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Letter to the Editor

Distributive network model of Banavar, Damuth, Maritan and Rinaldo (2002): Critique and perspective

In a recent paper (Makarieva et al., 2005a) we criticized the distributive network model of Banavar, Maritan and Rinaldo (BMR) (1999). We demonstrated that the proposed derivation of the 3/4 scaling for whole-body metabolic rate B, $B \propto M^{3/4}$, where M is body mass, is mathematically controversial. We also stated that the controversy persists in the subsequent development of the model by Banavar, Damuth, Maritan and Rinaldo (BDMR) (2002). In their response Banavar et al. (2006) accepted our criticisms of the 1999 model but disagree with our criticisms of the 2002 model. In the present paper we undertake a detailed analysis of the BDMR model to support our earlier conclusion.

1. Critique

Both BMR in 1999 and BDMR in 2002 consider a network delivering metabolites or energy to individual consumers evenly distributed in a D-dimensional space of linear size L (L corresponds to linear body size in animals). The nature of consumers is very general, from households consuming running water to microscopic transfer sites (e.g. cells) in the living tissues, where the uptake of energy from the distributive network occurs. An essential feature of both models is the presence of a size-invariant parameter. In the BMR model it is denoted as l and is explicitly defined as the mean distance between neighboring transfer sites, so that $(L/l)^D$ gives the total number of individual consumers in the system. In the BDMR model the size-invariant parameter is denoted as u, to which no explicit definition is given. It is characterized generally as "the basic length unit" and as "a length based on the size of a typical house and its immediate environs". However, the statement of BDMR that the number of individual consumers in the network scales as $(L/u)^D$ makes it clear that u in the BDMR model, similar to l in the BMR model, is equal (to the accuracy of a dimensionless numeric coefficient) to the distance between the neighboring consumers. Namely this distance determines the spatial density of consumers and their total number $N_s = (L/u)^D$ in a D-dimensional system of linear size L.

The key result of the BMR model is that the total volume C of the network (e.g. blood volume in mammals), denoted as V_d by Makarieva et al. (2005a), scales as the total number of consumers N_s multiplied by the linear size of the system L,

$$C \propto LN_s. \tag{1}$$

This result is readily illustrated by a simple network conforming to the main requirement of the BMR and BDMR models where "the flow of metabolites is always away from the source". We consider a central source of metabolites (e.g. a lake), from which the network pipes go to individual consumers (houses) that are evenly distributed in the two-dimensional space ($D = 2$) with a mean density $1/u^2$, Fig. 1a. Total number of consumers in the system (houses in the neighborhood) is $N_s = (L/u)^2$. It is clear that the total volume of the network is equal to the total number of pipes, which is N_s, multiplied by the mean volume of one pipe. Mean length of pipes is equal to L with a numeric coefficient of the order of unity, so mean volume of one pipe can be written as LR^2, where R is pipe radius. We thus have for the network volume $C = LR^2N_s$. If R is independent of total system size L, then the scaling $C \propto LN_s$ follows. Note that it corresponds to $C \propto LB$ if each consumer takes in energy at a size-independent rate.

Instead of building their further considerations on this important relationship, BDMR introduce a new variable F as "the sum of all individual flow rates" in pipes connecting the adjacent nodes of the network, dimension unit mass or volume per unit time (e.g. kg or liter blood per hour). BDMR state that BMR proved as a mathematical theorem that

$$F \propto (L/u)B, \tag{2}$$

where B is whole-body metabolic rate. We stated (Makarieva et al., 2005a) that this relationship is incorrect and is not equivalent to the result obtained by BMR. The network shown in Fig. 1a illustrates this point. In this simple network F, the sum of all individual flow rates, is equal to the sum of flow rates F_s in the N_s pipes, which, in its turn, is equal to the the sum of individual metabolic rates of the N_s consumers, i.e. to B. So we have $F = N_sF_s = B$ and not $F \propto (L/u)B$. Our first conclusion is therefore that the basic equation of the BDMR model, Eq. (2), is generally invalid for networks with directed flow. We stress that for the same network, Fig. 1a, the key result of BMR, Eq. (1), remains valid.

We now examine the physical meaning of variable F. Let each individual consumer (house) in Fig. 1a have a pump inside, which pumps water from the central source (lake) at

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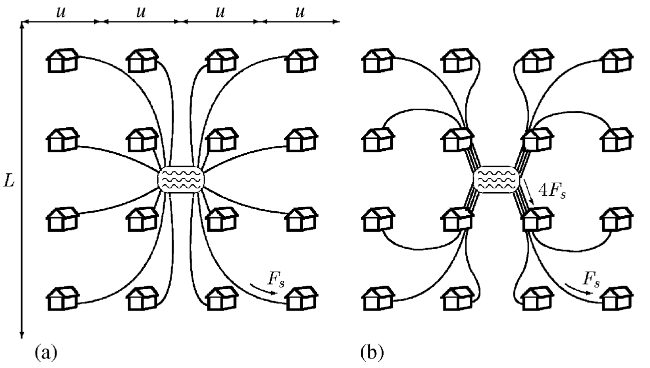

Fig. 1. A simple directed-flow network which illustrates general invalidity of Eq. (2) and ambiguity of definition of variable F ("sum of individual flow rates") in the model of Banavar et al. (2002). L is linear size of the distributive network, u is mean distance between individual consumers (houses) taking in metabolites (water) from a central source (lake) at a rate F_s ($\mathrm{l\,s^{-1}}$). In neighborhood **a** each house is connected to the lake by its own pipe; the same in neighborhood **b**, but the pipes are combined by four and enclosed in large tubes between the lake and the four nearest houses. Despite equivalent energetics of neighborhoods **a** and **b**, their F values are drastically different. See text for further details.

a certain rate $F_s = vR^2$, where v (m/s) is flow velocity (v was denoted as u_c by Makarieva et al. (2005a)). Each of the $N_s = 16$ houses is connected to the lake by its own pipe, so, as discussed above, in neighborhood **a** we have $F \equiv F_a = N_s\,F_s = 16\,F_s$.

Let us now enclose the four pipes going from the lake to the four houses situated in the right-hand lower quarter of the neighborhood into one large tube, Fig. 1b. This tube, as well as one of the four pipes within it, terminates in the nearest to the lake house. The remaining three pipes go to the remaining more distant houses. The same procedure is applied to the other three quarters of neighborhood **b**. In this new configuration the four houses that are nearest to the lake can be considered as new nodes of the network. If so, applying BDMR's procedure of calculating F, its value is now equal to the sum of flow rates in the four tubes connecting the lake to the nearest houses plus the sum of flow rates in the 12 pipes, which do not terminate where the tubes do, but go further to the 12 distant houses. As far as within each tube the flow rate is $4F_s$, while within each pipe it is F_s, for neighborhood **b** we have $F \equiv F_b = 4 \times 4F_s + 12\,F_s = 28\,F_s \neq F_a$.

The neighborhoods shown in Figs. 1a and b are identical in terms of energy consumption. The same pumps bring water to the same houses at the same rates via the same pipes; the network volume C is the same; total "metabolic rate" of the two neighborhoods is the same. The only thing that was changed by housekeepers in neighborhood **b** was the external design of the network—individual pipes were combined by four and enclosed (e.g. for the sake of decorum) by tubes along some part of the distance between the lake and the houses. In the meantime, the value of F has nearly doubled in neighborhood **b** as compared to neighborhood **a**. The value of F depends therefore on our subjective decision whether or not we consider the four nearest to the lake houses as nodes of the network.

This subjectivity of F definition can be illustrated for biological systems as well. For example, in many trees individual leaves are connected to the root system by individual capillaries, which can be traced within the trunk and branches along the entire path from the underground to the leaf. Thus, one can envisage tree as neighborhood **a**, where each leaf (house) is directly connected to the source of biogens (water) by its own capillary (pipe) with no intermediate network nodes. At the same time, as far as these capillaries are spatially bunched first within the trunk, then within the branches, we can consider the tree as neighborhood **b**, where before reaching the leaf (house) the flow of biogens (water) passes through one or more nodes where the network branches. Depending on our subjective vision, F values calculated as prescribed by BDMR will be drastically different.

Our second conclusion is therefore that F is an ambiguously defined variable, which, in contrast to the strictly defined network volume C, does not capture physics of the spatial resource distribution problem.

We now turn to the details of BDMR's derivation of the 3/4 scaling for metabolism from Eq. (2). BDMR introduce a new variable $r_1 \equiv F/M \propto (L/u)E$, where M is body mass and $E \equiv B/M$ is mass-specific metabolic rate. BDMR describe r_1 as "a rate, associated with the scaling of the capacity of the network to supply metabolites." r_1 has the dimension of inverse time. BDMR introduce another variable l_s, which is linear size of such a body volume, which consumes 1 unit metabolite mass per unit time, so that $El_s^D \equiv 1$ unit mass per unit time. Ultimately, BDMR introduce a third variable, r_2. Unlike the previous two, it has no explicit definition, is called "demand" rate (BDMR's quotes), and is set to be proportional to l_s/u, $r_2 \propto l_s/u$. BDMR then postulate that supply and demand are matched when $r_1 \propto r_2$. This yields a proportionality $(L/u)E \propto l_s/u$. Recalling that $l_s \propto E^{-1/D}$ (from the definition of l_s) and that $L \propto M^{1/D}$, this proportionality yields $E^{1+1/D} \propto L^{-1} \propto M^{-1/D}$ and $B \equiv EM \propto M^{1-1/(D+1)} = M^{D/(D+1)} = M^{3/4}$ for $D = 3$.

The critical relationship in the above derivation is $r_1 \propto r_2$, which is interpreted by BDMR as demand–supply balance. However, r_1 is not the rate of actual delivery of metabolites to a unit live mass, as admitted by BDMR themselves. Neither is the unmeasurable variable r_2 the demand rate. It is introduced as follows: "Noting that 1 time unit is associated with the length l_s, the time scale corresponding to the length scale u must be proportional to u/l_s, so that the "demand" rate (measured in inverse time units) is given by $r_2 \propto l_s/u$."

As far as the ratio l_s/u is dimensionless, in order to obtain a dimension of inverse time for r_2, to match the same dimension in r_1, it is necessary to multiply l_s/u by a size-invariant parameter having the dimension of inverse time. In the considered problem the only basic variable including time in its dimension is flow velocity v ($\mathrm{m\,s^{-1}}$).

The dimension of inverse time can be obtained from v by dividing it by u (m). We have shown (Makarieva et al., 2005a) that the BMR model implicitly assumes a size-invariant v. Had it been the case in the BDMR model as well, then one could write $r_2 = (v/u)\ (l_s/u)$, which has a dimension of inverse time, and, at a size-invariant u, preserve the proportionality $r_2 \propto l_s$, which is critical for the above derivation of $B \propto M^{3/4}$.

However, in the BDMR model flow velocity is not size invariant. BDMR state that in their model the network volume C, Eq. (1), is proportional to body mass, i.e. $C = LR^2N_s \propto M$. At the same time, they derive that $B = N_sF_s = N_svR^2 \propto M^{3/4}$. This gives $C/B = L/v \propto M^{1/4}$, from which, at $L \propto M^{1/3}$, one obtains that $v \propto L^{-1/4} \propto M^{-1/12}$.

Putting now $r_2 = (v/u)\ (l_s/u)$ to obtain the needed dimension of inverse time for r_2, we obtain from $r_1 \propto r_2$ (ignoring everywhere the size-invariant u) that $LE \propto v\ l_s$. As far as $l_s \propto E^{-1/3}$ (for $D = 3$) and $v \propto L^{-1/4}$, this gives $E^{4/3} \propto L^{-4/3}$, i.e. $E \propto L^{-1} \propto M^{-1/3}$, and, ultimately, $B = EM \propto M^{2/3}$.

Thus, having derived $v \propto M^{-1/12}$ from the model's basic relationships, $B \propto M^{3/4}$ and $C \propto M$, and using this very scaling in the model's derivations one obtains that $B \propto M^{2/3}$. This illustrates that the BDMR model is mathematically controversial, similar to the BMR model, where from $B \propto M^{3/4}$ and $C \propto M$ one can obtain that $B \propto M$ (Makarieva et al., 2005a).

Absence of physical content and the arbitrary nature of the particular scaling $r_2 \propto l_s/u$ chosen by BDMR for the "demand" rate r_2 (BDMR's quotes) also becomes clear from the following consideration. Supply–demand balance implies equal spatial dimensions of the matched supply and demand rates, e.g. the rate of supply per unit area must be equal to the rate of demand per unit area; the rate of supply per unit mass must be equal to the rate of demand per unit mass, etc. Supply and demand rates pertaining to different spatial dimensions cannot be equal to each other and are not expected to scale isometrically. In this sense r_1, which has an exemplary dimension of kg blood per kg live mass per hour, physically pertains to unit mass (or unit spatial volume), although one can formally cancel mass units in its dimension. In the meantime, there are no grounds to consider the "demand" rate r_2, which is proportional to the linear scale l_s, as pertaining to unit volume. BDMR explain their choice of $r_2 \propto l_s/u$ by noting, referring to the definition of l_s as $El_s^D \equiv 1$ unit mass per unit time, that scale l_s is "associated" with 1 time unit. However, one could write, referring to the same definition and equally without physical grounds, that 1 time unit is "associated" with spatial volume l_s^D and introduce r_2 as $r_2 \propto (l_s/u)^D$; or that 1 time unit is "associated" with spatial area l_s^{D-1} and introduce r_2 as $(l_s/u)^{D-1}$, etc. Introduced in such an arbitrary manner r_2 can give rise to any pre-set value of the scaling exponent for B. In science one operates with clearly defined notions as equality, proportionality or, in the most general case, functional dependence. The notion of "association" lacks a formal scientific definition and cannot be used as the basis for introducing physically meaningful variables.

We ultimately conclude that the derivation of $B \propto M^{3/4}$ in the BDMR model is a mathematical manipulation with formally introduced variables and arbitrarily postulated, mathematically controversial relationships deprived of physical content.

2. Discussion and perspective

In their 1999 work BMR showed that the total mass of distributive network grows faster with system size than the total mass of objects that are supplied by that network, Eq. (1). On the other hand, the distributive network must be contained within the body which it supplies. These two statements reflect the essential properties of the studied objects. All mathematical, physical and biological inconsistencies inherent to the models of BMR and BDMR, as well as to the model of West et al. (1997) (Makarieva et al., 2005a, b) ultimately result from, and can be traced to, the attempts to superimpose on the above statements an additional implicit and unjustified assumption that all organismal tissues feature a uniform mass-specific metabolic rate. Indeed, in all the three models the objects that are supplied by the network are evenly distributed within the body and consume energy at equal rates. Besides causing controversies in theory, this assumption strongly contradicts the empirical evidence (Makarieva et al., 2003, 2005a–c). While subsidiary mechanical tissues in both plants and animals may have negligible mass-specific metabolic rates that may change freely with body size, the critically important tissues like plant leaves or animal brains are maintained at a nearly universal mass-specific metabolic rate of around 1–10 W kg^{-1}. This rate supports viability of organisms as diverse in size as bacteria and whales (Makarieva et al., 2005c) and as diverse in biology as plants and animals, unicellular and multicellular organisms (Makarieva et al., 2005a, b). As we have shown (Makarieva et al., 2005a, b), recognizing this ubiquitous feature of organization of higher organisms allows to avoid all controversies and obtain realistic values of scaling exponents for whole-body metabolic rate B making use of the important result, Eq. (1), obtained by Banavar et al. (1999).

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