The global biomass of wild mammals

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Wild mammals are icons of conservation efforts, yet there is no rigorous estimate available for their overall global biomass. Biomass as a metric allows us to compare species with very different body sizes, and can serve as an indicator of wild mammal presence, trends, and impacts, on a global scale. Here, we compiled estimates of the total abundance (i.e., the number of individuals) of several hundred mammal species from the available data, and used these to build a model that infers the total biomass of terrestrial mammal species for which the global abundance is unknown. We present a detailed assessment, arriving at a total wet biomass of ≈20 million tonnes (Mt) for all terrestrial wild mammals (95% CI 13-38 Mt), i.e., ≈3 kg per person on earth. The primary contributors to the biomass of wild land mammals are large herbivores such as the white-tailed deer, wild boar, and African elephant. We find that even-hoofed mammals (artiodactyls, such as deer and boars) represent about half of the combined mass of terrestrial wild mammals. In addition, we estimated the total biomass of wild marine mammals at ≈40 Mt (95% CI 20-80 Mt), with baleen whales comprising more than half of this mass. In order to put wild mammal biomass into perspective, we additionally estimate the biomass of the remaining members of the class Mammalia. The total mammal biomass is overwhelmingly dominated by livestock (≈630 Mt) and humans (≈390 Mt). This work is a provisional census of wild mammal biomass on Earth and can serve as a benchmark for human impacts.

ecology | biomass | biosphere | quantitative biology

It is becoming critically urgent to take stock of the remaining wildlife on Earth and use it as a benchmark to evaluate recent and future trends. Although wild mammals are of great public interest, often serving as the target of conservation efforts, their rates of extinction have increased sharply over the past two centuries (1, 2), and shrinking population sizes amount to a massive anthropogenic erosion of biodiversity (3).

A large body of literature describes ecological parameters such as phylogenetic diversity (4, 5) and species richness (6) as indicators of the state of wild mammals. While these parameters are useful, especially at a regional or ecosystem scale, they can be limited or even misleading at a global scale. For example, the list of known, extant mammalian species is growing, rather than shrinking, due to taxonomic redefinitions despite a decline in wild mammal populations (3, 7). Thus, species richness metrics do not necessarily reflect the status of mammals on the global scale. Moreover, various diversity metrics are often less meaningful for assessing ecological impacts on ecosystems (8). All other things being equal, rare species with few individuals affect ecosystems much less than common ones (9, 10).

Estimating the number of individual organisms is technically challenging even for a single species, due to issues such as detectability, interannual and seasonal variability, and the lack of standardization in measurement methods (11), especially for small-bodied species. Quantifying the biomass of all mammals allows us to compare species with very different body sizes. Biomass is, therefore, complementary to species richness and other diversity metrics, and can serve as an indicator of wild mammals' abundance and ecological footprint on a global scale, as a benchmark to follow the temporal dynamics of the global wildlife state, and as an intuitive datasource for conservation efforts.

Some attempts have been made to quantify the global biomass of wild land mammals (12–13). However, these estimates are usually very crude and have large uncertainties, with none so far addressing the quantification of wild mammal biomass as their main effort. Furthermore, no comparative estimate has been reported for mammalian orders or families.

Constructing accurate estimates of the total biomass of any taxon is challenging. However, for wild mammals, a relatively large amount of census data are available, which makes such an effort more feasible. Here, we compiled available data on species-specific estimates for the total abundance (i.e., the number of individuals) of wild mammals. We used these estimates to build a model that infers the total abundance of terrestrial mammal species for which the global abundance is unknown. We used the global abundance data,

Significance

Mammals include some of the best-known species of animals, and are icons of conservation efforts. Despite their status, there is no rigorous estimate available for their overall global biomass. We quantified absolute wild mammalian biomass and its distribution across different taxa and continents. Such data can serve as a holistic benchmark to analyze temporal trends. This quantitative global view of wildlife, when contrasted for example to the mass of humanity and its livestock, can help dispel notions about the seemingly endless ubiquity of wildlife and provide a quantitative argument for the urgency of nature conservation efforts.

and provides a global view of current mammalian wildlife, to help prepare for its uncharted future.

To estimate the total biomass of wild mammals on Earth, we manually collected species-specific global population estimates. Overall, we were able to collect reports on the global population sizes of 392 land mammal species, representing ≈6% of all wild land mammal species (14). In terms of mass, these 392 species have a total biomass of ≈12 Mt. We also obtained a combination of species-specific properties influencing animal abundance, for each wild land mammal as detailed in *Materials and Methods*. As shown in Fig. 1*A*, using the species-specific properties and the global population reports, we constructed a machine learning model that infers the global populations of the remaining ≈94% of species, which lack global abundance estimates. Our estimate includes 4,805 wild land mammal species, out of ≈6,400 known and extant wild land mammal species (15), excluding species for which data are unavailable due to scarcity and lack of research. Because these tend to be low-abundance species, we consider their effect on the overall biomass to be negligible.

Results

We estimate the total biomass of wild land mammals at ≈22 Mt wet weight (equivalent to ≈7 Mt dry weight or ≈3 Mt carbon content). Despite representing a small fraction of all land mammals species (6%), species with reported abundances constitute ≈55% of the total wild land mammal biomass (12 Mt vs. 22 Mt). The remaining 94% of species amount to ≈45% of the total biomass, or ≈10 Mt (Fig. 1*B*). We found that the majority of the wild land mammal biomass is concentrated in a small number of large-bodied (>10 kg per individual) species, whereas species with a body mass below 1 kg, while comprising >95% of all individuals, contribute only one-fifth to the total biomass (*SI Appendix*). Bats (Chiroptera), for example, comprise one-fifth of species and two-thirds in terms of individual mammals, but only contribute less than one-tenth of the total biomass of wild land mammals, as shown in Fig. 2.
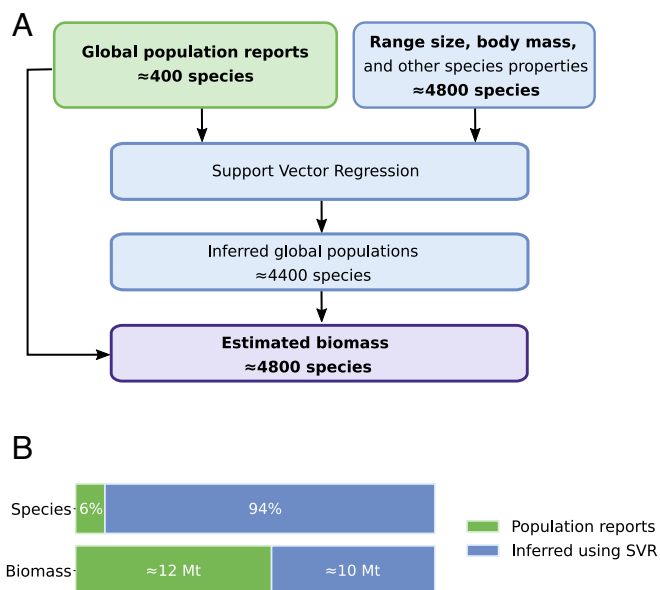
Fig. 1. (*A*) Outline of the process of quantifying the total biomass of all wild land mammals (*SI Appendix,* Fig. S3). (*B*) The number of species and total biomass of all wild land mammals by estimation method. For 392 species, global population reports are available (green). The total mass of each of the remaining 4,413 species (blue) was estimated using our model. The 392 species were not selected randomly, but selected based on data availability. This dataset therefore tends to contain more large-bodied species at greater risk of extinction, or species with a small range compared to the species where no global abundance data are available (*Materials and Methods*). Our estimate excludes ≈1,500 known wild land species for which there is a lack of range data due to scarcity and lack of research. We estimate their global biomass to be negligible, since their abundance is typically low.

along with the inferred abundance estimates and each species' body mass, to achieve a global wild mammal biomass estimate. This study thus provides an estimate of the total wild mammal mass, displays its distribution across different taxonomic groups, and

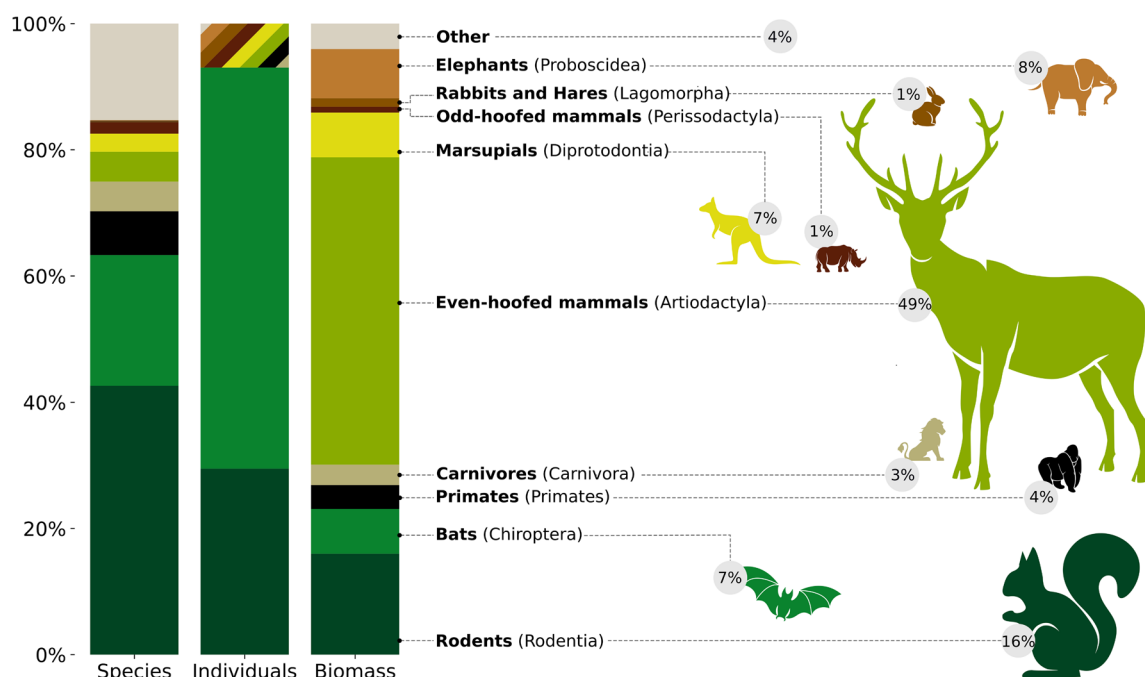**Fig. 2.** The relative number of species, number of individuals, and total biomass of each taxonomic order of wild land mammals. Due to the uncertainty associated with the number of individuals, we combine together the contribution of all but the two most individual-rich orders. The relative biomass contribution of each order is also indicated by the animal silhouette sizes and corresponding percentages.

Table 1. Top 10 contributors to global wild land mammal biomass, ranked by total species biomass. These 10 species represent ≈40% of the estimated global wild land mammal biomass, with white-tailed deer alone contributing ≈10% of the estimated global wild land mammal biomass.

Rank	Name	Binomial name	Total species mass (Mt)	Individuals (millions)
1	White-tailed deer	*Odocoileus virginianus*	2.7	45
2	Wild boar*,†	*Sus scrofa*	1.9	30
3	African savanna elephant	*Loxodonta africana*	1.3	0.5
4	Eastern gray kangaroo	*Macropus giganteus*	0.6	20
5	Mule deer	*Odocoileus hemionus*	0.5	7
6	Moose	*Alces alces*	0.5	1.5
7	Red deer	*Cervus elaphus*	0.5	2
8	European roe deer	*Capreolus capreolus*	0.4	20
9	Red kangaroo	*Macropus rufus*	0.4	10
10	Common warthog*	*Phacochoerus africanus*	0.3	5

*Species estimated using Support Vector Regression model.
†Including *S. scrofa* in Australia and North America, commonly known as feral pigs.

When considering which taxonomic order contributes the most, we find that even-hoofed mammals, Artiodactyla, comprise ≈50% of the total land mammal biomass (Fig. 2), followed by rodents (Rodentia). The order Proboscidea (elephants, the largest terrestrial mammals) comprises ≈8%.

We find that ≈40% of the biomass of all wild land mammals is concentrated in just 10 species (Table 1). Seven of these top contributors are even-hoofed mammals (wild boar, warthog, and five deer species). The species with the highest overall biomass is the white-tailed deer (*Odocoileus virginanus*), whose population in North America has recovered dramatically over the past century, reaching numbers similar to those before European colonization (16).

Many mammal species interact with, and benefit from, human surroundings and activities. These so-called synanthropic mammals, like the Northern raccoon (*Procyon lotor*), tend to have higher population densities in human surroundings than in the wild (17). Most synanthropic species lack population reports and are generally hard to quantify due to their wide distribution and large population size. Three prominent synanthropic species, known to have high population densities in urban environments, were removed from the final tally of wild mammals: the black and brown rats (*Rattus rattus* and *Rattus norvegicus*, respectively) and the house mouse (*Mus musculus*). For a number of other synanthropic species, we performed a dedicated manual analysis to evaluate their contribution to the global mammal biomass (*SI Appendix*).

Fig. 3 depicts the global geographic distribution of the wild land mammal biomass density if the biomass of each species was equally spread throughout its range. While simplistic, it provides a spatial perspective on the geographical distribution of the wild mammal biomass and the dominance of a few wild land mammal species on a global and continental scale. For example, the dense areas in sub-Saharan Africa consist mostly of the African savanna and forest elephants, which inhabit multiple disjoint ranges.

We also analyzed the total marine mammal biomass. In contrast to wild land mammals, population reports for marine mammals cover a much greater portion of the tallied marine species: ≈60% of marine-mammal species have global population reports (72 out of the 121 marine mammal species) and an additional 23 have partial reports on the International Union for Conservation
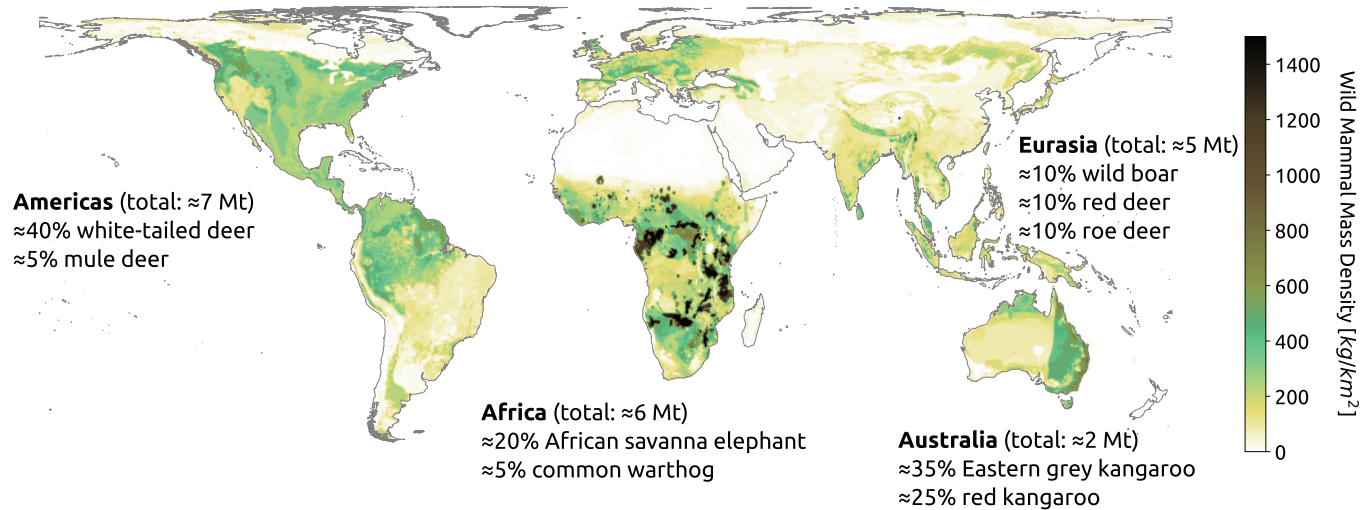
Fig. 3. A simplistic depiction of the global distribution of wild land mammal biomass density, based on overlaying the biomass and ranges of all species and assuming that each species is evenly spread throughout its range. Although this assumption can create unrealistically uniform patches across large areas, it provides a holistic overview and displays the dominance of the species with the largest overall biomass. The estimated total biomass is noted for each continent, together with the name of the top mass contributor and its relative biomass contribution to the said continent. This analysis excludes the feral pig (*Sus scrofa*) biomass in North America and Australia due to lack of range data.

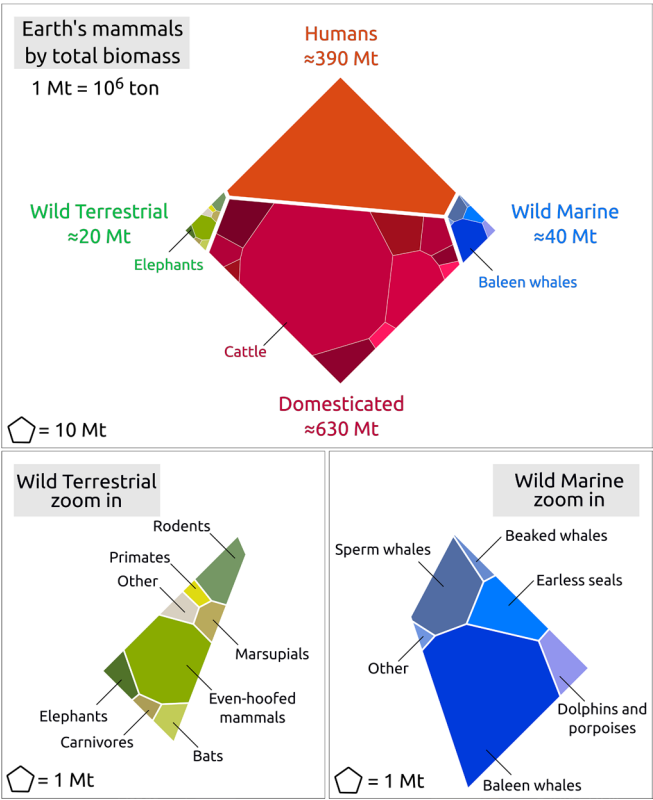**Fig. 4.** *Top*: the global biomass distribution of the mammalian class, represented by a Voronoi diagram. The area of each cell is proportional to the biomass contribution of each group. The global mammalian biomass distribution is dominated by humans and domesticated mammals, including livestock and pets (illustrated at the species level in *SI Appendix*). *Bottom*: enlarged view of the biomass of wild terrestrial (*Left*, grouped by order) and marine mammals (*Right*, grouped by family, or few families).

of Nature (IUCN) Red List website. The remaining species lack data due to scarcity and lack of research; as the typical abundance of such species is low, we estimate their global biomass to be negligible (*Materials and Methods*). While marine mammals comprise a substantially smaller number of species and number of individuals than wild land mammals, their total mass of ≈39 Mt outweighs that of wild land mammals, as shown in Fig. 4. We find that ≈60% (≈23 Mt) of the global marine-mammal biomass is contributed by the baleen whale families (Balaenidae, Balaenopteridae, Neobalaenidae, and Eschrichtiidae). Two of the top three mass contributors, the fin whale (*Balaenoptera physalus*) and the humpback whale (*Megaptera novaeangliae*), are members of baleen whale families, contributing ≈8 and ≈4 Mt, respectively

(Table 2), and the other is the sperm whale (*Physeter macrocephalus*, ≈7 Mt, a toothed whale).

In order to put the total biomass of wild terrestrial and marine mammals (≈22 Mt and ≈39 Mt, respectively) in perspective, we compared them to domesticated mammals (Fig. 4). Many domesticated mammal species outweigh the top wild mammal biomass contributors by 10 to 1,000 fold (*SI Appendix*, Fig. S8). The most significant mammal biomass contributors are cattle (≈420 Mt), humans (≈390 Mt), and other livestock species most commonly reared for meat or dairy (including buffaloes, pigs, sheep, and goats). These are followed by pack animals (e.g., horses, camels, and donkeys). Domesticated pigs alone weigh ≈40 Mt, almost double the combined mass of all terrestrial wild mammals.

Common pet species (e.g., cats and dogs) also are major contributors on a mass basis. Domestic dogs (*Canis lupus familiaris*) have a total mass of ≈20 Mt, similar to the combined biomass of all wild terrestrial mammals. Domestic cats (*Felis catus*) have a total biomass of ≈2 Mt, almost double that of the African savanna elephant and four times that of all moose (*Alces alces*, *SI Appendix*). These domesticated-to-wild mass ratios emphasize the active role humans play in shaping the abundance of mammals on Earth.

Discussion

We compiled available data on the abundance of wild and domesticated mammals and used them to estimate their global biomass. Portraying the distribution of biomass between different members of the class Mammalia gives a broad view of the current state of wild mammals as a whole and of the dominance of human-associated mammals worldwide. Human activities have been the main driver of wild mammal extinctions since the late Pleistocene (18), and continue to cause severe damage to many mammal populations. The blue whale, for example, which currently contributes a tenth of the total wild marine-mammal biomass, is estimated to have been more than 10-fold more abundant prior to industrial whaling (19). A recent analysis of ≈200 wild land mammal species showed that the extinction of mammal populations is rapidly unfolding (3). The global composition of mammal biomass reflects human-induced pressures on wild mammal populations: the increasing human population, the growing global demand for animal-based products, and the related expansion of factory farms (20), leading for example to the result where domesticated mammals now outweigh wild land mammals 30 to 1.

Biomass is reported in wet weight. Alternative options used elsewhere to report biomass include dry weight or carbon content (12). We chose to use wet weight as the measure of biomass for

Table 2. Top 10 contributors to global wild marine mammal biomass, ranked by total species biomass

Rank	Name	Binomial name	Total species mass (Mt)	Individuals (millions)
1	Fin whale	*Balaenoptera physalus*	8	0.1
2	Sperm whale	*Physeter macrocephalus*	7	0.4
3	Humpback whale	*Megaptera novaeangliae*	4	0.1
4	Antarctic minke whale	*Balaenoptera bonaerensis*	3	0.5
5	Blue whale	*Balaenoptera musculus*	3	0.05
6	Crabeater seal	*Lobodon carcinophaga*	2	10
7	Bryde's whale	*Balaenoptera edeni*	1.3	0.1
8	Common minke whale	*Balaenoptera acutorostrata*	1.3	0.2
9	Harp seal	*Pagophilus groenlandicus*	1.2	10
10	Bowhead whale	*Balaena mysticetus*	1.1	0.05

the class Mammalia as it is a relatively intuitive metric. All of our reported wet weight values can be easily converted to dry weight to a good approximation by dividing by a factor of 3, as two-thirds of the body content is water. Dry mass can be further converted to carbon content to a good approximation by dividing by 2, the characteristic conversion factor between carbon and total dry mass.

Our analysis of the distribution of biomass across wild land mammal orders and species reveals that ≈40% of the global biomass of wild land mammals is concentrated in only 10 species, four of which are deer species that have likely benefited from declining populations of keystone predators like the gray wolf (*Canis lupus*) (21). The global distribution of wild mammals' biomass highlights the dominance of a small number of species over other mammals in the wild (Fig. 3). An example of this pattern is the fact that the total biomass of the three elephant species is similar to that of all ≈1,200 bat species combined.

We find that most of the biomass of wild land mammals is concentrated in relatively abundant, large-ranged and large-body-sized species. Although reports are available for many large-bodied species, we estimate that only ≈55% of the biomass of land mammals is represented by species with global population reports, which is concentrated in a small subset of 6% of species that tend to have large body weight. This calls for more species-specific global abundance assessments, as some of the highest mass contributors (e.g., the common warthog, *Phacochoerus africanus*) still lack species-specific global abundance reports, and were, therefore, estimated in this work. A specific assessment of their global abundance would provide a more accurate view on significant species in terms of overall biomass, and on the distribution of mass across species, clades, and geographical regions. In addition, global abundance reports for widely distributed small-sized mammals, such as many bat species (Chiroptera), are lacking; thus, their global biomass estimates contain a high degree of uncertainty. Measuring the abundance of these small species is challenging, but could improve the global quantification of mammalian biomass. Since the methods used in this study are both easily repeatable and readily scalable, additional mammal population reports can easily be incorporated to improve our estimates.

The influence of human activities on animal abundance is evident even for species usually viewed as wild. We find that ≈30% of wild land mammal species reside in both human-dominated (plantations, urban areas, etc.) and natural habitats. Some wild land mammal species thrive in these human-dominated environments. A few of the top mass contributors on land, including the white-tailed deer and the wild boar, are considered pests and are exterminated regularly in some locations (22, 23). This, in addition to the clear dominance of domesticated mammals and humans over wild land mammals (Fig. 4), highlights the dominance of human-associated mammals over wildlife globally. While biomass is not a direct indicator of conservation status or anthropogenic pressures, we suggest that the ratio between the biomass of wild and domesticated species biomass provides further perspective on the extraordinary increase in humanity's impact on our planet.

There are several qualitative notions about the world that we tend to internalize, that decrease the apparent need and urgency of nature conservation efforts. Notably that the world is enormous and by corollary that natural things, shown in their explosive diversity in many natural history movies, textbooks, and museums, are seemingly endless and intuitively much more abundant than anything humanity creates. Rigorous estimates of the biomass of various components of the living world, when contrasted to human-associated masses, help dispel these erroneous notions and conclusions. Such estimates thus have utility independent of their direct ecological implications. Concrete examples are the findings that the mass

of human-made things, so-called anthropogenic mass, now exceeds the mass of all living things (24) or the current finding that there is only ≈3 kg of wild land mammals per person on earth and that the mass of dogs or sheep outweighs all wild mammals combined.

The global distribution of mammals and their biomass can also serve as a step toward assessing future risks from emerging zoonotic diseases. In the past century, many of the viral epidemics spread by viruses, including HIV, Ebola and, most recently, SARS-CoV-2, crossed from wild mammal carriers to humans. Other viruses, such as the H1N1 influenza A virus (commonly known as "swine flu"), crossed from livestock to humans (25). A joint estimate of the geographic distributions of wild and domesticated mammal biomass can be informative in assessing and monitoring zoonotic disease reservoirs.

This study achieves a comprehensive census of the biomass distribution of wild mammals on Earth. Its results can be relevant both for assessing wild mammals' global status as a whole and for evaluating and comparing different mammalian groups and species. Wild mammals serve as a source of inspiration for humanity and are often used as flagship species to support and raise awareness for wildlife conservation. The results presented here could be used for global ecology research and to monitor the fate of wild mammals on the global scale.

Materials and Methods

All of the data used to generate our estimates, as well as the code used for analysis, are open sourced and available at https://gitlab.com/milo-lab-public/mammal_biomass.

The biomass of ≈6% of land mammal species was calculated directly from global population reports. The biomass of the remaining wild land mammal species was estimated using a Support Vector Regression model (*SI Appendix*). Our model was built using a dataset of population abundances, along with several datasets of species-specific properties influencing animal abundance. The biomass of wild marine mammal species was calculated directly from global population reports (*SI Appendix*).

Wild Land Mammal Species-Specific Global Population Reports. The population abundance dataset contains global population reports at the species level. We manually extracted population reports from the IUCN website (26), which, at the time of extraction (April 2019), contained total population reports for 382 species. In addition, we collected population reports from sources outside the IUCN database specifically for 10 mammalian species we suspected of being high biomass contributors based on their large body masses and range sizes, such as the white-tailed deer (*SI Appendix*). None of these 10 species had their global abundance recorded in the IUCN database.

Inferring the Biomass of Wild Land Mammal Species Lacking Global Population Reports. We inferred population abundances for species lacking global population reports using a Support Vector Regression (27) model based on the dataset of global abundances. We assigned a mean density for each of the 392 species in the global population abundance dataset (population abundance divided by the range size in units of individuals per square kilometer), and the model was built to infer the mean population density of the species that lack global population reports (*SI Appendix, Inferring the biomass of wild land mammal species lacking population reports*). In order to arrive at the total biomass for each of the species that lack global population reports, we multiplied the inferred population density of each species by its range size and mean body mass.

Six parameters suspected to affect population density or sizes were analyzed and considered as predictors: range size, body mass, Red List category, taxonomic order, trophic level, and generation time (26, 28, 29). All of those, except for generation time, were found relevant based on the model fit (*SI Appendix*, Table S3).

Due to the special attention given to highly visible and threatened species, our global population abundance dataset tends to focus more on large-bodied species at greater risk of extinction, or species with a small range compared to the species where no global abundance data is available. We anticipated

that data scarcity might pose a problem when trying to infer the abundances of species which are not at risk, have small body sizes, or have large ranges. Using IUCN categories, which classify species according to the risk of global extinction as a model predictor, could help reduce some of the bias of estimating total abundances of species at different levels of risk of extinction, but does not fully account for a potential bias for small-bodied mammals with large ranges (*SI Appendix,* Fig. S1). Therefore, we opted for a simpler model when inferring the global biomass of small-bodied mammals (<1 kg): A Support Vector Regression model identical to the one described above, except that one of the input parameters, range size, was removed. A sensitivity analysis was performed on the 1-kg threshold (*SI Appendix*).

Due to the limited amount of training data (392 species), both models were crossvalidated using random resampling of training and testing data (10% of the data were used for validation in each draw), and each model's root mean square log error (RMSLE, natural log) score is the mean of 1,000 train-test draws. We assessed each model's performance using the RMSLE between the expected mean density and the inferred mean population density. The model that includes the range size feature yielded an RMSLE of ≈ 1.7, whereas the model that does not include the range size feature yielded an RMSLE of ≈ 2.3. We additionally used bootstrapping to determine the CI of each estimate, using random sampling of population abundances for each of the species in the population abundance dataset, for 1,000 model runs.

Log Transformation Correction for Inferred Population Abundances. We back-transformed our model estimates using the unbiased estimator of the mean (30):

$$E(x) = e^{\left(\mu + \frac{\sigma^2}{2}\right)} \quad [\mathbf{1}]$$

with modeled log-transformed mean μ, and SD σ. This assumes that the errors in the population reports are log-normally distributed. The model's RMSLE was used to replace the SD.

Final Biomass Estimate and Uncertainty. The total biomass of wild mammals is the sum of estimated biomass for each mammal species. Population size reports for most species did not report the uncertainty. We therefore analyzed and collected the available uncertainty reports for the species with the largest mass contribution for which CIs were available (*SI Appendix,* Table S2) and found that all of them were smaller than twofold. To be conservative, for each of the species with reported population abundances, we set a 95% CI within an upper and lower bound of twofold above and below the estimated size. Due to lack of better data, we assumed that uncertainties in the population reports are log-normally distributed. For species lacking population reports, we used bootstrapping based on 1,000 runs of our model to establish a 95% CI (see *Inferring the Biomass of Wild Land Mammal Species Lacking Global Population Reports* for a full description of the models). From each distribution, we extracted the mean and random errors (the means and medians of these distributions were almost identical). The uncertainty ranges for the total biomass of wild land and marine mammals were calculated summing the lower or upper bounds of the 95% CIs for each such distribution. We used this sum of bounds of the 95% CIs to account for both random, and possible systematic, errors, as this way of summing includes possible correlations between the underlying statistical errors.

Estimating the Mean Body Mass of Wild Mammal Species. To estimate the mean wet body mass of each wild land mammal species, we estimated the fraction of nonadult individuals using the mean fraction of nonadult individuals in a set of wild land mammal species for which data were available (*SI Appendix*), arriving at $\approx 40\%$ of non-adult individuals and $\approx 60\%$ adult individuals as a characteristic depiction of wild land mammal species. We then estimated the mean body mass of each wild land mammal species using:

$$\text{mean body mass} = 0.6 \times \text{adult body mass} + 0.4 \times \left(\frac{\text{adult body mass}}{2}\right) \quad [\mathbf{2}]$$

Due to interannual and seasonal variability, it is challenging to estimate the average body mass of a nonadult individual. We therefore assume that nonadults weigh one-half as much as an average adult. Adult body mass data were taken from the PanTHERIA database (31). To estimate the total biomass of wild marine mammals, we multiplied the population estimates obtained from the IUCN website by the mean body mass of wild marine mammal species (32), as described in the results section.

Mammal Ranges. The IUCN database contains, for each wild mammal species, geographic polygons describing the known Extent of Occurrences (EOO), denoting the area with the shortest continuous boundary that includes all the occurrences of a species. A more precise estimate for a species range size would be its Areas of Occupancy (AOO), the area within the EOO actually occupied by a species. Estimating AOOs, however, is extremely sensitive to sampling effort and can be successfully achieved only for a small subset of the best-studied species–or for species known from a tiny range only. To get an approximation of the AOO, we cropped EOO polygons to only contain suitable habitats for each species to obtain Extent of Suitable Habitat (ESH) maps (33).

To create these modified ranges, we used two additional datasets compiled by the IUCN. The first is a gridded (raster) dataset containing a global map of habitats (34). This dataset describes the type of habitat for each grid cell, at a fine spatial resolution (≈ 1 km^2 at the equator). The second dataset contains a list of suitable habitats for each vertebrate species (26). Using these datasets, we replaced the EOO polygons with gridded range data. For each species, we found the intersection between its EOO polygon and its suitable habitats, then assigned the output as the species' adapted range. For ≈ 450 out of 4,805 species, the intersection was empty. For those species, $\approx 90\%$ of which have very small ranges (<1,000 km^2), we took the EOO as our ESH estimate. All geographic datasets were projected to the Equal-Area Scalable Earth grid 2.0 projection (35, 36), at a spatial resolution of approximately 12.5 × 12.5 km^2.

Data, Materials, and Software Availability. Code, csv, data have been deposited in GitLab (https://gitlab.com/milo-lab-public/mammal_biomass/) (37).

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