

Metabolic theories in ecology

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The Metabolic Theory of Ecology (MTE) and the earlier theory of Dynamic Energy Budgets (DEB) are both founded on simple mechanistic descriptions of how individual organisms take up and use energy and material. Such descriptions should enable predictions to be made of pools and flows of energy and matter in populations, communities and ecosystems. MTE builds on the idea that the transport of resources through a fractal-like branching network causes the supply rate to cells to scale as a $\frac{3}{4}$ power of body mass, whereas DEB is based on the concept that rates of basic physiological processes are proportional to surface area or to body volume. Here, I critically compare both theories, highlight similarities and inconsistencies, and show where the approaches deviate. I argue that, to arrive at a sound theoretical basis of the energy budget of individual organisms, both views should be tested fully, but only after inconsistencies have been addressed.

Two theories

Recently, Brown *et al.* [1] proposed a Metabolic Theory of Ecology (MTE), the core of which is a mechanistic description of how the metabolic rate of individual organisms varies with body size and temperature [2–4]. Whole-organism metabolic rate is assumed to be limited by the internal delivery of resources to cells. Resources have to be distributed through branching networks, and it was suggested that the fractal-like designs of these networks cause the supply rate and, hence, the metabolic rate, to scale as a $\frac{3}{4}$ power of body volume [3]. This idea should provide the long-sought-for theoretical underpinning of Kleiber's law, that is, the observation that the metabolic rate of an organism is proportional to its mass raised to the $\frac{3}{4}$ power [5–7]. Brown and co-workers proceeded by arguing that the effects of body size and temperature (Box 1) on the metabolic rate of individual organisms govern features at the level of populations, communities and ecosystems [1]. For example, by using the additional assumption that the total supply rate of resources is the same for all populations, it is predicted that population density should vary inversely with body size, with a scaling coefficient of $-\frac{3}{4}$.

In an interesting commentary on Brown's paper, Harte [8] stated that a similar metabolic theory of ecology based on surface:volume ratios could have been constructed, but never was. In fact, such a theory is available. Almost two decades ago, Kooijman [9–11] presented a theory of

Dynamic Energy Budgets (DEB), which also takes the energetics of the individual organism as the starting point. The theory assumes that the various energetic processes, such as food intake rate, are dependent on either surface area or body volume. DEB theory predicts many types of intra- and interspecific scaling relationships, and also proceeds from the level of the individual organism to the population and beyond [12–16].

As MTE and DEB theory both aim for a general theory of energy budgets based on the energy conservation law, a comparison of them could provide a research agenda toward a broadly accepted metabolic theory of ecology. The topic is diverse and here I compare only the basis of the two theories (i.e. the energetics of the individual organism), with an emphasis on ontogenetic growth. Both theories describe energy supply rate and maintenance rate as functions of body size. Because the difference between these terms is the energy available for growth, both theories result in growth models containing fundamental energy budget parameters (Table 1). I pay particular attention to Kleiber's law and discuss whether a theory based on surface- and volume-related processes can be in accordance with the empirical finding of a $\frac{3}{4}$ power scaling of metabolic rate [17], or whether Harte [8] is correct in his suggestion that such a theory, if it had been constructed, would already have been falsified. Finally, I discuss the question of whether the model parameters are directly calculable from fundamental cellular parameters and still provide good fits to empirical data [4]. I do not discuss issues as development, reproduction, and stoichiometry (but see [18–23]).

The MTE growth model

The MTE assumes that the energy supply rate to the cells follows a $\frac{3}{4}$ scaling relationship with body mass W . The maintenance rate, defined here as the power needed to sustain the organism in all its activities, is proportional to the number of cells, because the rate per cell is assumed constant throughout growth and development. Because the mass per cell is also assumed to be constant, the maintenance rate is proportional to body mass. Hence, the growth equation corresponds to Equation I:

$$\frac{dW}{dt} = \frac{aW^{\frac{3}{4}} - mW}{g} \quad [\text{Eqn I}]$$

where a is the supply rate per mass ^{$\frac{3}{4}$} , m is the maintenance rate per unit mass and g is the energetic growth cost per unit growth in mass.

Growth ceases when the supply rate equals the maintenance and, from Equation I, it follows

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Box 1. The dependence of physiological rates on temperature

The MTE and DEB theory both use the van't Hoff-Arrhenius equation to describe the dependence of physiological rates on temperature. This equation has its origin in statistical thermodynamics, where the behaviour of a system containing a very large number of a single type of molecule is predicted from statistical considerations of the behaviour of individual molecules [46]. Glasstone *et al.* [47] showed that the van't Hoff-Arrhenius equation is approximate for bimolecular reactions in the gas phase, whereas Kooijman [13,14] emphasizes the enormous step from a single reaction between two types of particle in the gas phase to physiological rates where many compounds are involved and gas kinetics do not apply. He therefore regards the application of the van't Hoff-Arrhenius relation to physiological rates as an approximation only, for which the parameters have to be determined empirically for each species.

The more candid view of Gillooly *et al.* [2], who stated that the van't Hoff-Arrhenius equation must be applied because it links whole-organism metabolism directly to the kinetics of the underlying biochemical reactions, has been criticized by Clarke [48,49] and Marquet *et al.* [50]. Similar to Kooijman, Clarke [48,49] and Marquet *et al.* [50] stress that the van't Hoff-Arrhenius equation is only a valuable statistical generalization, and they conclude that we still lack a clear understanding of the relationship between temperature and metabolism at the organismal scale.

that the ultimate size that a species can reach equals $W_{\infty} = (a/m)^4$. Hence, differences in ultimate size among species are a result of differences in either size-specific supply rate a or size-specific maintenance rate m . MTE has not always been clear about whether the supply or maintenance parameter scales with ultimate size. In the original growth paper, West *et al.* [4] write that, among species within a taxon, the supply parameter a should be approximately independent of the ultimate size. This means that the parameter m should scale as $W_{\infty}^{-1/4}$. However, they further write that the parameter a should vary among groups, but it remains unclear whether they imply a relationship with ultimate size. No biological arguments are given as to why a should be independent of ultimate size among species within a taxon, but should vary between groups. They are also not specific about what they mean by a 'taxon' or by a 'group'. In a second paper, they are more explicit and state that a does not scale with asymptotic mass, whereas m decreases as

$W_{\infty}^{-1/4}$ [24]. Hence, some species grow bigger than others, because their volume-specific maintenance rate is lower (Figure 1).

The idea that a fractal-like network causes the uptake to scale as $3/4$ power of body mass has been criticized for mathematical flaws [25–28]. Another point of criticism concerns the proposed branching structure, which is different from what is found in true organisms [14]. In fact, many organisms (e.g. mollusks) do not have branching structures [14]. Finally, it has been argued that a $3/4$ rule for the supply rate to the cells does not require the idea of a fractal-like branching structure, but is also obtained for more general types of networks, for example, one in which the flow is sequential from one unit (e.g. a cell) to another and where the total volume of the network is proportional to body size [29–32]. Cyr and Walker therefore conclude that the idea of a fractal-like branching structure is interesting, but that the claim of a mechanistic basis to the MTE is premature [33].

The DEB growth model under constant food conditions

DEB theory describes the individual organism in terms of structural body size and reserve density, which is the amount of reserves per volume unit of the structural body. DEB theory assumes that, within a species, the energy assimilation rate A is proportional to the surface area of the organism $V^{2/3}$. Assimilation rate is also related to food density through a functional response curve. Hence, $A = faV^{2/3}$, where a is the maximum assimilation rate per unit of surface area and f is the scaled functional response (which can vary between 0 and 1). The assimilated products enter a reserve pool and the reserve density follows first-order dynamics. At constant food density, reserve density quickly reaches equilibrium at $fR_{\max}$. Hence, the equilibrium reserve density is proportional to the scaled functional response f , which implies that the maximum reserve density $R_{\max}$ is only reached at maximum food conditions. At constant food density, the rate at which energy is utilized from the reserves, can be written as Equation II:

$$C = faV^{2/3} - fR_{\max}dV/dt \quad [\text{Eqn II}]$$

Table 1. Comparison of the growth models of MTE and DEB theory

	MTE	DEB
State variables	Body mass	Structural body size and reserves
Feeding module, which makes growth sensitive to food availability	No	Yes
Supply (or assimilation) rate	Proportional to body mass ^{3/4} (within species)	Proportional to surface area of the structural body (within species)
Maintenance rate	Proportional to body mass (within species)	Proportional to structural body volume (within species)
Size-specific supply (or assimilation) rate parameter a	Does not scale with ultimate size (between species)	Scales with $V_{\infty}^{1/3}$ (between species)
Size-specific maintenance rate parameter m	Scales with $W_{\infty}^{-1/4}$ (between species)	Does not scale with ultimate size (between species)
Costs for growth parameter g	Energy content of the newly produced tissue	Sum of the energy content of the newly produced tissue and the overhead costs required for this production
Intraspecific scaling parameter for metabolic rate	1	Between $2/3$ and 1
Interspecific scaling parameter for metabolic rate	$3/4$	Between $2/3$ and 1

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