

#### The biomass distribution on Farth

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A census of the biomass on Earth is key for understanding the structure and dynamics of the biosphere. However, a global, quantitative view of how the biomass of different taxa compare with one another is still lacking. Here, we assemble the overall biomass composition of the biosphere, establishing a census of the ≈550 gigatons of carbon (Gt C) of biomass distributed among all of the kingdoms of life. We find that the kingdoms of life concentrate at different locations on the planet; plants (\$\approx 450 Gt C, the dominant kingdom) are primarily terrestrial, whereas animals (\$2 Gt C) are mainly marine, and bacteria (\$\approx 70 Gt C) and archaea (\$\approx 7 Gt C) are predominantly located in deep subsurface environments. We show that terrestrial biomass is about two orders of magnitude higher than marine biomass and estimate a total of ≈6 Gt C of marine biota, doubling the previous estimated quantity. Our analvsis reveals that the global marine biomass pyramid contains more consumers than producers, thus increasing the scope of previous observations on inverse food pyramids. Finally, we highlight that the mass of humans is an order of magnitude higher than that of all wild mammals combined and report the historical impact of humanity on the global biomass of prominent taxa, including mammals, fish, and plants.

ecology | biomass | biosphere | quantitative biology

One of the most fundamental efforts in biology is to describe the composition of the living world. Centuries of research have yielded an increasingly detailed picture of the species that inhabit our planet and their respective roles in global ecosystem. In describing a complex system like the biosphere, it is critical to quantify the abundance of individual components of the system (i.e., species, broader taxonomic groups). A quantitative description of the distribution of biomass is essential for taking stock of biosequestered carbon (1) and modeling global biogeochemical cycles (2), as well as for understanding the historical effects and future inmacts of human activities.

Earlier efforts to estimate global biomass have mostly focused on plants (3-5). In parallel, a dominant role for prokaryotic biomass has been advocated in a landmark paper by Whitman et al. (6) entitled "Prokaryotes: The unseen majority." New sampling and detection techniques (7, 8) make it possible to revisit this claim. Likewise, for other taxa, such as fish, recent global sampling campaigns (9) have resulted in updated estimates, often differing by an order of magnitude or more from previous estimates. For groups such as arthropods, global estimates are still lacking (10, 11).

All of the above efforts are each focused on a single taxon. We are aware of only two attempts at a comprehensive accounting of all biomass components on Earth: Whittaker and Likers (12) made a remarkable effort in the early 1970, noting even then that their study was "intended for early obsolesse nee." It did not include, for example, bacterial or fungal biomass. The other attempt, by Smil (13), was included as a subsection of a book intended for a broad readership. His work details characteristic values for the biomass of various taxa in many environments. Finally, Wikipedia serves as a highly effective platform for making accessible a range of estimates on various taxa (https://en.wikipedia.org/wiki/Biomass. (ecology)#Global\_biomass) but currently falls short of a comprehensive or integrated view.

In the past decade, several major technological and scientific advances have facilitated an improved quantitative account of the biomass on Earth. Next-generation sequencing has enable d a more detailed and cultivation-independent view of the composition of natural communities based on the relative abundance of genomes (14). Better remote sensing tools enable us to probe the environment on a global scale with unprecedented resolution and specificity. The Tam Oceans expedition (15) is among recent efforts at global sampling that are expanding our view and coverage. Continental counterpart efforts, such as the National Ecological Observatory Network in North America, add more finely resolved, continent-specific details, affording us more robust descriptions of natural habitats.

Here, we either assemble or generate estimates of the biomass for each of the major taxonomic groups that contribute to the global biomass distribution. Our analysis (described in detail in \$I\$

\*Appendix\*) is based on hundreds of studies, including recent studies that have overturned earlier estimates for many taxa (e.g., fish, subsurface prokaryotes, marine eukaryotes, soil fauna).

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The Biomass Distribution of the Biosphere by Kingdom. In Fig. 1 and Table 1, we report our best estimates for the biomass of each taxon analyzed. We use biomass as a measure of abundance, which allows us to compare taxa whose members are of very different sizes. Biomass is also a useful metric for quantifying stocks of elements sequestered in living organisms. We report biomass using the mass of carbon, as this measure is independent of water content and has been used extensively in the literature of the content and has been used extensively in the literature was the content and has been used extensively in the literature was the content and has been used extensively in the literature of the literature of the literature of the literature was the literature of the literature of the literature was report biomass in gigatons of carbon, with 1 Gt C = 10<sup>15</sup> g of carbon. We supply additional estimates for the number of individuals of different taxa in \$1.4 morabils. Table \$1.

#### Significano

The composition of the biosphere is a fundamental question in biology, yet a global quantitative account of the biomass of each taxon is still lacking. We assemble a census of the biomass of all kingdoms of life. This analysis provides a holistic view of the composition of the biosphere and allows us to observe broad patterns over taxonomic categories, geographic locations, and trophic modes.

Author contributions: Y.M.B.-O., R.P., and R.M. designed research; Y.M.B.-O. and R.M. performed research; Y.M.B.-O. and R.M. analyzed data; and Y.M.B.-O., R.P., and R.M. wrote the pager.

The authors declare no conflict of interest.

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Data deposition: All of the data used to generate our estimates, as well as the code used for analysis, are available on GitHub at https://github.com/milo-lab/biomass, distribution.

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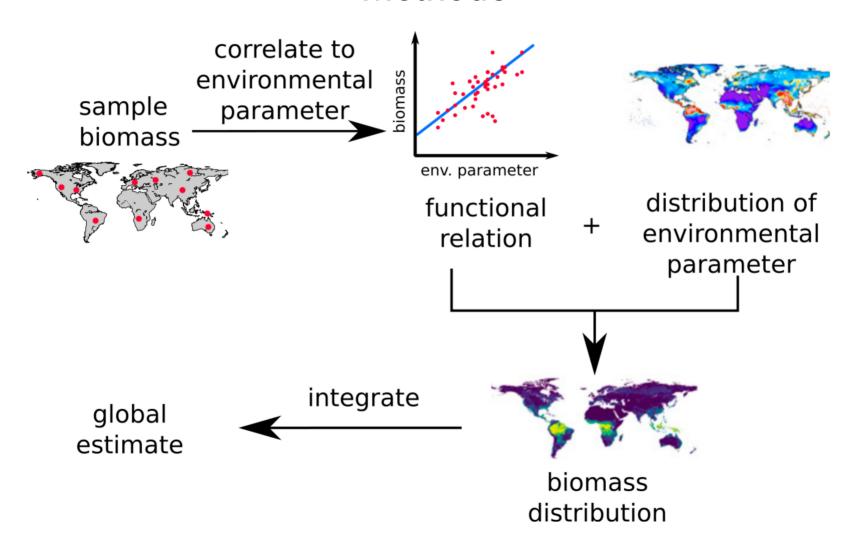
This article contains supporting information on line at www.pnas.org/lookup/suppildoi:10.1073/pnas.17118421154.DCSupplemental.

www.pnas.org/cgi/doi/10.1073/pnas.1711842115 PNAS Latest Articles | 1 of 6

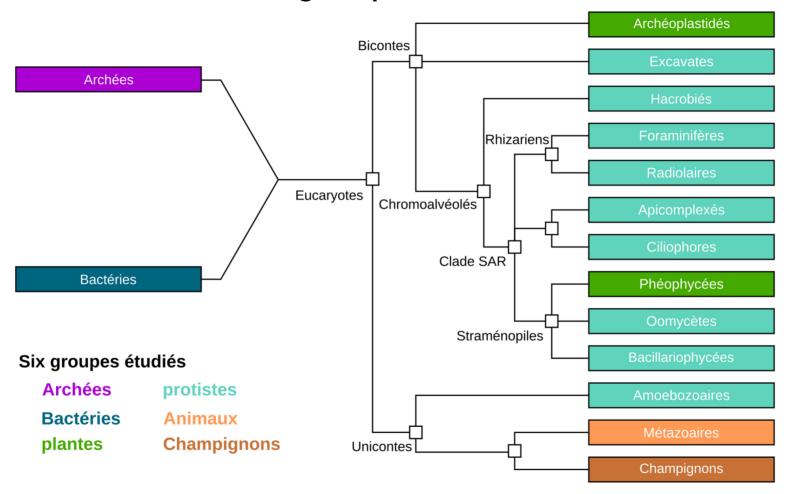
#### **L'étude**

The biomass distribution on Earth Yinon M. Bar-On, Rob Phillips, Ron Milo PNAS, juin 2018, DOI: 10.1073/pnas.1711842115

## Méthode

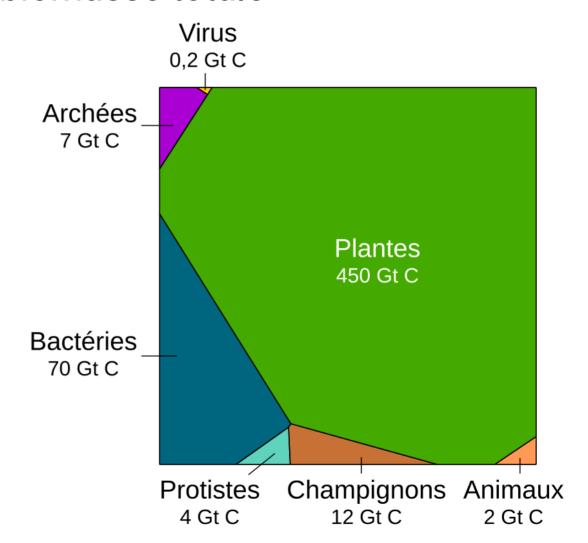


# Les groupes étudiés

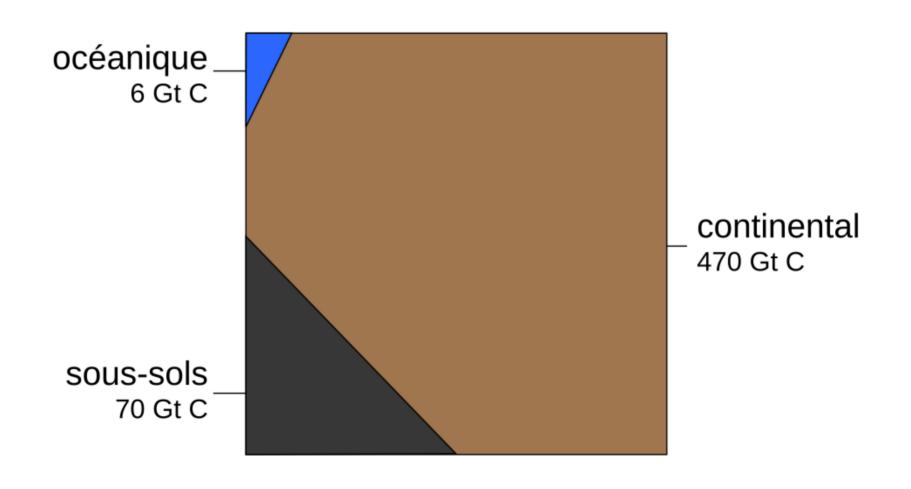


#### La biomasse totale

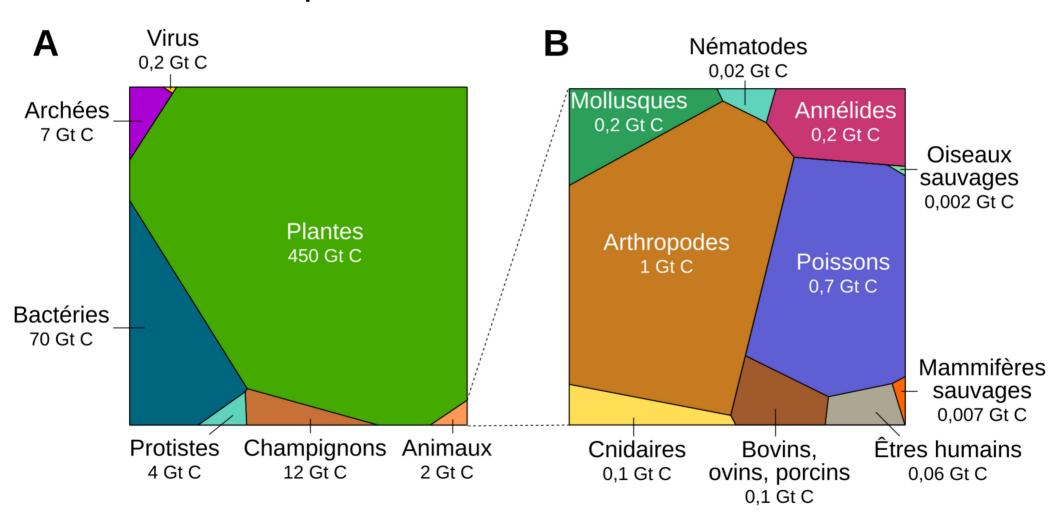
Biomasse totale 550 Gt C



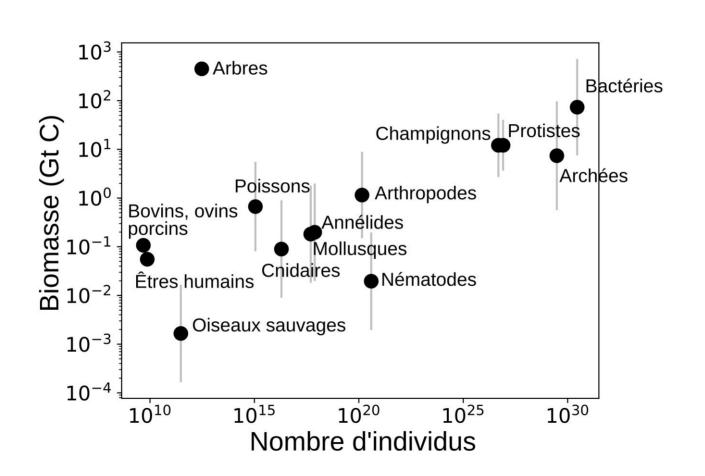
## Répartition de la biomasse en fonction des milieux de vie



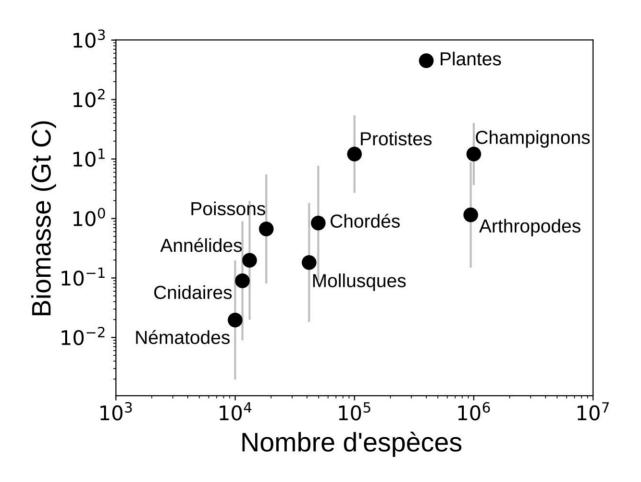
## Le cas particulier de la biomasse animale



### Biomasse vs. abondance

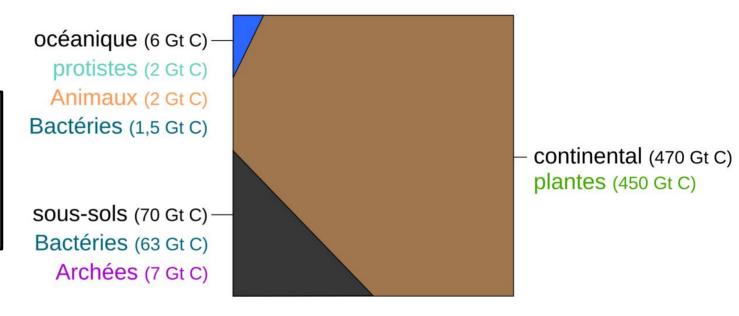


## Biomasse vs. diversité spécifique



### Idées clés

Biomasse totale 550 Gt C



- Des valeurs utiles pour contraindre les modèles climatiques.
- Bien distinguer **biomasse**, **abondance** et **biodiversité spécifique** d'un groupe d'êtres vivants.
- L'espèce humaine influence la biomasse des autres groupes d'êtres vivants.