

## 1 **Biomass of a trophic level increases with maximum body size, but less than proportionally**

2 Henrique C. Giacomini

3 *Ontario Ministry of Natural Resources and Forestry, 2140 East Bank Drive, Peterborough, ON, Canada,*  
4 *K9J 7B8*

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6 A recent paper by Enquist and colleagues<sup>1</sup> took a very important step in predicting the  
7 ecosystemic effects of species losses on a global scale. Using Metabolic Scaling Theory (MST), they  
8 concluded that large-sized species contribute disproportionately to several ecosystem functions. One of  
9 their key predictions is that total biomass of animals in a trophic level ( $M_{Tot}$ , using their notation) should  
10 increase more than proportionally with its maximum body size ( $m_{max}$ ), following the relationship  
11  $M_{Tot} \propto m_{max}^{5/4}$ . Here I argue that this superlinear scaling results from an incorrect representation of  
12 the individual size distribution and that the exponent should be 1/4, implying a sublinear scaling. The  
13 same reasoning applies to total energy flux or metabolism  $B_{Tot}$ , which should be invariant to maximum  
14 size according to the energetic equivalence and perfect compensatory responses entailed by MST.

15 The total biomass within a size interval characterizing a trophic level is calculated by integrating  
16 the product of individual mass  $m$  by its density function  $f(m)$ , also known as size spectrum or individual  
17 size distribution:

$$M_{Tot} = \int_{m_0}^{m_{max}} m f(m) dm \quad (1)$$

18 where  $m_0$  and  $m_{max}$  are the lower and upper limits of the size interval. To be an appropriate density  
19 function,  $f(m)$  must be measured as number of individuals per unit space (area or volume) per unit  
20 mass (ref. 2), so that, when integrated over a size interval, it gives the total number of individuals per

21 unit space (denoted here by  $N_{Tot}$ ). This is also a necessary condition for  $M_{Tot}$  in equation (1) to be  
22 measured in the correct scale, in total mass per unit space.

23 Based on MST, the authors define the size spectrum of animals as a power function, i.e.,  
24  $f(m) = cm^{-\epsilon}$ , with  $\epsilon = 3/4$ . However, the exponent  $-3/4$  typically describes changes in abundance  
25 along logarithmic intervals of body size<sup>3,4</sup>, the so-called abundance spectrum<sup>5</sup>, in this case for a single  
26 trophic level (for multiple trophic levels the exponent is more negative due to energy losses from trophic  
27 transfers<sup>6</sup>). Such abundance already represents an integration over a size interval and is measured as  
28 number of individuals per unit space, so it is not suitable as a density function to calculate biomass in  
29 equation (1). The abundance spectrum of a trophic level can be represented as a function of the  
30 interval's maximum size as  $N_{Tot} = \delta m_{\max}^{-3/4}$  (which reference size is used, whether maximum,  
31 minimum or a mid-point, does not change the exponent<sup>7</sup>). The relationship between  $N_{Tot}$  and  $f(m)$  can  
32 be thus expressed as:

$$N_{Tot} = \int_{m_0}^{m_{\max}} f(m) dm = \int_{m_{\max}/a}^{m_{\max}} cm^{-\epsilon} dm = \delta m_{\max}^{-3/4} \quad (2)$$

33 where  $a > 1$  is a constant defining the ratio  $m_{\max}/m_0$ , or the logarithmic range of the size interval; and  
34  $\delta$  is a coefficient given by  $\delta = 4c(a^{3/4} - 1)/3$ . Most importantly, the exponent satisfying equation (2) is  
35  $-\epsilon = -7/4$ , one unit lower than the value used by Enquist et al. Similar demonstrations can be found in  
36 refs. 7-8.

37 The value of  $\epsilon$  can be derived from more fundamental principles of MST if we assume a constant  
38 resource supply rate ( $J_{Tot}$ , in mass per time per unit space)<sup>3</sup>. At equilibrium, the total metabolism or  
39 energy flux of a trophic level,  $B_{Tot}$ , should be equal to their shared  $J_{Tot}$  (assuming further that  $J_{Tot}$   
40 corresponds to assimilated energy), so that biomass remains constant in time:

$$\frac{dM_{Tot}}{dt} = J_{Tot} - B_{Tot} = 0 \quad (3)$$

41 The total metabolism is equal to individual metabolism integrated over the size spectrum  $f(m)$ .

42 Individual metabolism is expected to scale as  $\propto m^{3/4}$  (ref. 3), so equation (3) can be expressed as:

$$J_{Tot} = B_{Tot} \propto \int_{m_{\max}/a}^{m_{\max}} m^{3/4} c m^{-\epsilon} dm \propto m_{\max}^{7/4-\epsilon} \quad (4)$$

43 As  $J_{Tot}$  is invariant with respect to size ( $J_{Tot} \propto m^0$ ), the equilibrium condition requires that  $\epsilon = 7/4$ .

44 The assumption of constant resource supply underlies the energetic equivalence rule or  
45 hypothesis<sup>4</sup> and explains the commonly observed scaling of  $N_{Tot}$  with an exponent -3/4 within a trophic  
46 level (or, more generally, with the reciprocal of individual metabolism's). The reasons for energetic  
47 equivalence are still a debated topic, and the hypothesis have found mixed empirical support (e.g., refs.  
48 9-10). It is nonetheless a prediction emerging from MST if all physiological processes determining the  
49 rates of energy gains and losses are proportional to individual metabolism and scale with the same  
50 exponent (e.g., 3/4). In this case, the efficiency with which energy is made available to biomass  
51 production, i.e., trophic transfer efficiency, can be represented by:

$$\Lambda = \frac{\gamma_i m^{3/4} - \sum_k \gamma_k m^{3/4}}{\gamma_i m^{3/4}} \quad (5)$$

52 where  $\gamma_i$  is the coefficient for energy input (e.g., ingestion), and  $\gamma_k$  are the coefficients representing all  
53 processes leading to energy losses (i.e., not used by the next trophic level), including respiration,  
54 excretion, egestion, and mortality from causes other than predation. Given a common exponent, the  
55 body size component cancels out and efficiency becomes a constant:  $\Lambda = (\gamma_i - \sum_k \gamma_k) / \gamma_i$ . Therefore,  
56 the amount of energy that is taken from a lower trophic level and metabolized remains the same (i.e.,

57 constant  $J_{Tot}$  and  $B_{Tot}$ ) regardless of which body sizes characterize the trophic level, and the resulting  
58 size spectrum scales as  $f(m) \propto m^{-7/4}$  (equation 4), implying  $N_{Tot} \propto m^{-3/4}$  (equation 2).

59 The total biomass calculated from equation (1) will be thus given by:

$$M_{Tot} = \int_{m_0}^{m_{max}} m c m^{-7/4} dm = 4c \left( m_{max}^{1/4} - m_0^{1/4} \right) \approx 4c m_{max}^{1/4} \quad (6)$$

60 where the resulting power function is an approximation for small  $m_0$ . It predicts an increase of biomass  
61 with maximum body size, but in a sublinear way.

62 It is important to recognize that the increase in biomass predicted by MST in equation (6) does  
63 not involve changes in ecological function. It results purely from the fact that larger organisms have  
64 slower turnover rates, which leads to greater biomass accumulation. From a community perspective, it  
65 implies perfect compensatory responses to species losses, as total resource utilization rate remains  
66 unchanged. Energy equivalence, constant trophic efficiency, and power-law size spectra are intrinsically  
67 related aspects of MST and all result from a common scaling of energetic processes. While there may be  
68 reasons for common scaling to result from long-term evolutionary processes<sup>11</sup> or broad-scale  
69 macroecological averaging, many real cases of ecological interest involve transient short- or mid-term  
70 changes that deviate from MST assumptions. For instance, trophic interactions are generally size-  
71 structured, so smaller predators in a trophic level cannot immediately compensate for the loss of large  
72 ones. Due to the increased proportion of uneaten prey, trophic efficiency (equation 5) would decrease  
73 nonlinearly with size, preventing analytical solutions in the form of simple power functions and limiting  
74 the scope of MST. In those cases, MST predictions are not expected to match empirical data or  
75 simulations from more realistic models. One example is the 18% decline in total heterotrophic  
76 metabolism that resulted from megaherbivore losses in the General Ecosystem Model simulations by  
77 Enquist et al., in contrast with the MST expectation of no change. Nonetheless, MST still serves as a

78 usefull baseline for comparison, one that controls for purely energetic processes but leaves out other  
79 important factors such as specialized ecological interactions and transient dynamics.

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