

Distribution of biomass on the planet

Auteur :

JOYARD Jacques, Directeur de recherche honoraire au CNRS, Laboratoire de Physiologie cellulaire et végétale, Université Grenoble Alpes

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What does the biosphere represent on Earth? How is the biomass distributed between oceans and continents? While hiking in the mountains, in the forest or while scuba diving, we appreciate the diversity of nature: the colorful flora of an alpine meadow, the incredible diversity of the fauna of a lagoon and the discreet tracks of animals in a forest! The contrast between biomes{end-text}A set of

ecosystems characteristic of a biogeographic area. A biome is the expression of the ecological conditions of the place (climate, soils, etc.); it is defined by a vegetation presenting a dominant form of life (trees, shrubs, herbaceous plants) which remains stable over generations. Tropical or temperate deciduous forests (i.e. populated by very large deciduous trees), mangroves, tundra are examples of biomes.{end-tooltip} marine and terrestrial is striking, but quantifying these differences remains difficult. Our vision of the species that inhabit the planet is biased. We notice the most visible organisms - or the largest - but we are far from imagining the importance of "the invisible majority" [1], the prokaryotes{end-text}Microorganisms (generally unicellular) with a simple cell structure, with no nucleus, and almost never any internal compartmentalization (an exception being the thylakoids in cyanobacteria). Two of the three groups constituting life are prokaryotes, the Archaea and the Bacteria {end-tooltip} or more broadly the microorganisms, especially in soils. How to correctly estimate the global biomass of all living organisms and quantify the abundance of the biosphere's constituents? This is a fundamental question in biology. The quantification of the biomass of living organisms on Earth presented here - broken down by major taxonomic groups{end-text}Relates to taxonomy or taxonomy, the branch of biological sciences that involves describing living organisms and organizing them into hierarchical categories called taxa. Generally the term "taxon" is used at the specific (the species) and subspecific (the subspecies) levels.{end-tooltip}, ecological strategies and global environments - provides a basis for exploring today's major environmental issues.

1. Biodiversity, living matter and biomass

1.1. From biodiversity to the quantitative account of the biomass

Centuries of observation of nature have led to an increasingly detailed - but still incomplete - picture of the species that inhabit

our planet and their respective roles in the various ecosystems (see [What is biodiversity?](#)). Since the beginning of the century, several major technological and scientific advances have expanded our understanding of biodiversity on Earth:

New **approaches to genome sequencing** have enabled a more detailed view of the composition of many natural communities. By characterizing short fragments of their DNA that persist in the environment, it is thus possible to inventory the biodiversity of an ecosystem from samples of water, soil, etc. (See [DNA barcoding to characterize biodiversity](#)) ;

Recent **global sampling efforts**, such as those of the *Tara Oceans* expedition (Figure 1) and its continental counterparts around the world, are providing more robust descriptions of the populations of natural habitats (See [When the Tara Oceans expedition explores plankton diversity](#)) ;

Better **remote sensing tools** enable to probe the environment on a global scale with unprecedented resolution and specificity. [See for example the *NASA Earth Observatory* video on ocean phytoplankton: [Feeding the Sea: Phytoplankton Fuel Ocean Life](#)]



Figure 1. On the deck of the schooner Tara during sampling in the Labrador Sea during a sampling station of the Tara Oceans campaign.
[Source: photo © Francois Aurat / Tara Expeditions Foundation - NASA Goddard Space Flight Center, CC BY 2.0]

In describing a complex system such as the biosphere, it is critical to quantify the abundance of individual components of the system (i.e., species, broader taxonomic groups...) within the various ecosystems. A quantitative description of biomass distribution is essential for taking stock of biosequestrated carbon [\[2\]](#) and modelling global biogeochemical cycles [\[3\]](#), as well as for understanding the past and future impact of human activities.

Such a comprehensive quantitative analysis of the biomass of each taxon{end-text}Unit of the hierarchical classifications of living things. Generally the term is used at the specific (species) and subspecific (subspecies) ranks.{end-tooltip} was recently proposed by an Israeli team [\[4,5\]](#): through a meta-analysis of published data, Bar-on *et al.* have assembled a census of the biomass of all kingdoms of life and have provided a holistic view of the composition of the biosphere on land and in the oceans, a theory or approach that focuses on an object as a whole, as a constituent of a whole. This has allowed the construction of specific models of taxonomic categories, geographical locations and trophic modes. The general framework of this strategy is summarized in the associated focus (See [How to estimate global biomass?](#)).

1.2. Carbon as a marker of organic matter and life

Microbial, plant or animal **biomass** is mostly **composed of water, minerals and organic compounds**; it therefore contains a large amount of hydrogen, oxygen, **carbon** and, to a lesser extent, nitrogen (Table 1). Life concentrates some of the elements that are not abundant on the Earth as a whole. For example, the atmosphere is rich in nitrogen and oxygen but contains little carbon and hydrogen, while the Earth's crust, although containing oxygen and a small amount of hydrogen, contains little carbon and nitrogen. Thus, **carbon** is a sort of **marker of organic matter** (living or dead organisms).

Table 1. Approximate percentage of elements in living organisms (e.g., humans) compared to the earth's crust or atmosphere [\[6\]](#).

Element	Life (Humans)	Atmosphere	Earth's Crust
Oxygen (O)	65%	21%	46%
Carbon (C)	18%	trace	trace
Hydrogen (H)	10%	trace	0.1%
Nitrogen (N)	3%	78%	trace

Biosequestered carbon is directly related to the biomass formed by photosynthetic organisms (cyanobacteria, green plants...). They absorb the sun's energy, capture water (H_2O) and carbon dioxide (CO_2) and convert them into sugars and oxygen (O_2) in a process called **photosynthesis** (See [Shedding light on photosynthesis](#) and [The path of carbon in photosynthesis](#)). The equation for photosynthesis can be summarized as follows:



The colossal amounts of living matter made continuously by photosynthesis are then used every day in a vast dynamic balance of life, death, nutrition, metabolism, growth, and decay [7]. Thus, the carbon fixed in plant biomass (*i.e.* biosequestered carbon) enters the food chain as it is used by a wide variety of organisms linked together by trophic relationships. Plants (producer organisms) are consumed by herbivorous animals (consumer organisms) with the help of associated microorganisms (microbiota). In the oceans, biomass enters the food chain through phytoplankton. Most living organisms use aerobic respiration{end-text}Characterizes a system (*e.g.*, a living organism) or process (*e.g.*, respiration) that requires O_2 oxygen. The term aerobic is also used in aeronautics, in the field of propulsion: an aerobic engine uses the oxygen of the ambient air as oxidizer for its operation. {end-tooltip}Aerobic respiration is a process which transfers chemical energy from glucose into ATP, the key molecule of cellular energy metabolism. Aerobic respiration is the catabolism of nutrients (glucose) into carbon dioxide, water and ATP, and involves an electron transport system in which oxygen is the final electron acceptor. The overall reaction of respiration is as follows:



1.3. Measuring biomass: dry weight and carbon content

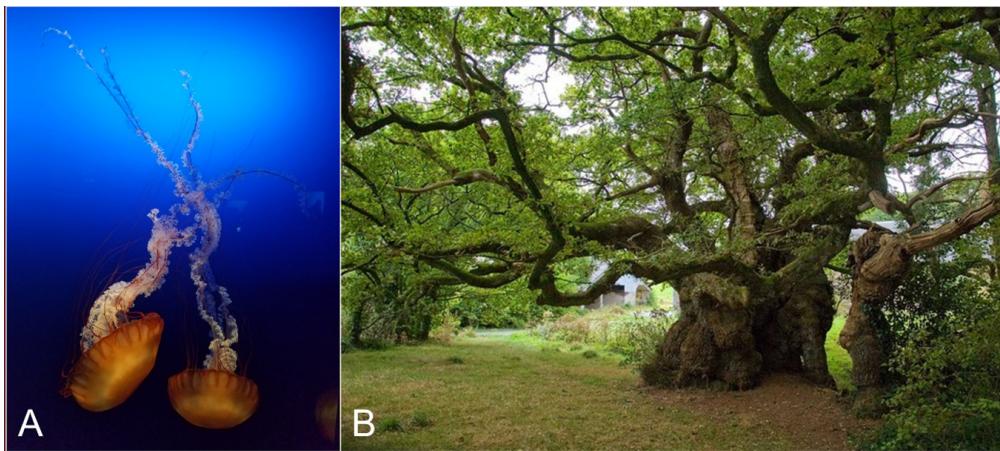


Figure 2. Water is the majority constituent of living organisms. A, Jellyfish (*Chrysaora fuscescens*) [Source: photo taken at the Omaha Aquarium © Betty Steffens, via Pexels]; B, Remarkable pedunculate oak (*Quercus robur*) from the Tronjoly forest, 1500 to 1700 years old [Source: Michel Lefrancq, CC BY-SA 3.0, via Wikimedia Commons]

The water content is very variable from one living organism to another: a jellyfish is composed of about 95% water while a living tree is more than two thirds water by mass (Figure 2)! It is therefore preferable to use a water-independent parameter to give an overview of the biomass. This is the case for both dry weight and carbon content. By the way, a good approximation of the characteristic conversion factor between carbon and total dry mass has a value of 2. Let's take a 100 year old oak tree with 20 tons of wood (dry weight). This corresponds to about 10 tons of carbon, mainly contained in the cellulose and lignin molecules, the main constituents of wood.

In their meta-analysis of the biomass of living organisms in the biosphere on the whole planet, Bar-on *et al* [4.5] expressed the biomass in gigatons of carbon, with 1 Gt C = 10^{15} g of carbon.

This reference to the quantity of carbon is thus a way of estimating (i) what the different taxa represent in terms of biomass and (ii) their relative importance within the biosphere. Of course, the carbon contained in living organisms does not represent the totality of the carbon in soil organic matter. This organic matter, which comes mainly from the decomposition of plants in the soil, constitutes considerable stocks of carbon (see [La place des sols dans le cycle du carbone](#)). Similarly, the organic matter accumulated in the oceans represents quantities of carbon far greater than that which can be measured in living organisms (See [The biological carbon pump of the ocean](#)).

2. Distribution of biomass in the biosphere

2.1. Plants dominate in terms of biomass

The best estimates of the biomass of each taxon{end-text}Unit in hierarchical classifications of living things. Generally the term is used at the specific (species) and subspecific (subspecies) ranks.{end-tooltip} [8] analyzed are shown in Figure 3 [9]. The sum of the biomass across all taxa on Earth is estimated to be about 550 Gt C, of which:

≈80% (≈450 Gt C) are plants [10];

≈15% (≈70 Gt C) are bacteria, the second major component of biomass ;

the remainder is due to other groups; in descending order: fungi (≈12 Gt C), archaea{end-text}Nucleus-free single-celled microorganisms often (but not always) living in extreme environments (anaerobic, high salinity, very hot...). The phylogenetic research of Carl Woese and George E. Fox (1977) allowed to differentiate the archaea from other organisms. Currently, it is considered that life is made up of three groups: archaea, bacteria and eukaryotes.{end-tooltip} (≈8 Gt C), protists{end-text}Eukaryotic microorganisms with a so-called simple cellular organization, unicellular most often, multicellular sometimes but without specialized tissues. They are eukaryotes other than an animal, a fungus or a plant. This group is very heterogeneous, both anatomically and physiologically. Some protists are autotrophic organisms (called protophytes), others are heterotrophic (called protozoa) and still others are mixotrophic as some dinoflagellates. The term "protophyte" was coined by Ernst Haeckel in 1866, from the Greek *proto*stos, superlative of *proto*, "first," the biologist placing in this taxon the organisms he considered the first living things on Earth.{end-tooltip} (≈4 Gt C), animals (≈2 Gt C) and viruses (≈0.2 Gt C).

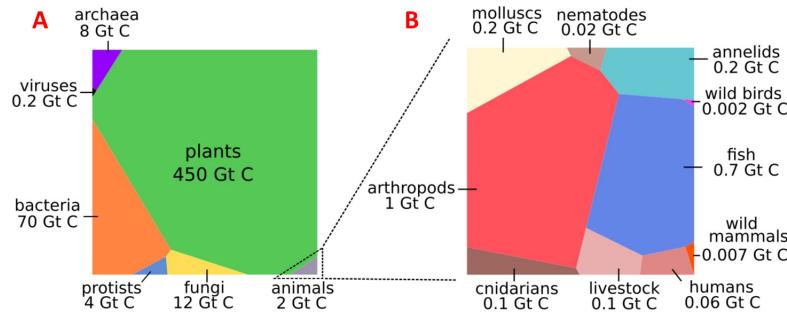


Figure 3. Graphical representation of global biomass distribution by taxa. (A) Absolute biomasses are represented using a Voronoi diagram where the area of each surface is proportional to the biomass of the group of living organisms considered. (B) Biomass of different groups of animals. Groups with negligible biomass are not shown. The diagrams were generated from the Proteomaps tool (see ref. [9]). Related groups such as vertebrates (birds, fish, mammals) are located next to each other. The contribution of reptiles and amphibians to the total animal biomass is negligible. [Source: diagram after Bar-On *et al.* ref [4]; Open Access article distributed under CC BY-NC-ND 4.0 license]

Estimates of global biomass vary according to the amount of information on which they are based and, consequently, their uncertainty (See Focus [How to estimate global biomass?](#)). One estimate with a **relatively high degree of certainty** is that of **plants**, which is based on many independent sources allowing a robust assessment of total plant biomass [11]. On the other hand, a typical case of **greater uncertainties** is illustrated by **marine prokaryotes**, whose cell concentrations are measured at various locations around the world and classified according to depth.

Thus, despite the large uncertainty associated with the total biomass of bacteria [10], plants are the dominant group in terms of

biomass with a probability of $\approx 90\%$.

Plant biomass is dominated by terrestrial plants, specifically vascular plants, with only a minor contribution from bryophytes{end-text} A branch of the plant kingdom, bryophytes (mosses, liverworts, sphagnum mosses...) do not possess a true vascular system (lack of roots and vessels). They have thallus (plant tissues composed of undifferentiated cells where we recognize neither leaves, nor stems) or small leaves. Among the current plants, the terrestrial and aquatic bryophytes are those which preserved the most characters of the first plants having colonized the dry land. The ancestors of all terrestrial plants, and therefore of bryophytes, are the green algae *Charophyceae*.{end-tooltip} (e.g. mosses) and of all marine plant biomass. This plant biomass represents that of forest and non-forest ecosystems and takes into account the impacts of land-use change.[\[12\]](#) Plant tissues are composed of an extracellular scaffold made out of cell walls (mainly cellulose and lignin), enclosing a cytoplasmic network, termed the protoplasm. The ratio of protoplasm to cell wall varies between plant compartments, with leaves containing the least amount of supporting tissue, while the stems of woody plants (such as trees) are primarily composed of supporting tissue:

$\approx 70\%$ of the plant biomass are due to the stems and trunks of trees, and are therefore relatively metabolically inert;

The remaining $\approx 30\%$ is concentrated in highly metabolically active plant tissues (mainly leaves and metabolically active root parts).

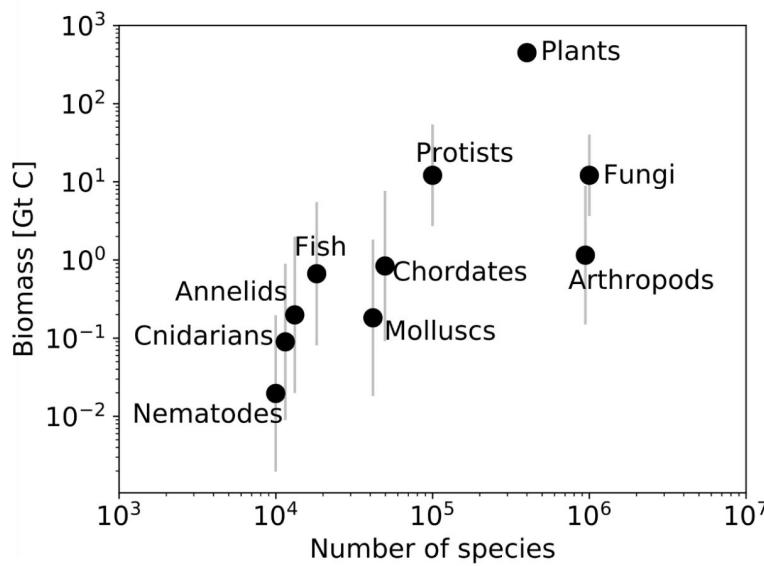


Figure 4. Relationship between species richness and biomass of different taxa. The total number of species in each taxon is plotted against the total biomass of the taxon. Error bars reflect our projection of uncertainty in the biomass estimate. [Source: diagram after Bar-On et al. ref [4]; Open Access article distributed under CC BY-NC-ND 4.0 license]

Aboveground biomass (≈ 320 Gt C) accounts for $\approx 60\%$ of the global biomass, with belowground biomass being mainly composed of plant roots (≈ 130 Gt C) and microbes residing in the soil and deep subsurface (≈ 100 Gt C).

Bacteria include about 90% of the biomass in deep subsurface (primarily in aquifers and beneath the seafloor), which have very slow metabolic activity and associated biomass carbon turnover times of months to thousands of years. Excluding these contributions, global biomass is still dominated by plants, consisting mainly of ≈ 150 Gt C of plant roots and leaves and ≈ 9 Gt C of terrestrial and marine bacteria whose contribution is nearly equal to the ≈ 12 Gt C of fungi.

2.2. Biomass is not directly related to the number of species

At present, about 1.7 to 2 million species have been described, but the number is estimated to be between 3 and 100 million species. Figure 3 represents the relationship between species richness and biomass of different taxa. Bacteria, archaea, and viruses are not included in this representation because species definition is problematic for these organisms.

Fungi, arthropods{end-text} Branch of invertebrate animals (insects, spiders, millipedes, crustaceans ...) whose organizational plan is characterized by a segmented body with articulated appendages and covered with a cuticle or a rigid carapace, which constitutes their exoskeleton, in most cases consisting of chitin. Appearing 543 million years ago, the phylum of arthropods is by far the one with the most species and the most individuals in the entire animal kingdom (80% of known species) [\[13\]](#) and plants

present the largest number of species. Flowering plants account for most of the terrestrial biomass, distributed among about 380,000 species [14].



Figure 5. Antarctic krill *Euphausia superba*. It lives in large groups, called "swarms", sometimes reaching densities of 10,000 to 30,000 individuals per cubic meter. [Source: Krill666.jpg: Uwe Kils, CC BY-SA 3.0, via Wikimedia Commons]

Whereas groups like insects (a class of arthropods) dominate in terms of species richness (with about 1 million described species) [15], their relative biomass fraction is minuscule. Some species contribute much more than families or even entire classes. For example, the Antarctic krill species *Euphausia superba* (Figure 5) contributes ≈ 0.05 Gt C to global biomass [16], on par with other prominent species such as humans (≈ 0.06 Gt C) or cows.

This value is comparable to the contribution of other members of the arthropod phylum, termites [17], which contain many species, and far exceeds the biomass of entire vertebrate classes such as birds (≈ 0.002 Gt C).

Other groups, such as nematodes [18], surpass any other animal species in terms of number of individuals, but constitute only about 1% of the total animal biomass (Figure 6).

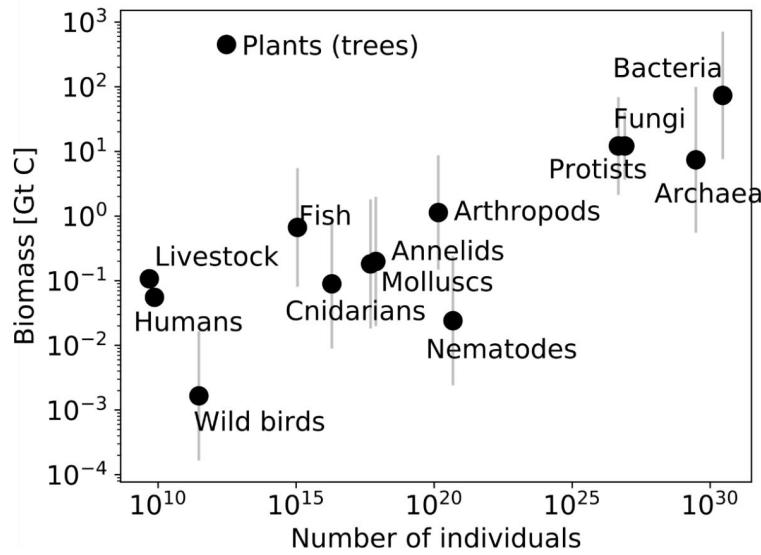


Figure 6. Relationship between abundance and biomass of different taxa. The total number of individuals in each taxon is plotted against the total biomass of the taxon. Error bars reflect the projected uncertainty in the biomass estimate. [Source: diagram after Bar-On et al. ref [4]; Open Access article distributed under CC BY-NC-ND 4.0 license]

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 (see Figure 4). This survey puts into perspective claims of the dominance of groups such as termites [16],

ants [19], nematodes [20] and prokaryotes [21].

In contrast, the biomass of amphibians{end-text}Formerly known as batrachians, amphibians are a class of tetrapod vertebrates with approximately 7000 species. The frog, the toad, the newt, the salamander are amphibians. They have the particularity of having an aquatic larval life and an aerial adult life {end-tooltip} (like the frog), whose population is in spectacular decline [22], remains poorly characterized.

3. Distribution of biomass across biotopes and trophic modes

3.1. Biomass of organisms living in different environments

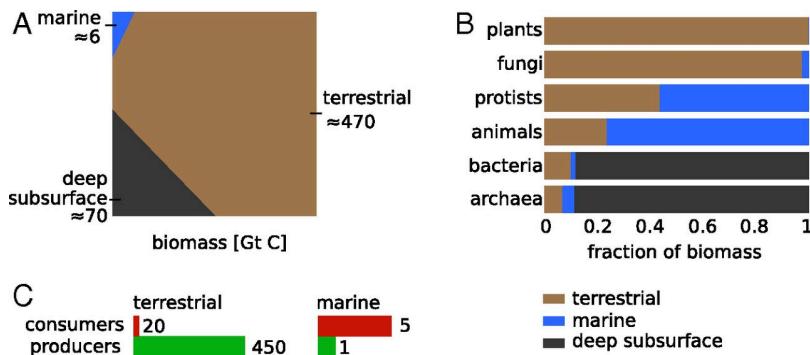


Figure 7. Biomass distribution of organisms living in different environments (marine -blue-, terrestrial -brown- and deep subsurfaces -black). (A) Absolute biomass is represented using a Voronoi diagram, with the area of each cell proportional to the overall biomass in each environment. (B) Fraction of the biomass of each group concentrated in the terrestrial, marine, or deep subsurface environment. Numbers are expressed in gigatons of carbon. [Source: diagram after Bar-On et al. ref [4]; Open Access article distributed under CC BY-NC-ND 4.0 license]

The differences in global biomass between terrestrial and marine environments are highly marked (Figure 7 and Table 2). The ocean covers 71% of the Earth's surface and occupies a much larger volume than the terrestrial environment, yet the terrestrial biomass, at ≈ 470 Gt C, is about two orders of magnitude higher than the ≈ 6 Gt C of the marine biomass, as shown in Figure 7A. In contrast, the primary productivity of the two environments is roughly equal [23].

For plants, most biomass is concentrated in terrestrial environments (plants are only a small fraction of marine biomass, <1 Gt C, in the form of algae -green and red- and seagrass; Figure 7B).

For animals, most biomass is concentrated in the marine environment, from fish (≈ 0.7 Gt C), marine arthropods (≈ 1 Gt C), molluscs, and annelids.

For bacteria and archaea, most of the biomass is concentrated in deep subsurface environments [24],[25], such as deep aquifers and the ocean's crust, which may hold the largest aquifer on Earth [26].

Table 2. Global biomass of taxa in terrestrial, marine, or deep subsurface environments. [Table based on data from Bar-On et al. ref [4]; Open access article distributed under CC BY-NC-ND 4.0 license]

Terrestrial		Marine		Deep subsurface
Taxon	Biomass [Gt C]	Taxon	Biomass [Gt C]	Taxon
Plants	450	Fish	0.7	
Soil fungi	12	Marine fungi	0.3	
Soil bacteria	7	Marine bacteria	1.3	Terrestrial deep subsurface bacteria Marine deep subsurface bacteria
Terrestrial protists	1.6	Marine protists	2	
Soil archaea	0.5	Marine archaea	0.3	Terrestrial deep subsurface archaea Marine deep subsurface archaea
Terrestrial arthropods	0.2	Marine arthropods	1	
Wild mammals	0.003	Marine mammals	0,004	
Terrestrial nematodes	0.006	Marine nematodes	0.01	
Annelids	0.2			
Livestock	0.1			
Humans	0.06			
Wild birds	0.002			
		Marine molluscs	0.2	
		Cnidaria	0.1	
Sum	470	Sum	6	Sum

However, several of the results in Figure 7B should be interpreted with caution due to the large uncertainty associated with some of the estimates, primarily those for total terrestrial protists, marine fungi, and -more broadly- contributions from deep subsurface environments (See Focus [How to estimate global biomass?](#)).

3.2. Biomass of organisms living in the oceans

In the oceans (Figure 8), the biomass of living organisms decreases in the following order

Animals, mainly represented by Crustacea (a sub-branch of the Arthropoda; mainly copepods, shrimps and krill, see Figure 5) and fishes (mainly small fishes of the mesopelagic zone);

Protists, both unicellular with, in particular, the Diatoms, Coccolithophorids and Dinoflagellates... and multicellular organisms with, essentially, the Phaeophyceae [\[27\]](#) (such as kelp and other brown algae);

Bacteria, and in particular the cyanobacteria of the genera *Prochlorococcus* and *Synechococcus* whose biomass is estimated at $\approx 15\%$ of the marine bacterial biomass;

Plants (in the broad sense - the Archaeoplastids - including green and red algae [\[24\]](#) as well as flowering plants such as eelgrass or posidonia beds);

Archaea, whose biomass corresponds to $\approx 20\%$ of the marine bacterial biomass;

Viruses, in particular phages, which play an important role in the recycling of nutrients during the lysis of marine bacteria (See focus [Ocean viruses](#) & [The biological carbon pump of the oceans](#)). While marine viruses outnumber bacteria and archaea by about an order of magnitude in various habitats [\[28\]](#), in terms of biomass in the ocean, they constitute only a tiny fraction, $\approx 1\%$, of the total biomass.

Fungi, found both in the deep ocean and in coastal waters such as mangroves or low salinity estuaries.

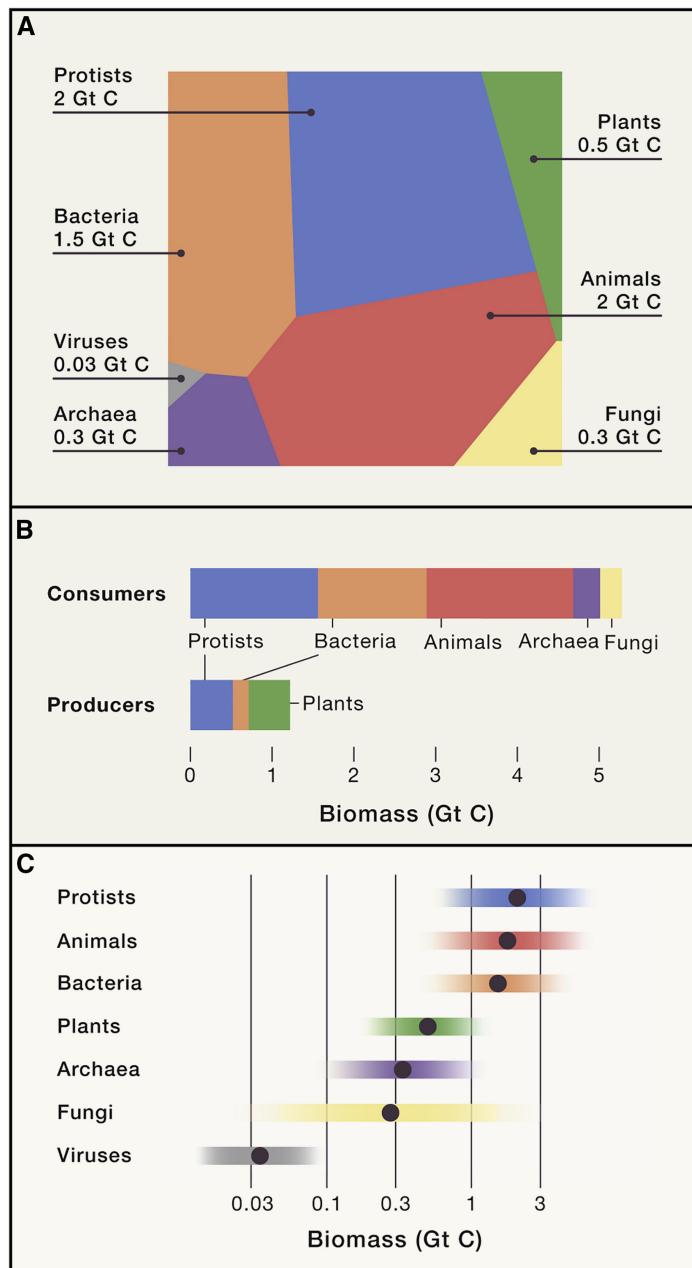


Figure 8. Biomass of the oceans. A. Biomasses of each group of living things are represented using a Voronoi diagram, where the area of each surface is proportional to the biomass of the group of living organisms considered. B. Distribution of biomasses of different producer and consumer groups in ocean environments. C. Representation of the uncertainties as gradients around the values estimated in A. [Source: Baron and Milo, ref [5], License: CC-BY-SA]

The first three groups of this classification (Animals, protists and bacteria) represent alone nearly 80% of the oceanic biomass while they form only 2% of the continental biomass! Conversely, plants, which largely dominate terrestrial ecosystems by constituting more than 80% of the biomass, represent only a small fraction of the oceanic biomass (less than 10%). Moreover, two thirds of the oceanic biomass is made up of unicellular organisms.

In terms of habitat, the majority of marine biomass is planktonic (transported by ocean currents), a much smaller fraction belongs to neoton{end-text}A set of marine organisms whose swimming ability is such that they can move against currents (fish, some crustaceans, cephalopods, and marine mammals).{ Then there are the organisms attached to particles (attached to micro- or macro-aggregates in the open sea) and finally the organisms living on the sea floor (or benthic). This global representation varies according to the kingdom. Thus, macroalgae can be both benthic and planktonic (for example, the common genus of brown algae *Sargassum*). In contrast, most plant biomass is benthic and not planktonic. However, this distribution must take into account the large uncertainties associated with the analyses (see Focus on [How to estimate the global biomass?](#)) and the fact that the global biomass of the many hot spots on the ocean floor (submarine canyons for example) is still largely unknown.

By providing a better understanding of the structure of ocean ecosystems and their biomass, this study allows us to better parameterize the carbon stock of these environments. This is an important element for climate models.

3.3. Biomass of producers and consumers

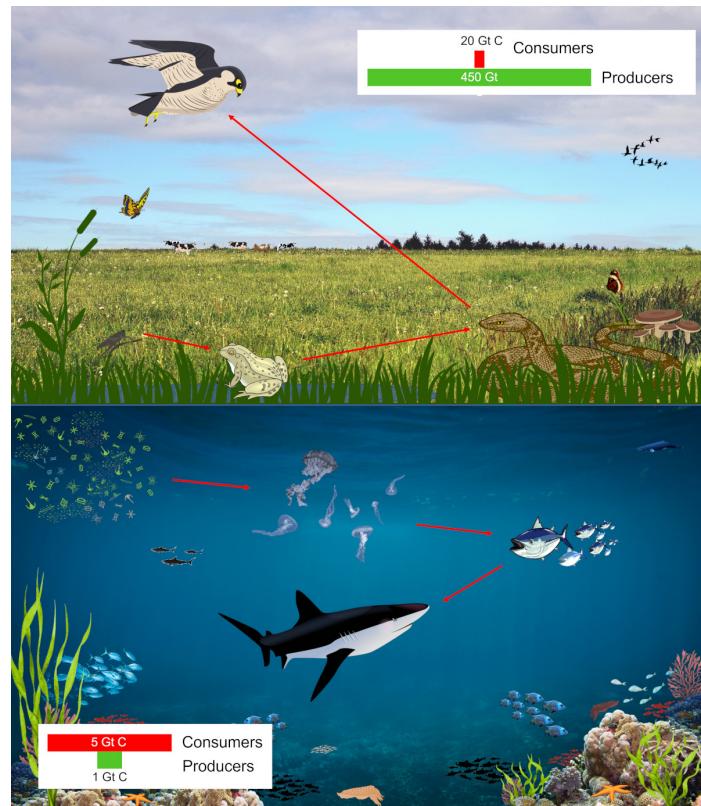


Figure 9. Example of food chains and biomass distribution (in Gt C) in terrestrial (top) and marine (bottom) environments. The producers are autotrophs, mainly photosynthetic, and the consumers are heterotrophs. [Source: © EEnv diagrams]

Figure 9 shows the distribution of biomass between producers (autotrophs) and consumers (heterotrophs) in the terrestrial and marine ecosystems. All heterotrophic organisms, including detritivores, are part of the consumer biomass.

In the terrestrial environment, plant biomass represents the total biomass of terrestrial autotrophs. The remaining terrestrial biomass, including soil bacteria (≈ 7 Gt C), soil archaea (≈ 0.5 Gt C), soil fungi (≈ 12 Gt C), soil protists (≈ 1.5 Gt C), and terrestrial animals (≈ 0.5 Gt C), are considered terrestrial heterotrophs (See Focus [Soil biomass](#)).

In the marine environment, the total biomass of seagrasses (≈ 0.1 Gt C), macroalgae (≈ 0.1 Gt C), picoplankton (≈ 0.4 Gt C), diatoms (≈ 0.3 Gt C), and *Phaeocystis* (≈ 0.3 Gt C) yields an estimate of total marine autotroph biomass of ≈ 1.3 Gt C. The remaining marine biomass of ≈ 5 Gt C including marine bacteria (≈ 1.3 Gt C), archaea (≈ 0.3 Gt C), fungi (≈ 0.3 Gt C), heterotrophic protists (≈ 1.1 Gt C), and animals (≈ 2 Gt C), was considered as marine heterotrophic biomass.

This study confirms a well-known observation in ecology: in oceans, the biomass of consumers far exceeds that of producers (≈ 5 Gt C versus ≈ 1 Gt C). Conversely, on land, the biomass of primary producers is much larger than that of primary and secondary consumers (Figure 9).

Such inverted biomass distribution in the oceans can be explained by a higher turnover rate of producers than consumers: marine primary producers renew their biomass rapidly (on the order of a few days [\[29\]](#), whereas consumers renew their biomass only much more slowly, a few years in the case of mesopelagic fish [\[30\]](#)). Thus, the standing stock of consumers is larger, even though the productivity of producers is necessarily higher. Inverted consumer/producer ratio has also been described for the global plankton biomass [\[31\]](#). This holds true when considering the overall biomass of all producers and consumers in the marine environment.

It should be noted that the biomass of parasites is not yet separated from that of their hosts. It might be larger than the biomass of top predators in some environments [\[32\]](#).

4. The impact of humanity on the biosphere

4.1. Humans represent only a small fraction of animal biomass

Over the relatively short period of human history, major innovations, such as the domestication of livestock, the adoption of an agricultural lifestyle, and the industrial revolution, have allowed for dramatic increases in human population and have had radical

Today, human biomass (≈ 0.06 Gt C) and livestock biomass (≈ 0.1 Gt C, dominated by cattle and pigs) far exceed that of wild mammals, whose mass is ≈ 0.007 Gt C.

The same is true for wild and domesticated birds, for which the biomass of domesticated poultry (≈ 0.005 Gt C, dominated by chickens) is about three times higher than that of wild birds (≈ 0.002 Gt C).

In fact, the biomass of humans and livestock exceeds that of all vertebrates combined, except fish.

Although humans and livestock dominate the mammalian biomass, they represent only a small fraction of the ≈ 2 Gt C of animal biomass, which primarily includes arthropods (≈ 1 Gt C), followed by fish (≈ 0.7 Gt C).

4.2. Humans reshaped the planet's biomass

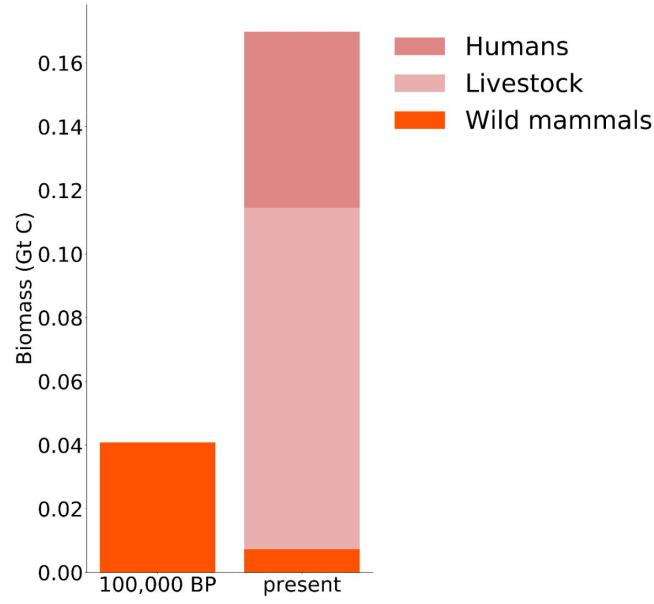


Figure 10. Impact of human civilization on mammal biomass. Biomass of wild mammals, livestock (dominated by cattle), and humans before human civilization (BP, Before Present) and at the present time. [Schematic after Bar-On et al. ref [4]; Open access article distributed under CC BY-NC-ND 4.0 license]

Comparison of current global biomass with pre-human values (which are very difficult to estimate accurately) allows us to assess the impact of humans on the biosphere (Figure 10):

Human activity contributed to the **Quaternary megafauna extinction** between $\approx 50,000$ and $\approx 3,000$ years ago, which took away about half of the large (>40 kg) terrestrial mammal species [33]. The biomass of wild terrestrial mammals prior to this extinction period was estimated by Barnosky [29] to be ≈ 0.02 Gt C. The current biomass of wild terrestrial mammals would be about seven times lower, at ≈ 0.003 Gt C.

Intense whaling and exploitation of other marine mammals have resulted in an approximately fivefold decrease in overall marine mammal biomass (from ≈ 0.02 Gt C to ≈ 0.004 Gt C [34]).

While the total biomass of wild mammals (marine and terrestrial) has decreased by about a factor of 6, the total mammal mass increased approximately fourfold, from ≈ 0.04 Gt C to ≈ 0.17 Gt C due to the vast increase in 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 total biomass remaining in fisheries and to the gain in the total mammal biomass due to livestock husbandry.

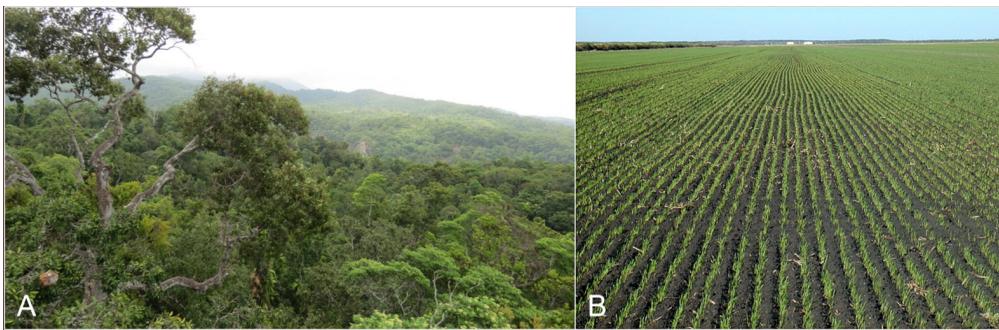


Figure 11. Agriculture reshaped plant biomass. A, Daintree Rainforest, Queensland, Australia, the world's oldest continuously surviving rainforest [Photo © Robert Linsdell from St. Andrews, Canada, CC BY 2.0, via Wikimedia Commons]. B, winter wheat germination at Open Grounds Farm in Beaufort, North Carolina, USA [Soil-Science.info, CC BY 2.0, via Wikimedia Commons]

The impact of human civilization on global biomass has not been limited to mammals but has also profoundly reshaped the total amount of carbon sequestered by plants (Figure 11). A global census of the total number of trees [35], as well as a comparison of actual and potential plant biomass [6], suggested that total plant biomass (and, by extension, total biomass on Earth) has been cut roughly in half from its value before the onset of human civilization. The total biomass of plants grown by humans is estimated to be ≈ 10 Gt C, which is only $\approx 2\%$ of the total existing plant biomass [6].

5. Take-home messages

The census of biomass distribution (≈ 550 Gt C) on Earth provides an integrated global picture of the relative and absolute abundances of all kingdoms of life: plants (≈ 450 Gt C), bacteria (≈ 70 Gt C), archaea (≈ 7 Gt C), and animals (≈ 2 Gt C) ;

Terrestrial biomass is about two orders of magnitude higher than marine biomass, and a total of ≈ 6 Gt C is estimated in marine organisms;

Plant biomass (which dominates the biosphere) is mostly located on land; it accounts for less than 10% of the total biomass in the ocean.

Animals, protists, and bacteria together account for $\approx 80\%$ of marine biomass, whereas on land they account for only $\approx 2\%$.

The animal biomass is predominantly marine; it consists of small mesopelagic fish and crustaceans, mainly copepods, shrimp, and krill.

The marine environment is primarily occupied by microbes, primarily bacteria and protists, which account for $\approx 70\%$ of the total marine biomass. The remaining $\approx 30\%$ is primarily composed of arthropods and fish.

Viruses dominate the ocean in terms of numbers but constitute only $\approx 1\%$ of the total biomass.

The deep subsurface holds $\approx 15\%$ of the total biomass of the biosphere. It is mainly composed of bacteria and archaea.

The global marine biomass pyramid contain much more consumers (≈ 5 Gt C) than producers (≈ 1 Gt C). Conversely, on land, the biomass of primary producers (≈ 450 Gt C) is much larger than that of primary and secondary consumers (≈ 20 Gt C).

The mass of humans is an order of magnitude greater than that of all wild mammals combined.

Humans have had a historical impact on the overall biomass of most important taxa, namely:

The huge decrease in total biomass of wild animals, including fish;

The gain in total mammalian biomass due to livestock husbandry;

The profound reshaping in the total quantity of carbon sequestered by plants.

The main gaps in our knowledge concern the distribution of biomass among different microbial taxa, such as bacteria, archaea,

protists and fungi.

Our knowledge of the biomass composition of the different taxa is mainly determined by our ability to sample, for example, in deep marine subsurface environments.

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Bar-On Y.M., Phillips R. & Milo R. (2018) The biomass distribution on Earth. Proc. Nat. Acad. Sci. U.S.A. 115:6506-6511 ; DOI: 10.1073/pnas.1711842115

Bar-On, Y.M. & Milo R. (2019) The biomass composition of the oceans: A blueprint of our blue planet, Cell, 179 :1451-1454; https://doi.org/10.1016/j.cell.2019.11.018

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Notes and references

Cover image. A certain idea of biomass: Zebra (*Equus zebra*) and wildebeest (*Connochaetes taurinus*) in the African savannah, *Masai Mara National Reserve*, Kenya. [Source: photo © Jacques Joyard]

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[8] Our knowledge of the biomass composition of different taxa is mainly determined by the ability to sample their biomass in nature, for example in deep ocean and crustal environments. The main gaps in our knowledge concern the distribution of biomass among different microbial taxa, such as bacteria, archaea, protists and fungi.

[9] The data set collected and analyzed by Bar-on *et al* [4,5] is available on [GitHub](#). The data representation for the figures is done using the [Proteomaps](#) tool.

[10] What Bar-On *et al.* (ref. [4]) define as plants are the set of Embryophytes (which are called land plants), green algae and red algae. For French-speaking authors (Romaric Forêt and his *Dictionnaire de sciences de la vie*, Le Guyader & Lecointre and their *Classification phylogénétique du vivant*), the term plants is synonymous with Embryophytes. For Wikipedia, the term plants is synonymous with Archaeoplastids (green lineage).

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associated with the bacterial biomass estimate is much larger (≈ 9 times) (see ref. [4]).

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