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# Anthropogenic disruptions to longstanding patterns of trophic-size structure in vertebrates

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Diet and body mass are inextricably linked in vertebrates: while herbivores and carnivores have converged on much larger sizes, invertivores and omnivores are, on average, much smaller, leading to a roughly U-shaped relationship between body size and trophic guild. Although this U-shaped trophic-size structure is well documented in extant terrestrial mammals, whether this pattern manifests across diverse vertebrate clades and biomes is unknown. Moreover, emergence of the U-shape over geological time and future persistence are unknown. Here we compiled a comprehensive dataset of diet and body size spanning several vertebrate classes and show that the U-shaped pattern is taxonomically and biogeographically universal in modern vertebrate groups, except for marine mammals and seabirds. We further found that, for terrestrial mammals, this U-shape emerged by the Palaeocene and has thus persisted for at least 66 million years. Yet disruption of this fundamental trophic-size structure in mammals appears likely in the next century, based on projected extinctions. Actions to prevent declines in the largest animals will sustain the functioning of Earth's wild ecosystems and biomass energy distributions that have persisted through deep time.

oth the ecology and evolution of organisms are substantially shaped by diet and body size. Diet constrains the energy that is available for essential processes, such as metabolism and growth. At the same time, body size constrains the types and volumes of food that can be obtained, processed and are required to survive<sup>1</sup>. Together, these two sets of constraints define the classical conception of the ecological 'niche' and form the basis of much of modern ecology (Fig. 1 and Extended Data Table 1). Therefore, diet and body size are inextricably linked across scales, from across an individual's lifespan to macroevolutionary timescales2. Previous studies including different trophic guilds highlighted a fundamental trophic-size structure for modern terrestrial mammals, where invertivores are limited almost exclusively to very small sizes, omnivores occupy small to medium sizes and only specialist carnivores and herbivores attain the largest sizes<sup>2-4</sup>. We found that the highest and lowest trophic levels (herbivores and carnivores) have greater median and maximum body sizes than the intermediate trophic levels (omnivores and invertivores), leading to a relationship that is roughly U-shaped when trophic guilds are ordered along a plant-to-protein dietary gradient (Fig. 1 and Methods). Past literature has sometimes referred to and figured this relationship as V-shaped (for example, Hiiemae et al.<sup>3</sup>). While this relationship is not always symmetrical and depends on the order of trophic guilds applied, for the sake of clarity, brevity and visualization we will refer to this trophic-body size relationship as U-shaped throughout the text.

This U-shaped relationship between body size and trophic status can be explained by multiple physiological constraints and mechanisms (Fig. 1 and Extended Data Table 1). For example, as nutrient concentrations in tissues accumulate with increasing trophic level (from primary producers to carnivores), herbivores must contend with a generally nutrient-poor diet5. Thus, herbivores tend to be large to both (1) allow for increased foraging over a wider home range to maximize the amount of food consumed and (2) accommodate long and/or complex digestive systems that can maximize nutrient extraction (the Jarman-Bell principle<sup>6-8</sup>). Consequently, carnivores must be large enough to traverse the same ranges as their prey and also to take down these larger-bodied herbivores (the Red Queen hypothesis9,10). By contrast, invertivores achieve much smaller sizes by specializing on small protein-rich invertebrates whose abundance, distribution and energy content are insufficient to support larger body masses<sup>10</sup>. In comparison to these specialist dietary strategies, omnivores readily switch between plants and animals depending on availability and therefore face fewer constraints<sup>11</sup>. Still, the relatively high energy requirements of omnivores mean that they must be selective about the nutritional quality of their food-often focusing on smaller but denser diet items, such as seeds, nuts and insects<sup>12</sup>. Given the universality of these shared constraints irrespective of taxa or geography, we expect a consistent U-shaped trophic-size structure across taxonomic, biogeographical and temporal scales within vertebrates.

In this study, we tested the universality of this U-shaped trophic-size structure among vertebrates in the present and, for terrestrial mammals, the consistency across deep time and towards future centuries. We started by examining the robustness of the relationship across extant vertebrate species with available data (5,033 mammals, 8,991 birds, 7,356 reptiles and 2,795 fish). We also

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**Fig. 1** | Observed limits and conceptual mechanisms relating body size to trophic guild across the world's terrestrial mammals. The white boxes indicate maximum body size when including prehistoric and historic extinct species. The grey boxes indicate the potential maximum body size decreases if all IUCN threatened (vulnerable, endangered, critically endangered) species are lost. Mass limits (vertical bars) are based on data from Smith et al.<sup>21</sup>, while the mechanisms (horizontal lines and associated labels) are conceptual and based on the literature (Extended Data Table 1). Silhouettes represent the smallest and largest species for each trophic guild. Icons are all from PhyloPic.org. Creator credits: (top, left to right) US National Park Service; xgirouxb; Xvazquez; Tracy A. Heath; (bottom, left to right) Daniel Jaron; Natasha Vitek; Becky Barnes; Ferran Sayol.

tested whether the abiotic environment interacted with the U-shape since environmental conditions are known to constrain body size (for example, Bergmann's rule<sup>13</sup>), by examining trophic-size structure within and across all global biomes. For the evolutionary past, we investigated the emergence of this trophic-size structure from fossil mammal records (5,427 species, Early Cretaceous to the present). Finally, we examined the future of the U-shape structure by simulating projected mammalian extinctions to determine if recent human-driven changes in extinction bias have the potential to disrupt the existing trophic-size structure.

#### Results

**Taxonomic universality.** In terrestrial mammals, herbivores and carnivores converge on the largest body sizes (for both median and maximum values), while omnivores and invertivores are limited to much smaller sizes, confirming the roughly U-shaped trophic-size structure described previously (Fig. 2a and Pineda-Munoz et al.<sup>4</sup>). Furthermore, this trophic-size structure is nearly universal among other modern vertebrate consumers, including terrestrial birds,

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reptiles and marine fish (Fig. 2c,e,f). The convergence towards this trophic-size structure suggests that its development and generality are robust to the highly variable life histories and evolutionary trajectories of these groups. Even so, we found deviation from this structure in marine birds and marine mammals (Fig. 2b,d), probably due to the additional body size constraints imposed on vertebrates that have evolved secondarily aquatic lifestyles (for example, thermoregulation and lung capacity; see Gearty et al.<sup>14</sup> and Gearty and Payne<sup>15</sup>). Moreover, invertivores in marine groups often achieve much larger sizes due to the exploitation of unique filter-feeding opportunities (for example, bulk plankton feeding) and the fact that the water medium can support much larger weights, making them non-analogous to the terrestrial invertivore guilds<sup>16</sup>.

Biogeographical universality. When we broke down the general patterns by individual biomes, we still consistently found the U-shaped trophic-size structure for extant terrestrial mammals (Fig. 3), birds (Extended Data Fig. 1) and marine fish (Extended Data Fig. 2), despite the varying ecological and evolutionary histories, degrees and types of disturbance and stability, climate, habitat structure and available energy for these systems and discrepancies between dominant taxa. Minor deviations from this trend are evident for the tundra and taiga biomes (herbivore median size was lower than that of omnivores) and the temperate grassland biome (herbivore-omnivore non-significant; further details in the Discussion). Still, changes in the relative frequencies of species per guild across biomes did not appear to generally impact this relationship (Fig. 3). Thus, the near-universality of trophic-size structure across biomes, particularly in terrestrial mammals, suggests that it is fundamental to the structure and ultimately functioning of communities across the planet.

**Temporal universality.** When we extended our analysis in terrestrial mammals over geological timescales, we found that the U-shape developed before the Palaeocene Epoch (and potentially as early as the Early Cretaceous, 145–100.5 million years ago (Ma)) and has persisted for at least the last 66 million years (Fig. 4 and Extended Data Figs. 3–5). Therefore, the development of this trophic-size structure seems to have preceded the establishment of mammals as the dominant terrestrial fauna after the end-Cretaceous mass extinction 66 million years ago, when the largest land animals until then, the dinosaurs, disappeared<sup>17</sup>. Terrestrial mammals reflect this trophic-size structure in most epochs since then (exceptions: herbivore median size lower than that of omnivores in the Oligocene; non-significant trophic-structure during the Pliocene; see Discussion for further details).

Effects of projected extinctions. The U-shaped trophic-size structure has been a feature of terrestrial mammals for millions of years. Yet, we also revealed major disruptions to trophic-size structure. For instance, the median and range of body sizes for herbivores and omnivores (approximately 100-fold) and median body size for carnivores (approximately tenfold), have generally decreased through the Pleistocene and Holocene in parallel with the rise of early humans (Fig. 4), demonstrating a potentially important role for human exploitation and other impacts in altering trophic-size structure<sup>18</sup>. Into the future, we expect continued disruption; indeed, extinction simulations suggest that many large- and medium-sized herbivores are likely to be lost, especially within the next 100-200 years (Fig. 5). These future predicted extinctions (based on current International Union for the Conservation of Nature (IUCN) extinction categorizations) suggest a continued and rapid reduction in herbivore median and maximum body size over the next century further disrupting the U-shaped relationship (Fig. 5). This reduction in mammal body sizes may be at rates even greater than those experienced during

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Fig. 2 | Contemporary global trophic-size structure across taxa. a-f, Body size distributions per trophic guild for 5,033 terrestrial mammal species (a),

the Pleistocene and Holocene extinction events for all trophic guilds and for most continents (Extended Data Fig. 6).

#### Discussion

Taken together, these taxonomic, biogeographical and temporal patterns demonstrate that a combination of evolutionary, physiological and ecological pressures have driven a similar trophic-size structure across nearly all modern vertebrates (Fig. 1 and Extended Data Table 1). While the average and maximum body sizes of terrestrial mammals have indeed increased over the Cenozoic<sup>19-21</sup>, this structure appears to have manifested during the Cretaceous (Fig. 4), before the rapid diversification of mammals that followed the extinction of non-avian dinosaurs<sup>22,23</sup>. The fact that the different trophic guilds consistently maintained their relative body size relationships to one another even when mammals were limited to smaller sizes during the reign of dinosaurs suggests that evolutionary and physiological pressures (Fig. 1) alone cannot explain this pattern. Furthermore, the consistency of this pattern across biomes in multiple classes of modern vertebrates (Fig. 3 and Extended Data

Figs. 1 and 2) suggests that ecological assembly processes and the distribution of niches within local areas play an important role in maintaining this pattern.

Although trophic-size structure is consistent across vertebrates, biomes and epochs, we identified some notable deviations. For instance, secondarily marine mammals and birds do not exhibit the same structure. This can be explained by a combination of strong physiological constraints imposed on 'warm-blooded' species living in the oceans (for example, limited capacity to buffer body temperature), the relaxation of the maximum body size due to living in the aquatic medium (for example, because mass is displaced by water) and the exploitation of unique filter-feeding opportunities where high-quality food is available in large quantities14,15,24,25. In addition, omnivorous mammals in the cold and dry tundra and taiga biomes tend to be larger than omnivores in other biomes, although this difference was not statistically significant (Supplementary Table 1). This is likely due to the seasonality of high-quality plant sources, which constrain omnivores to diets consisting of low-quality plants or vertebrates for much of

118 marine mammal species (b), 8,991 terrestrial bird species (c), 281 marine bird species (d), 7,356 reptile species (e) and 2,795 fish species (f). Trophic guilds are ordered according to a gradient of plant-based to animal-based diets and increasing average trophic level (Methods); labels indicate the number of species per trophic guild. Note that the (log) body size scale is taxonomic group-specific. The asterisks represent P values from pairwise, two-sided Mann-Whitney U-tests (bottom) and 90th quantile two-sided permutation tests (top) after correcting for multiple comparisons (\*P < 0.05, \*\*P < 0.01, \*\*\*P<0.001) and are located between the test pairs (Methods). The box plot elements are as follows: centre line, median; box limits, upper and lower quartiles; whiskers, 1.5x interquartile range. Silhouettes show example species for each taxonomic group. Icons are all from PhyloPic.org. Creator credits: a,b,d,e, Steven Traver; f, Xavier Giroux-Bougard.



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Fig. 3 | Trophic-size structure across global biomes for terrestrial mammals. Body mass distributions (log scale) per trophic guild for 5,033 terrestrial mammal species across biomes. Mammals were assigned to all biomes where they occur. Labels indicate the number of species per trophic guild. Biomes are ordered by their absolute latitudinal distribution. Box plot elements and asterisks as in Fig. 2.

the year<sup>26,27</sup>, tipping them towards strategies that characterize large herbivores and carnivores. The species trophic guild assignments in our database are coded at the global scale, so they might not account for dietary differences or prey switching such as this at the biome level. Therefore, it is also possible that these species are entirely or nearly entirely herbivorous or carnivorous in these biomes; if so, this would explain why they exhibit similar sizes to these other trophic guilds. Furthermore, it is also possible that the small sample sizes of omnivorous species in these biomes (tundra n=7, taiga n=15) might be leading to less accurate results than would be derived from larger sample sizes. Temperate grasslands also show no clear difference between herbivores and omnivores. We attribute this to the loss of many large herbivores across this biome during the late Pleistocene extinctions (for example, several species of mammoth, bison and horses)28,29. Finally, the average invertivore size varies significantly between some biomes (21 of 91 pairwise comparisons; Supplementary Table 1). Eight of these 21 comparisons include the tundra biome, indicating that invertebrate diets in the tundra potentially cannot sustain sizes as large as those in other biomes. For the remainder of these comparisons, we propose that the narrow distribution of invertivore body sizes combined with large sample sizes may be leading to spurious Mann-Whitney U-test results. Outside these differences among invertivores, the distributions (medians and 90th quantiles) of mammal body sizes within trophic guilds are similar between biomes (Supplementary Tables 1 and 2).

While the different trophic guilds have similar distributions during the Cretaceous period, some of their 90th quantiles are statistically different. With larger sample sizes during this period, we expect the differences in medians would become statistically significant. During the Oligocene, omnivores exhibit larger average sizes than herbivores (although not significantly). These results may be related to climatic cooling<sup>30</sup> during this time period, although fossil preservation and sampling biases can lead to unexpected results when examining patterns in the fossil record (Methods and Extended Data Figs. 3–5). However, rather than cause the consistent trophic-size structure we observed, fossil preservation biases are most likely to introduce noise, including through time averaging<sup>31</sup>, and obscure ecological signals (Methods). Despite this and other minor deviations, we observed statistically different 90th quantiles between herbivores and omnivores and between carnivores and insectivores across the entire Cenozoic (66 Ma to the present), indicating that the U-shape is persistent across this era.

Recent and projected future extinctions (Fig. 5) indicate that this longstanding near-universal U-shaped structure may be disrupted by anthropogenic activities. Past downsizing of terrestrial herbivores—driven by the extinction of larger species—has previously altered ecosystems by reducing seed dispersal distances, modifying fire regimes and transforming vegetation structure<sup>32–34</sup>. These ecosystem changes could be exacerbated in the future through predicted extinctions of many of the remaining larger herbivores (Fig. 5); such extinctions may also result in other negative ecosystem changes. For example, large-bodied herbivores exploit large amounts of resources over broad scales, leading to important contributions to nutrient transfer over vast distances<sup>35</sup>. The extinction of these herbivores will likely result in reduced energy transfer and thus reduced ecosystem productivity, degraded ecological interactions and reduced ecosystem resilience to climate change<sup>35,36</sup>. Similar changes are expected

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**Fig. 4 | Trophic-size structure of 5,427 terrestrial mammal species through time.** Body mass distributions (log scale) across trophic guilds for terrestrial mammals since the Early Cretaceous, 145 Ma (Supplementary Table 5). Coloured numbers represent sample sizes corresponding to trophic guilds. Box plot elements and asterisks as in Fig. 2. Silhouettes show example species for each time interval. Icons are all from PhyloPic.org. Creator credits: (left to right) T. Michael Keesey; Scott Hartman; Heinrich Harder; Zimices; Christine Axon; T. Michael Keesey; US National Park Service; Steven Traver; Steven Traver.

to occur in the marine realm due to the loss of marine herbivores, such as a reduction in the capacity of large fish to control algal overgrowth and produce carbonate sediments on coral reefs<sup>37,38</sup>.

At the same time, the introduction and increase in vertebrate livestock (most of which are herbivores) across the globe, in both agricultural and wilderness areas, could further exacerbate these changes through associated overgrazing and indirect effects, such as eutrophication, erosion and increased carbon emissions<sup>39</sup>. Other management actions, such as fencing, may also introduce barriers to dispersal, which will likely alter the biome-level patterns documented in this study<sup>40</sup>. Moreover, livestock are protected (for example, from disease) by and support humans (omnivores) and thus represent a collapsed food web and focused energy transfer.

The projected loss of wild herbivores (Fig. 5) also has the potential to trigger coextinctions of large carnivores, which depend on lower trophic levels to meet their nutritional needs<sup>41,42</sup>. These potential coextinctions are not directly accounted for in our extinction forecast, that is, the IUCN Red List does not directly incorporate prey abundance, and could further disrupt trophic-size structure and compromise ecosystem functioning<sup>43</sup>. Furthermore, the effects of downsizing and coextinctions could be amplified by possible impacts of future climate change on body size that have also been hypothesized to lead to smaller body mass in mammals (for example, Hoy et al.<sup>44</sup>) and ectotherms<sup>45</sup>.

The predicted future decline and extinction of wild mammals described in this study, which is likely underestimated by not including coextinctions, could generate strong ecological and trophic consequences for wilderness areas, comparable to those triggered by past megafaunal extinctions<sup>18,46–49</sup>. Moreover, these changes are currently being seen in marine environments, such as the loss of otters in Pacific kelp ecosystems<sup>37,50</sup>. Thus, fundamental ecological assembly rules that have been in operation since before the beginning of the age of mammals are likely to be disrupted. While we have not examined the same future trajectories for taxa other than mammals due to data limitations, we know that similar extinctions are expected for marine fish, reptiles and birds due to global change drivers, such as habitat loss, over-exploitation, disease and climate change<sup>51</sup>. Thus, we surmise that the shared

**Fig. 5 | Change in mass into the future. a,b**, Percentage change in the median (**a**) and 90th quantile (**b**) of wild terrestrial mammal body mass per trophic guild predicted up to 500 years into the future. The solid bold lines show the mean trajectory and the envelopes show the 95% CIs per year across 10,000 simulations; the dashed lines show the present-day body mass value (median or 90th quantile) for each trophic guild. **c**, Illustration showing examples of large terrestrial mammals lost during the Pleistocene (light shading), those that are forecast to be lost in the future (medium shading; probability of extinction > 50%) and those likely to persist (dark shading; probability of extinction < 20%) (Supplementary Table 6). The smallest mammals of each guild, magnified in the insets, show little change across these intervals. Panel **c** credit: Julius Csotonyi.

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U-shaped trophic-size structure exhibited by these groups (Fig. 1) is also likely to continue to be disrupted in the coming decades, leading to a dramatic global shift in Earth's ecosystem processes not seen in at least 66 million years.

#### Methods

Briefly, we summarized trophic-size structure for mammals through time, with body mass comparisons across four trophic guilds—herbivores, omnivores, invertivores, and carnivores. We assessed the consistency of emergent patterns across biomes and taxa. We compared the rate of extinction in the different trophic guilds through the past and future. We used R v.4.1.0 (ref. <sup>52</sup>) for all our analyses. The R code summarizing the major analytical steps can be accessed at https://github.com/willgearty/Trophic-Extremes.

Consistency of U-shape across taxa. To evaluate the consistency of the U-shape across vertebrate consumers, and across endothermic and ectothermic animals from both marine and terrestrial realms, we undertook global analyses of trophic-size structure for mammals (terrestrial), marine mammals, birds (terrestrial), marine birds, reptiles and fish (Fig. 2) (see below for the data sources). We analysed marine birds and marine mammals separately from their terrestrial relatives due to the different energetic constraints across marine and terrestrial realms14,15. We defined marine birds as those birds that feed at sea, either nearshore or offshore53-the families Alcidae, Anhingidae, Diomedeidae, Fregatidae, Gaviidae, Hydrobatidae, Laridae, Oceanitidae, Pelecanidae, Phaethontidae, Phalacrocoracidae, Podicipedidae, Procellariidae, Spheniscidae, Stercorariidae and Sulidae. We defined marine mammals as those mammals that generally inhabit marine and/or freshwater systems-the families Balaenidae, Balaenopteridae, Cetotheriidae, Delphinidae, Dugongidae, Eschrichtiidae, Iniidae, Kogiidae, Lipotidae, Monodontidae, Odobenidae, Otariidae, Phocidae, Phocoenidae, Platanistidae, Pontoporiidae, Trichechidae and Ziphiidae.

We used the best available diet and body size data for each taxonomic group (we only included species with complete diet and body size data): terrestrial mammals (5,033 species; using a previously collated database<sup>54</sup> and primarily derived from 4 datasets<sup>55–58</sup>), marine mammals (118 species<sup>55–58</sup>), terrestrial birds (8,991 species<sup>54</sup>), marine birds (281 species<sup>54</sup>), reptiles (7,356 species<sup>59</sup>) and fish (2,795 species<sup>60</sup>). For fish, estimates of body mass are scarce, so we used maximum body length, which is a more commonly measured value of body size for fish and is known to scale predictably with size. We classified species into 4 trophic guilds based on diet proportions where available (mammals and birds<sup>57</sup>): herbivores (>50% use of plants, including plant material, fruits, nectar and seeds); invertivores (>50% use of invertebrates); carnivores (>50% use of vertebrates, including endotherms, ectotherms, fish and carrion); and omnivores ( $\leq$ 50% use of plants, invertebrates and vertebrates). We translated the reported diet data for reptiles to match the trophic guilds for mammals and birds; however, this was not possible for fish.

Our trophic guild classification and trophic guild order (herbivore, omnivore, invertivore, carnivore) were selected to characterize a gradient from plant-based to animal-based diets. This plant-animal gradient represents a transition between high carbohydrate and high protein dietary materials<sup>3</sup>; hence, it reflects changes in dietary nutritional content5. In addition, the gradient reflects a general shift in trophic level from primary consumers (that is, herbivores) to secondary and tertiary consumers. This shift in trophic level underpins the separation of invertivores from carnivores. While these two guilds have been combined in other work<sup>2</sup>, this ignores the fact that they have differing average trophic levels, differing ecological roles and differing ecophysiological body size constraints (Tucker and Rogers16; Fig. 1 and Extended Data Table 1). In this study, we used a coarse trophic guild classification, which would inevitably lose some of the finer dietary specialization between species<sup>61</sup> but allowed us to analyse broad patterns in the relationship between body mass and diet across vertebrates<sup>2</sup>. Overall, our trophic guild classification and guild order, which reflects diet nutritional content and the average trophic level of consumers, captures major ecological differences between species and is underpinned by multiple ecophysiological constraints (Fig. 1 and Extended Data Table 1).

We used Mann–Whitney *U*-tests to assess whether pairwise trophic guilds had statistically different body size distributions. We used non-parametric permutation tests to assess whether the 90th quantiles of the body size distributions of pairwise trophic guilds were statistically different. We performed 5,000 random permutations to establish a null distribution of 90th quantile differences, then compared the observed 90th quantile difference to estimate the probability (*P* value) that this difference occurred due to random chance. The *P* values from these two sets of tests have been corrected for multiple tests within each taxonomic group (n = 3) using the Holm method<sup>62</sup> and are displayed in Fig. 2.

**Consistency of U-shape across biomes.** To test for spatial (biogeographical) consistency in the U-shape across biomes with markedly different environmental characteristics, we analysed extant terrestrial mammal (Fig. 3) and extant terrestrial bird (Extended Data Fig. 1) species pools for each terrestrial biome<sup>63</sup>, and extant fish (Extended Data Fig. 2) species pools for each marine biome (Spalding

et al. <sup>64</sup>; although not strictly equivalent, for simplicity, we treated the realms of Spalding et al. <sup>64</sup> as marine biomes). We assigned mammals and birds to all global terrestrial biomes<sup>63</sup> where they occur based on their geographical distributions (only including areas where the species is native or reintroduced) obtained from the IUCN (https://www.iucnredlist.org/resources/spatial-data-download). We assigned fish to global marine biomes<sup>64</sup> where they were surveyed<sup>60</sup>. We performed Mann–Whitney *U*-tests and 90th quantile permutation tests as described above. The resulting *P* values were corrected for the number of pairwise tests across all biomes (n = 42). We also performed similar tests to compare the distributions of mammal body sizes within individual trophic guilds between different biomes (Supplementary Tables 1 and 2). For the permutation tests, we performed 100,000 replicates. The number of replicates was increased in this case (compared to the 5,000 described above) to increase the power of the test after correcting for the large number of pairwise tests performed (n = 364). The resulting *P* values were corrected for the total number of pairwise tests performed (n = 364).

Consistency of U-shape across time. For the temporal analysis, we used body mass and fossil range data previously compiled for 5,236 mammals since the Cretaceous<sup>19,21</sup>. Within this dataset, mammals were classified into one of four trophic guilds: herbivores (primarily browsers or grazers); omnivores (ambiguous or mixed diet); invertivores (exclusively eat invertebrates); and carnivores (primarily meat eaters, excluding insects and earthworms). We supplemented these data by obtaining body size estimates for 191 additional mammals using osteological measurements and allometric equations from the primary literature (Supplementary Tables 3 and 4). Diets for all mammals were based on expert opinions in the Paleobiology Database (https://paleobiodb.org/#/, downloaded on 8 June 2021) using the trophic guild classification scheme outlined above. Fossil ranges for these mammals were also obtained from the Paleobiology Database assuming the oldest possible origination and the youngest possible extinction. We used the first and last fossil appearances of each mammal to code their presence or absence in each epoch from the Early Cretaceous to the Holocene (Fig. 4 and Supplementary Table 5). We performed Mann-Whitney U-tests and 90th quantile permutation tests as described above within each epoch. The resulting P values were corrected for the number of pairwise tests across all epochs (n = 27).

For each trophic guild within each epoch that had at least five species, we performed a bootstrapping approach to assess uncertainty in their body mass distributions. We performed 1,000 bootstraps and calculated the means and s.d. for each bootstrap replicate. The distributions of the means are reported in Extended Data Fig. 3 and the weighted means and s.d. are reported in Extended Data Fig. 4. Finally, we performed a subsampling approach where we took random samples of increasing size from each trophic guild within each epoch. We repeated this 100 times and then calculated the mean and s.d. for each sample (Extended Data Fig. 5).

Potential effects of biases in fossil data. We considered potential biases in the fossil record and how they might affect documented patterns and our interpretation of those patterns. For the purposes of the analyses included in this study, the main issue was the bias against preservation of small-bodied species65. However, live-dead studies have shown that the ecological structures of mammalian communities are retained in death assemblages66 suggesting that the ecological signal is recoverable from fossil data. Regardless, if there were to be such a bias against smaller-sized species in our sampling, invertivores would be preferentially impacted since they tend to be small-bodied (Fig. 2; Smith et al.67). However, even with this potential bias, invertivores were consistently (and statistically) the smallest trophic guild through time (Fig. 4) and would possibly be even smaller on average without this preservation bias. Also, we did not exclude species below a certain size because that would have differentially biased our estimates of the body size distributions of the different trophic guilds since they do not encompass the same body size ranges. Bootstrap and subsetting analyses indicated that the identified patterns are robust (Extended Data Figs. 3-5). Moreover, they suggested that deviations from the overall U-shape in the Oligocene are not statistically significant and may be a result of a low omnivore sample size during this epoch. Importantly, these biases in fossil data should introduce noise into these patterns and are unlikely to cause a U-shaped pattern in body size among trophic guilds.

**Consistency of U-shape in the future.** We simulated yearly future extinction scenarios for 4,804 terrestrial mammal species, that is, those with data available for diet, body mass, generation length<sup>46</sup> and IUCN status, over a 500 year time horizon using the iucn\_sim program v.2.1.1 (Andermann et al.<sup>68</sup>) 10,000 extinction simulations. The iucn\_sim program uses extinction probabilities derived from the IUCN Red List<sup>60</sup> (for example, least concern, near threatened, vulnerable, endangered, critically endangered, extinct/extinct in the wild) to simulate future extinctions<sup>68</sup>. Specifically, the history of the Red List, that is, historic status changes and cumulative amount of time spent in each status, is used to inform potential status transitions away from a species<sup>2</sup> current status (for example, through time<sup>68</sup>. Therefore, historic status changes are assumed to characterize the potential for future status changes. Species<sup>2</sup> generation lengths were used to adjust the time

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frame associated with the transitions<sup>68</sup>. The simulations could then be used to estimate extinction probabilities, based on transitions to the extinct status. For further details of the extinction models see Andermann et al.<sup>68</sup>.

We quantified the median and 90th quantile body mass trajectories using the diet and body mass data for extant terrestrial mammals<sup>24</sup> and the estimated extinction dates generated by iucn\_sim<sup>68</sup>. We calculated the mean and 95% confidence interval (CI) (that is, the 2.5th and 97.5th percentiles) of these two statistics across the 10,000 simulations per trophic guild per year. The median extinction probabilities across all extant mammals are reported in Supplementary Table 6.

**Comparison of U-shape future changes to Pleistocene changes.** We calculated the median body size for each continent before and after the Pleistocene extinctions based on mammal body sizes in the updated MOM database (v10; ref. <sup>21</sup>). We then calculated the median body size for each continent before and after the predicted future extinctions based on extant species (before) and extant species minus species identified as threatened on the IUCN Red List (after), again using the MOM database<sup>21</sup>. The lengths of the continent-specific Pleistocene extinctions were estimated based on Barnosky et al.<sup>29</sup>). The lengths of the predicted future extinctions were set to 500 years to correspond to the projections in Fig. 5. Rates were calculated as the changes in median body size across the extinctions divided by the lengths of the extinctions (Extended Data Fig. 6).

**Reporting Summary.** Further information on research design is available in the Nature Research Reporting Summary linked to this article.

#### **Data availability**

All data are available at https://github.com/willgearty/Trophic-Extremes.

#### Code availability

All code is available at https://github.com/willgearty/Trophic-Extremes.

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#### **Author contributions**

R.C., W.G., A.S.A.C., J.D., G.J.E., J.S.L., G.R., C.R.M., R.D.S.-S., S.K.L. and A.E.B. conceived the project. R.C., W.G., S.K.L., A.E.B., G.J.E., R.D.S.-S., G.R. and J.S.L. contributed the data. R.C., W.G., S.K.L. and A.E.B. developed the methodology and performed the statistical analyses. R.C. and W.G. created the visualizations. A.S.A.C. and A.E.B. acquired the funding for the project. S.K.L. and A.E.B. jointly supervised the project. R.C. and W.G. wrote the original draft of the manuscript. R.C., W.G., A.S.A.C., J.D., G.J.E., J.S.L., G.R., C.R.M., R.D.S.-S., S.K.L. and A.E.B. helped revise the manuscript.

#### **Competing interests**

The authors declare no competing interests.

#### Additional information

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**Extended Data Fig. 1 | Trophic-size structure across global biomes for terrestrial birds.** Body mass distributions per trophic guild for 8,991 terrestrial bird species across biomes. Birds were assigned to all biomes in which they occur. Labels indicate the number of species per boxplot. Biomes are ordered by their absolute latitudinal distribution. Boxplot elements and stars as in Fig. 2.

## **NATURE ECOLOGY & EVOLUTION**



**Extended Data Fig. 2 | Trophic-size structure across global marine biomes for fishes.** Maximum body length distributions per trophic guild for 2,795 fish species across marine biomes. Fishes were assigned to all biomes in which they occur. Labels indicate the number of species per boxplot. Marine biomes are ordered by their absolute latitudinal distribution. Boxplot elements and stars as in Fig. 2.



**Extended Data Fig. 3 | Distributions of bootstrap means of terrestrial mammal body masses by trophic guild since the Early Cretaceous, 145 million years ago.** Each boxplot represents the results of 1,000 bootstrap replicates. Silhouettes show example species for each time interval. Boxplot elements as in Fig. 2. Silhouettes show example species for each time interval. Icons are all from PhyloPic.org. Creator credits: (left to right) T. Michael Keesey; Scott Hartman; Heinrich Harder; Zimices; Christine Axon; T. Michael Keesey; US National Park Service; Steven Traver, Steven Traver.



Extended Data Fig. 4 | Weighted bootstrap means (±1.96 weighted standard deviation) of terrestrial mammal body masses by trophic guild since the Early Cretaceous, 145 million years ago. Silhouettes show example species for each time interval. Icons are all from PhyloPic.org. Creator credits: (left to right) T. Michael Keesey; Scott Hartman; Heinrich Harder; Zimices; Christine Axon; T. Michael Keesey; US National Park Service; Steven Traver, Steven Traver.



**Extended Data Fig. 5 | Distributions of subsample means of terrestrial mammal body masses by trophic guild since the Early Cretaceous, 145 million years ago.** Each boxplot represents the results of 100 subsamples. Each panel indicates the increasing size of the subsamples (indicated by the panel titles). Boxplot elements as in Fig. 2.

• Pleistocene • Future



**Extended Data Fig. 6 | Comparison of effects of predicted future extinctions and observed Pleistocene extinctions on rate of change of median body** size split by trophic guild and continent. Text near points corresponds to the continent names (AF: Africa, AUS: Australia, EA: Eurasia, NA: North America, SA: South America). Pleistocene extinctions are blue, predicted future extinctions are green. Dashed lines indicate 5th and 95th quantile regressions of Pleistocene extinctions.

Trophic Guild	Type of Constraint	Mechanism	References
Herbivores	Minimum Size	Physiology: Need to be big enough to have digestive systems efficient (large) enough to extract enough energy; smallest herbivores are eating fruit or seeds which are energy dense	8
	Promotes Smaller	High quality plant resources (fruit/seeds) are lower in abundance and seasonal	5
	Size	Higher population sizes and lower extinction risk	71
	Promotes Larger Size	Jarman-Bell principle (larger species can survive on lower quality forage)	6,7
		Able to travel farther (and migrate)	72
		Large size is a generally effective strategy for protection against predators	33
	Maximum Size	Lower quality resource availability	12
		Biomechanical (bone density/structure, heart size/circulation, overheating)	73,74
		Plant fermentation efficiency limit	72
Omnivores	Minimum Size	Physiology: High mass-specific metabolism, need very high protein food source	11
	Promotes Smaller Size	Higher population sizes and lower extinction risk	71
	Promotes Larger Size	Larger size leads to lower mass-specific metabolic rate, higher efficiency	10
	Maximum Size	Resource availability: Larger than max size of carnivores (for example, bears) because they can rely on plants when animals are unavailable; smaller than max size of herbivores because they lack the digestive systems required to process bulk energy-poor foods	12
Invertivores	Minimum Size	Physiology: High mass-specific metabolism, need very high protein food source	11
		Need to be larger than their prey	9
	Promotes Smaller Size	Higher population sizes and lower extinction risk	71
	Promotes Larger Size	Larger size leads to lower mass-specific metabolic rate, higher efficiency	10
	Maximum Size	For terrestrial mammalian invertivores, the abundance, distribution and energy content of terrestrial invertebrates are not sufficient to support body masses above 20 kg	10
Carnivores	Minimum Size	Need to be larger than their prey (at least at these sizes)	9
	Promotes Smaller Size	Higher population sizes and lower extinction risk	71
	Promotes Larger Size	Patchiness of food favors fasting and starvation resistance afforded by larger sizes	75
		Larger size leads to lower mass-specific metabolic rate, higher efficiency	10
	Maximum Size	1,100 kg limit due to tradeoff of high hunting costs versus payoff	10

### Extended Data Table 1 | Theoretical mechanisms of body size constraints in vertebrates by trophic guild from the primary literature

# nature portfolio

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# **Reporting Summary**

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	$\square$	A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
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$\boxtimes$		For null hypothesis testing, the test statistic (e.g. <i>F</i> , <i>t</i> , <i>r</i> ) with confidence intervals, effect sizes, degrees of freedom and <i>P</i> value noted Give <i>P</i> values as exact values whenever suitable.
$\boxtimes$		For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
$\boxtimes$		For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
$\boxtimes$		Estimates of effect sizes (e.g. Cohen's d, Pearson's r), indicating how they were calculated
		Our web collection on <u>statistics for biologists</u> contains articles on many of the points above.

## Software and code

Policy information	about <u>availability of computer code</u>
Data collection	Custom R code (version 4.1.0) was used to aggregate previously published data and newly collected data (https://github.com/willgearty/ Trophic-Extremes).
Data analysis	Custom R code (version 4.1.0) was used to analyze aggregated data (https://github.com/willgearty/Trophic-Extremes).

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# Ecological, evolutionary & environmental sciences study design

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Study description	We aggregated previously collected body size and trophic level data for vertebrates. We then assessed patterns between these two attributes across different biomes and vertebrate orders and through time. We then assessed how these patterns would be impacted by projected biased mammalian extinctions.
Research sample	Our dataset covers mammals (5,151 extant and 5,427 extinct species), birds (9,272 extant species), reptiles (7,356 extant species), and fishes (2,795 extant species). All data come from previously published datasets, except for 191 extinct mammal species which were added for this study (see Methods).
Sampling strategy	No sample-size calculations were performed beforehand; we used all of the data that was available. We discuss (for the fossil analyses) how some time intervals may have insufficient sampling.
Data collection	Osteological measurements were collected from literature for 191 extinct mammal species. Allometric equations based on extant species were used to estimate the body mass of these species. Details are available in Supplementary Table 1.
Timing and spatial scale	The extant data are global. The fossil data are global and range from 0 to 145 million years old.
Data exclusions	We did not exclude any available data from our analyses.
Reproducibility	No experiments were conducted for this study.
Randomization	No experiments were conducted for this study.
Blinding	Measurements were taken from previously published literature and blinding was not relevant.
Did the study involve field	d work? 🗌 Yes 🛛 No

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	Animals and other organisms		'	
$\boxtimes$	Human research participants			
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## Palaeontology and Archaeology

Specimen provenance	No new palaeontological specimens were collected for this study.
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No ethical approval or guidance was required.

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