The biomass distribution on Earth

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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 (≈450 Gt C, the dominant kingdom) are primarily terrestrial, whereas animals (≈2 Gt C) are mainly marine, and bacteria (≈70 Gt C) and archaea (≈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 analysis 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 ecosystems. 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 impacts 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 Likens (12) made a remarkable effort in the early 1970s, noting even then that their study was "intended for early obsolescence." 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 enabled 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 *Tara* 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 *SI 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).

Results

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 (6, 16, 17). Alternative measures for biomass, such as dry weight, are discussed in *Materials and Methods*. For ease of discussion, we report biomass in gigatons of carbon, with $1 \text{ Gt C} = 10^{15}$ g of carbon. We supply additional estimates for the number of individuals of different taxa in *SI Appendix*, Table S1.

Significance

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.

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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.

See Commentary on page 6328.

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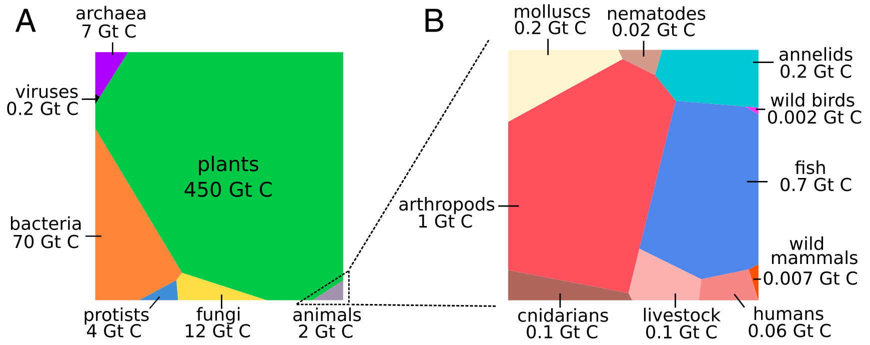

Fig. 1. Graphical representation of the global biomass distribution by taxa. (*A*) Absolute biomasses of different taxa are represented using a Voronoi diagram, with the area of each cell being proportional to that taxa global biomass (the specific shape of each polygon carries no meaning). This type of visualization is similar to pie charts but has a much higher dynamic range (a comparison is shown in *SI Appendix*, Fig. S4). Values are based on the estimates presented in Table 1 and detailed in the *SI Appendix*. A visual depiction without components with very slow metabolic activity, such as plant stems and tree trunks, is shown in *SI Appendix*, Fig. S1. (*B*) Absolute biomass of different animal taxa. Related groups such as vertebrates are located next to each other. We estimate that the contribution of reptiles and amphibians to the total animal biomass is negligible, as we discuss in the *SI Appendix*. Visualization performed using the online tool at bionic-vis.biologie.uni-greifswald.de/.

The sum of the biomass across all taxa on Earth is ≈550 Gt C, of which ≈80% (≈450 Gt C; *SI Appendix*, Table S2) are plants, dominated by land plants (embryophytes). The second major biomass component is bacteria (≈70 Gt C; *SI Appendix*, Tables S3–S7), constituting ≈15% of the global biomass. Other groups, in descending order, are fungi, archaea, protists, animals, and viruses, which together account for the remaining <10%. Despite the large uncertainty associated with the total biomass of bacteria, we estimate that plants are the dominant kingdom in terms of biomass at an ≈90% probability (more details are provided in the *SI Appendix*). Aboveground biomass (≈320 Gt C) represents ≈60% of global biomass, with belowground biomass composed mainly of plant roots (≈130 Gt C) and microbes residing in the soil and deep subsurface (≈100 Gt C). Plant biomass includes ≈70% stems and tree trunks, which are mostly woody, and thus relatively metabolically inert. Bacteria include about 90% deep subsurface biomass (mostly in aquifers and below the seafloor), which have very slow metabolic activity and associated turnover times of several months to thousands of years (18–22). Excluding these contributions, global biomass is still dominated by plants (*SI Appendix*, Fig. S1), mostly consisting of ≈150 Gt C of plant roots and leaves and ≈9 Gt C of terrestrial and marine bacteria whose contribution is on par with the ≈12 Gt C of fungi (*SI Appendix*, Table S8).

Table 1. Summary of estimated total biomass for abundant taxonomic groups

Taxon	Mass (Gt C)	Uncertainty (-fold)
Plants	450	1.2
Bacteria	70	10
Fungi	12	3
Archaea	7	13
Protists	4	4
Animals	2	5
Arthropods, terrestrial	0.2	
Arthropods, marine	1	
Chordates, fish	0.7	
Chordates, livestock	0.1	
Chordates, humans	0.06	
Chordates, wild mammals	0.007	
Chordates, wild birds	0.002	
Annelids	0.2	
Molluscs	0.2	
Cnidarians	0.1	
Nematodes	0.02	
Viruses	0.2	20
Total	550	1.7

Values are based on an extensive literature survey and data integration as detailed in the *SI Appendix*. Reported values have been rounded to reflect the associated level of uncertainty. We report an uncertainty projection for each kingdom as a fold-change factor from the mean, representing a range akin to a 95% confidence interval of the estimate. The procedure for deriving these projections is documented in detail in *Materials and Methods* and *SI Appendix*.

Whereas groups like insects dominate in terms of species richness [with about 1 million described species (23)], their relative biomass fraction is miniscule. Some species contribute much more than entire families or even classes. For example, the Antarctic krill species *Euphausia superba* contributes ≈0.05 Gt C to global biomass (24), similar to other prominent species such as humans or cows. This value is comparable to the contribution from termites (25), which contain many species, and far surpasses the biomass of entire vertebrate classes such as birds. In this way, the picture that arises from taking a biomass perspective of the biosphere complements the focus on species richness that is commonly held (*SI Appendix*, Fig. S3).

The Uncertainty Associated with Global Biomass Estimates. The specific methods used for each taxon are highly diverse and are given in detail in the *SI Appendix*, along with data sources. Global biomass estimates vary in the amount of information they are based on and, consequently, in their uncertainty. An estimate of relatively high certainty is that of plants, which is based on several independent sources. One of these is the Forest Resource Assessment, a survey on the state of world forests conducted by the international Food and Agriculture Organization (FAO). The assessment is based on a collection of country reports that detail the area and biomass density of forests in each country (26) using a standardized format and methodology. The FAO also keeps a record of nonforest ecosystems, such as savannas and shrublands, in each country. Alternatively, remote sensing data give high coverage of measurements that indicate plant biomass (27–29). Remote sensing is used to measure, for example, the height of trees or the number of tree stems per unit area. Biomass is inferred by field measurements establishing a connection between tree plant biomass and satellite-based remote sensing measurements. Combining data from independent sources such as these enables a robust assessment of the total plant biomass (17).

A more characteristic case with larger uncertainties is exemplified by marine prokaryotes, where cell concentrations are measured in various locations and binned based on depth. For each depth range, the average cell concentration is calculated and the total number of marine prokaryotes is estimated through multiplication by the water volume in each depth range. The total number of cells is converted to biomass by using the characteristic carbon content per marine prokaryote. In cases where there are fewer measurements (e.g., terrestrial arthropods, terrestrial protists), the possibility of systematic biases in the estimate is greater and the uncertainty larger. To test the robustness of our estimates, we used independent approaches and analyzed the agreement between such independent estimates. Details on the specific methodologies used for each taxon are provided in the *SI Appendix*. Because most datasets used to estimate global biomass rely on fragmentary sampling, we project large uncertainties that will be reduced as additional data become available.

The Impact of Humanity on the Biosphere. Over the relatively short span of human history, major innovations, such as the domestication of livestock, adoption of an agricultural lifestyle, and the Industrial Revolution, have increased the human population dramatically and have had radical ecological effects. Today, the biomass of humans (≈0.06 Gt C; *SI Appendix*, Table S9) and the biomass of livestock (≈0.1 Gt C, dominated by cattle and pigs; *SI Appendix*, Table S10) far surpass that of wild mammals, which has a mass of ≈0.007 Gt C (*SI Appendix*, Table S11). This is also true for wild and domesticated birds, for which the biomass of domesticated poultry (≈0.005 Gt C, dominated by chickens) is about threefold higher than that of wild birds (≈0.002 Gt C; *SI Appendix*, Table S12). In fact, humans and livestock outweigh all vertebrates combined, with the exception of fish. Even though humans and livestock dominate mammalian biomass, they are a small fraction of the ≈2 Gt C of animal biomass, which primarily comprises arthropods (≈1 Gt C; *SI Appendix*, Tables S13 and S14), followed by fish (≈0.7 Gt C; *SI Appendix*, Table S15). Comparison of current global biomass with prehuman values (which are very difficult to estimate accurately) demonstrates the impact of humans on the biosphere. Human activity contributed to the Quaternary Megafauna Extinction between ≈50,000 and ≈3,000 y ago, which claimed around half of the large (>40 kg) land mammal species (30). The biomass of wild land mammals before this period of extinction was estimated by Barnosky (30) at ≈0.02 Gt C. The present-day biomass of wild land mammals is approximately sevenfold lower, at ≈0.003 Gt C (*SI Appendix*, *Pre-human Biomass* and *Chordates* and Table S11). Intense whaling and exploitation of other marine mammals have resulted in an approximately fivefold decrease in marine mammal global biomass [from ≈0.02 Gt C to ≈0.004 Gt C (31)]. While the total biomass of wild mammals (both marine and terrestrial) decreased by a factor of ≈6, the total mass of mammals increased approximately fourfold from ≈0.04 Gt C to ≈0.17 Gt C due to the vast increase of the biomass of humanity and its associated livestock. Human activity has also impacted global vertebrate stocks, with a decrease of ≈0.1 Gt C in total fish biomass, an amount similar to the remaining total biomass in fisheries and to the gain in the total mammalian biomass due to livestock husbandry (*SI Appendix, Pre-human Biomass*). The impact of human civilization on global biomass has not been limited to mammals but has also profoundly reshaped the total quantity of carbon sequestered by plants. A worldwide census of the total number of trees (32), as well as a comparison of actual and potential plant biomass (17), has suggested that the total plant biomass (and, by proxy, the total biomass on Earth) has declined approximately twofold relative to its value before the start of human civilization. The total biomass of crops cultivated by humans is estimated at ≈10 Gt C, which accounts for only ≈2% of the extant total plant biomass (17).

The Distribution of Biomass Across Environments and Trophic Modes. Examining global biomass in different environments exposes stark differences between terrestrial and marine environments. The ocean covers 71% of the Earth's surface and occupies a much larger volume than the terrestrial environment, yet land biomass, at ≈470 Gt C, is about two orders of magnitude higher than the ≈6 Gt C in marine biomass, as shown in Fig. 2*A*. Even though there is a large difference in the biomass content of the terrestrial and marine environments, the primary productivity of the two environments is roughly equal (33). For plants, we find that most biomass is concentrated in terrestrial environments (plants have only a small fraction of marine biomass, <1 Gt C, in the form of green algae and seagrass; Fig. 2*B*). For animals, most biomass is concentrated in the marine environment, and for bacteria and archaea, most biomass is concentrated in deep subsurface environments. We note that several of the results in Fig. 2*B* should be interpreted with caution due to the large uncertainty associated with some of the estimates, mostly those of total terrestrial protists, marine fungi, and contributions from deep subsurface environments.

When analyzing trophic levels, the biomass of primary producers on land is much larger than that of primary and secondary consumers. In stark contrast, in the oceans, ≈1 Gt C of primary producers supports ≈5 Gt C of consumer biomass, resulting in an inverted standing biomass distribution as shown in Fig. 2*C*. Such inverted biomass distributions can occur when primary producers have a rapid turnover of biomass [on the order of days (34)], while consumer biomass turns over much more slowly [a few years in the case of mesopelagic fish (35)]. Thus, the standing stock of consumers is larger, even though the productivity of producers is necessarily higher. Previous reports have observed inverted biomass pyramids in local marine environments (36, 37). An additional study noted an inverted consumer/producer ratio for the global plankton biomass (16). Our analysis suggests that these observations hold true when looking at the global biomass of all producers and consumers in the marine environment.

Discussion

Our census of the distribution of biomass on Earth provides an integrated global picture of the relative and absolute abundances of all kingdoms of life. We find that the biomass of plants dominates the biomass of the biosphere and is mostly located on land. The marine environment is primarily occupied by microbes, mainly bacteria and protists, which account for ≈70% of the total marine biomass. The remaining ≈30% is mainly composed of arthropods and fish. The deep subsurface holds ≈15% of the total biomass in the biosphere. It is chiefly composed of bacteria and archaea, which are mostly surface-attached and turn over their biomass every several months to thousands of years (18–22).

In addition to summarizing current knowledge of the global biomass distribution, our work highlights gaps in the current understanding of the biosphere. Our knowledge of the biomass composition of different taxa is mainly determined by our ability to sample their biomass in the wild. For groups such as plants, the use of multiple sources to estimate global biomass increases our confidence in the validity of current estimates. However, for other groups, such as terrestrial arthropods and protists, quantitative sampling of biomass is limited by technical constraints, and comprehensive data are thus lacking. Beyond specific taxa, there are entire environments for which our knowledge is very

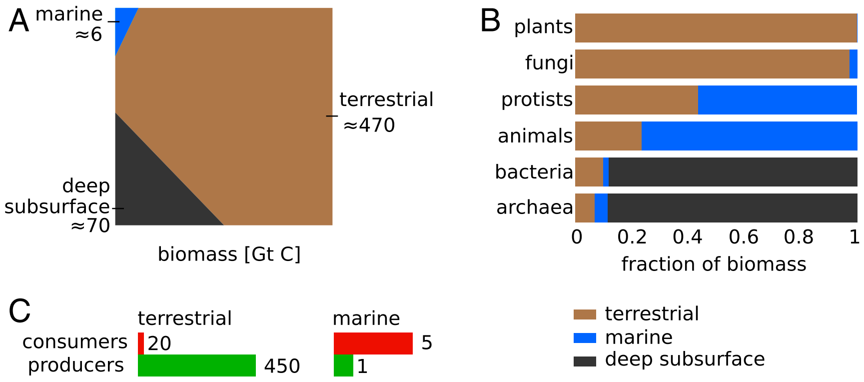

Fig. 2. Biomass distributions across different environments and trophic modes. (*A*) Absolute biomass is represented using a Voronoi diagram, with the area of each cell being proportional to the global biomass at each environment. Values are based on *SI Appendix*, Table S23. We define deep subsurface as the marine subseafloor sediment and the oceanic crust, as well as the terrestrial substratum deeper than 8 m, excluding soil (6). (*B*) Fraction of the biomass of each kingdom concentrated in the terrestrial, marine, or deep subsurface environment. For fungi and protists, we did not estimate the biomass present in the deep subsurface due to data scarcity. (*C*) Distribution of biomass between producers (autotrophs, mostly photosynthetic) and consumers (heterotrophs without deep subsurface) in the terrestrial and marine environments. The size of the bars corresponds to the quantity of biomass of each trophic mode. Numbers are in gigatons of carbon.

limited, namely, the deep subsurface environments such as deep aquifers and the ocean's crust, which might hold the world largest aquifer (38). Studies in these environments are scarce, meaning that our estimates have particularly high uncertainty ranges and unknown systematic biases. Main gaps in our knowledge of these environments pertain to the distribution of biomass between the aquifer fluids and the surrounding rocks and the distribution of biomass between different microbial taxa, such as bacteria, archaea, protists, and fungi. Scientists have closely monitored the impact of humans on global biodiversity (39–41), but less attention has been given to total biomass, resulting in high uncertainty regarding the impact of humanity on the biomass of vertebrates. Our estimates for the current and prehuman biomasses of vertebrates are only a crude first step in calculating these values (*SI Appendix*, *Prehuman Biomass*). The biomass of amphibians, which are experiencing a dramatic population decline (42), remains poorly characterized. Future research could reduce the uncertainty of current estimates by sampling more environments, which will better represent the diverse biosphere on Earth. In the case of prokaryotes, some major improvements were recently realized, with global estimates of marine deep subsurface prokaryote biomass reduced by about two orders of magnitude due to an increased diversity of sampling locations (7).

Identifying gaps in our knowledge could indicate areas for which further scientific exploration could have the biggest impact on our understanding of the biosphere. As a concrete example, we identify the ratio between attached to unattached cells in the deep aquifers as a major contributor to the uncertainties associated with our estimate of the biomass of bacteria, archaea, and viruses. Improving our understanding of this specific parameter could help us better constrain the global biomasses of entire domains of life. In addition to improving our reported estimates, future studies can achieve a finer categorization of taxa. For example, the biomass of parasites, which is not resolved from their hosts in this study, might be larger than the biomass of top predators in some environments (43).

By providing a unified, updated, and accessible global view of the biomass of different taxa, we also aim to disseminate knowledge of the biosphere composition to a wide range of students and researchers. Our survey puts into perspective claims regarding the overarching dominance of groups such as termites and ants (44), nematodes (45), and prokaryotes (6). For example, the biomass of termites [≈0.05 Gt C (25)] is on par with that of humans but is still around an order of magnitude smaller than that of other taxa, such as fish (≈0.7 Gt C; *SI Appendix*, Table S15). Other groups, such as nematodes, surpass any other animal species in terms of number of individuals (*SI Appendix*, Fig. S2) but constitute only about 1% of the total animal biomass.

The census of biomass distribution on Earth presented here is comprehensive in scope and based on synthesis of data from the recent scientific literature. The integrated dataset enables us to draw basic conclusions concerning kingdoms that dominate the biomass of the biosphere, the distribution of biomass of each kingdom across different environments, and the opposite structures of the global marine and terrestrial biomass pyramids. We identify areas in which current knowledge is lacking and further research is most required. Ideally, future research will include both temporal and geographic resolution. We believe that the results described in this study will provide students and researchers with a holistic quantitative context for studying our biosphere.

Materials and Methods

Taxon-Specific Detailed Description of Data Sources and Procedures for Estimating Biomass. The complete account of the data sources used for estimating the biomass of each taxon, procedures for estimating biomass, and projections for the uncertainty associated with the estimate for the biomass of each taxon are provided in the *SI Appendix*. To make the steps for estimating the biomass of each taxon more accessible, we provide supplementary tables that summarize the procedure as well as online notebooks for the calculation of the biomass of each taxon (see data flow scheme in *SI Appendix, Overview*). In Table 1, we detail the relevant supplementary table that summarizes the steps for arriving at each estimate. All of the data used to generate our estimates, as well as the code used for analysis, are open-sourced and available at https://github.com/milo-lab/biomass_distribution.

Choice of Units for Measuring Biomass. Biomass is reported in gigatons of carbon. Alternative options to represent biomass include, among others, biovolume, wet mass, or dry weight. We chose to use carbon mass as the measure of biomass because it is independent of water content and is used extensively in the literature. Dry mass also has these features but is used less frequently. All of our reported values can be transformed to dry weight to a good approximation by multiplying by 2, the characteristic conversion factor between carbon and total dry mass (46–48).

We report the significant digits for our values throughout the paper using the following scheme: For values with an uncertainty projection that is higher than twofold, we report a single significant digit. For values with an uncertainty projection of less than twofold, we report two significant digits. In cases when we report one significant digit, we do not consider a leading "1" as a significant digit.

General Framework for Estimating Global Biomass. In achieving global estimates, there is a constant challenge of how to move from a limited set of local samples to a representative global value. How does one estimate global biomass based on a limited set of local samples? For a crude estimate, the average of all local values of biomass per unit area is multiplied by the total global area. A more effective estimate can be made by correlating measured values to environmental parameters that are known at a global scale (e.g., temperature, depth, distance from shore, primary productivity, biome type), as shown in Fig. 3. This correlation is used to extrapolate the biomass of a taxon at a specific location based on the known distribution of the environmental parameter (e.g., the temperature at each location on the globe). By integrating across the total surface of the world, a global estimate is derived. We detail the specific extrapolation procedure used for each taxon in both the *SI Appendix* and supplementary tables (*SI Appendix*, Tables S1–S23). For most taxa, our best estimates are based on a geometric mean of several independent estimates using different methodologies. The geometric mean estimates the median value if the independent estimates are log-normally distributed or, more generally, the distribution of estimates is symmetrical in log space.

Uncertainty Estimation and Reporting. Global estimates such as those we use in the present work are largely based on sampling from the distribution of biomass worldwide and then extrapolating for areas in which samples are missing. The sampling of biomass in each location can be based on direct biomass measurements or conversion to biomass from other types of measurement, such as number of individuals and their characteristic weight. Some of the main sources of uncertainty for the estimates we present are the result of using such geographical extrapolations and conversion from number of individuals to overall biomass. The certainty of the estimate is linked to the amount of sampling on which the estimate is based. Notable locations in which sampling is scarce are the deep ocean (usually deeper than 200 m) and deep layers of soil (usually deeper than 1 m). For some organisms, such as annelids and marine protists and arthropods, most estimates neglect these environments, thus underestimating the actual biomass. Sampling can be biased toward places that have high abundance and diversity of wildlife. Relying on data with such sampling bias can cause overestimation of the actual biomass of a taxon.

Another source of uncertainty comes from conversion to biomass. Conversion from counts of individuals to biomass is based on either known average weights per individual (e.g., 50 kg of wet weight for a human, which averages over adults and children, or 10 mg of dry weight for a "characteristic" earthworm) or empirical allometric equations that are organism-specific, such as conversion from animal length to biomass. When using such conversion methods, there is a risk of introducing biases and noise into the final estimate. Nevertheless, there is often no way around using such conversions. As such, we must be aware that the data may contain such biases.

In addition to describing the procedures leading to the estimate of each taxon, we quantitatively survey the main sources of uncertainty associated with each estimate and calculate an uncertainty range for each of our biomass estimates. We choose to report uncertainties as representing, to the best of our ability given the many constraints, what is equivalent to a 95% confidence interval for the estimate of the mean. Uncertainties reported in our analysis are multiplicative (fold change from the mean) and not additive (± change of the estimate). We chose to use multiplicative uncertainty as it is more robust to large fluctuations in estimates, and because it is in accord with the way we generate our best estimates, which is usually by using a geometric mean of different independent estimates. Our uncertainty projections are focused on the main kingdoms of life: plants, bacteria, archaea, fungi, protists, and animals.

The general framework for constructing our uncertainties (described in detail for each taxon in the *SI Appendix* and in the online notebooks) takes into account both intrastudy uncertainty and interstudy uncertainty. Intrastudy uncertainty refers to uncertainty estimates reported within a specific study, whereas interstudy uncertainty refers to variation in estimates of a certain quantity between different papers. In many cases, we use several independent methodologies to estimate the same quantity. In these cases, we can also use the variation between estimates from each methodology as a measure of the uncertainty of our final estimate. We refer to this type of uncertainty as intermethod uncertainty. The way we usually calculate uncertainties is by taking the logarithm of the values reported either within studies or from different studies. Taking the logarithm moves the values to log-space, where the SE is calculated (by dividing the SD by the square root of the number of values). We then multiply the SE by a factor of 1.96 (which would give the 95% confidence interval if the transformed data were normally distributed). Finally, we exponentiate the result to get the multiplicative factor in linear space that represents the confidence interval (akin to a 95% confidence interval if the data were log-normally distributed).

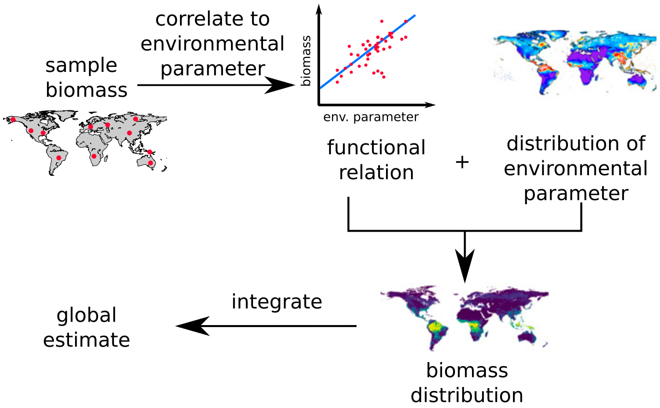

Fig. 3. General framework for estimating global biomass. The procedure begins with local samples of biomass across the globe. The more representative the samples are of the natural distribution of the taxon biomass, the more accurate the estimate will be. To move from local samples to a global estimate, a correlation between local biomass densities and an environmental parameter (or parameters) is established. Based on this correlation, in addition to our knowledge of the distribution of the environmental parameter, we extrapolate the biomass across the entire globe. The resolution of the resulting biomass distribution map is dependent on the resolution at which we know the environmental parameter. Integrating across the entire surface of the Earth, we get a global estimate of the biomass of the taxon.

Most of our estimates are constructed by combining several different estimates (e.g., combining total number of individuals and characteristic carbon content of a single organism). In these cases, we use intrastudy, interstudy, or intermethod variation associated with each parameter that is used to derive the final estimate and propagate these uncertainties to the final estimate of biomass. The uncertainty analysis for each specific biomass estimate incorporates different components of this general scheme, depending on the amount of information that is available, as detailed on a case-by-case basis in the *SI Appendix*.

In cases where information is ample, the procedure described above yields several different uncertainty estimates for each parameter that we use to derive the final estimate (e.g., intrastudy uncertainty, interstudy uncertainty). We integrate these different uncertainties, usually by taking the highest value as the best projection of uncertainty. In some cases, for example, when information is scarce or some sources of uncertainty are hard to quantify, we base our estimates on the uncertainty in analogous taxa and consultation with relevant experts. We tend to round up our uncertainty projections when data are especially limited.

Taxonomic Levels Used. Our census gives estimates for the global biomass at various taxonomic levels. Our main results relate to the kingdom level: animals, archaea, bacteria, fungi, plants, and protists. Although the division into kingdoms is not the most contemporary taxonomic grouping that exists, we chose to use it for the current analysis as most of the data we rely upon does not provide finer taxonomic details (e.g., the division of terrestrial protists is mainly based on morphology and not on taxonomy). We supplement these kingdoms of living organisms with an estimate for the global biomass of viruses, which are not included in the current tree of life but play a key role in global biogeochemical cycles (49). For all kingdoms except animals, all taxa making up the kingdom are considered together. For estimating the biomass of animals, we use a bottom-up approach, which estimates the biomass of key phyla constituting the animal kingdom. The sum of the biomass of these phyla represents our estimate of the total biomass of animals. We give estimates for most phyla and estimate bounds for the possible biomass contribution for the remaining phyla (*SI Appendix, Other Animal Phyla*). Within chordates, we provide estimates for key classes, such as fish, mammals, and birds. We estimate that the contribution of reptiles and amphibians to the total chordate biomass is negligible, as we discuss in the *SI Appendix*. We divide the class of mammals into wild mammals and humans plus livestock (without a contribution from poultry, which is negligible compared with cattle and pigs). Even though livestock is not a valid taxonomic division, we use it to consider the impact of humans on the total biomass of mammals.

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