

ECOLOGY

Functional diversity of marine megafauna in the Anthropocene

C. Pimiento^{1,2*}, F. Leprieur^{3,4}, D. Silvestro^{5,6†}, J. S. Lefcheck⁷, C. Albouy⁸, D. B. Rasher⁹, M. Davis^{10,11}, J.-C. Svenning¹⁰, J. N. Griffin¹

Marine megafauna, the largest animals in the oceans, serve key roles in ecosystem functioning. Yet, one-third of these animals are at risk of extinction. To better understand the potential consequences of megafaunal loss, here we quantify their current functional diversity, predict future changes under different extinction scenarios, and introduce a new metric [functionally unique, specialized and endangered (FUSE)] that identifies threatened species of particular importance for functional diversity. Simulated extinction scenarios forecast marked declines in functional richness if current trajectories are maintained during the next century (11% globally; up to 24% regionally), with more marked reductions (48% globally; up to 70% at the poles) beyond random expectations if all threatened species eventually go extinct. Among the megafaunal groups, sharks will incur a disproportionate loss of functional richness. We identify top FUSE species and suggest a renewed focus on these species to preserve the ecosystem functions provided by marine megafauna.

INTRODUCTION

Marine megafauna comprise all large-bodied organisms (body mass, ≥ 45 kg) inhabiting the coastal and open oceans, including bony fishes, elasmobranchs (sharks and rays), mammals (whales, seals, sea cows, and the polar bear), reptiles (sea turtles), a species of sea bird (i.e., the emperor penguin), and a few species of mollusks (clams, squids, and octopuses) (*1*). Megafauna affect ocean ecosystems by (i) consuming large amounts of biomass; (ii) transporting nutrients within and between habitats via excretion; (iii) connecting ocean ecosystems via long-distance migration; and (iv) physically modifying habitats by way of their feeding, locomotion, and mortality (*2, 3*). Moreover, marine megafauna include many charismatic species that are socially, economically, and culturally important (*1*). Despite their immense ecological and societal value, marine megafauna are currently threatened by human exploitation, habitat loss, pollution, and ocean warming, which together have triggered population declines and local extinctions of many species over just the past century (*1, 4–7*).

Scientists have long focused on species diversity as a barometer for ecosystem integrity and the success of conservation initiatives. However, the ecology of a species is not necessarily governed by its nomenclature, but instead by its functional traits (*8*). Traits such as body size, feeding behavior/diet, and mobility broadly determine what, how, and where resources are acquired, consumed, and trans-

ported. In turn, the diversity of traits (functional diversity) in a community dictates the ability of communities to fill diverse niches, assimilate energy, and transfer it within and across ecosystems, and enhance and stabilize ecosystem processes (*8–11*). Furthermore, functional traits differentiate species in terms of how ecologically redundant or unique they are irrespective of taxonomic affiliation (*12*). Hence, measuring functional diversity allows us to generalize the functional contributions of species to ecosystems and contemplate the potential ecological consequences of their extinction.

While terrestrial megafauna suffered widespread anthropogenic extinctions in the prehistoric Late Quaternary (*13*), most marine megafauna survived into historical times (*14, 15*). Yet, in the past few centuries, the industrialization of whaling and fishing led to functional extinctions [i.e., extreme population declines (*6, 16, 17*), local (*18*) and commercial extinctions (*16, 19*)], as well as the global extinction of a few species (*1*). Notwithstanding recovery of several populations following harvest moratoria, overexploitation remains a leading threat to marine megafauna (and indeed many smaller marine taxa). Today, one-third of marine megafaunal species evaluated by the International Union for Conservation of Nature (IUCN) are deemed at risk of extinction based on their rarity, rate of population decline, population size, area of geographic distribution, and degree of population fragmentation (*20*). How the extinction of these species could affect the functional diversity of marine megafauna—and their potential to maintain global ecological processes—has yet to be evaluated.

In theory, megafaunal functional diversity might be resilient to some degree of extinction if remaining species have similar traits (or trait combinations). However, even then, extinctions would reduce the availability of these more similar, relatively “redundant” species increasing ecosystem vulnerability to further losses (*12, 21–24*). The study of past extinction events indicates that marine megafaunal functional diversity is highly sensitive to extinctions at the global scale (*25*). Moreover, regions with lower species richness, such as those near the poles, could prove particularly vulnerable to species losses (*26*) and consequent changes to ecosystem processes (*11*). Given the accelerated rate of extinctions in today’s oceans (*6, 27*), documenting regional and global patterns of functional redundancy

¹Department of Biosciences, Swansea University, Wallace Building, Singleton Park, Swansea SA2 8PP, UK. ²Smithsonian Tropical Research Institute, Box 2072, Balboa, Panama. ³MARBEQ, Université de Montpellier, CNRS, Ifremer, IRD, Montpellier, France. ⁴Institut Universitaire de France (IUF), Paris, France. ⁵Department of Biological and Environmental Sciences, University of Gothenburg and Global Gothenburg Biodiversity Centre, 41319 Gothenburg, Sweden. ⁶Department of Computational Biology, University of Lausanne, Lausanne 1015, Switzerland. ⁷Tennenbaum Marine Observatories Network, MarineGEO, Smithsonian Environmental Research Center, Edgewater, MD 21037, USA. ⁸IFREMER, Unité Ecologie et Modèles pour l’Halieutique, Nantes Cedex 3, France. ⁹Bigelow Laboratory for Ocean Sciences, 60 Bigelow Drive, East Boothbay, ME 04544, USA. ¹⁰Center for Biodiversity Dynamics in a Changing World (BIOCHANGE) and Section for Ecoinformatics and Biodiversity, Department of Biology, Aarhus University, 8000 Aarhus C, Denmark. ¹¹Natural History Museum of Los Angeles County, 900 Exposition Blvd., Los Angeles, CA 90007, USA.

*Corresponding author. Email: c.pimiento@swansea.ac.uk

†Present address: Department of Biology, University of Fribourg (Ch. de Musee 10), 1700 Fribourg, Switzerland.

among the marine megafauna is therefore a crucial step toward predicting the potential impacts of future extinctions on ocean ecosystems and prioritizing species of particular conservation concern.

Here, we combine the functional traits and extinction risk status of each megafaunal species in the ocean to predict the potential functional consequences associated with their extinction and to identify threatened species that contribute disproportionately to functional diversity. To do so, we first compile a species-level trait dataset for all known extant marine megafauna ($n = 334$ species) to characterize the current structure of their functional space. Then, we simulate future extinction scenarios and quantify the impact of potential species losses on megafaunal functional diversity at global and regional scales. Last, we introduce a new index to inform conservation priorities. Our results reveal a diverse range of functional traits exhibited by the global marine megafauna, as well as how the current extinction crisis might affect the functional diversity—with all its associated benefits, both ecological and societal—of this iconic group of animals.

RESULTS AND DISCUSSION

Contemporary patterns of functional diversity

For our analysis, we selected 10 traits that characterize marine megafaunal functional diversity (table S1). We repeated all of our analyses using a subset of traits (herein referred to as “marine-only” traits) to assess how extinctions threaten strictly marine-based ecosystem processes (see Materials and Methods). There is great variation in traits among

extant megafauna, providing evidence for their diverse range of niches (fig. S1A). A principal coordinates analysis (PCoA) revealed that the global marine megafauna can be represented within a reduced six-dimensional trait space (representing 71% of the total inertia; table S2). The first axis of the trait space is strongly related to terrestriality (i.e., the ability to move between marine and terrestrial or riverine realms) and vertical position in the water column (table S2). The mostly fresh water and benthic Julien’s golden carp scored the lowest value along the first axis, and the fully marine and pelagic pygmy right whale scored the highest (Fig. 1A). The second axis of the trait space revealed a strong compartmentalization, with mammals occupying an area separate from that of fishes and sharks. This axis is mostly related to breeding site and thermoregulation (table S2), two traits that separate endothermic mammals, many of which breed on sea ice (e.g., crabeater seal, the lowest value; Fig. 1A), from ectothermic species that breed in coastal environments (e.g., whale shark, the highest value; Fig. 1A). Last, the third axis of the trait space is mostly related to feeding mode (table S2). Accordingly, the filter-feeding fin whale occupies the highest end of this axis, whereas the active predatory butterfly kingfish occupies the lowest end (Fig. 1A). The remaining three axes of the functional space are weakly associated with individual species traits (table S2) and together represented 21% of the total inertia.

Marine mammals span the largest extent of global trait space (25% of the total volume occupied; Fig. 1B) despite the fact that bony fishes have the highest species richness (Fig. 1C). The broader spread of mammalian species in trait space reflects their diverse adaptations

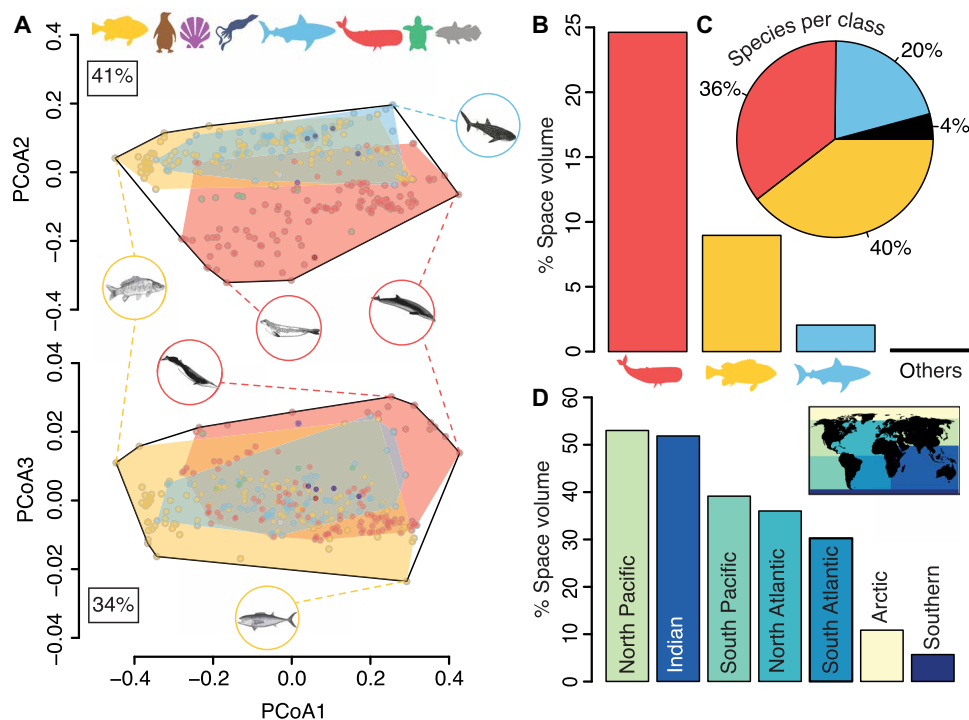


Fig. 1. Composition of marine megafauna in the Anthropocene. (A) Structure of a three-dimensional functional space for the global megafauna. The percentages in the squares denote total inertia represented in the pair of axes of each plot, where PCoA1 independently represents 25%; PCoA2, 16%; and PCoA3, 9%. Colors denote taxonomic class, as provided by animal shapes: yellow, Actinopterygii (bony fish); brown, Aves (sea birds); purple, Bivalvia (giant clam); dark blue, Cephalopoda (squids and octopus); light blue, Elasmobranchii (sharks and rays); red, Mammalia (whales, seals, sea cows, and polar bear); green, Reptilia (sea turtles); gray, Sarcopterygii (coelacanth). (B) Proportional taxonomic richness of main taxonomic classes: bony fishes (yellow), sharks and rays (blue) and mammals (red), and all other groups (black). (C and D) Percentage of the space volume occupied using six dimensions, which altogether represent 71% of the total inertia. (C) Volume occupied by the main taxonomic classes and (D) by the different oceanic regions (ordered by volume). All plots show mean values across 1000 imputations. Error bars are not shown in bar plots as they are negligible (from 0.003 to 0.01).

and ecological habits, including exploitation of the terrestrial realm, a trait also shared with the less speciose sea turtles. The higher contribution of mammals to the trait space is maintained using marine-only traits (mammals: 8%; fish: 7%; sharks: 4%). Endothermy may explain the capacity of marine mammals to exploit a broader range of habitats than ectothermic megafauna (e.g., most fish, invertebrates, most sharks, and sea turtles) (28), including the poles. Marine mammals are the only group to occupy all oceanic regions (fig. S1). Notably, of all regions, the North Pacific and Indian oceans host the most taxonomic groups of marine megafauna and the highest overall taxonomic diversity (fig. S1). Consequently, taxa from these regions span the largest extent of the trait space (54% each; Fig. 1D).

Forecasted changes in functional diversity following potential species loss

To understand the future of marine megafaunal functional diversity, we use a scenario-based approach (29) at global and regional scales. The first scenario (herein referred to as “IUCN 100”) is based on the estimated probability of extinction for each species within 100 years given their current IUCN status (30–32). The second scenario (herein referred to as “IUCN AT”) assumes the extinction of all threatened (IUCN status: vulnerable, endangered, and critically endangered) species (27, 30). While IUCN 100 is a realistic proxy of species extinctions, IUCN AT uses the threatened status as a broad indicator of species’ risk under human pressures and serves to illustrate the collective contribution of threatened species to functional diversity (33). For each scenario ($n = 1000$ iterations; see Materials and Methods), we quantified functional richness (FRic), expressed as the total volume of the trait space occupied (21), and functional uniqueness (FUn), expressed as the overall isolation of a species within the total trait space, which is an indicator of functional redundancy (22).

Under the IUCN 100 scenario, on average, 18% of species are predicted to go extinct within the next 100 years (Fig. 2A), which, in turn, would reduce FRic, on average, by 11% (or by 15% using marine-only traits; Fig. 2B). Such contractions of functional space indicate a marked decline in the variety of ecological functions we will observe in ocean ecosystems. Furthermore, as species go extinct, leaving the remaining species more isolated in trait space, FUn would increase

(i.e., functional redundancy will decline), on average, by 9% over the same time period (Fig. 2C). This loss of species occupying similar functional niches could destabilize ecological processes (23) and leave ecosystems more vulnerable to further species loss as pressures continue to mount over the next century (21). These functional diversity changes reflect the general sensitivity of FRic and—to a lesser degree—FUn to species loss (fig. S2A).

The vulnerability of global functional diversity is more markedly illustrated under the IUCN AT scenario. The loss of 40% of all extant species (Fig. 2A) would cause FRic to contract by 48% (or by 62% when using marine-only traits; Fig. 2B). This loss is 15% greater than expected under random extinction scenarios (Fig. 2B). The loss of FRic is due not only to limited overall functional redundancy but also to the tendency of those species that are going extinct to be more functionally unique (i.e., to lack close neighbors; fig. S2B) under this scenario. Concomitantly, FUn would increase by 16% (Fig. 2C), which is 9% less than expected by chance, indicating that, while overall functional redundancy declines, the extinction of species is not random and particular combinations of traits are selectively lost. Under the IUCN AT scenario, the loss of FRic is greater than the loss of species richness (Fig. 2, A and B) and exceeds observations from marine megafaunal extinction events in the geological past (25). While this scenario represents an extreme, it serves to warn that currently threatened species account for a substantial and larger-than-expected portion of functional diversity. Many of these species already have severely depleted population sizes and distributions. The global extinction of these species would permanently remove almost half of megafaunal FRic from the world’s oceans.

Across both global extinction scenarios, sharks are expected to suffer the largest changes relative to bony fishes and mammals (Fig. 3). It has been shown that sharks are the most threatened marine vertebrate group in the world (7). Under the IUCN 100 scenario, both bony fish and sharks lose, on average, 19% of their species diversity (Fig. 3A), which results in a 15% FRic loss for bony fish and a 44% FRic loss for sharks. The loss of the functional space occupied by sharks under this scenario is 18% higher than expected by chance (Fig. 3B), suggesting that extinction projections for the next century selectively affect shark species holding extreme trait combinations.

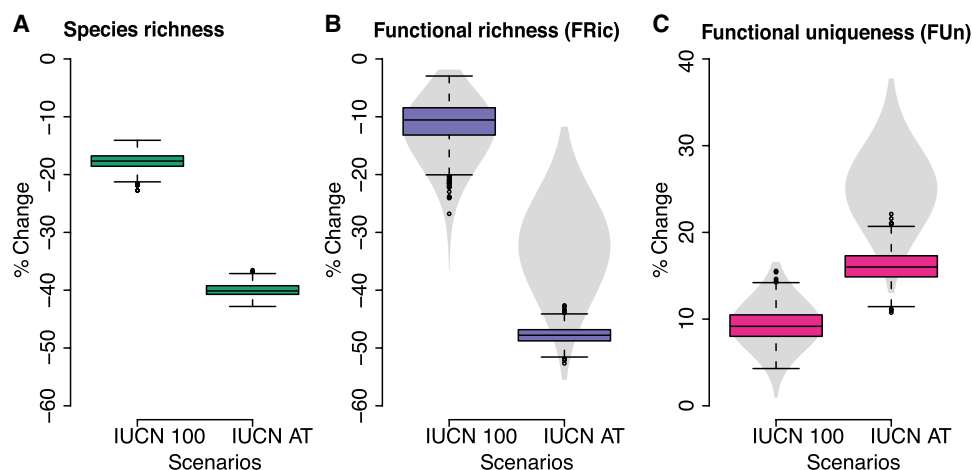


Fig. 2. Forecasted changes in global diversity across extinction scenarios: IUCN 100 and IUCN AT. (A) Proportional changes in species richness. (B) Proportional changes in FRic (% volume of functional space). (C) Proportional changes in FUn (mean distance to five nearest neighbors). Boxplots show values across 1000 imputations. Violin plots show values obtained by randomized species loss. P values for all pairwise comparisons [empirical data (boxplots) versus randomized data (violin plots)] are <0.05 ; $\alpha = 0.05$.

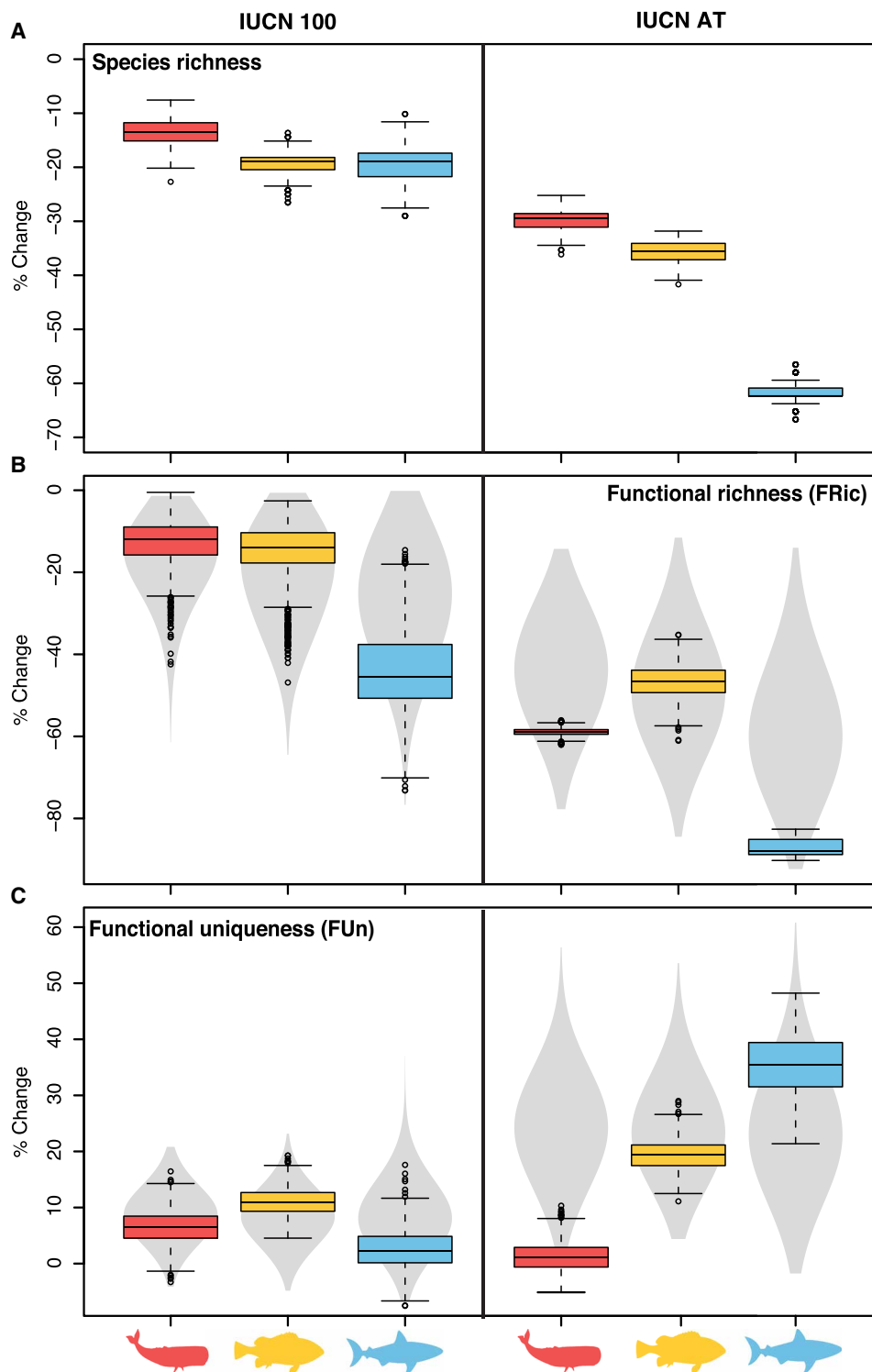


Fig. 3. Global diversity changes in main taxonomic groups. (A) Proportional changes in species richness. (B) Proportional changes in FRic (% volume of functional space). (C) Proportional changes in FU (mean distance to five nearest neighbors). Boxplots show values across 1000 imputations. Violin plots show values obtained by randomized species loss. *P* values for all pairwise comparisons [empirical data (boxplots) versus randomized data (violin plots) and between groups (among boxplots)] are <0.05; $\alpha=0.05$. Colors denote taxonomic class, as provided by animal shapes: yellow, Actinopterygii (bony fish); red, Mammalia (whales, seals, sea cows, and polar bear); blue, Elasmobranchii (sharks and rays).

FUn increases by 11% for bony fish and only by 2% for sharks (Fig. 3C), indicating that despite losing less overall functional volume, bony fish species become more isolated inside the trait space compared with shark species. Under the IUCN AT scenario, 62% of all shark species are predicted to go extinct (Fig. 3A), which would approach levels of a mass extinction (27). Such loss of taxonomic diversity would result in an 87% contraction of shark functional trait space (Fig. 3B) and a 35% increase in FUn (Fig. 3C). These functional changes are 30 and 11% greater (respectively) than expected from random species loss, indicating a highly disproportionate loss of sharks' FRic and redundancy and signifying even worse-than-expected consequences for marine food webs (34).

Regional—or ocean basin—scale forecasts of proportional species loss under the IUCN 100 scenario are generally smaller than those at the global level (maximum = 17% in North Pacific; Fig. 4A), as most regional assemblages are restricted subsets of the larger global species pool. However, the resulting changes in FRic at the regional scale are larger than those at the global scale, between 12% in the North Atlantic and 24% in the South Pacific (Fig. 4B). As at the global level, the remaining species within each region generally become more functionally isolated—particularly in the polar oceans (up to 16% increase in FUn in the Southern Ocean; Fig. 4C). Under the IUCN AT scenario, FRic losses would range between 49% (Southern Ocean) and 70% (Arctic Ocean), surpassing the level of taxonomic loss in all oceans (Fig. 4, A and B). These FRic losses exceed the global estimate and are larger than expected from random species loss (except in the Southern Ocean; Fig. 4B). Furthermore, under the IUCN AT scenario, species become more functionally isolated (i.e., redundancies are lost), as FUn increases between 9% (South Atlantic) and 33% (Southern Ocean; Fig. 3). Therefore, FRic appears even more sensitive to species loss at the regional level than that at the global scale, probably because of lower initial species richness at these smaller scales affording less potential for functional redundancy, evolutionary selection for adapted traits in extreme environments (e.g., the poles), and potentially restricted dispersal among regions due to physiological intolerances (23).

These regional patterns may have serious implications for ecosystem functioning, given that ocean basins are likely the spatial scale at which many megafauna exert their effects on ecosystems. The general relationships between species loss and FRic are more linear at the regional scale than those at the global scale (fig. S2C). The forecasted increases in FUn in the polar oceans—particularly under the IUCN AT extinction scenario—also show that functional redundancies can be rapidly lost in lower-diversity regions, as has been shown for other assemblages (fig. S1) (11). Thus, extinctions at the regional scale push assemblages closer to the exponential phase of the species loss–FUn relationship (fig. S3). Future studies might wish to consider whether these results are consistent at smaller scales when considering local extinctions (24) and how functional diversity is altered by range shifts under climate change (35).

The ecosystem consequences of extinction are determined not only by the loss of functional diversity but also by declines in particular trait modalities (36). Unexpectedly, contrary to previous studies on marine vertebrates [e.g., (37)], neither scenario showed extinction selectivity with respect to body size among these—by definition—large marine megafauna, except within a single class: bony fishes [fig. S4, A and J; see also (38)]. Most other traits showed clear differences in extinction probabilities across modalities (fig. S4). For instance, over the next 100 years, species occupying benthic habitats in the coastal shelf zone and those undertaking movements between

marine and terrestrial realms are particularly vulnerable to extinction (fig. S4, B to F). Under the IUCN AT extinction scenario, ectothermic, nonsocial species and those with specialized diets (i.e., higher-vertebrates and vascular plant feeders; fig. S4, G to I) are also highly vulnerable. Associations between traits and extinction risk arose independently: Functional traits were used to capture the ecological roles of megafauna (table S1), whereas distinct population-level criteria were used to assign species' extinction risk [IUCN status; (20)]. The extinction of realm-crossing megafauna would weaken nutrient transfer, compromising ecosystem diversity, productivity, and stability (39). Furthermore, losses of apex predators and megaherbivores can trigger ecological cascades down- and upward through marine food webs (5). For example, within sharks, the group displaying the highest loss of FRic across extinction scenarios, the highly migratory great white shark and whale shark, are predicted to be lost, along with their impacts as apex predator and giant filter feeder, respectively. Accordingly, extinctions will not only threaten the FRic and redundancy of megafauna—they will also selectively affect trait modalities that strongly influence ecosystem structure and function. Regional-scale extinctions of megafauna have already been found to influence ocean ecosystems. For example, the functional extinction of the sea otter (*Enhydra lutris*) in Southwest Alaska triggered a trophic cascade within nearshore kelp forests, resulting in habitat collapse and the decline of myriad ecosystem processes (5). Likewise, functional extinction of the bumphead parrotfish (*Bolbometopon muricatum*) on Indo-Pacific coral reefs has compromised a key process in the region [i.e., reef bioerosion and sediment transport; (40)]. In both cases, functions carried out by these megafauna were not subsumed by smaller-bodied taxa.

Recent syntheses emphasize that current and projected global species extinction rates in the Anthropocene are at least as great as those of previous mass extinctions (27, 41). Yet, biodiversity is multidimensional, and embracing the functional dimension—as done here—can elucidate the potential ecosystem consequences of species extinctions (21, 25). As emphasized by our results, species loss can drive steep and unanticipated declines in functional diversity, depending on both the underlying functional structure of the community (e.g., degree of redundancy) and the pattern of extinction. Connecting actual and potential species extinctions with functional diversity develops a more complete picture of Earth's changing biodiversity in the Anthropocene.

Contribution of species to functional diversity and conservation priorities

The above-described extinction scenarios underline the vulnerability of marine megafaunal functional diversity across the globe and especially within each ocean basin. We next investigated the contribution of individual species to overall functional diversity to assess which species losses would most rapidly erode the integrity of functional space. We did so by quantifying species' FUn and functional specialization (FSp; i.e., distance of each individual species from the centroid of the global trait space; (21)). It is worth noting that these metrics were quantified treating all traits equally and therefore do not reflect the functional relevance of individual traits (e.g., those related with trophic level).

Species-level FUn and specialization vary among taxonomic groups, with reptiles and mammals having higher FUn and specialization, respectively (fig. S5). Despite the large contributions of marine mammal and sea turtle species to global functional diversity, an array

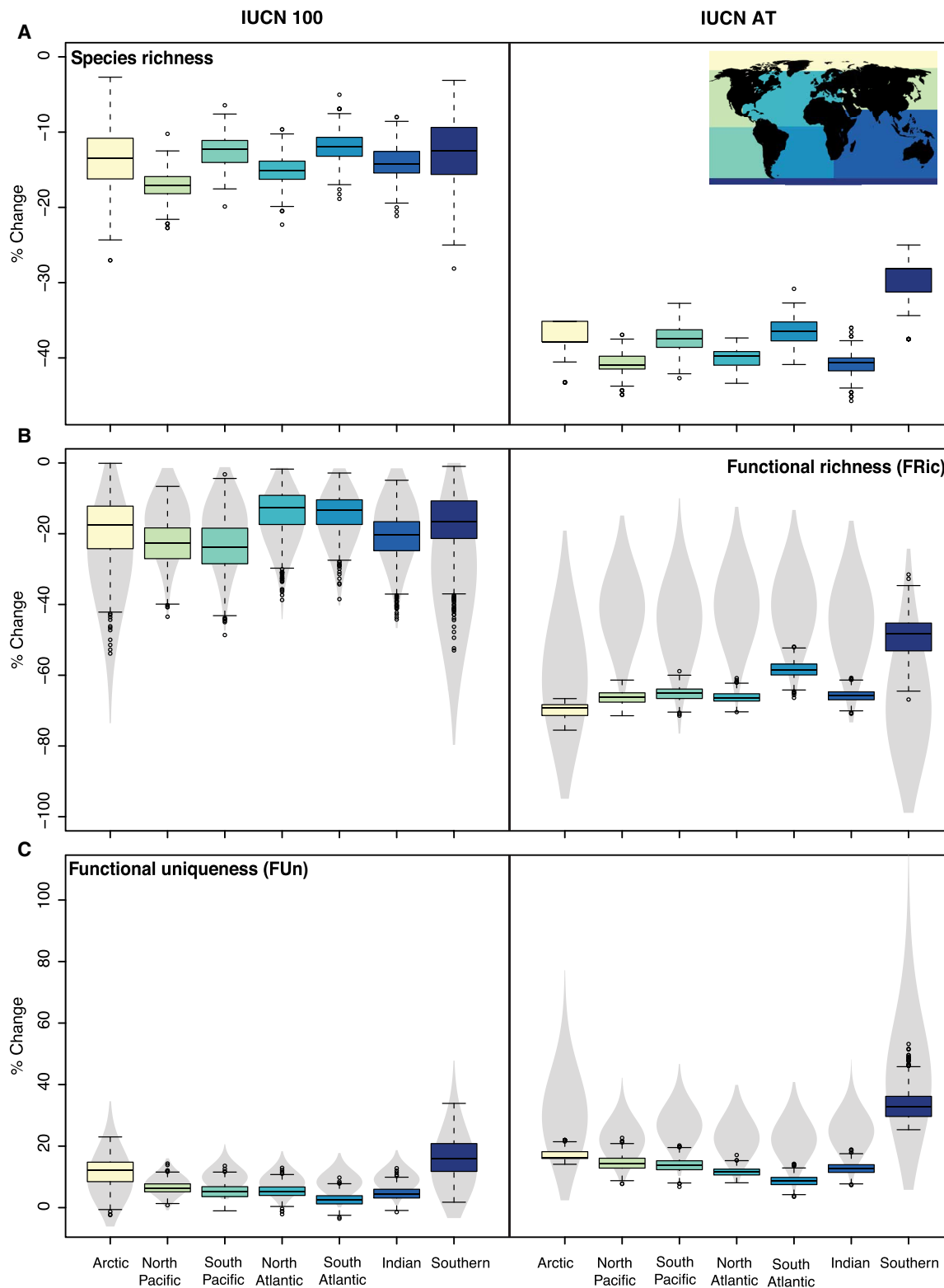


Fig. 4. Regional diversity changes. (A) Proportional changes in species richness. (B) Proportional changes in FRic (% volume of functional space). (C) Proportional changes in FUN (mean distance to five nearest neighbors). Boxplots show values across 1000 imputations. Violin plots show values obtained by randomized species loss. *P* values for all pairwise comparisons [empirical data (boxplots) versus randomized data (violin plots)] are <0.05 ; $\alpha = 0.05$. Colors denote ocean as shown in map in the upper right corner.

of taxonomic groups was among the most important contributors. The dugong, green sea turtle, and giant clam are the three most functionally unique (Fig. 5A), while the crabeater seal, Antarctic fur seal, and Julien's golden carp are the most functionally specialized (Fig. 5B). The uniqueness of the dugong and green sea turtle likely derives from the rarity of benthic herbivores among the marine megafauna (42). Furthermore, the uniqueness of the giant clam probably stems from its planktonic diet and sessile benthic lifestyle (most plankton-feeding megafauna reside in the pelagic zone) (43). The FSp of the crabeater and Antarctic fur seals may relate to their krill-dominated diet via filter feeding (44) and of Julien's golden carp to their omnivorous diet. The use of marine-only traits reveals that the Chilean devil and giant oceanic manta rays (fig. S6) are the most functionally unique and specialized species (respectively) in strictly marine environments. Unlike other species, which are mostly coastal, these species mainly use offshore and continental slope habitats.

To integrate species FUn and specialization in the assessment of marine megafauna conservation priorities, we combined FUn and FSp with IUCN extinction threat status in a new index: FUSE (functionally unique, specialized and endangered). Although high-scoring FUSE species are threatened by extinction, the top FUSE species are not necessarily at the highest level of risk (Fig. 5C) as the index integrates both the vulnerability of a species and the overall distinctiveness of its functional contribution. The green sea turtle, Julien's golden carp, dugong, sea otter, and giant clam have the five highest FUSE scores (Fig. 5C). When only marine traits are considered, the Chilean devil ray, the coelacanth, and the whale shark have the highest FUSE values (fig. S6). As expected, high FUSE scores are associated with traits found to be linked with IUCN status, e.g., body size, reflecting size-biased overharvesting (37), and nonmigration, possibly reflecting the inherent vulnerability of populations with small home ranges such as the sea otter (table S3 and fig. S7, A and B) (45). However, FUSE scores are also related to additional traits, most clearly move-

ment from the sea to land (table S3 and fig. S7C) and, when considering marine traits only, a diet based on high vertebrates, fish, or seagrass (table S3 and fig. S7D). Species that move from marine to terrestrial systems (e.g., sea turtles) or that consume seagrass (e.g., dugong) face not only high levels of human exploitation but also loss or modification of coastal habitats by human development, pollution, and climate change (13). Moreover, species feeding high in the food web compete for prey increasingly depleted by fishing and bycatch (7). Therefore, while direct overharvesting is often cited as the major driver of marine megafauna depletion (6, 46), preserving FUSE species will require conservation initiatives that embrace a broader range of drivers.

The new index (FUSE) that we propose is inspired by previous phylogeny-based metrics used in the EDGE (evolutionarily distinct and globally endangered) program, which identifies threatened species representing unique evolutionary histories (47). The two approaches are complementary, with EDGE aiming to capture a species' contribution to the broad diversity of evolutionarily conserved features and FUSE more directly capturing species' contributions to functional diversity and potentially ecosystem functioning. Because high-scoring EDGE or FUSE species are, by definition, threatened with extinction, many have depleted populations, which may limit their current ecological impacts. Conservation actions that allow high-scoring FUSE species to not only avoid extinction but also undergo population recoveries would restore their unique and specialized functional roles in future oceans. FUSE is a flexible metric, as it that can be applied across different taxa and scales according to particular conservation and management challenges.

CONCLUSIONS

Functional trait analyses have long been used to gauge the consequences of species loss for ecosystem functioning, because traits

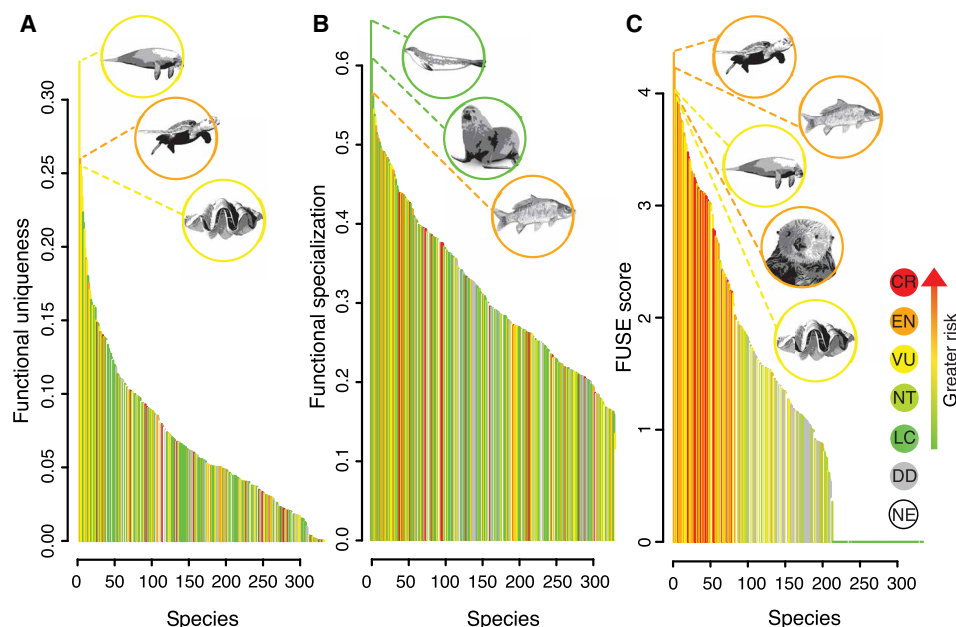


Fig. 5. Species contribution to functional diversity and their current conservation status. Bars represent mean values for each species across all imputations. (A) FUn. Top species: Dugong (*Dugong dugong*), green sea turtle (*Chelonia mydas*) and giant clam (*Tridacna gigas*). (B) FSp. Top species: Crabeater seal (*Lobodon carcinophaga*), Antarctic fur seal (*Arctocephalus gazelle*), and Julien's golden carp (*Probarbus jullieni*). (C) FUSE scores. Top species: Green sea turtle, Julien's golden carp, dugong, sea otter (*E. lutris*), and giant clam. Bar colors represent species' original, nonimputed IUCN status (see Materials and Methods).

better define how organisms interact with their environment and each other than do simple taxonomic measures (48). This trait-based approach may be especially relevant for marine megafauna, which, because of their size and mobility, are difficult to study using traditional experimental approaches (1, 49). Current global marine megafaunal functional diversity is highly influenced by traits associated with cross-realm movements. Consequently, marine mammals—which distinctively exploit the terrestrial realm and occur in all oceanic regions—disproportionately contribute to overall megafaunal functional diversity and include the most functionally unique and specialized species.

Our analyses forecast a marked loss of marine megafauna taxonomic and functional diversity over the next century. Among the different groups, sharks are predicted to be the most affected, with losses of FRic far beyond those expected under random extinctions. Among all megafaunal groups, under a scenario in which all currently threatened species go extinct, almost half of the global FRic (and 70% in the Arctic) would be lost. Again, these forecasted contractions of trait space do not merely reflect the expected decline in functional diversity following species loss but rather are compounded by a disproportionate extinction of functionally unique species. Accordingly, we might expect a worse-than-expected loss of ecological processes associated with these extinctions (1). Such ecological changes are likely to precede global extinction, instead occurring when a species falls to low abundance. Therefore, the disproportionate volume of functional space held by threatened species may already be largely compromised across much of the global oceans. Fortunately, given that only a few species of marine megafauna have been driven to complete extinction (6), rapid efforts to curb overharvesting, climate change, and associated degradation of coastal habitats have the potential to resurrect the diverse functional roles and beneficial effects of many marine megafauna.

On the basis of our findings, we recommend that resource managers and conservation practitioners consider not only the population trends of marine megafauna but also their importance for the maintenance of global functional diversity, as provided by their FUSE scores. This new index is associated with traits beyond those determining species' current IUCN status and is therefore useful in identifying traits and species of special concern. As demonstrated in our analysis of trait drivers of FUSE, conservation efforts to preserve marine megafaunal functional diversity need to consider threats to species' ability to move across ecosystems. The new FUSE index can be applied to diverse taxonomic groups in both terrestrial and marine ecosystems, as the functional roles of species are now being more recognized as pivotal in spatial conservation planning (50).

MATERIALS AND METHODS

All analyses were performed in the R environment (51).

Trait dataset

We gathered a list of 334 marine megafauna species (Supplementary Materials; table S1), as defined (maximum reported size, ≥ 45 kg) and provided by Estes *et al.* (1). A dozen of these species use the marine environment marginally (i.e., brackish waters). We assigned 10 functional traits to each species. These traits were selected to capture the ecological roles of megafaunal species in marine systems (table S1). Trait scores were assigned based mainly on the species information provided by FishBase (www.fishbase.org/) and IUCN

Red List of Threatened Species (www.iucnredlist.org/), as well as on primary literature (Supplementary Materials). In addition to traits, IUCN Red List status was gathered from Estes *et al.* (1) and updated (51 cases) using the IUCN website (last accessed April 2019). All 51 statuses updated progressed to a higher-risk category (e.g., the whale shark, from vulnerable to endangered). On the basis of country-based distribution information provided by FishBase and IUCN, we assigned species to the following oceanic regions: North Pacific, South Pacific, North Atlantic, South Atlantic, Indian, Southern, and Arctic.

Multiple imputations

There were 51 species missing one or more trait scores (Supplementary Materials). We inferred missing scores by performing multiple imputations in which we resampled missing scores value based on the empirical frequency of the trait combinations in each taxonomic order. For example, for a species that lacked trait A but had trait B = 1, we resampled A on the basis of the empirical frequencies of A scores associated with B = 1, where species A and B belong to the same order. This procedure has the benefit of avoiding "impossible" trait combinations, assuming that all possible trait combinations are observed in the set of species. Concurrently, we inferred the IUCN status of the species that were not evaluated (NE) or data deficient (DD) (24 and 48, respectively) by resampling each missing status based on the empirical distribution of the other IUCN status in each order. We ran multiple imputations for traits and IUCN status simultaneously, 1000 times.

Extinction scenarios

Parallel to the multiple imputations, we simulated two extinction scenarios. The first scenario (IUCN 100) was based on the probability of extinction of IUCN categories as in (30–32, 52, 53). We followed Davis *et al.* (31), who converted categorical IUCN ranks into estimates of extinction probability given 100 years of status quo conservation, assuming for simplicity that species populations followed exponential decay. These extinction probabilities are likely conservative as they predict fewer species going extinct than actual status changes would suggest (54). Thus, under IUCN 100, the status of species (extinct or extant) was assigned on the basis of the extinction probability of the respective IUCN category. For example, because VU (IUCN status = Vulnerable) species are estimated to have at least 10% probability of going extinct in the next 100 years (30, 32, 52), in our 1000 iterations (see above), we randomly assigned, on average, 10% of VU species as extinct. The second scenario (IUCN AT) assumes the extinction of all currently threatened species (27) with the objective of illustrating their collective contribution functional diversity (33). Therefore, under IUCN AT, we assigned all threatened species as extinct in all iterations. It is worth noting that even though there is no variation in the status of species (extinct or extant) under IUCN AT, there is a range of species loss produced by the NE and DD imputations (see above). All the following analyses are based on the iterations from multiple imputations and extinction scenarios, which were run simultaneously (total: 1000).

Generalized linear models

We used a binomial generalized linear models (GLM) to explore how species extinction probabilities (averaged over all iterations) are associated with their traits. A linear mixed model (LMM), considering taxonomic order as a random effect, was also used to evaluate how species' traits are associated with their IUCN status [modeled as a

continuous variable: LC (Least Concern) = 0; NT (Near Threatened) = 1; VU (Vulnerable) = 2; EN (Endangered) = 3; and CR (Critically Endangered) = 4].

Functional diversity analyses

For each iteration (see above), we calculated the FRic to evaluate the changes of the overall functional volume, FUn to quantify the changes in the interior of the functional space, and FSp to identify species contributing the most to FRic. We first created a species trait distance matrix using a modified version of Gower's distance ("dist.ktab" function of the ade4 package), which allows the treatment of various types of variables (see table S1), e.g., quantitative, ordinal, nominal, multichoice nominal, binary (55). From this functional dissimilarity matrix, we then built a multidimensional Euclidean space based on a PCoA (56). We retrieved the PCoA axes using the "dudi.pco" function of the ade4 package. Using the method proposed by Maire *et al.* (56), we determined that the marine megafaunal functional space is best represented by seven dimensions (i.e., lowest mean squared deviation between the initial trait distance and standardized distance in the functional space given by the PCoA). However, we built our space using six dimensions because (i) the difference between mean squared deviations of a seven-dimensional space and a six-dimensional space was negligible (i.e., 0.0001), and (ii) 71.15% of the total inertia is represented in the first six axes. We assessed the relationship between axes and traits using a linear model (table S2).

On the basis of the multidimensional trait space, we calculated FRic, which measures the volume of functional space occupied, i.e., the convex hull volume whose vertices are delimited by the species at the edge of multidimensional trait space (and therefore, those farthest away from the center of the space) (57), capturing the whole range of species' functional strategies (58). For each extinction scenario, we calculated the FRic of the main three main megafaunal taxonomic classes (mammals, fish, and sharks) and oceans as the proportional convex hull volume occupied relative to the current global assemblage (where the current global assemblage is 100% of the trait space volume; FRic = 1). FUn *sensu* (21) measures the level of isolation of each species inside the functional space, which allows quantifying the level of species' uniqueness or redundancy (24). For each extinction scenario, and as in (59), we calculated mean FUn considering the five nearest neighbors (but see complementary analyses below). Last, we calculated FSp as the Euclidean distance of each species to the center of the multidimensional trait space (21), which allows distinguishing between those close to the center of the space (displaying average trait combinations, or generalists) and those near the edges of the space (displaying extreme trait combinations, or specialists). FSp was calculated only at the species level and not per scenario. FUn and FSp calculations were based on the current global trait distance matrix. Differences between mean FUn and FSp per taxonomic group were statistically compared using a Mann-Whitney-Wilcoxon test.

Random simulations

We performed three sets of random simulations. (i) We simulated the two extinction scenarios explained above, but the identity of species going extinct was randomized to test whether observed losses were more extreme than expected purely by chance. For each randomized extinction scenario, we calculated FRic and FUn and statistically compared the results against what we obtained empirically using a Wilcoxon signed-rank test because the data were not normally distributed (Shapiro-Wilk normality test, $P < 0.05$). We re-

peated these simulations per taxonomic group and per region. (ii) We calculated FUn separately for extinct and extant species across extinction scenarios (fig. S2B) using the 1000 resampled datasets described above. We computed the frequency of $FUn(\text{extant}) > FUn(\text{extinct})$ to assess whether the uniqueness of extinct and extant species was significantly different. (iii) We simulated changes in FRic and FUn by randomizing a sequence of species loss, from 10 to the total number of species (334), 1000 times each for both the global and the regional assemblages.

FUSE index

We introduced an index that combines the uniqueness and specialization of each individual species within the global assemblage, and their extinction risk, FUSE, which aims to inform conservation prioritization by linking traditional extinction threat measures with species' contribution to functional diversity. FUSE consists in adding the product between species' uniqueness and specialization scores (47) and their IUCN Red List status as follows

$$FUSE = FUGE + FSGE \quad (1)$$

where

$$FUGE = \ln(1 + (FUn \times GE)) \quad (2)$$

and

$$FSGE = \ln(1 + (FSp \times GE)) \quad (3)$$

FUn and FSp are the standardized FUn and FSp, respectively, multiplied by 4. GE is the IUCN scores, from LC = 0 to CR = 4 (see above). We used an LMM implemented in lme4 (60) to explore how species' FUSE scores are associated with their traits, accounting for taxonomic order as a random effect.

The FUSE index must be interpreted as a relative measure. A species having a high FUSE score indicates that it is highly threatened globally, and simultaneously, that it displays more extreme and unique combination of traits. This implies that there are none or just a few species at the global scale that could play a similar functional role in case of extinction. Nevertheless, FUSE scores can also be calculated at smaller spatial scales (i.e., considering different species-pool sizes) according to the goal of the study. For example, a given species can be both more threatened and more functionally unique or specialized at the regional scale than at the global scale because of local threats and/or the absence of functionally similar species. Last, FUSE is a dynamic measure that would change as species' IUCN statuses are updated.

Complementary analyses

We conducted two sets of complementary analysis. (i) We limited the traits used to those exclusively containing marine modalities (i.e., excluding terrestriality, breeding site, and migration) because adaptations for cross-realm movements are disproportionately represented within certain taxonomic groups (e.g., pinnipeds) and within species strongly affiliated with coastal habitats (fig. S1). These marine-only analysis reveals how extinctions threaten strictly marine ecosystem functions. There is only a moderate correlation between the values obtained from these two functional spaces (FSp rho = 0.62 and FUn rho = 0.67; fig. S14). Deviation between values varies strongly within taxonomic class (fig. S14). Despite a reordering of the top FUSE species (see main text), overall FUSE values remained fairly

robust, with a high correlation between the values obtained from the two spaces ($\rho = 0.92$; fig. S14). Using marine-only traits, mammals occupied the largest percentage of the functional space (8%), followed by fish (7%) and sharks (4%). (ii) Because we calculated FUn as the mean distance of each species to five nearest neighbors, we reanalyzed our data varying the number of neighbors to test how the selected number of neighbors influenced our FUn results. We found that the identity of the three most functionally unique species remains unchanged when estimating it based on 1, 3, or 10 neighbors (fig. S6). There is a strong correlation between FUn using five neighbors and using 1 ($\rho = 0.84$), 3 ($\rho = 0.98$), and 10 ($\rho = 0.97$; fig. S15). Overall, our additional analyses show that our metric for FUn is robust to the number of neighbors used.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at <http://advances.sciencemag.org/cgi/content/full/6/16/eaay7650/DC1>

REFERENCES AND NOTES

- J. A. Estes, M. Heithaus, D. J. McCauley, D. B. Rasher, B. Worm, Megafaunal impacts on structure and function of ocean ecosystems. *Annu. Rev. Env. Resour.* **41**, 83–116 (2016).
- C. E. Doughty, J. Roman, S. Faurby, A. Wolf, A. Haque, E. S. Bakker, Y. Malhi, J. B. Dunning Jr., J.-C. Svenning, Global nutrient transport in a world of giants. *Proc. Natl. Acad. Sci. U.S.A.* **113**, 868–873 (2016).
- N. Hammerschlag, O. J. Schmitz, A. S. Flecker, K. D. Lafferty, A. Sih, T. B. Atwood, A. J. Gallagher, D. J. Irschick, R. Skubel, S. J. Cooke, Ecosystem function and services of aquatic predators in the anthropocene. *Trends Ecol. Evol.* **34**, 369–383 (2019).
- J. A. Estes, A. Burdin, D. F. Doak, Sea otters, kelp forests, and the extinction of Steller's sea cow. *Proc. Natl. Acad. Sci. U.S.A.* **113**, 880–885 (2016).
- J. A. Estes, J. Terborgh, J. S. Brashares, M. E. Power, J. Berger, W. J. Bond, S. R. Carpenter, T. E. Essington, R. D. Holt, J. B. C. Jackson, R. J. Marquis, L. Oksanen, T. Oksanen, R. T. Paine, E. K. Pikitch, W. J. Ripple, S. A. Sandin, M. Scheffer, T. W. Schoener, J. B. Shurin, A. R. E. Sinclair, M. E. Soulé, R. Virtanen, D. A. Wardle, Trophic downgrading of planet Earth. *Science* **333**, 301–306 (2011).
- D. J. McCauley, M. L. Pinsky, S. R. Palumbi, J. A. Estes, F. H. Joyce, R. R. Warner, Marine defaunation: Animal loss in the global ocean. *Science* **347**, 1255641–1255641 (2015).
- N. K. Dulvy, S. L. Fowler, J. A. Musick, R. D. Cavanagh, P. M. Kyne, L. R. Harrison, J. K. Carlson, L. N. K. Davidson, S. V. Fordham, M. P. Francis, C. M. Pollock, C. A. Simpfendorfer, G. H. Burgess, K. E. Carpenter, L. J. V. Compagno, D. A. Ebert, C. Gibson, M. R. Heupel, S. R. Livingstone, J. C. Sanciangco, J. D. Stevens, S. Valenti, W. T. White, Extinction risk and conservation of the world's sharks and rays. *eLife* **3**, e00590 (2014).
- J. S. Lefcheck, J. E. Duffy, Multitrophic functional diversity predicts ecosystem functioning in experimental assemblages of estuarine consumers. *Ecology* **96**, 2973–2983 (2015).
- V. Gagic, I. Bartomeus, T. Jonsson, A. Taylor, C. Winqvist, C. Fischer, E. M. Slade, I. Steffan-Dewenter, M. Emmerson, S. G. Potts, T. Tschirntke, W. Weisser, R. Bommarco, Functional identity and diversity of animals predict ecosystem functioning better than species-based indices. *Proc. R. Soc. B. Biol. Sci.* **282**, 20142620 (2015).
- L. E. Dee, S. J. Miller, L. E. Peavey, D. Bradley, R. R. Gentry, R. Startz, S. D. Gaines, S. E. Lester, Functional diversity of catch mitigates negative effects of temperature variability on fisheries yields. *Proc. Biol. Sci.* **283**, 20161435 (2016).
- J. E. Duffy, J. S. Lefcheck, R. D. Stuart-Smith, S. A. Navarrete, G. J. Edgar, Biodiversity enhances reef fish biomass and resistance to climate change. *Proc. Natl. Acad. Sci. U.S.A.* **113**, 6230–6235 (2016).
- D. Mouillot, S. Villéger, V. Parravicini, M. Kulbicki, J. E. Arias-González, M. Bender, P. Chabanet, S. R. Floeter, A. Friedlander, L. Vigliola, D. R. Bellwood, Functional over-redundancy and high functional vulnerability in global fish faunas on tropical reefs. *Proc. Natl. Acad. Sci. U.S.A.* **111**, 13757–13762 (2014).
- Y. Malhi, C. E. Doughty, M. Galetti, F. A. Smith, J.-C. Svenning, J. W. Terborgh, Megafauna and ecosystem function from the Pleistocene to the Anthropocene. *Proc. Natl. Acad. Sci. U.S.A.* **113**, 838–846 (2016).
- S. T. Turvey, C. L. Risley, Modelling the extinction of Steller's sea cow. *Biol. Lett.* **2**, 94–97 (2006).
- A. S. L. Rodrigues, A. Charpentier, D. Bernal-Casasola, A. Gardeisen, C. Norez, J. A. Pis Millán, K. McGrath, C. F. Speller, Forgotten Mediterranean calving grounds of grey and North Atlantic right whales: Evidence from Roman archaeological records. *Proc. Biol. Sci.* **285**, 20180961 (2018).
- A. M. Springer, J. A. Estes, G. B. van Vliet, T. M. Williams, D. F. Doak, E. M. Danner, K. A. Forney, B. Pfister, Sequential megafaunal collapse in the North Pacific Ocean: An ongoing legacy of industrial whaling? *Proc. Natl. Acad. Sci. U.S.A.* **100**, 12223–12228 (2003).
- R. A. Myers, B. Worm, Rapid worldwide depletion of predatory fish communities. *Nature* **423**, 280–283 (2003).
- B. Worm, D. P. Tittensor, Range contraction in large pelagic predators. *Proc. Natl. Acad. Sci. U.S.A.* **108**, 11942–11947 (2011).
- R. R. Reeves, T. D. Smith, Commercial whaling, especially for gray whales, *Eschrichtius robustus*, and humpback whales, *Megaptera novaeangliae*, at California and Baja California shore stations in the 19th century (1854–1899). *Mar. Fish. Rev.* **72**, 1–25 (2010).
- IUCN, *Red List Categories and Criteria: Version 3.1* (Gland, Switzerland and Cambridge, UK, ed. 2, 2012).
- D. Mouillot, N. A. J. Graham, S. Vileger, N. W. H. Mason, D. R. Bellwood, A functional approach reveals community responses to disturbances. *Trends Ecol. Evol.* **28**, 167–177 (2013).
- D. Mouillot, D. R. Bellwood, C. Baraloto, J. Chave, R. Galzin, M. Harmelin-Vivien, M. Kulbicki, S. Lavergne, S. Lavorel, N. Mouquet, C. E. T. Paine, J. Renaud, W. Thuiller, Rare species support vulnerable functions in high-diversity ecosystems. *PLOS Biol.* **11**, e1001569 (2013).
- F. Micheli, B. S. Halpern, Low functional redundancy in coastal marine assemblages. *Ecol. Lett.* **8**, 391–400 (2005).
- R. P. Leirão, J. Zuanon, S. Villéger, S. E. Williams, C. Baraloto, C. Fortunel, F. P. Mendonça, D. Mouillot, Rare species contribute disproportionately to the functional structure of species assemblages. *Proc. Biol. Sci.* **283**, 20160084 (2016).
- C. Pimiento, J. N. Griffin, C. F. Clements, D. Silvestro, S. Varela, M. D. Uhen, C. Jaramillo, The Pliocene marine megafauna extinction and its impact on functional diversity. *Nat. Ecol. Evol.* **1**, 1100–1106 (2017).
- M. Aberhan, W. Kiessling, Persistent ecological shifts in marine molluscan assemblages across the end-Cretaceous mass extinction. *Proc. Natl. Acad. Sci. U.S.A.* **112**, 7207–7212 (2015).
- A. D. Barnosky, N. Matzke, S. Tomiya, G. O. U. Wogan, B. Swartz, T. B. Quental, C. Marshall, J. L. McGuire, E. L. Lindsey, K. C. Maguire, B. Mersey, E. A. Ferrer, Has the Earth's sixth mass extinction already arrived? *Nature* **471**, 51–57 (2011).
- J. Rolland, D. Silvestro, D. Schluter, A. Guisan, O. Broennimann, N. Salamin, The impact of endothermy on the climatic niche evolution and the distribution of vertebrate diversity. *Nat. Ecol. Evol.* **2**, 459–464 (2018).
- S. Naeem, J. E. Duffy, E. Zavaleta, The functions of biological diversity in an age of extinction. *Science* **336**, 1401–1406 (2012).
- A. Ø. Mooers, D. P. Faith, W. P. Maddison, Converting endangered species categories to probabilities of extinction for phylogenetic conservation prioritization. *PLOS ONE* **3**, e3700 (2008).
- M. Davis, S. Faurby, J.-C. Svenning, Mammal diversity will take millions of years to recover from the current biodiversity crisis. *Proc. Natl. Acad. Sci. U.S.A.* **115**, 11262–11267 (2018).
- D. W. Redding, A. Ø. Mooers, Incorporating evolutionary measures into conservation prioritization. *Conserv. Biol.* **20**, 1670–1678 (2006).
- A. Toussaint, N. Charpin, S. Brosse, S. Villéger, Global functional diversity of freshwater fish is concentrated in the Neotropics while functional vulnerability is widespread. *Sci. Rep.* **6**, 22125 (2016).
- R. A. Myers, J. K. Baum, T. D. Shepherd, S. P. Powers, C. H. Peterson, Cascading effects of the loss of apex predatory sharks from a coastal ocean. *Science* **315**, 1846–1850 (2007).
- M. Barbet-Massin, W. Jetz, The effect of range changes on the functional turnover, structure and diversity of bird assemblages under future climate scenarios. *Glob. Change. Biol.* **21**, 2917–2928 (2015).
- P. L. Thompson, F. Isbell, M. Loreau, M. I. O'Connor, A. Gonzalez, The strength of the biodiversity-ecosystem function relationship depends on spatial scale. *Proc. Biol. Sci.* **285**, 20180038 (2018).
- P. G. Harnik, H. K. Lotze, S. C. Anderson, Z. V. Finkel, S. Finnegan, D. R. Lindberg, L. H. Liow, R. Lockwood, C. R. McClain, J. L. McGuire, A. O'Dea, J. M. Pandolfi, C. Simpson, D. P. Tittensor, Extinctions in ancient and modern seas. *Trends Ecol. Evol.* **27**, 608–617 (2012).
- J. D. Olden, Z. S. Hogan, M. J. Vander Zanden, Small fish, big fish, red fish, blue fish: Size-biased extinction risk of the world's freshwater and marine fishes. *Glob. Ecol. Biogeogr.* **16**, 694–701 (2007).
- N. A. J. Graham, S. K. Wilson, P. Carr, A. S. Hoey, S. Jennings, M. A. MacNeil, Seabirds enhance coral reef productivity and functioning in the absence of invasive rats. *Nature* **559**, 250–253 (2018).
- D. R. Bellwood, A. S. Hoey, T. P. Hughes, Human activity selectively impacts the ecosystem roles of parrotfishes on coral reefs. *Proc. Biol. Sci.* **279**, 1621–1629 (2012).
- G. Ceballos, P. R. Ehrlich, A. D. Barnosky, A. Garcia, R. M. Pringle, T. M. Palmer, Accelerated modern human-induced species losses: Entering the sixth mass extinction. *Sci. Adv.* **1**, e1400253 (2015).

42. J. Wyneken, K. J. Lohmann, J. A. Musick, The biology of sea turtles: volume III, in *Marine Turtle Newsletter* (CRC Press, 2014), vol. 141, pp. 18–19.
43. M. L. Neo, C. C. Wabnitz, R. D. Braley, G. A. Heslinga, F. Cécile, S. Van Wynsberge, A. Serge, C. Waters, A. S. H. Tan, E. D. Gomez, M. J. Costello, P. A. Todd, Giant clams (Bivalvia: Cardiidae: Tridacninae): A comprehensive update of species and their distribution, current threats and conservation status: An annual review. *Oceanogr. Mar. Biol.* **55**, 87–387 (2017).
44. W. F. Perrin, B. Würsig, J. Thewissen, *Encyclopedia of Marine Mammals* (Academic Press, 2009).
45. S. Finnegan, S. C. Anderson, P. G. Harnik, C. Simpson, D. P. Tittensor, J. E. Byrnes, Z. V. Finkel, D. R. Lindberg, L. H. Liow, R. Lockwood, H. K. Lotze, C. R. McClain, J. L. McGuire, A. O'Dea, J. M. Pandolfi, Extinctions. Paleontological baselines for evaluating extinction risk in the modern oceans. *Science* **348**, 567–570 (2015).
46. J. L. Payne, A. M. Bush, N. A. Heim, M. L. Knope, D. J. McCauley, Ecological selectivity of the emerging mass extinction in the oceans. *Science* **353**, 1284–1286 (2016).
47. N. J. B. Isaac, S. T. Turvey, B. Collen, C. Waterman, J. E. M. Baillie, Mammals on the EDGE: Conservation priorities based on threat and phylogeny. *PLOS ONE* **2**, e296 (2007).
48. B. J. McGill, B. J. Enquist, E. Weiher, M. Westoby, Rebuilding community ecology from functional traits. *Trends Ecol. Evol.* **21**, 178–185 (2006).
49. D. C. Tavares, J. F. Moura, E. Acevedo-Trejos, A. Merico, Traits shared by marine megafauna and their relationships with ecosystem functions and services. *Front. Mar. Sci.* **6**, 262 (2019).
50. F. T. Brum, C. H. Graham, G. C. Costa, S. B. Hedges, C. Penone, V. C. Radeloff, C. Rondinini, R. Loyola, A. D. Davidson, Global priorities for conservation across multiple dimensions of mammalian diversity. *Proc. Natl. Acad. Sci. U.S.A.* **114**, 7641–7646 (2017).
51. R Development Core Team. A language and environment for statistical computing (R Foundation for Statistical Computing, Vienna, Austria, 2017).
52. O. Kindvall, U. Gärdenfors, Temporal extrapolation of PVA results in relation to the IUCN Red List criterion E. *Conserv. Biol.* **17**, 316–321 (2003).
53. N. Teichert, M. Lepage, A. Sagouis, A. Borja, G. Chust, M. T. Ferreira, S. Pasquaud, R. Schinegger, P. Segurado, C. Argillier, Functional redundancy and sensitivity of fish assemblages in European rivers, lakes and estuarine ecosystems. *Sci. Rep.* **7**, 17611 (2017).
54. M. Di Marco, L. Boitani, D. Mallon, M. Hoffmann, A. Iacucci, E. Meijaard, P. Visconti, J. Schipper, C. Rondinini, A retrospective evaluation of the global decline of carnivores and ungulates. *Conserv. Biol.* **28**, 1109–1118 (2014).
55. S. Pavoine, J. Vallet, A.-B. Dufour, S. Gachet, H. Daniel, On the challenge of treating various types of variables: Application for improving the measurement of functional diversity. *Oikos* **118**, 391–402 (2009).
56. E. Maire, G. Grenouillet, S. Brosse, S. Villéger, How many dimensions are needed to accurately assess functional diversity? A pragmatic approach for assessing the quality of functional spaces. *Glob. Ecol. Biogeogr.* **24**, 728–740 (2015).
57. S. Villéger, N. W. H. Mason, D. Moullot, New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* **89**, 2290–2301 (2008).
58. W. K. Cornwell, D. W. Schilck, D. D. Ackerly, A trait-based test for habitat filtering: Convex hull volume. *Ecology* **87**, 1465–1471 (2006).
59. M. McWilliam, M. O. Hoogenboom, A. H. Baird, C.-Y. Kuo, J. S. Madin, T. P. Hughes, Biogeographical disparity in the functional diversity and redundancy of corals. *Proc. Natl. Acad. Sci. U.S.A.* **115**, 3084–3089 (2018).
60. D. Bates, M. Mächler, B. Bolker, S. Walker, Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**, 1–48 (2014).
61. S. L. Lewis, M. A. Maslin, Defining the Anthropocene. *Nature* **519**, 171–180 (2015).
62. C. Albouy, V. L. Delattre, B. Mérigot, C. N. Meynard, F. Leprieur, Multifaceted biodiversity hotspots of marine mammals for conservation priorities. *Divers. Distrib.* **23**, 615–626 (2017).
63. L. J. Compagno, V. M. Dando, S. Flower, *Sharks of the World* (Princeton Univ. Press, Princeton, New Jersey, 2005).
64. D. M. P. Jacoby, D. P. Croft, D. W. Sims, Social behaviour in sharks and rays: Analysis, patterns and implications for conservation. *Fish Fish.* **13**, 399–417 (2012).
65. Commission SSGotSS. Review of Migratory Chondrichthyan Fishes. *CMS Technical Series 5* (United Kingdom, 2007).
66. B. A. Block, F. G. Carey, Warm brain and eye temperatures in sharks. *J. Comp. Physiol. B* **156**, 229–236 (1985).
67. F. G. Carey, J. M. Teal, Mako and porbeagle: Warm-bodied sharks. *Comp. Biochem. Physiol.* **28**, 199–204 (1969).
68. D. Bernal, D. Smith, G. Lopez, D. Weitz, T. Grimminger, K. Dickson, J. B. Graham, Comparative studies of high performance swimming in sharks II. Metabolic biochemistry of locomotor and myocardial muscle in endothermic and ectothermic sharks. *J. Exp. Biol.* **206**, 2845–2857 (2003).
69. D. Bernal, C. A. Sepulveda, Evidence for temperature elevation in the aerobic swimming musculature of the common thresher shark, *Alopias vulpinus*. *Copeia* **2005**, 146–151 (2005).
70. D. Bernal, J. M. Donley, R. E. Shadwick, D. A. Syme, Mammal-like muscles power swimming in a cold-water shark. *Nature* **437**, 1349–1352 (2005).
71. D. Bernal, J. K. Carlson, K. J. Goldman, C. G. Lowe, Energetics, metabolism, and endothermy in sharks and rays, in *Biology of sharks and their relatives* (CRC Press, Boca Raton, ed. 2, 2012), pp. 211–237.
72. C. A. Sepulveda, N. C. Wegner, D. Bernal, J. B. Graham, The red muscle morphology of the thresher sharks (family Alopiidae). *J. Exp. Biol.* **208**, 4255–4261 (2005).
73. K. Dickson, J. Graham, Evolution and consequences of endothermy in fishes. *Physiol. Biochem. Zool.* **77**, 998–1018 (2004).
74. B. A. Block, Thermogenesis in muscle. *Annu. Rev. Physiol.* **56**, 535–577 (1994).
75. B. A. Block, J. R. Finnerty, Endothermy in fishes: A phylogenetic analysis of constraints, predispositions, and selection pressures. *Environ. Biol. Fishes* **40**, 283–302 (1994).
76. N. C. Wegner, O. E. Snodgrass, H. Dewar, J. R. Hyde, Whole-body endothermy in a mesopelagic fish, the opah, *Lampris guttatus*. *Science* **348**, 786–789 (2015).
77. F. V. Paladino, M. P. O'Connor, J. R. Spotilla, Metabolism of leatherback turtles, gigantothermy, and thermoregulation of dinosaurs. *Nature* **344**, 858–860 (1990).
78. C. G. Lowe, K. J. Goldman, Thermal and bioenergetics of elasmobranchs: Bridging the gap. *Environ. Biol. Fishes* **60**, 251–266 (2001).
79. J. C. Carrier, J. A. Musick, M. R. Heithaus, *Biology of sharks and their relatives* (CRC Marine Biology Series, 2012).
80. R. L. Alexander, Evidence of a countercurrent heat-exchanger in the ray, *Mobula tarapacana* (Chondrichthyes: Elasmobranchii: Batoidea: Myliobatiformes). *J. Zool.* **237**, 377–384 (1995).
81. R. L. Alexander, Evidence of brain-warming in the mobulid rays, *Mobula tarapacana* and *Manta birostris* (Chondrichthyes: Elasmobranchii: Batoidea: Myliobatiformes). *Zool. J. Linn. Soc.* **118**, 151–164 (1996).
82. S. R. Thorrold, P. Afonso, J. Fontes, C. D. Braun, R. S. Santos, G. B. Skomal, M. L. Berumen, Extreme diving behaviour in devil rays links surface waters and the deep ocean. *Nat. Commun.* **5**, 4274 (2014).
83. M. Thums, M. Meekan, J. Stevens, S. Wilson, J. Polovina, Evidence for behavioural thermoregulation by the world's largest fish. *J. Royal. Soc. Interface* **10**, 20120477 (2013).
84. M. Meekan, L. Fuiman, R. Davis, Y. Berger, M. Thums, Swimming strategy and body plan of the world's largest fish: Implications for foraging efficiency and thermoregulation. *Front. Mar. Sci.* **2**, 64 (2015).
85. Y. Y. Watanabe, K. J. Goldman, J. E. Caselle, D. D. Chapman, Y. Papastamatiou, Comparative analyses of animal-tracking data reveal ecological significance of endothermy in fishes. *Proc. Natl. Acad. Sci. U.S.A.* **112**, 6104–6109 (2015).
86. E. A. Schreiber, J. Burger, *Biology Of Marine Birds* (CRC Press, 2001).
87. R. Froese, D. Pauly, FishBase World Wide Web electronic publication, version (01/2017); www.fishbase.org. [accessed January 2019].
88. E. Paig-Tran, A. Summers, Comparison of the structure and composition of the branchial filters in suspension feeding elasmobranchs. *Anat. Rec.* **297**, 701–715 (2014).
89. A. D. Davidson, A. G. Boyer, H. Kim, S. Pampa-Mansilla, M. J. Hamilton, D. P. Costa, G. Ceballos, J. H. Brown, Drivers and hotspots of extinction risk in marine mammals. *Proc. Natl. Acad. Sci. USA* **109**, 3395–3400 (2012).
90. M. González-Suárez, A. Gómez, E. Revilla, Which intrinsic traits predict vulnerability to extinction depends on the actual threatening processes. *Ecosphere* **4**, 1–16 (2013).
91. R. H. Peters, The ecological implications of body size. *The Ecological Implications of Body Size* (Cambridge Univ. Press, 1983).
92. G. Woodward, B. Ebenman, M. Emmerson, J. M. Montoya, J. M. Olesen, A. Valido, P. H. Warren, Body size in ecological networks. *Trends Ecol. Evol.* **20**, 402–409 (2005).
93. W. B. Vernberg, F. J. Vernberg, *Environmental Physiology of Marine Animals* (Springer Science & Business Media, 2012).
94. S. Bouchard, K. Bjørndal, Sea turtles as biological transporters of nutrients and energy from marine to terrestrial ecosystems. *Ecology* **81**, 2305–2313 (2000).
95. G. A. Polis, F. Sánchez-Piñero, P. T. Stapp, W. B. Anderson, M. D. Rose, in *Food Webs at the Landscape Level* (University of Chicago Press, Chicago, Illinois, USA, 2004), pp. 200–216.
96. S. Bokhorst, P. Convey, R. Aerts, Nitrogen inputs by marine vertebrates drive abundance and richness in antarctic terrestrial ecosystems. *Curr. Biol.* **29**, 1721–1727.e3 (2019).
97. V. Rosset, B. Oertli, Freshwater biodiversity under climate warming pressure: Identifying the winners and losers in temperate standing waterbodies. *Biol. Conserv.* **144**, 2311–2319 (2011).
98. K. L. Laidre, I. Stirling, L. F. Lowry, O. Wiig, M. P. Heide-Jørgensen, S. H. Ferguson, Quantifying the sensitivity of arctic marine mammals to climate-induced habitat change. *Ecol. Appl.* **18**, S97–S125 (2008).
99. R. A. García, M. B. Araújo, N. D. Burgess, W. B. Foden, A. Gutsche, C. Rahbek, M. Cabeza, Matching species traits to projected threats and opportunities from climate change. *J. Biogeogr.* **41**, 724–735 (2014).
100. M. J. A. Christianen, P. M. J. Herman, T. J. Bouma, L. P. M. Lamers, M. M. van Katwijk, T. van der Heide, P. J. Mumby, B. R. Silliman, S. L. Engelhard, M. van de Kerk, W. Kiswara, J. van de Koppel, Habitat collapse due to overgrazing threatens turtle conservation in marine protected areas. *Proc. Biol. Sci.* **281**, 20132890 (2014).
101. F. J. R. Meysman, J. J. Middelburg, C. H. R. Heip, Bioturbation: A fresh look at Darwin's last idea. *Trends Ecol. Evol.* **21**, 688–695 (2006).

102. E. Milner-Gulland, J. M. Fryxell, A. R. Sinclair, *Animal migration: A Synthesis* (Oxford Univ. Press, 2011).
103. G. C. Hays, L. C. Ferreira, A. M. M. Sequeira, M. G. Meekan, C. M. Duarte, H. Bailey, F. Bailleul, W. D. Bowen, M. J. Caley, D. P. Costa, V. M. Eguiluz, S. Fossette, A. S. Friedlaender, N. Gales, A. C. Gleiss, J. Gunn, R. Harcourt, E. L. Hazen, M. R. Heithaus, M. Heupel, K. Holland, M. Horning, I. Jonsen, G. L. Kooyman, C. G. Lowe, P. T. Madsen, H. Marsh, R. A. Phillips, D. Righton, Y. Ropert-Coudert, K. Sato, S. A. Shaffer, C. A. Simpfendorfer, D. W. Sims, G. Skomal, A. Takahashi, P. N. Trathan, M. Wikelski, J. N. Womble, M. Thums, Key questions in marine megafauna movement ecology. *Trends Ecol. Evol.* **31**, 463–475 (2016).
104. K. S. McCann, J. B. Rasmussen, J. Umbanhowar, The dynamics of spatially coupled food webs. *Ecol. Lett.* **8**, 513–523 (2005).
105. J. Terborgh, R. D. Holt, J. A. Estes, Trophic cascades: What they are, how they work, and why they matter. *Trophic cascades: Predators, prey, and the changing dynamics of nature*, J. Terborgh, J. A. Estes, Eds. (Island Press, Washington, DC, 2010), pp. 1–18.
106. B. C. Chessman, Identifying species at risk from climate change: Traits predict the drought vulnerability of freshwater fishes. *Biol. Conserv.* **160**, 40–49 (2013).
107. Y. P. Papastamatiou, B. M. Wetherbee, C. G. Lowe, G. L. Crow, Distribution and diet of four species of carcharhinid shark in the Hawaiian Islands: Evidence for resource partitioning and competitive exclusion. *Mar. Ecol. Prog. Ser.* **320**, 239–251 (2006).
108. M. R. Heithaus, J. J. Vaudo, S. Kreicker, C. A. Layman, M. Krützen, D. A. Burkholder, K. Gastrich, C. Bessey, R. Sarabia, K. Cameron, A. Wirsing, J. A. Thomson, M. M. Dunphy-Daly, Apparent resource partitioning and trophic structure of large-bodied marine predators in a relatively pristine seagrass ecosystem. *Mar. Ecol. Prog. Ser.* **481**, 225–237 (2013).
109. P. Matich, J. S. Ault, R. E. Boucek, D. R. Bryan, K. R. Gastrich, C. L. Harvey, M. R. Heithaus, J. J. Kiszka, V. Paz, J. S. Rehage, A. E. Rosenblatt, Ecological niche partitioning within a large predator guild in a nutrient-limited estuary. *Limnol. Oceanogr.* **62**, 934–953 (2017).
110. K. A. Bjorndal, Foraging ecology and nutrition of sea turtles. *The biology of sea turtles* (CRC Press, Boca Raton, 1997).
111. K. A. Burek, F. M. D. Gulland, T. M. O'Hara, Effects of climate change on Arctic marine mammal health. *Ecol. Appl.* **18**, S126–S134 (2008).
112. F. L. Felleman, J. R. Heimlich-Boran, R. W. Osborne, The feeding ecology of killer whales (*Orcinus orca*) in the Pacific Northwest, in *Dolphin societies. Discoveries and Puzzles*, K. Pryor, K. S. Norris, Eds. (University of California Press, Berkeley, 1991), pp. 113–147.

Acknowledgments: We thank J. Joos for help in collecting the trait data. **Funding:** C.P. was partially funded by the Alexander von Humboldt Foundation and the Federal Ministry for Education and Research (Germany). DS received funding from the Swedish Research Council 23 (2015-04748), the Swedish Foundation for Strategic Research, and the Swiss National Science Foundation (PCEFP3_187012) as a third funder for D.S. J.S.L. was supported by the Michael E. Tennenbaum Secretarial Scholar gift to the Smithsonian Institution. D.B.R. was supported by the NSF (PLR-1316141) and the Bigelow Laboratory for Ocean Sciences. J.-C.S. was supported by the Carlsberg Foundation Semper Ardens project MegaPast2Future (grant CF16-0005) and the VILLUM Investigator project “Biodiversity Dynamics in a Changing World” (grant 16549). This project has received funding from the European Union’s Horizon 2020 research and innovation programme under the Marie Skłodowska-Curie grant agreement no. 663830. **Competing interests:** The authors declare that they have no competing interests. **Author contributions:** C.P. and J.N.G. conceived the study. C.P. and J.N.G. designed the study with contributions from F.L., J.S.L., D.B.R., and J.-C.S. C.P., F.L., and C.A. collected the data. C.P., F.L., D.S., J.N.G., J.S.L., C.A., and M.D. analyzed the data. C.P. and J.N.G. led the writing with input from all authors. **Data and materials availability:** All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials. Additional data related to this paper may be requested from the authors.

Submitted 23 July 2019
Accepted 13 January 2020
Published 17 April 2020
10.1126/sciadv.aay7650

Citation: C. Pimiento, F. Leprieur, D. Silvestro, J. S. Lefcheck, C. Albouy, D. B. Rasher, M. Davis, J.-C. Svenning, J. N. Griffin, Functional diversity of marine megafauna in the Anthropocene. *Sci. Adv.* **6**, eaay7650 (2020).

Functional diversity of marine megafauna in the Anthropocene

C. Pimiento, F. Leprieur, D. Silvestro, J. S. Lefcheck, C. Albouy, D. B. Rasher, M. Davis, J.-C. Svenning and J. N. Griffin

Sci Adv **6** (16), eaay7650.
DOI: 10.1126/sciadv.aay7650

ARTICLE TOOLS <http://advances.sciencemag.org/content/6/16/eaay7650>

SUPPLEMENTARY MATERIALS <http://advances.sciencemag.org/content/suppl/2020/04/13/6.16.eaay7650.DC1>

REFERENCES This article cites 95 articles, 23 of which you can access for free
<http://advances.sciencemag.org/content/6/16/eaay7650#BIBL>

PERMISSIONS <http://www.sciencemag.org/help/reprints-and-permissions>

Use of this article is subject to the [Terms of Service](#)

Science Advances (ISSN 2375-2548) is published by the American Association for the Advancement of Science, 1200 New York Avenue NW, Washington, DC 20005. The title *Science Advances* is a registered trademark of AAAS.

Copyright © 2020 The Authors, some rights reserved; exclusive licensee American Association for the Advancement of Science. No claim to original U.S. Government Works. Distributed under a Creative Commons Attribution NonCommercial License 4.0 (CC BY-NC).