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 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 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:

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

where *a* is the supply rate per mass³/₄, *m* is the maintenance rate per unit mass and *g* is the energetic growth cost per unit growth in mass.

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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 Gilloolly *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 $W_{\infty}^{-\nu_4}$ [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 $\frac{3}{4}$ 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 $\frac{3}{4}$ 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 $V^{\frac{2}{3}}$. 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 $R_{\rm max}$ 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:

$$C = f a V^{4} - f R_{\text{max}} dV / dt$$

[Eqn II]

	MTE	DEB
State variables	Body mass	Structural body size and reserves
Feeding module, which makes growth sensitive to food availability	Νο	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 <i>a</i>	Does not scale with ultimate size (between species)	Scales with $V^{1/3}_{\infty}$ (between species)
Size-specific maintenance rate parameter <i>m</i>	Scales with $W^{\!$	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 $\frac{2}{3}$ and 1
Interspecific scaling parameter for metabolic	3/4	Between $\frac{2}{3}$ and 1

Table 1. Comparison of the growth models of MTE and DEB theo
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Figure 1. Supply rate (solid lines) and maintenance rate (dotted lines) versus body size on a double log-scale. MTE (a) states that species differing in ultimate size have different maintenance curves, whereas according to DEB theory (b) supply curves differ. Ultimate size is obtained where the two lines cross. In (a) and (b), circles indicate the ultimate size for three different species. The difference between supply and maintenance is available for growth, but, according to DEB theory, part of it is dissipated as heat.

The term $fR_{\text{max}}dV/dt$ is necessary to prevent dilution of the reserves as a result of growth.

A fixed proportion κ of utilized energy is spent on growth plus maintenance plus (for endotherms) heating, the rest goes to maturation (for embryos and juveniles) or to reproduction (for adults). Maintenance costs mV are proportional to structural body volume (where m is the maintenance cost per unit of volume), and heating costs $hV^{\frac{3}{2}}$ are proportional to body surface area (where h is the heating cost per unit of surface area). Thus (Equation III):

$$\kappa C = g dV / dt + mV + hV^{\frac{2}{3}}$$
 [Eqn III]

where g is the energetic growth cost per unit of growth in structural body volume. Substituting Equation II in Equation III gives the growth equation (Equation IV):

$$\frac{dV}{dt} = \frac{(\kappa f a - h)V^{z_3} - mV}{\kappa f R_{\max} + g}$$
 [Eqn IV]

This growth model is mathematically equivalent to the well-known Von Bertalanffy growth model [34], but based on a different biological rationale. Von Bertalanffy did not apply the energy conservation law to the overall organism, but defined growth as the difference between anabolism (synthesis) and catabolism (breakdown) [35].

DEB theory makes a strong plea for the similarities of cells, independent of species: that is, cells of the same size have similar maintenance costs. As the maintenance of cells is probably a major part of the maintenance of the whole individual, DEB theory states that the volume-specific maintenance rate (given by the parameter m) is independent of ultimate body size. This implies that the area-specific assimilation rate a must be proportional to the cubic root of the ultimate volume. Hence, some species grow bigger, because their area-specific assimilation rate is higher (Figure 1). DEB theory also predicts that species with a large ultimate structural volume have a higher maximum energy density than do species that remain small.

Scaling of metabolic rate

For animals, metabolic rate is the rate at which chemical energy is transformed into heat, and is usually indirectly measured by the rate of oxygen consumption. DEB theory is clear about the intraspecific scaling relationship of metabolic rate [9,14]. Maintenance costs are proportional to structural body volume, but there are other costs contributing to the oxygen consumption. For example, only part of the energy that is allocated to growth is fixed in new body tissue, the rest is dissipated as overhead costs [36,37]. These overhead costs are proportional to the difference between a surface area-related term and a volume-related term. For endotherms, the heating costs, which scale with surface area, contribute to the total oxygen use. Taking all these other costs into account, DEB theory predicts that the total metabolic rate will scale (if individuals of different size within the same species are compared) with body volume with a power somewhere between $\frac{2}{3}$ and 1.

Surprisingly, MTE is ambiguous about how metabolic rate scales with body size when individuals of the same species are compared. This ambiguity has its origin in inconsistencies in the definition of metabolic rate in the MTE papers [1,3,4]. In the original paper by West *et al.* [3], metabolic rate was assumed to be equivalent to the supply rate of energy and materials to the cells. In a subsequent paper on growth [4], the term 'metabolic rate' was, however, used for the supply rate of energy ('the average resting metabolic rate') and also for the maintenance rate (the 'metabolic rate of a single cell' summed over the total number of cells, where 'the sum is over all types of tissue'). At the same time, the difference between these two rates was supposed to be used for the build-up of new body tissue, and, thus, not lost as dissipating heat. Yet you cannot (almost literally) have your cake and eat it, and the only valid way out of this ambiguity is to realize that, within the MTE approach, it is not the supply rate, but the maintenance rate that must be equated to the metabolic rate. Consequently, MTE predicts that the intraspecific scaling power of metabolic rate equals 1 [38].

But what about Kleiber's law of the ³/₄ power scaling of metabolic rate, which was not based on an intraspecific but on an interspecific comparison? Assuming that such a comparison concerns full-grown adult organisms, the predicted metabolic rate equals a^4/m^3 according to MTE, and is equivalent to both the supply rate $aW_{\infty}^{3/4}$ and the maintenance rate mW_{∞} . Growth has ceased, and all supplied energy is needed for maintenance and is finally lost as dissipating heat. Combining this result with the additional assumption that cellular maintenance costs scale interspecifically with a $-\frac{1}{4}$ power (i.e. the maintenance costs of a lizard are much higher than those of a baby crocodile of the same size), reveals Kleiber's law. Hence, the idea in itself that the transport of resources to the cells through a hierarchy of branching vessels causes the supply to scale as ³/₄ power of body mass does not suffice to predict Kleiber's law.

DEB theory predicts (for convenience restricted here to well-fed ectotherms) a metabolic rate at ultimate size that is proportional to ultimate structural body volume. However, DEB also predicts that species with a large ultimate structural volume have a higher maximum energy density than do species that remain small. The observed interspecific scaling power of metabolic rate to body mass (which includes not only structure, but also reserves) will therefore be <1. For endotherms, heating costs, which are related to surface area, have to be added.

Parameter estimation

West et al. [4] claim that the MTE growth model parameters do not have to be derived from fits of growth trajectories, but are directly calculable from fundamental cellular parameters. But are they? And what about the DEB parameters? Unfortunately, most DEB parameters, such as the fraction of the utilized energy spent on growth and maintenance κ and the maintenance rate per unit of volume m, cannot be measured directly. One problem is that most conceptual model processes do not have a one-toone relationship with easily measurable processes. Oxygen consumption, for example, represents not only maintenance costs, but also overhead costs of growth and reproduction. Kooijman and co-workers therefore had to put much effort and ingenuity in estimating DEB parameters [23,39,40]. They used, for example, data on growth and oxygen consumption of embryos in eggs. Embryos do not feed, but use their high initial reserves for growth and maintenance [41,42]. This phenomenon simplifies reserve dynamics considerably and reduces scatter related to variable food intake.

The more optimistic view of West *et al.* [4], that the MTE growth model parameters are directly calculable from cellular parameters, is problematic. The MTE growth model uses three parameters: the energy supply rate per unit of mass^{3/4} *a* (B_0 in the original notation), the power per unit of mass needed to sustain the organism in all of its activities *m* (originally B_c/m_c), and the energetic costs per unit of mass to create new tissue *g* (originally E_c/m_c). West *et al.* [4] derived the parameter *g* from the energy content of mammalian tissue. They used

a value of 7 kJ g⁻¹, the same as had been estimated for birds [43]. Yet, this approach ignores all overhead costs of growth. The parameter *a* was set to 0.019 W, for which reference was made to Peters' compendium of scaling relationships [44]. This procedure contains at least three inaccuracies. First, a dimensional error is made. The unit of the parameter *a* should have been W kg⁻³/₄. Second, the reported value cannot have been derived from fundamental cellular parameters (such parameters are not given by Peters), but must have been based on allometric curve fitting of probably ingestion rates (these are the most relevant data that Peters provides). Third, an interspecific relationship of ingestion versus body mass was used, where in fact intraspecific ones are needed, and these are not provided by Peters.

The third parameter *m* was also not predicted from the cellular level, but from curve fitting of the growth trajectory. In any case, it would have been difficult to derive this parameter from cellular processes. To my knowledge, no data at the cellular level are available to prove that the costs of cellular processes should obey the supposed $-\frac{1}{4}$ scaling relationship. Recall that the MTE growth model predicts that the maintenance cost of, for example, a single lizard cell is much higher than that of a crocodile cell $(m \propto W_{\infty}^{-1/4})$, independent of the actual size of the animal (Figure 1). The supposed $-\frac{1}{4}$ scaling relationship should thus also hold for the maintenance costs of in vitro cells. West and Brown [45], when presenting the empirical result that the metabolic rate of in vitro cultured cells is constant among species differing in ultimate size, nevertheless stated that such a result is predicted by MTE theory and refer to the constraints set by the supply rate which would cause a $-\frac{1}{4}$ scaling relationship for cells in vivo. Apparently, they equate the metabolic rate with the supply rate, and the contradiction is thus the result of the same inconsistency in the definition of metabolic rate, which I was referring to above.

Conclusion

A new theory should be judged on a variety of criteria: it should be internally consistent, it should be as simple and general as possible, it should be in accordance with broadly accepted and more fundamental theories, and it should be in line with empirical observations. Last, but not least, it should be new.

At least at the level of the organism, the MTE has provided few insights that DEB theory has not already offered. The new insights that MTE proposes appear to be inconsistent under closer scrutiny. Contrary to its claims, MTE does not imply a $\frac{3}{4}$ scaling law of metabolic rate, when organisms of different size of one species are compared. Neither is the law predicted for interspecific comparisons, unless the biologically questionable assumption is made that cellular maintenance costs scale with a $-\frac{1}{4}$ power. Recently, West and Brown [45] oppose the distinction between supply- and demand-driven processes, thereby (unintentionally) dismissing their own growth model and increasing the level of inconsistency.

The proponents of MTE have succeeded in getting the idea of a mechanistic and dynamic theory of energy

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budgets onto the research agenda of ecology. This agenda should now include the two opposing views (i.e. the earlier and simpler DEB theory based on surface area- and volume-related processes and the MTE based on fractallike branching structures) being tested fully, but only if the inconsistencies in MTE can be repaired. If that is not possible, MTE should be removed from this agenda. A sound theoretical basis of the energy budget of the individual organism is a prerequisite for further journeys into the realm of populations, communities and ecosystems.

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