabolism (Demetrius 2006), the MLB hypothesis (Glazier 2010) and the cell-size model by Kozlowski et al. (2003) relax the strict $3/4$ power law and predict scaling exponents that vary within the range between $2/3$ and $3/4$ or 1 (MLB hypothesis and cell-size model). While seven allometric exponents fell within this predicted range, two of the phylogenetic groups of the present study exhibited exponents with 95% confidence limits lower than $2/3$ (see discussion below) thus suggesting that none of the models might be able to explain their metabolic scaling. Moreover, the nonlinearities detected in our analyses suggest more complex mechanistic relationships between body masses and standard metabolic rates accounting for differences among organisms concerning their morphology, ecology, lifestyle and physiology. Here, we followed prior studies (Meehan 2006; Chown et al. 2007; White et al. 2007; Irlich et al. 2009; Isaac & Carbone 2010) and aggregated these differences in phylogenetic signals included in metabolic scaling relationships.

Our analyses indicate that the incorporation of phylogenetic groups is essential for predicting the standard metabolic rates of different groups of invertebrates, because the phylogenetic model provided the best fit to the data and removed curvatures in the scaling relationship. We explain our results with the different body architectures and metabolic strategies of the invertebrates included in our study. Invertebrates possess (1) partially or entirely open tracheal and body-fluid transport systems that are heterogeneous across their body parts, and dramatically different across differently sized species from different phylogenetic groups and (2) different ecological lifestyles and habitats. Together, these two characteristics may be responsible for the different scaling exponents of the phylogenetic groups, and they prevent a general scaling relationship across phylogenetic groups. Similarly, prior studies have also documented the importance of phylogenetic signals in the metabolic scaling relationships (Kozlowski & Konarzewski 2005; Meehan 2006; Chown et al. 2007; White et al. 2007; Irlich et al. 2009; Isaac & Carbone 2010). However, until more complex metabolic scaling models accounting for phylogenetic differences in body architecture as well as ecological lifestyle or habitat are developed the fitted exponents of our phylogenetic model remain descriptive. Nevertheless, we anticipate that the data set sampled for the present study may provide an important benchmark against which such more complex metabolic models should be tested.

The allometric exponents of some phylogenetic groups reported here are lower than those of prior studies (e.g. Meehan 2006; Pennington & Meehan 2007; Glazier 2010; but see the lower exponent for orbited mites by Wood & Lawton 1973). In case of the chilopods, we caution that this might be caused by the low species number in our study. However, as the data of Meehan (2006) and Wood & Lawton (1973) are included in our data set, other differences in fitted exponents are more likely to be explained by (1) the larger range in body masses and (2) parameter estimation via mixed effect models with maximum likelihood in our study. Re-analyses of our data with sums of squares statistics yielded higher estimates of the exponents more consistent with prior publications, which suggests differences in statistical methodology as the main explanation for the disparity in exponents between studies. However, more detailed analyses of allometric exponents for individual phylogenetic groups were beyond the scope of this study.

For six of nine invertebrate groups the activation energies for the fluid transport systems that are heterogeneous across their body parts, and dramatically different across differently sized species from different phylogenetic groups and (2) different ecological lifestyles and habitats. Together, these two characteristics may be responsible for the different scaling exponents of the phylogenetic groups, and they prevent a general scaling relationship across phylogenetic groups. Similarly, prior studies have also documented the importance of phylogenetic signals in the metabolic scaling relationships (Kozlowski & Konarzewski 2005; Meehan 2006; Chown et al. 2007; White et al. 2007; Irlich et al. 2009; Isaac & Carbone 2010). However, until more complex metabolic scaling models accounting for phylogenetic differences in body architecture as well as ecological lifestyle or habitat are developed the fitted exponents of our phylogenetic model remain descriptive. Nevertheless, we anticipate that the data set sampled for the present study may provide an important benchmark against which such more complex metabolic models should be tested.

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For six of nine invertebrate groups the activation energies for
three phylogenetic groups exhibited activation energies in the more narrow range for metabolic processes between 0.6 and 0.7 eV (Gillooly et al. 2001). This is consistent with the substantial variation in metabolic activation energies found in prior studies (Meehan 2006; Terblanche et al. 2007; Irlich et al. 2009; Isaac & Carbone 2010). However, even the narrow range for metabolic activation energy is within the confidence limits of the parameter estimates of our analyses for each of the nine phylogenetic groups as well as for the linear model. This suggests that despite substantial variation in activation energies across phylogenetic groups the universal temperature dependence of metabolic processes as predicted by the MTE (Gillooly et al. 2001) is not rejected by our analyses.

In addition to testing for curvature in the body-mass scaling, we have documented nonlinearities in the scaling of invertebrate standard metabolic rates with the environmental temperature. We found the most pronounced deviations from the predictions of the linear model at high temperatures, where the linear model overestimated the invertebrate standard metabolic rates drastically. In part, this severe overestimation might be overcome by thermal adaptation processes (Terblanche et al. 2005, 2009; Lachenicht et al. 2010). While such thermal adaptation processes may be important for our understanding of temperature effects on metabolism, we chose to focus the present study on standard metabolic rates excluding possible acclimation effects. One important aspect of the standardisation involved in our

Figure 2 Accuracy of polynomial and phylogenetic models: distributions of the residuals for the polynomial (a, b) and the phylogenetic model (c, d) across the natural logarithms of body mass (a, c) and temperature (b, d). Systematic deviations of the data from model predictions are characterised by loess fits (brown curves). See Table 2 for parameters of the fitted polynomial (eqn 2) and phylogenetic model (eqn 3).

Figure 3 Distribution of fitted metabolic scaling parameters and their 95% confidence limits in the phylogenetic model across phylogenetic groups: (a) intercepts, (b) allometric exponents and (c) activation energies. Parameters of the linear model (all groups) have been included. Indications of model predictions: (b) dashed line equals $\gamma_0$ (MTE); grey and dark grey areas indicate ranges $1/2$–$1$ and $\gamma_0^2/\gamma_0$ respectively (alternative models); (c) the dark grey area indicates range $0.46$ to $0.96$ eV and the dashed line the mean 0.65 eV (MTE); the light grey area depicts range $0.65$ to $0.96$ eV. MTE, metabolic theory of ecology.
own study was to start the metabolic measurements with organisms of the same standardised initial conditions [see Appendix S1(b) for details]. This implied keeping them at the same temperature prior to the measurement.

Consistent with a prior study (Knies & Kingsolver 2010), a polynomial model provided a better fit to the data than the simple linear model. While the phylogenetic model could remove most of the curvature in the metabolic scaling relationship, a systematic negative deviation of the metabolic data from the model predictions at the highest temperatures (> 30 °C) remained. These temperatures are probably close to the edge of the species’ thermal windows (Pörtner et al. 2006; Pörtner & Farrell 2008) or the ‘biologically relevant’ temperature range (Gillooly et al. 2001), which causes down regulation of the metabolism when approaching lethal temperatures. Metabolic down regulation at high temperatures (Gillooly et al. 2001) is thus the reasonable explanation for the nonlinearities remaining in the temperature scaling of the phylogenetic model.

CONCLUSIONS

A comparison of the three tested models clearly shows that the linear and the polynomial model do not fit the metabolic data equally well as the phylogenetic model. The linear model employs the least parameters, which came at the cost of curved residuals across the body mass and temperature axes. Hence, the linear model sacrifices detail for the sake of generality (i.e. residual variation of the linear model was 12% higher than that of the phylogenetic model). In contrast, the introduction of polynomials removed most of the curvature in the residuals while lacking a mechanistic basis. Our analyses demonstrated that a phylogenetic model accounting for differences in allometric exponents, activation energies and normalisation constants between phylogenetic groups provided the best fit to the data and also removed most of the curvature in the residuals. Although this does not provide the critically needed, novel mechanistic model for the scaling of invertebrate metabolic rates, our analyses suggest that differences in body architectures as well as ecological lifestyles and habitats among phylogenetic groups could be centrally important to such novel models.

ACKNOWLEDGEMENTS

Funding has been provided by the DFG Priority Program 1374 "Infrastructure-Biodiversity-Exploratories" (BR 2315/7-1) and the German Research Foundation (BR 2315/8-1, BR 2315/13-1). Field work permits were given by the responsible state environmental offices of Baden-Württemberg, Thüringen and Brandenburg (according to § 72 BbgNatSchG). We appreciate the data provided by T. Meehan and S.C. Chown. We thank S. Scheu, M. Marau, M.M. Marau, G. Ermann, B. Kranner, B. Eitzinger for helpful comments, T. Volovei for help with the respiration measurements, and M. Reichstein for helpful comment on an earlier draft. We are grateful to Jan Kozłowski and two anonymous referees whose comments on an earlier version greatly improved this manuscript.

AUTHOR CONTRIBUTIONS

R.B.E. collected literature data and ran the respiration measurements. R.B.E. and U.B. designed the study and wrote the manuscript. All authors carried out the statistical analysis, interpreted and discussed the results and commented on the manuscript.

REFERENCES


**SUPPORTING INFORMATION**

Additional Supporting Information may be found in the online version of this article:

**Appendix S1(a) Data set.**

**Appendix S1(b) Details on respiration measurement.**

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Editor, David Storch

Manuscript received 28 April 2011

First decision made 27 May 2011

Manuscript accepted 13 June 2011