

# The Global Body Size Biomass Spectrum is Multimodal

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## Article

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# The Global Body Size Biomass Spectrum is Multimodal

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## **Type**

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## **Author Contributions**

ET and MP conceived the project, ET, KC and AB compiled the data, all authors designed the analyses, ET conducted analyses, and all authors contributed to writing.

1 **Abstract**

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

## 13 Introduction

14 Body size is a fundamental metric in biodiversity and evolutionary sciences<sup>1</sup>. Size  
15 spectra—be they uniform, unimodal, or multimodal—help identify governing forces. Organisms  
16 range from  $10^{-17}$  (*Nanoarchaeum equitans*) to  $10^9$  g (*Sequoiadendron giganteum*) in carbon  
17 weight, but the global size-biomass distribution, or size spectrum, remains to be comprehensively  
18 explored across taxa<sup>2</sup>. Previously, empirical studies showed that biomass appears relatively  
19 equal across broad but still limited body size ranges either within habitat realms<sup>3</sup> or when  
20 averaged over species<sup>4</sup>. In other words, biomass has so far appeared to be nearly scale-invariant  
21 across many taxa.

22 Theories for the body size biomass spectrum have also been limited to specific taxa or  
23 focused on specific realms, but they can be roughly divided into evolutionary and ecological.  
24 Within taxa such as terrestrial mammals, macroevolutionary theory focusing on variations  
25 between species predicts a unimodal and right skewed spectrum of species richness<sup>5</sup> and hence  
26 a right skewed body size spectrum when combined with roughly equal species biomass across  
27 size<sup>4</sup> (high biomass at small sizes and some rare, very large sizes). Across taxa, the evolution of  
28 complexity<sup>6,7</sup> identifies several distinct life forms (simple unicellular, unicellular endosymbiotic,  
29 and complex multicellular) that each occupy different body sizes separated by rare and abrupt  
30 evolutionary transitions<sup>8,9,6</sup>. Within each life form, larger sizes may be selected for<sup>10</sup> up to an  
31 upper limit<sup>11-13</sup>, consistent with macroevolutionary theory. However, there is no quantitative theory  
32 for whether or how size modes may evolve – an open question that may determine their debated  
33 status as major transitions. The evolutionary perspective also does not explicitly account for  
34 ecological trophic interactions, unlike the following theories. In the marine realm, where primary  
35 producers tend to be small and trophic interactions are often governed strongly by size<sup>3,14</sup>,  
36 metabolic food web theory predicts a broad-scale power law with a small negative or zero  
37 exponent (called scale invariance). In addition, food web theory also predicts finer-scale modes<sup>15-</sup>  
38 <sup>17</sup> separated by predator-prey mass ratios of approximately three orders of magnitude, a

39 separation that increases with predator size<sup>18</sup>. In contrast, trophic interactions are not constrained  
40 by size in the terrestrial realm<sup>19</sup>, which would predict a relatively flat size spectrum without  
41 regularly spaced modes. Biophysics can also influence the size spectrum, as abundant primary  
42 producers are generally small in the ocean and large on land because of differences in  
43 competition for light, buoyancy, and nutrient diffusion rates<sup>20,21</sup>. However, due to different  
44 ecological efficiencies and rates of biomass turnover<sup>3,22,23</sup>, small body sizes can have relatively  
45 low standing biomass in the ocean. This pattern may therefore be similar to what is expected on  
46 land, where abundant primary producers like trees may generate a high biomass mode at large  
47 body sizes. The presence of decomposers, occupying high trophic levels among consumers,  
48 further complicates the spectral expectation, and smaller sizes may be over-represented  
49 compared to expectations from a simple trophic chain where size corresponds to trophic level<sup>19</sup>.

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

59

## 60 **Results and Discussion**

61         To compile the global aggregate body size biomass spectrum among biological groups  
62 defined by habitat and taxonomy, we used global biomass (gigatons [Gt] in carbon content)  
63 assessments and minimum, mean, and maximum body sizes (grams [g] in carbon content) within  
64 groups (Tables S1-3). We relied on the most comprehensive existing synthesis of global biomass

65 estimates, which incorporate uncertainties within and between multiple studies<sup>24</sup>, and then  
66 complemented these with improved estimates available for cryptogamic phototrophs<sup>25</sup>, hard  
67 corals<sup>26,27</sup>, mangroves<sup>28</sup>, and subterranean prokaryotes<sup>29</sup>. We allocated biomass as a skew  
68 normal distribution within each of the 36 groups shown in Figure 1 (legend) because this  
69 distribution is flexible and simple enough to incorporate previous observations and  
70 methods<sup>30,14,16,31,32</sup>. In addition, we extensively tested sensitivity to other distribution choices. For  
71 organisms that grow clonally and remain attached, such as plants, fungi, and corals, we used  
72 genet size as body size. We found that mean body size was closer to minimum than to maximum  
73 body size in 64% of the groups, which suggests limited to no evidence for widespread right  
74 skewed body size distributions that align with macroevolutionary theory at this biological scale ( $p$   
75 = 0.13 with  $n = 36$  from a binomial test).

76         Across terrestrial, marine, and subterranean (under both land and sea) organisms, the  
77 body sizes with the highest biomass were the small (mainly bacteria,  $10^{-14}$  g) and the large  
78 (mainly plants,  $10^6$  g), and these peaks (19 and 79 Gt) outweighed intermediate sizes (1.2 to 2.3  
79 Gt) by an order of magnitude. The pattern is particularly clear on a linear biomass scale (Figure  
80 1B). A third smaller peak occurs at  $10^{-9}$  g, which contains mainly fungi (2.3 Gt). The aggregate  
81 pattern featuring two major peaks was robust to substantial biomass uncertainties for individual  
82 groups, as assessed by resampling, whereas the intermediate-sized peak was not always higher  
83 in biomass compared to neighboring sizes (Figure 1A, 1B). On the other hand, uncertainty for  
84 individual groups (Tables S1-S3) was large enough in some cases that the ranking of groups by  
85 biomass for a given body size (as depicted in Figure 1) is itself uncertain. For example, according  
86 to the best available estimates, terrestrial microbes outweigh marine microbes by five-fold, but  
87 their data uncertainties (2- to 6-fold) make it possible that the true ranking is the opposite (Tables  
88 S1-S2).

89         The most diverse body size ( $10^4$  g with 53% of groups represented) was close to but did  
90 not coincide with the large body size peak ( $10^6$  g with 38% of groups represented), whereas the

91 small ( $10^{-14}$  g) and medium ( $10^{-9}$  g) body size peaks contained 19% and 44% of groups  
92 represented respectively (Figure 1C). This diversity pattern is likely influenced by the tendency to  
93 name organismal groups at finer resolution near our own size, illustrating a strong size bias in  
94 naming that does not correspond to the macroecological distribution of biomass.

95         The two highest peaks appear to correspond to major transitions in complexity. The  
96 peaks are represented primarily by unicellular organisms (prokaryotes) and by complex  
97 multicellular organisms (animals and plants), respectively. Intermediate sizes form a third, minor  
98 peak ( $10^{-9}$  g, 2.3Gt) that contains eukaryotic unicellular life (some fungi and protists), which is the  
99 simplest form of endosymbiotic life and has been discussed as either a major or minor  
100 evolutionary transition<sup>33,34</sup>. All peaks contain both producers and consumers. A statistical  
101 Gaussian mixture model (Supplementary Information Text) suggested that—whether including or  
102 excluding subterranean organisms—three modes provided the best statistical descriptions  
103 ( $R^2=0.97$  and  $0.98$  respectively, Figure S1A,D).

104         We also characterized size spectra allometrically using power functions with exponent  
105  $\beta^{15,35}$  (Figure S1). We fit power functions to the empirical spectra and bootstrapped the  
106 regressions across resampled within-group biomasses to obtain regression uncertainties  
107 (Supplementary Information Text). The overall exponent was  $0.067 \pm 0.011$  S.D. ( $R^2=0.28$ , Figure  
108 S1A), which is near zero as expected from metabolic food web theories applied across trophic  
109 levels<sup>35</sup>. This value is also close to the 0.05 exponent from previous body size biomass data  
110 compiled for individual species<sup>4</sup>. Despite the similar exponent, however, biomass was reported in  
111 the latter dataset as  $\text{g/m}^2$  of individual species present at sampled locations, and thus represents  
112 a conceptually different quantity than the global total biomass that we focus on here.

113         We found that the power exponents differed between habitat realms and trophic classes  
114 (Figure 2, Figure S1B-F). In particular, while the terrestrial realm had an exponent similar to the  
115 global aggregate ( $\beta=0.067 \pm 0.010$ ,  $R^2=0.36$ ), the marine realm had a slope at or near zero  
116 ( $\beta=0.00 \pm 0.011$ ,  $R^2=0.01$ ). The higher terrestrial exponent may be explained by the dominance of

117 large size producers, while the marine scale invariance is compatible with the expectations from a  
118 size-structured metabolic food web<sup>3</sup>.

119         The marine realm exhibited peaks at sizes of  $10^{-13}$ ,  $10^{-10}$ ,  $10^{-4}$ ,  $10^2$ , and  $10^6$  g (Figure 2A).  
120 The first and last represent the highest biomass peaks, consistent with the cross-realm pattern.  
121 Additionally, the first four peaks roughly correspond to green algae, protists, arthropods, and fish,  
122 resembling a trophic chain. These separations of 3 to 6 orders of magnitude increase with body  
123 size and roughly correspond to, but are larger than, empirical predator-prey size ratios<sup>18</sup> and  
124 trophic expectations<sup>19</sup>. This multimodal food chain pattern is anchored in the green algae that  
125 access sunlight efficiently as microscopic plankton near the ocean surface, but algae do not  
126 comprise the largest biomass peak because high ecological turnover and efficiencies mean they  
127 are rapidly consumed and converted to biomass in higher trophic organisms<sup>19,23</sup>. In addition, the  
128 marine realm also has some large producers and small consumers that complicate a simple food  
129 chain perspective. Producers like macroalgae, seagrass and mangroves, as well as corals that  
130 host symbiotic producers, represent a strategy that is different from planktonic primary production  
131 and that contributes to the largest body size peak. The most notable of these are mangroves,  
132 which are terrestrial-like producers that grow attached to the shallow benthos and become large  
133 to compete for light<sup>36</sup>. In addition, decomposer microbes near the top of food chains contribute to  
134 the smallest body size peak along with unicellular producers. Thus, likely for both trophic and  
135 non-trophic reasons, biomass spectra in the ocean are relatively flat but with the highest  
136 aggregate biomasses in the small and large size peaks.

137         The terrestrial realm has more strongly dominant peaks at sizes of  $10^{-14}$  and  $10^6$  g (Figure  
138 2B), as well as a minor peak at  $10^{-9}$  g, which are similar to the global pattern and to predictions  
139 based on evolutionary transitions. Ecological efficiencies are lower on land versus in the ocean,  
140 which allows producers to dominate. Terrestrial biophysics dictate that producers grow large to  
141 compete for light, in contrast to marine producers that can be small or large. However, animal  
142 consumers also share the large size peak. Prokaryotic decomposers dominate the smallest size

143 peak, while fungal and protist consumers as well as cryptogamic phototrophs occupy the minor  
144 intermediate size peak. Overall, trophic level and size do not strongly correlate on land<sup>19</sup>.  
145 Gaussian mixture models also identified three modes as the best description for terrestrial life  
146 ( $R^2=0.94$ , Figure S1B). Moreover, the three terrestrial size modes roughly line up with three of the  
147 more prominent marine size modes (prokaryotes, protists, and plants/animals), suggesting that  
148 even in the ocean where trophic-size structure is important, evolutionary transitions remain  
149 evident.

150 The size spectrum can also be divided by the major routes of energy acquisition:  
151 producers and consumers. Producers and consumers had, respectively, stronger positive  
152 ( $0.099\pm 0.008$ ,  $R^2=0.55$ ) and negative ( $-0.021\pm 0.010$ ,  $R^2=0.06$ ) scaling exponents (Figure S1E,F).  
153 The producer exponent largely reflects the dominance of large terrestrial trees and grasses, and  
154 the Gaussian mixture model identified only one mode (Figure S1E). In contrast, the consumer  
155 exponent is strongly shaped by trophic interactions and is compatible with metabolic food web  
156 theories that predict a slightly negative trend<sup>15-17</sup> with multiple modes (Figure S1F).

157 We note that compiling the global body size biomass spectrum required numerous  
158 choices and included substantial uncertainties. Within-group biomass uncertainties are high  
159 among some taxa, especially in microbes<sup>24</sup>, which we propagated throughout our analysis by  
160 resampling each group's error distribution independently to obtain cross-taxa confidence intervals  
161 and regression results. In addition, we explored uncertainty in body size definitions, biomass  
162 definitions, and size distributions using sensitivity analyses. Defining body size as individual  
163 clones (ramets) instead of genets (Table S4, Figure S2A), excluding mass with low metabolism  
164 (woody material, hard coral skeletons, and all subterranean microbes)<sup>37</sup> (Table S5, Figure S2B),  
165 using normal (Figure S2C) or uniform (Figure S2D) instead of skew normal within-group size  
166 biomass distributions, altering the distribution quantiles that correspond to the minimum and  
167 maximum sizes (Figure S2E), or coarsening the sampling resolution (Figure S2F) all had some  
168 effects but maintained the most prominent feature of at least two disparate size modes. These

169 sensitivity analyses therefore support the basic findings presented above. Unavoidably for a first  
170 global synthesis, potentially important sources of uncertainty like differences in the sampling of  
171 microbe versus macroorganism sampling, within-taxa sampling biases, and within-species size  
172 classes have not been quantified. Our treatment of uncertainty reflects the current state of the art  
173 knowledge – which is admittedly crude – and does not indicate where improved estimates may  
174 fall in the future. Quantifying and narrowing uncertainties remain priorities for macroecology<sup>38</sup>.

175         The empirical size spectra suggest similarities and differences between habitat realms,  
176 reflecting fundamental differences in the organization of trophic interactions, biophysics, and  
177 evolutionary history. Terrestrial systems are dominated by large producers that often compete for  
178 light by growing tall, while marine systems are strongly shaped by trophic interactions that  
179 efficiently transfer biomass to larger organisms<sup>3</sup> – but exceptions abound. In all major habitat  
180 realms and together globally, three common and prominent size modes match well to the  
181 evolutionary forms of prokaryotic unicellular, endosymbiotic (eukaryotic) unicellular, and complex  
182 multicellular body plans<sup>8,6</sup>. Their ecological prominence corroborates their status as distinct  
183 evolutionary transitions<sup>6,34,39</sup> – with the first and third modes being major transitions and the  
184 second mode being minor. Further exploration of the temporal evolution of empirical size spectra  
185 across Earth's history would facilitate the development and testing of a synthesis spanning  
186 microscopic and macroscopic biological dynamics from the origin of life to contemporary global  
187 change<sup>42</sup>, akin to the big-data approach to understanding the evolution and distribution of matter  
188 in modern cosmology<sup>43</sup>.

189

190 **Materials and Methods**

191 **Organismal Size.** Size is defined as the carbon content (grams) of a unicellular or multicellular  
192 organism. Defining an organism is not entirely straightforward for clonal life forms like grasses,  
193 corals, and fungi. Here, we used genets as our primary definition but also explore alternatives in  
194 sensitivity analyses (presented in a later section). Genet is a widely accepted functional definition  
195 of a biological unit because genetically identical cell agglomerates function as coherent units and  
196 actively share resources, and often seem like separate organisms only because the connecting  
197 tissues are invisible to us above the substrate<sup>44-46</sup>. We included the plant woody material and  
198 coral skeleton produced by a living individual as part of biomass in our primary analysis, as is  
199 conventional in previous works<sup>24</sup>, but also explore removing this biomass in sensitivity analyses.

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

206 (1) 
$$f(z) = Z \frac{2}{\omega} \phi\left(\frac{z-\xi}{\omega}\right) \Phi\left(\alpha \frac{z-\xi}{\omega}\right)$$

207 Eq. 1 describes a skew normal distribution of size on a log scale. We chose a skew-  
208 normal function for a number of reasons. Cross-taxa size-biomass relationships are often  
209 described in the literature using power laws or functions, with log biomass linearly decreasing  
210 with log body size<sup>14,31,32</sup>. These functions implicitly assume a minimum body size that is close to  
211 the body size with the most biomass, which can be represented with an extremely right skew  
212 normal distribution ( $\alpha > 0$ ). In addition, there is evidence that the size-biomass distribution  
213 becomes less consistently right-skewed ( $\alpha < 0$ ) as one descends into finer taxonomic  
214 classifications<sup>16,30</sup>. At the extreme, ontogeny within many species leads to a greater biomass for

215 large adults than for small larvae (left skew)<sup>16</sup>. This makes a simple skewed distribution like  
216 lognormal inappropriate, since it cannot be left skewed. Given the diversity of skewness values  
217 observed at different geographic and taxonomic ranges<sup>30</sup>, we determined that the skew normal  
218 distribution is a sufficiently flexible and parsimonious within-group description that does not  
219 impose multiple modes *a priori*, though we also explored alternative shapes in sensitivity  
220 analyses.

221 We fit skew normal distributions (Eq. (1)) to three observed reference sizes for each  
222 organismal group compiled from the literature: minimum, mean, and maximum sizes (Tables S1-  
223 3), with biomass and fold uncertainty (mean x fold and mean/fold corresponding to 95% CI of a  
224 log-normal error distribution) of groups derived from<sup>24</sup> unless noted. This fit was achieved by  
225 minimizing the sum of squares of the residuals between the three observed reference (log) sizes  
226 and the corresponding predicted sizes according to the skew normal model (size on log scale and  
227 biomass on linear scale). Three points for biomass distribution within each group is minimalistic,  
228 but given our current knowledge of most groups there are no other reliable size and biomass  
229 pairs to serve as additional reference points. For the main analyses, we fit each biological group's  
230 2.5<sup>th</sup> and 97.5<sup>th</sup> percentiles of the skew normal size-biomass distribution to the minimum and  
231 maximum sizes (delimiting 95% of group biomass). We obtained the mean body size of a  
232 biological group by dividing biomass by abundance when available<sup>24</sup>; otherwise, we used the size  
233 of the most representative species from an independent literature search (those mentioned as  
234 most "common" or "widespread"). In a body size-biomass graph and in subsequent discussions,  
235 "biomass" is short for biomass density, i.e., the biomass that is expected to be found within one  
236 log-biomass unit at a given body size.

237 The body sizes of some species were reported in units of grams carbon, but for many  
238 species we needed to extrapolate from wet or dry mass. When size estimates in the literature  
239 were reported in wet mass, we first searched the literature for a species-specific wet weight to  
240 grams carbon conversion. When a species-specific conversion was not available, we used the

241 conversion from the closest relative within the taxon (see online repository tables). When taxon-  
242 specific conversions were not available, we assumed 30% dry mass per wet mass unit, and 50%  
243 carbon per dry mass unit following previous conventions<sup>24</sup>. In some cases, body size was  
244 reported in units of length (particularly among annelids, nematodes, and fishes). For these taxa,  
245 we found existing length to weight conversions for the species or the closest relative within the  
246 taxon. If body size was reported in diameter, as was the case for most unicellular species, we  
247 found the volume assuming that the organism was either spherical<sup>47</sup> or tubular<sup>48</sup>, and then found  
248 existing biovolume to biomass conversions for the species or the closest relative within the taxon.  
249 For hard corals, since each corallite or colony is often tightly packed among other units, we  
250 estimated that volume as the cube of the reported diameter.

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

258 ***Cross-Taxa Spectrum.*** The cross-taxa spectrum was obtained by summing biomass of all  
259 groups within each size bin (one 40<sup>th</sup> of a log unit). We obtained 95% confidence bounds of the  
260 body size-biomass spectra using parametric bootstrapping, which involved sampling from the log-  
261 normal uncertainty in each biological group's biomass estimate<sup>24</sup>. We first generated 1000 sets of  
262 size-biomass distribution, each set consisting of each group being independently sampled  
263 according to the log-normal biomass error distribution with a standard deviation that corresponds  
264 to the biomass fold uncertainty. Since the fold uncertainty corresponds to the 95% confidence  
265 interval (with the log upper/lower bounds deviating from the log mean by  $\lambda$ ), we sampled in log  
266 space using standard deviation  $\sigma = \lambda/1.96$ . The group biomass uncertainty  $\lambda$  is based on <sup>24</sup>, which

267 incorporates both observational and systematic assumption uncertainties that can be qualitative.  
268 We then summed the size-biomass distributions of all groups to generate a single cross-taxa size  
269 spectrum for each bootstrap. This process was repeated for each of the 1000 sample sets. The  
270 2.5<sup>th</sup> and 97.5<sup>th</sup> percentiles at each size bin were recorded as the confidence bounds.

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

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

281 1) Genets can be dissolved into smaller units of clones or ramets for the definition of  
282 body size. Grassland plants, seagrass, soil fungi, and hard corals were affected by the switch to  
283 the ramet definition of size (Table S4). In particular, the original large size range for soil fungi was  
284 reduced but still remained the largest among all groups. This large size range reflects the group's  
285 unique history of having evolved and lost multicellularity many times<sup>7</sup>, and having indeterminate  
286 growth through hyphae<sup>49</sup> that manifest in all possible sizes up to the upper limits. The large size  
287 range for soil fungi (whether genets or ramets) is likely a reflection of reality and less of  
288 measurement uncertainty. Figure S2A shows the cross-taxa spectrum with body size measured  
289 at the ramet scale.

290 2) We re-calculated the biomass spectrum only including the portion of the world's  
291 biomass that is metabolically active, which would exclude skeletons and subterranean  
292 microbes<sup>37</sup>. An extreme of this logic would be that all biomass should be weighted by metabolism,

293 which decreases with body size<sup>35</sup>. This would create an *a priori* negative relationship between  
294 size and biomass. To avoid this conundrum and following previous works<sup>24</sup>, we chose to include  
295 skeletal mass in the main text to decouple biomass from metabolism. However, in Table S5 we  
296 provide new estimates for biomass and body sizes when the portion of biomass with low  
297 metabolism is excluded. This resulted in an alternative cross-taxa spectrum (Figure S2B).

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

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

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

312           All data, including datasheets for variations in body size definition, and Matlab code are  
313 available on an online Figshare repository at [10.6084/m9.figshare.12016437](https://doi.org/10.6084/m9.figshare.12016437).

314

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319 **Data availability:** All data and code are available on Figshare at [10.6084/m9.figshare.12016437](https://doi.org/10.6084/m9.figshare.12016437).

320

321

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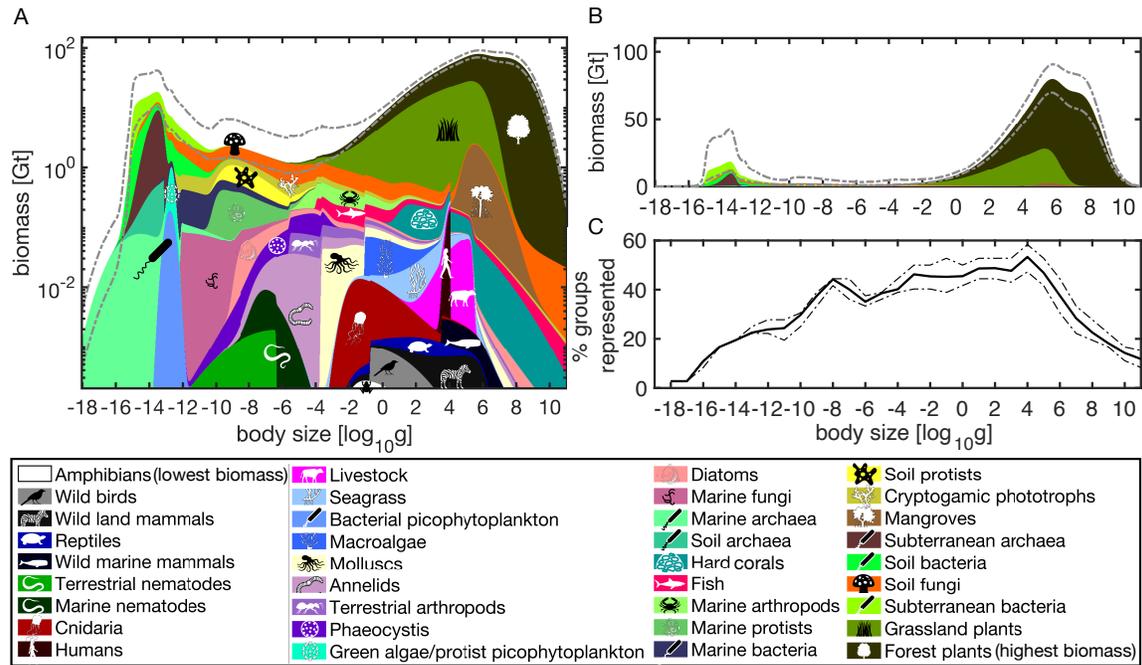
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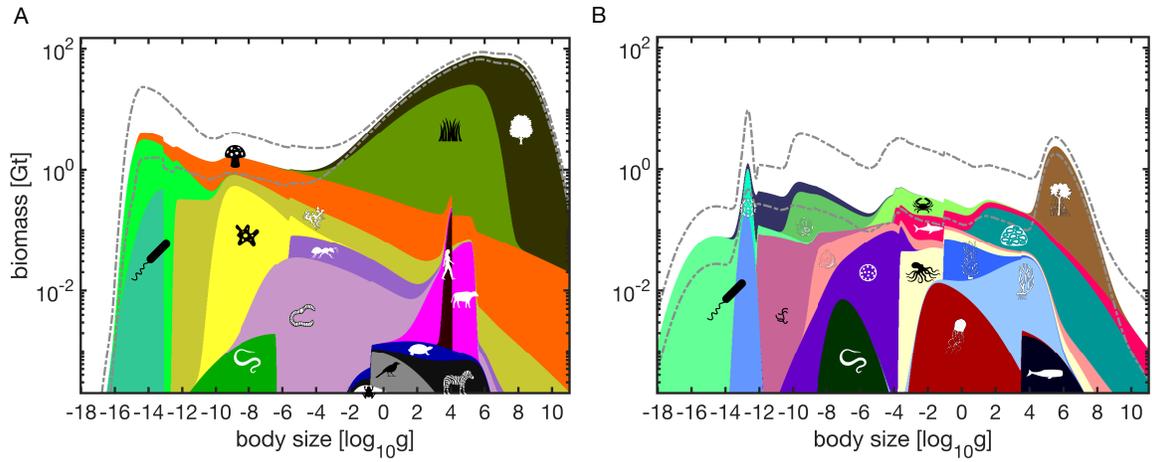
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428 **Figures and Tables**  
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430  
 431 **Figure 1. Global body size biomass spectrum. A.** Empirical carbon biomass (log scale) as a  
 432 function of body size with 95% confidence bounds (grey dotted curves) for the across-group  
 433 aggregate from 1000 bootstraps over within-group biomass error distributions. Groups were  
 434 organized from the least massive at the bottom to the most massive at the top for visibility on the  
 435 log scale (see color legend for group identity). See Tables S1-3 for within-group biomass  
 436 uncertainties, and Table S6 for icon sources. **B.** Biomass and 95% confidence bounds in linear  
 437 biomass scale. **C.** Mean (solid) and 95% confidence bounds (dotted) of diversity, or the  
 438 percentage of the 36 groups represented at >20000 t biomass at a given body size.

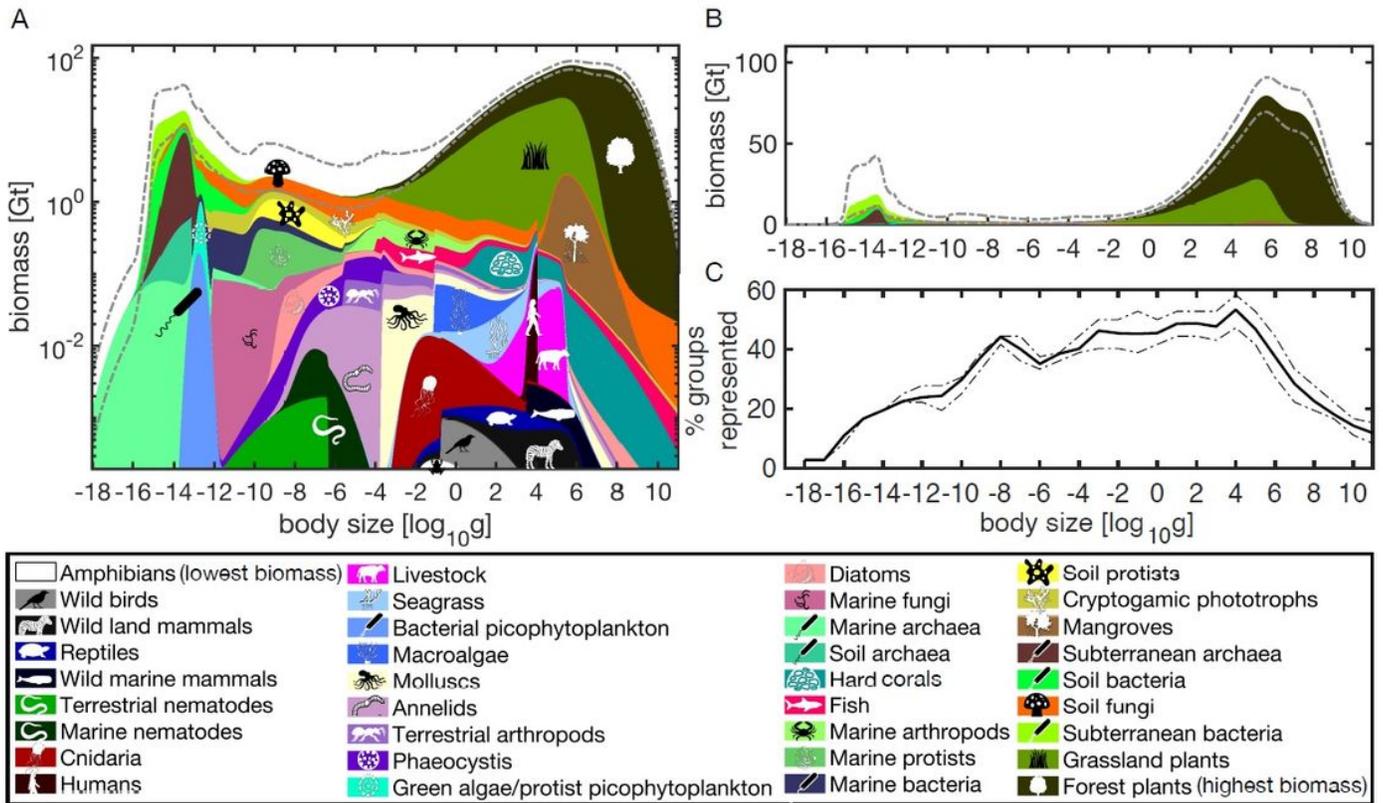


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440 **Figure 2. Body size spectra by habitat realms.** Groups with carbon biomass above 20000 t are  
 441 shown. Grey dotted curves are 95% confidence bounds from 1000 bootstraps. **A.** Terrestrial. **B.**  
 442 Marine. Subterranean prokaryotes are excluded. See Figure 1 for color reference.

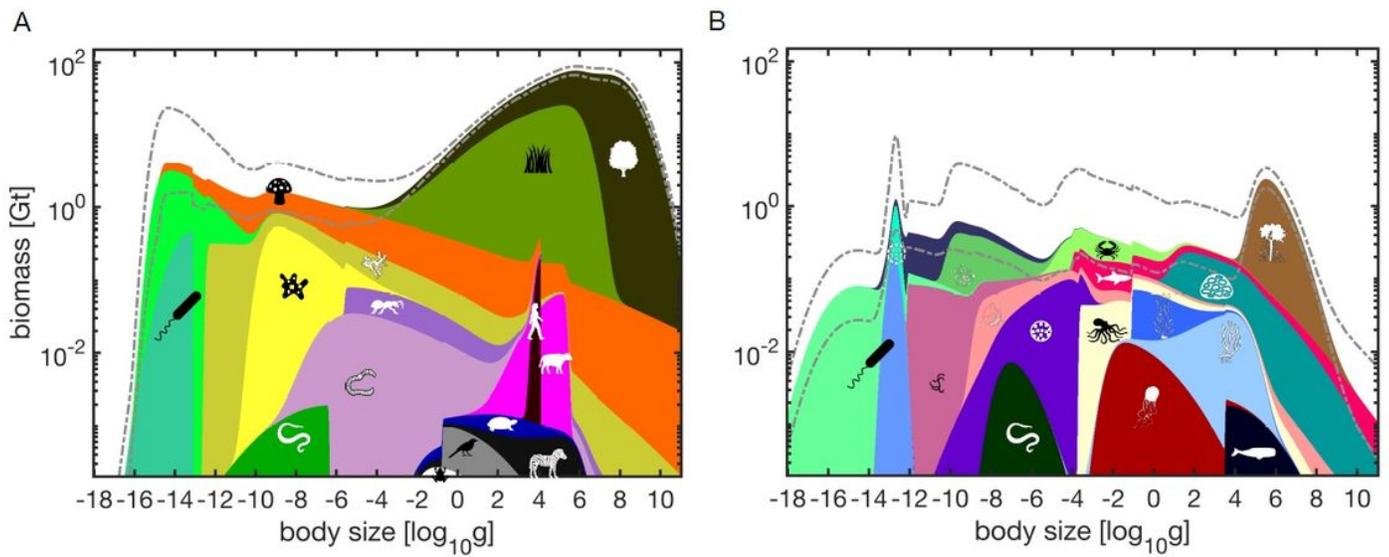
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# Figures



**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.

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