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

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A recent paper by Enquist and colleagues¹ took a very important step in predicting the ecosystemic effects of species losses on a global scale. Using Metabolic Scaling Theory (MST), they concluded that large-sized species contribute disproportionately to several ecosystem functions. One of their key predictions is that total biomass of animals in a trophic level (M_{Tot} , using their notation) should increase more than proportionally with its maximum body size (m_{max}), following the relationship $M_{Tot} \propto m_{max}^{5/4}$. Here I argue that this superlinear scaling results from an incorrect representation of the individual size distribution and that the exponent should be 1/4, implying a sublinear scaling. The same reasoning applies to total energy flux or metabolism B_{Tot} , which should be invariant to maximum size according to the energetic equivalence and perfect compensatory responses entailed by MST.

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

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

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

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

Based on MST, the authors define the size spectrum of animals as a power function, i.e., $f(m) = cm^{-\epsilon}$, with $\epsilon = 3/4$. However, the exponent $-3/4$ typically describes changes in abundance along logarithmic intervals of body size^{3,4}, the so-called abundance spectrum⁵, in this case for a single trophic level (for multiple trophic levels the exponent is more negative due to energy losses from trophic transfers⁶). Such abundance already represents an integration over a size interval and is measured as number of individuals per unit space, so it is not suitable as a density function to calculate biomass in equation (1). The abundance spectrum of a trophic level can be represented as a function of the interval's maximum size as $N_{Tot} = \delta m_{\max}^{-3/4}$ (which reference size is used, whether maximum, minimum or a mid-point, does not change the exponent⁷). The relationship between N_{Tot} and $f(m)$ can be thus expressed as:

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

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

The value of ϵ can be derived from more fundamental principles of MST if we assume a constant resource supply rate (J_{Tot} , in mass per time per unit space)³. At equilibrium, the total metabolism or energy flux of a trophic level, B_{Tot} , should be equal to their shared J_{Tot} (assuming further that J_{Tot} 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 hypothesis⁴ 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 γ_i is the coefficient for energy input (e.g., ingestion), and γ_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.,

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

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

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

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

It is important to recognize that the increase in biomass predicted by MST in equation (6) does not involve changes in ecological function. It results purely from the fact that larger organisms have slower turnover rates, which leads to greater biomass accumulation. From a community perspective, it implies perfect compensatory responses to species losses, as total resource utilization rate remains unchanged. Energy equivalence, constant trophic efficiency, and power-law size spectra are intrinsically related aspects of MST and all result from a common scaling of energetic processes. While there may be reasons for common scaling to result from long-term evolutionary processes¹¹ or broad-scale macroecological averaging, many real cases of ecological interest involve transient short- or mid-term changes that deviate from MST assumptions. For instance, trophic interactions are generally size-structured, so smaller predators in a trophic level cannot immediately compensate for the loss of large ones. Due to the increased proportion of uneaten prey, trophic efficiency (equation 5) would decrease nonlinearly with size, preventing analytical solutions in the form of simple power functions and limiting the scope of MST. In those cases, MST predictions are not expected to match empirical data or simulations from more realistic models. One example is the 18% decline in total heterotrophic metabolism that resulted from megaherbivore losses in the General Ecosystem Model simulations by Enquist et al., in contrast with the MST expectation of no change. Nonetheless, MST still serves as a

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

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