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Metabolic theory or metabolic models?

Carlos Martínez del Río

Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82070, USA

The metabolic theory of ecology (MTE) claims to derive ecological relationships from the structure of resource distribution networks, which is assumed to determine the scaling of metabolism with body mass, and from the effect of temperature on the rate of biological processes. MTE is controversial. I propose that some of the controversy stems from the implicit adoption of different views of science by the proponents and critics of MTE. The perspective of proponents is consistent with the theory-centric view of science called the received view, whereas many of the critics implicitly adopt an alternative view consistent with a model-centric view of science. I propose that adopting the model-centric view can help to settle some of the differences among proponents and critics of MTE.

Why is MTE controversial? A conjecture

The metabolic theory of ecology (MTE) is bold, big and contentious. It has been heralded by some as one of the greatest advances in ecology, and by others as a threat that will slow down conceptual progress [1]. The number of attacks and counterattacks that it has elicited is summarized in Refs [2,3]. A curious observation on the published critiques of MTE is that most include a sentence in which the authors applaud how the theory has sparked controversy and focused attention on a potentially important issue. I am less sanguine about the presumed benefits of heated debate, inasmuch as these are based on the assumption that scientific controversies are resolved rationally when logic and/or evidence hold sway. Scientific controversies are about facts, observations and methods, but they are also about complex implicit assumptions about how nature works and about how it should be studied [4]. I will hypothesize that at the heart of the debate about MTE are two conceptions of the meaning of the word ‘theory’ and the scientific practices that accompany these.

My conjecture has its origins in an exchange between Fox Keller [5], a philosopher of science, and Enquist and Stark [6], who are proponents of MTE. Fox Keller [5] questioned whether biology has universally applicable laws derived from first principles. Enquist and Stark [6] defended the quest for universal laws, such as those that they claimed are embodied in MTE, as a legitimate and useful goal for biology. Enquist and Stark [6] follow a long and distinguished intellectual tradition well exemplified by the ideas of the ‘organic physicists’ of the 19th century (e.g. Hermann von Helmholtz, Carl Ludwig and Ernst Brücke), who aimed to explain all living phenomena exclusively through the laws of physics and chemistry. The ideas

of the organic physicists were viewed with considerable skepticism by the physiologist Claude Bernard [7], who considered that physics and chemistry could only inform, but not be the foundation of, the models of physiology. Enquist and Stark [6] cite an organic physicist, D’Arcy Thompson, as a source of inspiration. Ironically, in a previous historical analysis, Fox Keller found that the research program of D’Arcy Thompson and other early 20th century organic physicists had little resonance in contemporary biology [8]. I will argue that some (although not all) of the controversy that surrounds MTE results from the fact that its approach contrasts with that of most biologists.

Theory- and model-centric views of science

Fox Keller [5] and Enquist and Stark [6] represent two perspectives of science. Enquist and Stark [6] have, consciously or not, adopted logical empiricism (or the ‘standard’ or ‘received’ view [9]) as a normative ideal for the scientific enterprise. The received view is ‘theory centric’ ([10], p. 33). It assumes that knowledge must be encapsulated in scientific theories understood as systems in which first principles act as axioms from which models are derived as theorems [10]. Thus, the main (or ‘master’) equation of metabolic theory (Box 1) is derived as a theorem that flows from three first principles (Box 1). Both the practitioners of metabolic theory and its popularizers often refer to Equation 1 in Box 1 as a master equation ([11] and references therein), and claim that it is derived from first principles.

In contrast with the theory centrism of the received view, Fox Keller and many contemporary philosophers of science give models a central role in scientific inquiry [9,12,13]. Models are representations of some aspect of nature for a purpose of investigation [13]. They are objects to inquire with and inquire into [14]. Models can be verbal accounts, mathematical formulations, computer programs, diagrams and physical/mechanical objects [13]. The relationship between a model and the world is mediated by assumptions of the form “model M is similar to system S in certain respects and degrees” [15]. We can classify models on the basis of their resemblance to other models devised to tackle similar problems and group them into families [16]. These families are sometimes called ‘theories’ [16], but the diversity of assumptions of the included models makes model families very different from the theories of the received view.

In a model-centric view of science there is no single best, all-purpose model. By contrast, there can be several models of the same phenomenon which represent separate aspects of the system [17]. A good example from physics is how water is sometimes modeled as a fluid using Navier-Stokes

Corresponding author: del Río, C.M. (cmedelrio@uwyo.edu).

Box 1. The master equation of metabolic theory

The use of the term 'master equation' in MTE differs from the usage in physics, where master equations are simply sets of differential equations that describe the evolution of a system. However, for consistency, and following [11] and the proponents of MTE, I will use the term to refer to the equation that summarizes the main results of MTE. The master equation of MTE (Equation 1) establishes that whole organism metabolic rate (I in Watts) is the product of an allometric equation that depends on mass (M [33]) and the Arrhenius equation, which depends on temperature (T in °K [29]),

$$I = I_0 M^{3/4} e^{-\frac{E}{kT}} \quad [1]$$

where I_0 is a normalization constant, E is an empirical constant that is assumed to be the average energy of activation of the respiratory complex ($E \approx 0.65$ eV [29]) and k is Boltzmann's constant (in eV \times K $^{-1}$). Proponents of MTE assume that the components of the master equation are a consequence of three first principles: (i) organisms rely on hierarchically branching and volume-filling resource distribution networks, (ii) natural selection has tended to maximize both metabolic capacity (by maximizing the scaling of exchange surface areas) and internal efficiency (by minimizing the scaling of transport distances and times) [28] and (iii) the rate coefficient for metabolism at all scales (from enzymes to organisms) depends on temperature following the Arrhenius equation ([29]; see also Refs [28,30,31]). Note that the exponent of Equation 1 is 3/4. Proponents of MTE derive a variety of 'quarter-power' rules from this exponent. We can call Equation 1 the universalist or received master equation of MTE. By substituting 3/4 and 0.65 eV by constants derived from each data set, we gain a form of the master equation that is (or should be) much less contentious.

equations, and at other times as a collection of particles using statistical mechanics [18]. Population biologists can model individuals as having ecologies but no genetics, or as having genetics but no ecologies [19]. Indeed, evolutionary population biology is a representative example of model-centric theories. Richard Levins [17] recognized that ecologists have a diversity of objectives and interests when they build models, and that this diversity imposes trade-offs. Levins's [20] well-known (and controversial; e.g. Ref. [21]) precision/realism/generalizability triangle clarifies the potential tradeoffs that modelers face. Models differ depending on whether the modeler aims to challenge existing theory, make predictions or simply make the interconnections among related concepts and processes intelligible. Hence, evaluation of the virtues of a model is crucially dependent on the purposes for which it was built [13]. Because models are built with a restricted set of objectives in mind, there is little room for universality claims in the model-centric view. By contrast, universality claims are prevalent in both popular accounts of the metabolic theory as well as in the rhetoric of its proponents [22,23].

Modes of inquiry and the metabolic theory controversy

I believe that the distinction between the theory-centric view and what I have called model-centric views of science illuminates the controversies that have plagued the metabolic theory. Readers might predict that I will equate proponents of the theory with the received and opponents with the model-centric views. However, I will pose a slightly more complex model in which proponents adopt

the received view but critics adopt stances that are compatible with both the model-centric and the received view. From its inception, the proponents of MTE have emphasized the law-like regularity of allometry (including the universality of quarter power exponents; see Box 1 and Refs [22,23]), as well as the virtues of models derived from the first principles from chemistry and physics [24]. Although I doubt that most of the biologists critical of MTE would immediately identify with a model view of science, their arguments are often compatible with this perspective. Thus, many biologists tend to question the universality of MTE [25], the need and wisdom of deriving from first principles a single master equation that serves all cases [26] and the existence of common mechanisms for the seeming allometric regularity of metabolism [2]. Philosophers of science also distrust the notion of a scientific law (e.g. note the titles of Refs [12,27]). For example, a prominent architect of the model view proposed that the notion of a scientific law was imported into science from theology in the 17th century ([10], p. 23).

I do not imply that scientists have taken sides in the battles over science philosophy [10]. Most biologists pay little attention to debates in philosophy, and we are, for the most part, none the worse for it. However, the attitudes of biologists about theory can often be identified with both how philosophers of science describe how biologists do science and how they believe that we should practice it. Although my primary objective is to diagnose why MTE is so controversial among biologists, this paper also has a prescriptive element. It will contend that progress in the development of MTE will be faster and less contentious if we adopt a model-centric, rather than a theory-centric, perspective.

Is the master equation of MTE a model – and if so, of what?

The master equation of MTE has two components: an allometric one that relates metabolism with body mass [28], and a thermodynamic one that establishes the relationship between metabolism and temperature [29]. Here I will emphasize its allometric component. Subsequently, I will deal with how it accounts for temperature. The three models that make up the foundation of the metabolic theory are grounded in the same set of principles but can be characterized as mammalian [30], plant [31] and a general model that is based on geometrical principles [28] but that seems to have been designed with unicellular organisms in mind [3]. The mammalian and plant models make predictions that apply only to the specific systems that they represent, but the models also have seemingly robust [20], general results that they share with the unicell model [28]. Importantly, the proponents of MTE note that an exponent equal to 3/4 was derived from the three models [32], and they interpret the putative prevalence of 3/4 as an allometric exponent in empirical data sets as evidence for the generality of the principles from which the models were derived [33]. The proponents of a universal MTE assume that the principles used to derive their three foundation models apply to most if not all organisms [28].

When West, Brown and Enquist derived the allometric component of MTE's master equation, they were aware

that changing the assumptions of the models could lead to differences in the 3/4 exponent. For example, in their plant model, they listed the potential ‘violations’ most likely to affect the model’s predictions (e.g. departure from precise volume filling) [31]. However, they concluded that “these complications... have small effects, because many quantities, such as scaling exponents, effectively average out over the whole plant” ([31], p. 667). This belief led them to postulate the generality of the 3/4 exponent for vascular plants [23]. Then, in 2006, Reich and colleagues [25] published a data set that demonstrated that in seedlings, saplings and small trees, the metabolic scaling exponent was 1 rather than 3/4. Because many plants are small [34], the complications identified by West and colleagues [31] proved to be important. In response to the observation by Reich and colleagues [25], Enquist and colleagues [35] pointed out that West and colleagues [31] had predicted the deviation from the 3/4 exponent. However, in recognition of the potential variation in the metabolic exponent, Enquist and colleagues [36] now use the expression $B = b_0 M^\theta$, and substitute the variable θ for the constant 3/4 in their models. The size dependency of θ in the plant model by West and colleagues [31] highlights the need to find out which assumptions of a model collection are central to a prediction and which are not. From a model-centric perspective, this can be elucidated by robustness analysis, as described below.

A case for robustness analysis

The model view can be critiqued as a piecemeal approach to investigate the world with no hope for generality. Richard Levins [20] proposed a way that general results can be obtained from similar, but distinct, models. Briefly, he proposed finding common predictions shared by members of model families: ‘If these models, despite their different assumptions, lead to similar results, we have... a robust theorem that is relatively free of the details of the model’ ([20], p. 20). Weisberg [37] summarized Levins’s [20] suggestion in a four-step program. In the case of MTE models, the first step would be to examine a sufficiently diverse group of independent models to determine whether they all predict a common result. Models are independent if they differ in some of their underlying assumptions. The second step requires looking into the models to find the common assumptions that produce the robust property. The first and second steps are then combined to formulate a robust prediction of the form “all else being equal, if organisms have fractal-like, hierarchically structured, space-filling, resource distribution systems with size-invariant terminal units, then metabolism and body mass will be related by a power function of the form $B = b_0 M^\theta$, and the value of θ will equal 3/4.”

This statement is abstract and general and might apply to a large set of organisms. The third step is to transform the robust statement into a set of predictions that can be tested empirically in real systems. The fourth step is a form of conceptual stability analysis: we find the conditions that break the connection between the assumptions and the robust prediction of the models. We ask under what conditions these assumptions do not yield the robust prediction. After step four, it might be possible to substitute the

‘all-else-being-equal’ clause by the specific conditions that cause the key assumptions to fail to give a robust result [37].

Because the master equation of MTE is the result of three models with similar, but not identical, assumptions (described in Refs [28,30,31]), it appears to be a summary of a robust statement [33]. However, I would argue that this robustness analysis is incomplete, as it does not include the large collection of other independent models that aim to explain the allometric dependence of metabolic rate on body mass (see Ref. [38]), but instead is based on three models only. An incomplete analysis can either miss assumptions that are essential, or identify assumptions that are unnecessary as pivotal. For example, a recent model [39] suggests that the requirement of MTE of natural selection to maximize both metabolic capacity and internal efficiency (see Box 1) is dispensable. By contrast, the episode elicited by the analysis by Reich and colleagues [25] suggests that the space-filling assumption is key [35]. A thorough rigorous robustness analysis of the multiple possible derivations of the master equation of MTE appears vital for the future development of MTE [38].

Only research into real organisms can determine whether a robust result is empirically sound [16,37]. We must evaluate whether model assumptions are faithful to the objects represented and, then, whether their predictions hold. Models with faulty assumptions and/or wrong predictions are eventually discarded. The goodness of a model or robust result is assessed by its fit with observations and experimental results [10]. Much discussion on MTE has been centered on the question of how general its three models are [2,38]. The critics question whether the seemingly robust results of the theory, such as the derivation of the 3/4 exponent, are based on a representative sample of models that capture the diversity of body plans found among organisms, or whether they are the result of the assumptions of a small and biased sample [2]. Given the large number of exceptions to the 3/4 exponent [40], this critique appears legitimate. For example, Glazier [40] found that roughly 50% of the intraspecific ontogenetic scaling exponents in 322 species were statistically different from 3/4. Progress in MTE depends on expanding the family of models that constitute the theory, as much as on the rigor with which we contrast its predictions with data and experimental results.

Is the metabolic theory based on first principles, and does it matter?

Often, scientists characterize models as either mechanistic or phenomenological [12]. Mechanistic models are based on a set of assumptions (often termed ‘first principles’) connected by causal links. The most commonly used phenomenological models are statistical descriptions of a pattern with no claim to causal connections among variables. The preference of some theoreticians for mechanistic models is based on the notion that phenomenological models are about superficial similarities, whereas mechanistic models are about the fundamental reality behind apparent similarities [12]. The proponents of MTE [24], and sometimes their critics [2], have emphasized the virtues of theories built on ‘mechanistic’ first principles [3]. A model view

adopts the more pragmatic view that mechanistic models are useful for two related reasons: first, their construction often allows us to peer more clearly into their internal structure, and second, because mechanistic models illuminate the causation pathways among variables that create a pattern, it is easier to evaluate each of these pathways empirically. We should often prefer mechanistic models not because there is something inherently virtuous in relying on first principles, but for clarity and because such models can be more easily compared and evaluated.

However, purely mechanistic models can be large and unwieldy [41], and sometimes we do not have all the elements to construct a fully mechanistic model and have to rely on phenomenological components. Therefore, models that mingle phenomenological and mechanistic elements are very common in the sciences. These hybrids can be very successful. For example, Gillooly and Allen [42] used a phenomenological statistical relationship between the change in body temperature and body mass in exercising mammals as an element in a model that explains why maximal respiration rate scales roughly with body mass to an exponent that ranges from 0.79 to 0.87, rather than with body mass to the 3/4th power. Another example is the use of the Arrhenius equation in the master equation of MTE (Box 1). Although the Arrhenius equation is claimed to be “firmly based on statistical thermodynamics” [3], most physical chemists consider it a phenomenological approximation [43]. Instead, they consider Eyring’s transition-state equation to be truly based on first principles [44]. In the model view, the advantage of the modeling mechanism depends on the purpose of the model, and therefore the inclusion of the Arrhenius equation in MTE’s master equation is an approximation that is good enough for many uses. From the model perspective, the universal superiority of mechanistic models is a red herring. Although the master equation of MTE is not a mechanistic model based solely on first principles, its hybrid nature is not a fatal flaw.

The role of MTE in macroecology

MTE has two components. First, it attempts to identify and explain the form of the relationship between metabolism and body size and temperature in organisms, and second, it characterizes the effect of body size and temperature at higher levels of organization such as populations, communities and ecosystems [33]. Proponents of MTE see these two components as linked, but critics argue that the link is tenuous [2]. Implicit in the perspective of the proponents, and consistent with the received view of science, is the assumption that the success of the application of MTE to higher levels validates the premises at the lower levels [22,33]. West and Brown [23], for example, argue that the scaling of many patterns in a forest, such as the abundance of trees as a function of the diameter of the trees, mimics that of the scaling of the number of branches in single trees on tree diameter. Furthermore, they propose that the similarities in scaling between the forest and the trees are a result of the same causes. Perhaps one of the most interesting outcomes of the development of MTE is the successful prediction of broad macroecological patterns from the simple premises embodied in MTE’s master

equation [33,36]. Two commendable instances of the application of the MTE equation as a component of models that explore high-level phenomena are the derivation by Enquist and colleagues [36] of a model that scales plant growth and carbon flux from spectra of functional traits, and Allen *et al.*’s [45] application of MTE to explain global biodiversity patterns.

How can we interpret the success of the application of MTE to higher levels of organization in light of the model view? Again, Richard Levins has a useful suggestion – he proposed the idea of a sufficient parameter (or equation [20]), which captures the effect of variation in a lower level for the purpose of building simpler models of upper-level phenomena [16]. I speculate that the metabolic equation of MTE is one such sufficient parameter or equation. If sufficient parameters are based on a robust result, they can lead to descriptions of upper-level phenomena that are independent of the fine details of variation at lower levels [17]. Even though 3/4 might not be a universal metabolic exponent [40], using it as a sufficient parameter in allometric equations that are components of more complex models can lead to adequate approximations (see Ref. [36]).

A caveat to the use of sufficient parameters in modeling is a consequence of the observation that their construction involves many-to-one, or many-to-few, transformations [20]. Parameter reductions create imprecision, and therefore the resulting upper-level patterns that result from using sufficient parameters give a coarser description of a phenomenon. Consequently, the descriptions produced by the application of MTE can be too rough except as first-order approximations [33]. The general relationships between body mass and temperature and population parameters [33], for example, might be too imprecise for use by wildlife/fisheries biologists interested in estimating accurate values of a species’ vital statistics. In this case, the patterns unveiled by the macroecological applications of MTE do not substitute for detailed studies summarized in more elaborate and detailed demographic models.

Coda: MTE, received or modeled?

I attempted to illuminate the controversy around MTE by placing it under the light of two competing views of science. I believe that if the architects of MTE had adopted a model view of MTE, the controversy would have been much less strident, but on the other hand, the impact of MTE would have been reduced. The big splash that MTE has made is a result of the still firm hold that the rhetoric of the received view has on science and culture. The promise of creating a Newtonian biology, or of transforming biology into a science with a big S [6], remains alluring [46]. However, as identified by Fox Keller, and as the reaction to MTE illustrates, many biologists have little patience with the received view [8]. Furthermore, it appears that the mode of inquiry that has dominated our discipline in the century when it acquired ascendancy [47] is more consistent with the model view than with the received view [17]. The theoretical bodies of even the most mathematized disciplines in biology, including population biology [48], population genetics [49], epidemiology [50] and ecosystems ecology [51] can be best characterized as collections of models, rather than assemblages of received theories.

Abandoning the received view will not make biology less mathematical, less quantitative and/or less predictive [52]. However, the model view of biology dims the outlook for a general law of the living. Richard Lewontin [46] has quipped that 'Newtonhood' might not be an option for biologists. We are blessed or condemned (depending on your temperament) to live a science without laws [53].

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