

Scaling body size fluctuations

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The size of an organism matters for its metabolic, growth, mortality, and other vital rates. Scale-free community size spectra (i.e., size distributions regardless of species) are routinely observed in natural ecosystems and are the product of intra- and interspecies regulation of the relative abundance of organisms of different sizes. Intra- and interspecies distributions of body sizes are thus major determinants of ecosystems' structure and function. We show experimentally that single-species mass distributions of unicellular eukaryotes covering different phyla exhibit both characteristic sizes and universal features over more than four orders of magnitude in mass. Remarkably, we find that the mean size of a species is sufficient to characterize its size distribution fully and that the latter has a universal form across all species. We show that an analytical physiological model accounts for the observed universality, which can be synthesized in a log-normal form for the intraspecies size distributions. We also propose how ecological and physiological processes should interact to produce scale-invariant community size spectra and discuss the implications of our results on allometric scaling laws involving body mass.

protist microcosms | allometry | finite size scaling | body mass | cell counter

Why should a continuous, gap-free spectrum of organismic sizes emerge from the ecological and evolutionary processes that shape their ecosystems? The origins and the implications of the absence of preferential body sizes, which is routinely observed across a variety of ecosystems regardless of broad differences in climatic and environmental conditions (1–5), have been attracting much interest from field and theoretical ecologists (6–13). Scale invariance, epitomized by power-law probability distributions (9, 12, 14–19), requires regularities of the component parts (the species' size distributions) making up the whole [the community size spectra (i.e., the probability distributions of size regardless of species)]. In particular, a necessary condition for scaling community size spectra is the lack of peaks that pinpoint frequent occurrences, and therefore excess abundance (and vice versa) within any given range of sizes. Such features are particularly interesting if robust to environmental fluctuations because their dynamic origin could lie in the self-organization of complex adaptive systems (6, 9, 15).

Body size distributions in natural ecosystems are strongly related to the life history of the organisms and to the dynamics of their living communities (18). Thereby, they modulate structure and function of the ecosystem at any scale. Size spectra, which display the relative abundance of organisms of different sizes within or across species, convey a synoptic and possibly taxon-independent image of ecological communities (1, 2, 20, 21). As such, they have long been attracting much interest in ecology because they hold important predictive power (e.g., fish stock projections from planktonic size spectra) (2, 5). Because examples and counterexamples of scaling spectra abound (2, 3, 5, 7, 21–24), it is an unsettled issue as to whether scaling size spectra represent some central tendency of statistically stationary states of natural ecosystems. For instance, the operational computation of mean phytoplankton size was shown to depend on the sample size typically (7) and scaling relationships were documented for interspecific plant biomass (20, 25, 26), whereas some terrestrial

ecosystems exhibit ubiquitous gaps in size and uneven relative abundances of organisms (1, 21).

Single species inhabiting communities, however, do exhibit a species-specific mean and variance of their sizes, as even common sense suggests. Thus, there naturally exists the mean size of a particular species, as usually implied by most, if not all, biological scaling laws (10, 27–31), wherein one typical mass subsumes a whole distribution of sizes. One thus wonders how evolutionary and ecological processes interact to modulate species' abundances, the range of sizes proper to each functional group, and the number of species existing within a given niche or range of sizes to concoct regular, taxon-independent, continuous size spectra. Moreover, one expects that the existence of a range of possible sizes for a species (and how such a range varies for different mean sizes) has to be taken into account when addressing scaling laws in biology (e.g., allometric scaling laws) (10, 11, 27–29, 32–39).

Here, we have precisely measured the intraspecies size distributions of 13 species of protists in isolation or in competition (40–42), covering a relatively broad set of field conditions (*Materials and Methods*). Examples of such distributions as functions of the linear size in standard environmental conditions are shown in Fig. 1. The corresponding transformed distributions as functions of volume span over four orders of magnitude and are shown in Fig. 2A. Let $p_k(m)$ denote the measured size spectrum of the k th species: Such a $p_k(m)$ measures the relative proportion of individuals of a given species k with mass belonging to $(m, m + dm)$, assuming a continuous distribution of sizes. We tested whether $p_k(m)$ exhibits a finite-size scaling form (22, 30, 36, 43, 44) obtained by the product of two terms, an algebraic power of size multiplied by a suitable scaling function F ; that is,

$$p_k(m) = \frac{1}{m^\Delta} F\left(\frac{m}{\langle m \rangle_k^\phi}\right), \quad [1]$$

where $\langle m \rangle_k$ is the mean mass of the k th species and $F(x)$, critically, is the same scaling function for all species (dimensional analysis and normalization conditions that F must satisfy are discussed in *SI Text*). Eq. 1 implies that the only species dependence of the size distribution occurs through the average mass $\langle m \rangle_k$ of species k . Note that the two exponents in Eq. 1, Δ and ϕ , are not independent. This follows from imposing $\int_{\mathcal{R}} dm m p_k(m) \propto \langle m \rangle_k$ (where \mathcal{R} is the suitable range of sizes); in fact, $\int_{\mathcal{R}} dm m p_k(m) = \int_{\mathcal{R}} dm m \frac{1}{m^\Delta} F\left(\frac{m}{\langle m \rangle_k^\phi}\right) \propto \langle m \rangle_k^{(2-\Delta)\phi}$ is proportional to $\langle m \rangle_k$ only if the two exponents satisfy $(2 - \Delta)\phi = 1$

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a peak at small sizes exist due to debris in the culture (*SI Text*) (61). Peaks at larger sizes are due to protists. To deconvolve the two peaks, we fit the debris peak with an exponential decay (in a region adjacent to the peak, where data lie on a straight line in a log-linear plot; *SI Text*) and subtracted the resulting curve from the overall spectrum. On the right side of the protist peak, we truncated the data when the measured frequency of a size channel was below 20 occurrences to separate it from the noise. Noise was uniformly distributed on all size channels with a frequency of ~10–20 counts per channel, as demonstrated by measuring pure buffer solution only. For each species, several measurements of different cultures (grown in the same

conditions) were collected and summed to get an ensemble average representative of the species.

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