The Global Body Size Biomass Spectrum is Multimodal
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Abstract

Recent research provides an unprecedented account of the diversity and biomass of life, but the data also suggest unexplained patterns such as the co-dominance of very different life forms. We compile the planetary body size biomass spectrum across all taxa and investigate possible underlying forces. We find that small ($10^{-14}$ g) and large ($10^6$ g) organisms vastly outweigh other sizes. The global spectrum reveals an allometric power exponent close to zero, with the marine spectrum in particular showing multiple closely packed modes that are compatible with metabolic food webs. All habitat realms share two distinct size modes that correspond well to the evolutionary innovations of unicellular and complex multicellular life forms, plus a smaller third mode representing unicellular endosymbiotic life. Each mode contains both producers and consumers. These findings show both differences and similarities across habitat realms and point to a size-based synthesis of microevolution, macroevolution, and macroecology.
**Introduction**

Body size is a fundamental metric in biodiversity and evolutionary sciences. Size spectra—be they uniform, unimodal, or multimodal—help identify governing forces. Organisms range from $10^{-17}$ (Nanoarchaeum equitans) to $10^9$ g (Sequoiadendron giganteum) in carbon weight, but the global size-biomass distribution, or size spectrum, remains to be comprehensively explored across taxa. Previously, empirical studies showed that biomass appears relatively equal across broad but still limited body size ranges either within habitat realms or when averaged over species. In other words, biomass has so far appeared to be nearly scale-invariant across many taxa.

Theories for the body size biomass spectrum have also been limited to specific taxa or focused on specific realms, but they can be roughly divided into evolutionary and ecological. Within taxa such as terrestrial mammals, macroevolutionary theory focusing on variations between species predicts a unimodal and right skewed spectrum of species richness and hence a right skewed body size spectrum when combined with roughly equal species biomass across size (high biomass at small sizes and some rare, very large sizes). Across taxa, the evolution of complexity identifies several distinct life forms (simple unicellular, unicellular endosymbiotic, and complex multicellular) that each occupy different body sizes separated by rare and abrupt evolutionary transitions. Within each life form, larger sizes may be selected for up to an upper limit, consistent with macroevolutionary theory. However, there is no quantitative theory for whether or how size modes may evolve—an open question that may determine their debated status as major transitions. The evolutionary perspective also does not explicitly account for ecological trophic interactions, unlike the following theories. In the marine realm, where primary producers tend to be small and trophic interactions are often governed strongly by size, metabolic food web theory predicts a broad-scale power law with a small negative or zero exponent (called scale invariance). In addition, food web theory also predicts finer-scale modes separated by predator-prey mass ratios of approximately three orders of magnitude, a
separation that increases with predator size\textsuperscript{18}. In contrast, trophic interactions are not constrained by size in the terrestrial realm\textsuperscript{19}, which would predict a relatively flat size spectrum without regularly spaced modes. Biophysics can also influence the size spectrum, as abundant primary producers are generally small in the ocean and large on land because of differences in competition for light, buoyancy, and nutrient diffusion rates\textsuperscript{20,21}. However, due to different ecological efficiencies and rates of biomass turnover\textsuperscript{3,22,23}, small body sizes can have relatively low standing biomass in the ocean. This pattern may therefore be similar to what is expected on land, where abundant primary producers like trees may generate a high biomass mode at large body sizes. The presence of decomposers, occupying high trophic levels among consumers, further complicates the spectral expectation, and smaller sizes may be over-represented compared to expectations from a simple trophic chain where size corresponds to trophic level\textsuperscript{19}.

A lack of cross-taxa data integration and coarse empirical size resolution has prevented further theoretical refinement and synthesis relevant to understanding the global distribution of body sizes on Earth. Further, size-biomass distributions are either non-existent or heavily biased even within well-studied taxonomic groups. Given that population census remains prohibitively expensive even for a few species, here we obtain a first global picture by pairing previous estimates of cross-taxa biomass with size distribution estimates based on key species within groups. We then examine the cross-taxa size-biomass patterns, offer preliminary mechanistic interpretations, and extensively test the sensitivity of the results to different methodological approaches.

**Results and Discussion**

To compile the global aggregate body size biomass spectrum among biological groups defined by habitat and taxonomy, we used global biomass (gigatons [Gt] in carbon content) assessments and minimum, mean, and maximum body sizes (grams [g] in carbon content) within groups (Tables S1-3). We relied on the most comprehensive existing synthesis of global biomass
estimates, which incorporate uncertainties within and between multiple studies, and then complemented these with improved estimates available for cryptogamic phototrophs, hard corals, mangroves, and subterranean prokaryotes. We allocated biomass as a skew normal distribution within each of the 36 groups shown in Figure 1 (legend) because this distribution is flexible and simple enough to incorporate previous observations and methods. In addition, we extensively tested sensitivity to other distribution choices. For organisms that grow clonally and remain attached, such as plants, fungi, and corals, we used genet size as body size. We found that mean body size was closer to minimum than to maximum body size in 64% of the groups, which suggests limited to no evidence for widespread right skewed body size distributions that align with macroevolutionary theory at this biological scale ($p = 0.13$ with $n = 36$ from a binomial test).

Across terrestrial, marine, and subterranean (under both land and sea) organisms, the body sizes with the highest biomass were the small (mainly bacteria, $10^{-14}$ g) and the large (mainly plants, $10^6$ g), and these peaks (19 and 79 Gt) outweighed intermediate sizes (1.2 to 2.3 Gt) by an order of magnitude. The pattern is particularly clear on a linear biomass scale (Figure 1B). A third smaller peak occurs at $10^{-9}$ g, which contains mainly fungi (2.3 Gt). The aggregate pattern featuring two major peaks was robust to substantial biomass uncertainties for individual groups, as assessed by resampling, whereas the intermediate-sized peak was not always higher in biomass compared to neighboring sizes (Figure 1A, 1B). On the other hand, uncertainty for individual groups (Tables S1-S3) was large enough in some cases that the ranking of groups by biomass for a given body size (as depicted in Figure 1) is itself uncertain. For example, according to the best available estimates, terrestrial microbes outweigh marine microbes by five-fold, but their data uncertainties (2- to 6-fold) make it possible that the true ranking is the opposite (Tables S1-S2).

The most diverse body size ($10^4$ g with 53% of groups represented) was close to but did not coincide with the large body size peak ($10^6$ g with 38% of groups represented), whereas the
small (10^{-14} g) and medium (10^{-9} g) body size peaks contained 19% and 44% of groups represented respectively (Figure 1C). This diversity pattern is likely influenced by the tendency to name organismal groups at finer resolution near our own size, illustrating a strong size bias in naming that does not correspond to the macroecological distribution of biomass.

The two highest peaks appear to correspond to major transitions in complexity. The peaks are represented primarily by unicellular organisms (prokaryotes) and by complex multicellular organisms (animals and plants), respectively. Intermediate sizes form a third, minor peak (10^{-9} g, 2.3Gt) that contains eukaryotic unicellular life (some fungi and protists), which is the simplest form of endosymbiotic life and has been discussed as either a major or minor evolutionary transition. All peaks contain both producers and consumers. A statistical Gaussian mixture model (Supplementary Information Text) suggested that—whether including or excluding subterranean organisms—three modes provided the best statistical descriptions (R^2=0.97 and 0.98 respectively, Figure S1A,D).

We also characterized size spectra allometrically using power functions with exponent β^{15,35} (Figure S1). We fit power functions to the empirical spectra and bootstrapped the regressions across resampled within-group biomasses to obtain regression uncertainties (Supplementary Information Text). The overall exponent was 0.067±0.011 S.D. (R^2=0.28, Figure S1A), which is near zero as expected from metabolic food web theories applied across trophic levels. This value is also close to the 0.05 exponent from previous body size biomass data compiled for individual species. Despite the similar exponent, however, biomass was reported in the latter dataset as g/m^2 of individual species present at sampled locations, and thus represents a conceptually different quantity than the global total biomass that we focus on here.

We found that the power exponents differed between habitat realms and trophic classes (Figure 2, Figure S1B-F). In particular, while the terrestrial realm had an exponent similar to the global aggregate (β=0.067±0.010, R^2=0.36), the marine realm had a slope at or near zero (β=0.00±0.011, R^2=0.01). The higher terrestrial exponent may be explained by the dominance of
large size producers, while the marine scale invariance is compatible with the expectations from a size-structured metabolic food web\(^3\).

The marine realm exhibited peaks at sizes of \(10^{-13}, 10^{-10}, 10^{-4}, 10^2, \) and \(10^6\) g (Figure 2A). The first and last represent the highest biomass peaks, consistent with the cross-realm pattern. Additionally, the first four peaks roughly correspond to green algae, protists, arthropods, and fish, resembling a trophic chain. These separations of 3 to 6 orders of magnitude increase with body size and roughly correspond to, but are larger than, empirical predator-prey size ratios\(^{18}\) and trophic expectations\(^{19}\). This multimodal food chain pattern is anchored in the green algae that access sunlight efficiently as microscopic plankton near the ocean surface, but algae do not comprise the largest biomass peak because high ecological turnover and efficiencies mean they are rapidly consumed and converted to biomass in higher trophic organisms\(^{19,23}\). In addition, the marine realm also has some large producers and small consumers that complicate a simple food chain perspective. Producers like macroalgae, seagrass and mangroves, as well as corals that host symbiotic producers, represent a strategy that is different from planktonic primary production and that contributes to the largest body size peak. The most notable of these are mangroves, which are terrestrial-like producers that grow attached to the shallow benthos and become large to compete for light\(^{38}\). In addition, decomposer microbes near the top of food chains contribute to the smallest body size peak along with unicellular producers. Thus, likely for both trophic and non-trophic reasons, biomass spectra in the ocean are relatively flat but with the highest aggregate biomasses in the small and large size peaks.

The terrestrial realm has more strongly dominant peaks at sizes of \(10^{-14}\) and \(10^6\) g (Figure 2B), as well as a minor peak at \(10^{-9}\) g, which are similar to the global pattern and to predictions based on evolutionary transitions. Ecological efficiencies are lower on land versus in the ocean, which allows producers to dominate. Terrestrial biophysics dictate that producers grow large to compete for light, in contrast to marine producers that can be small or large. However, animal consumers also share the large size peak. Prokaryotic decomposers dominate the smallest size
peak, while fungal and protist consumers as well as cryptogamic phototrophs occupy the minor intermediate size peak. Overall, trophic level and size do not strongly correlate on land\textsuperscript{19}. Gaussian mixture models also identified three modes as the best description for terrestrial life ($R^2=0.94$, Figure S1B). Moreover, the three terrestrial size modes roughly line up with three of the more prominent marine size modes (prokaryotes, protists, and plants/animals), suggesting that even in the ocean where trophic-size structure is important, evolutionary transitions remain evident.

The size spectrum can also be divided by the major routes of energy acquisition: producers and consumers. Producers and consumers had, respectively, stronger positive $(0.099\pm0.008, R^2=0.55)$ and negative $(-0.021\pm0.010, R^2=0.06)$ scaling exponents (Figure S1E,F). The producer exponent largely reflects the dominance of large terrestrial trees and grasses, and the Gaussian mixture model identified only one mode (Figure S1E). In contrast, the consumer exponent is strongly shaped by trophic interactions and is compatible with metabolic food web theories that predict a slightly negative trend\textsuperscript{15–17} with multiple modes (Figure S1F).

We note that compiling the global body size biomass spectrum required numerous choices and included substantial uncertainties. Within-group biomass uncertainties are high among some taxa, especially in microbes\textsuperscript{24}, which we propagated throughout our analysis by resampling each group’s error distribution independently to obtain cross-taxon confidence intervals and regression results. In addition, we explored uncertainty in body size definitions, biomass definitions, and size distributions using sensitivity analyses. Defining body size as individual clones (ramets) instead of genets (Table S4, Figure S2A), excluding mass with low metabolism (woody material, hard coral skeletons, and all subterranean microbes)\textsuperscript{37} (Table S5, Figure S2B), using normal (Figure S2C) or uniform (Figure S2D) instead of skew normal within-group size biomass distributions, altering the distribution quantiles that correspond to the minimum and maximum sizes (Figure S2E), or coarsening the sampling resolution (Figure S2F) all had some effects but maintained the most prominent feature of at least two disparate size modes. These
sensitivity analyses therefore support the basic findings presented above. Unavoidably for a first
38 global synthesis, potentially important sources of uncertainty like differences in the sampling of
microbe versus macroorganism sampling, within-taxa sampling biases, and within-species size
classes have not been quantified. Our treatment of uncertainty reflects the current state of the art
knowledge – which is admittedly crude – and does not indicate where improved estimates may
fall in the future. Quantifying and narrowing uncertainties remain priorities for macroecology.

The empirical size spectra suggest similarities and differences between habitat realms,
reflecting fundamental differences in the organization of trophic interactions, biophysics, and
evolutionary history. Terrestrial systems are dominated by large producers that often compete for
light by growing tall, while marine systems are strongly shaped by trophic interactions that
efficiently transfer biomass to larger organisms – but exceptions abound. In all major habitat
realms and together globally, three common and prominent size modes match well to the
38 evolutionary forms of prokaryotic unicellular, endosymbiotic (eukaryotic) unicellular, and complex
multicellular body plans. Their ecological prominence corroborates their status as distinct
38 evolutionary transitions – with the first and third modes being major transitions and the
second mode being minor. Further exploration of the temporal evolution of empirical size spectra
38 across Earth’s history would facilitate the development and testing of a synthesis spanning
38 microscopic and macroscopic biological dynamics from the origin of life to contemporary global
change, akin to the big-data approach to understanding the evolution and distribution of matter
in modern cosmology.
Materials and Methods

**Organismal Size.** Size is defined as the carbon content (grams) of a unicellular or multicellular organism. Defining an organism is not entirely straightforward for clonal life forms like grasses, corals, and fungi. Here, we used genets as our primary definition but also explore alternatives in sensitivity analyses (presented in a later section). Genet is a widely accepted functional definition of a biological unit because genetically identical cell agglomerates function as coherent units and actively share resources, and often seem like separate organisms only because the connecting tissues are invisible to us above the substrate⁴⁴–⁴⁶. We included the plant woody material and coral skeleton produced by a living individual as part of biomass in our primary analysis, as is conventional in previous works²⁴, but also explore removing this biomass in sensitivity analyses.

We used the skew normal distribution to describe the body size-biomass distribution (with size on a log scale) within biological groups for our main results, but also tested sensitivity of our results to other distribution choices. The skew normal biomass function \( f(z) \) is written in terms of log size \( z \), with \( \phi(x) \) and \( \Phi(x) \) indicating the PDF and CDF of the standard normal density function, \( Z \) being the total biomass of the group, and the three parameters \( \alpha, \omega, \) and \( \xi \) specifying the shape, scale, and location, respectively:

\[
(1) \quad f(z) = Z \omega \phi \left( \frac{z-\xi}{\omega} \right) \Phi \left( \alpha \frac{z-\xi}{\omega} \right)
\]

Eq. 1 describes a skew normal distribution of size on a log scale. We chose a skew-normal function for a number of reasons. Cross-taxa size-biomass relationships are often described in the literature using power laws or functions, with log biomass linearly decreasing with log body size¹⁴,³¹,³². These functions implicitly assume a minimum body size that is close to the body size with the most biomass, which can be represented with an extremely right skew normal distribution (\( \alpha > 0 \)). In addition, there is evidence that the size-biomass distribution becomes less consistently right-skewed (\( \alpha < 0 \)) as one descends into finer taxonomic classifications¹⁶,³⁰. At the extreme, ontogeny within many species leads to a greater biomass for
large adults than for small larvae (left skew). This makes a simple skewed distribution like lognormal inappropriate, since it cannot be left skewed. Given the diversity of skewness values observed at different geographic and taxonomic ranges, we determined that the skew normal distribution is a sufficiently flexible and parsimonious within-group description that does not impose multiple modes a priori, though we also explored alternative shapes in sensitivity analyses.

We fit skew normal distributions (Eq. (1)) to three observed reference sizes for each organismal group compiled from the literature: minimum, mean, and maximum sizes (Tables S1-3), with biomass and fold uncertainty (mean x fold and mean/fold corresponding to 95% CI of a log-normal error distribution) of groups derived from unless noted. This fit was achieved by minimizing the sum of squares of the residuals between the three observed reference (log) sizes and the corresponding predicted sizes according to the skew normal model (size on log scale and biomass on linear scale). Three points for biomass distribution within each group is minimalistic, but given our current knowledge of most groups there are no other reliable size and biomass pairs to serve as additional reference points. For the main analyses, we fit each biological group’s 2.5th and 97.5th percentiles of the skew normal size-biomass distribution to the minimum and maximum sizes (delimiting 95% of group biomass). We obtained the mean body size of a biological group by dividing biomass by abundance when available; otherwise, we used the size of the most representative species from an independent literature search (those mentioned as most “common” or “widespread”). In a body size-biomass graph and in subsequent discussions, “biomass” is short for biomass density, i.e., the biomass that is expected to be found within one log-biomass unit at a given body size.

The body sizes of some species were reported in units of grams carbon, but for many species we needed to extrapolate from wet or dry mass. When size estimates in the literature were reported in wet mass, we first searched the literature for a species-specific wet weight to grams carbon conversion. When a species-specific conversion was not available, we used the
conversion from the closest relative within the taxon (see online repository tables). When taxon-
specific conversions were not available, we assumed 30% dry mass per wet mass unit, and 50%
carbon per dry mass unit following previous conventions\textsuperscript{24}. In some cases, body size was
reported in units of length (particularly among annelids, nematodes, and fishes). For these taxa,
we found existing length to weight conversions for the species or the closest relative within the
taxon. If body size was reported in diameter, as was the case for most unicellular species, we
found the volume assuming that the organism was either spherical\textsuperscript{47} or tubular\textsuperscript{48}, and then found
existing biovolume to biomass conversions for the species or the closest relative within the taxon.
For hard corals, since each corallite or colony is often tightly packed among other units, we
estimated that volume as the cube of the reported diameter.

We excluded from our size datapoints non-free-living disease organisms, which are
mainly found within trematode, nematode, virus, bacterial, and fungal groups. Disease organisms
tend to represent extreme body sizes within their taxa. It is likely that the total biomass of disease
organisms is low\textsuperscript{39} within most groups and thus should not appreciably affect the cross-taxa
spectrum, but parasites and microbiome-associated organisms may have disproportionate effects
on the biomass of other organisms. Such questions represent an important future research venue
in the context of size spectra but are not addressed further in this paper.

\textbf{Cross-Taxa Spectrum.} The cross-taxa spectrum was obtained by summing biomass of all
groups within each size bin (one 40\textsuperscript{th} of a log unit). We obtained 95% confidence bounds of the
body size-biomass spectra using parametric bootstrapping, which involved sampling from the log-
normal uncertainty in each biological group’s biomass estimate\textsuperscript{24}. We first generated 1000 sets of
size-biomass distribution, each set consisting of each group being independently sampled
according to the log-normal biomass error distribution with a standard deviation that corresponds
to the biomass fold uncertainty. Since the fold uncertainty corresponds to the 95% confidence
interval (with the log upper/lower bounds deviating from the log mean by $\lambda$), we sampled in log
space using standard deviation $\sigma = \lambda / 1.96$. The group biomass uncertainty $\lambda$ is based on \textsuperscript{24}, which
incorporates both observational and systematic assumption uncertainties that can be qualitative. We then summed the size-biomass distributions of all groups to generate a single cross-taxon size spectrum for each bootstrap. This process was repeated for each of the 1000 sample sets. The 2.5th and 97.5th percentiles at each size bin were recorded as the confidence bounds.

For biological group diversity measures across size, a group was counted if it had a biomass greater than 20000 t within the size bin. The threshold was selected so that the least massive group (amphibians) would be counted.

**Sensitivity Analyses.** We performed six sensitivity analyses to test how different assumptions affect the cross-taxon size biomass spectrum. These are: 1) using ramets instead of genets for size measurements; 2) excluding biomass with low metabolism, which are skeletons and subterranean microbes; 3) normal instead of skew normal distribution for within-group biomass across size; 4) uniform instead of skew normal distribution for within-group biomass across size; 5) altering the percentiles of within-group biomass distributions that correspond to reported minimum and maximum sizes; and 6) coarse-graining the sampling resolution.

1) Genets can be dissolved into smaller units of clones or ramets for the definition of body size. Grassland plants, seagrass, soil fungi, and hard corals were affected by the switch to the ramet definition of size (Table S4). In particular, the original large size range for soil fungi was reduced but still remained the largest among all groups. This large size range reflects the group’s unique history of having evolved and lost multicellularity many times, and having indeterminate growth through hyphae that manifest in all possible sizes up to the upper limits. The large size range for soil fungi (whether genets or ramets) is likely a reflection of reality and less of measurement uncertainty. Figure S2A shows the cross-taxon spectrum with body size measured at the ramet scale.

2) We re-calculated the biomass spectrum only including the portion of the world’s biomass that is metabolically active, which would exclude skeletons and subterranean microbes. An extreme of this logic would be that all biomass should be weighted by metabolism,
which decreases with body size. This would create an *a priori* negative relationship between size and biomass. To avoid this conundrum and following previous works, we chose to include skeletal mass in the main text to decouple biomass from metabolism. However, in Table S5 we provide new estimates for biomass and body sizes when the portion of biomass with low metabolism is excluded. This resulted in an alternative cross-taxon spectrum (Figure S2B).

3) and 4) We tested the sensitivity of the size spectrum to the assumption of uniform or normal biomass distributions within groups. For a uniform distribution, biomass was identical across log sizes within groups. The results are in Figure S2C and D.

5) It is difficult to quantify uncertainties in the published minimum and maximum sizes since they generally correspond to single extreme samples within taxa. It may be reasonable to assume that the maximum sizes reported are mostly accurate because these taxa are easier to observe. On the other hand, the minimum sizes reported may be too large as a result of overlooking smaller specimens. We therefore also reconstructed the spectrum assuming that the minimum size corresponds to the 4.5\(^{th}\) (instead of 2.5\(^{th}\)) percentile and maximum sizes correspond to the 99.5\(^{th}\) (instead of 97.5\(^{th}\)) percentile, which preserved the original 95% coverage of biomass between the reported minimum and maximum sizes. These changes made right skews less common (47% instead of the original 64%) (Figure S2E).

6) To test whether resolution affects the general pattern, the cross-taxon spectrum was reconstructed with a sampling resolution of one per log size bin (Figure S2F).

All data, including datasheets for variations in body size definition, and Matlab code are available on an online Figshare repository at 10.6084/m9.figshare.12016437.
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Figure 1. Global body size biomass spectrum. A. Empirical carbon biomass (log scale) as a function of body size with 95% confidence bounds (grey dotted curves) for the across-group aggregate from 1000 bootstraps over within-group biomass error distributions. Groups were organized from the least massive at the bottom to the most massive at the top for visibility on the log scale (see color legend for group identity). See Tables S1-3 for within-group biomass uncertainties, and Table S6 for icon sources. B. Biomass and 95% confidence bounds in linear biomass scale. C. Mean (solid) and 95% confidence bounds (dotted) of diversity, or the percentage of the 36 groups represented at >20000 t biomass at a given body size.
Figure 2. Body size spectra by habitat realms. Groups with carbon biomass above 20000 t are shown. Grey dotted curves are 95% confidence bounds from 1000 bootstraps. A. Terrestrial. B. Marine. Subterranean prokaryotes are excluded. See Figure 1 for color reference.