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APPLIED ECOLOGY

A wide megafauna gap undermines China's expanding coastal ecosystem conservation

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To fulfill sustainable development goals, many countries are expanding efforts to conserve ecologically and societally critical coastal ecosystems. Although megafauna profoundly affect the functioning of ecosystems, they are neglected as a key component in the conservation scheme for coastal ecosystems in many geographic contexts. We reveal a rich diversity of extant megafauna associated with all major types of coastal ecosystems in China, including 218 species of mammals, birds, reptiles, cephalopods, and fish across terrestrial and marine environments. However, 44% of these species are globally threatened, and 78% have not yet been assessed in China for extinction risk. More worrisome, 73% of these megafauna have not been designated as nationally protected species, and <10% of their most important habitats are protected. Filling this wide "megafauna gap" in China and globally would be a leading step as humanity strives to thrive with coastal ecosystems.

INTRODUCTION

Conservation of coastal ecosystems plays critical roles in helping achieve many of the United Nations (UN) Sustainable Development Goals (*1*). These goals include zero hunger by supporting fisheries; safe-guarding public health and critical infrastructure through protection from storms; clean water and sanitation by purifying water; climate mitigation through carbon sequestration; and job creation and economic growth through fisheries, ecotourism, and restoration industries. Accordingly, the Kunming-Montreal Global Biodiversity Framework recently agreed upon by 196 countries set goals to protect at least 30% of the world's coastal areas in ecologically representative, well-connected systems and to restore at least 30% of degraded systems by 2030 (the "30 by 30" targets). To help fulfill these ambitious goals, countries are expanding efforts to conserve coastal ecosystems. However, whether these expanding efforts for coastal ecosystem conservation should cover or have well covered megafauna, large animals that profoundly affect the functioning of Earth's ecosystems (*2*), remains largely unknown.

In contrast to fully terrestrial and oceanic ecosystems, megafauna in coastal ecosystems, such as salt marshes and mangrove forests, can, in many geographic contexts, slip through the gaps for policymakers and conservation practitioners because of a lack of megafauna studies (*3*) and because management responsibilities are often organized along artificially constructed ministerial lines (e.g., departments of forestry and departments of oceans) (*4*). Megafauna are often perceived to use coastal areas as marginal habitats only occasionally or intermittently (*5*), making it difficult for scientists and/or the public to connect them with certain nearshore systems (except for some groups, such as sea turtles and seals, that are notable exceptions because they make more predictable and conspicuous visits to coastal habitats). Moreover, coastal ecosystems are often among the world's most densely populated and affected by humans (*6*), with the role of megafauna in coastal ecosystems unrecognized partly because their abundance, behavior, and habitats have been severely altered by human activities in what is a catastrophic example of shifting baselines (*7*–*9*).

Nonetheless, emerging research is revealing that many coastal ecosystems provide essential habitats for megafaunal species (*10*–*12*). For example, after successful population recovery, sea otters have expanded into salt marshes; river otters and alligators have expanded into coastal wetlands; and wolves, bears, and pumas have been sighted foraging along shorelines (*9*). Vegetated coastal wetlands, in particular, provide intermittent but important foraging and/or breeding habitats for at least 174 species of megafauna globally, accounting for over 13% of all extant marine megafauna (*12*). Megafauna, in turn, play important and unique roles in shaping coastal ecosystems and providing valuable ecosystem services where they reach naturally occurring densities (*13*–*15*). For example, high abundance of large predatory sharks and tunas can act as a stabilizing force in coastal fish communities through top-down control (*16*), and whale watching is estimated to generate more than $2.5 billion in yearly tourism revenue worldwide (*17*), providing substantial economic benefits to coastal communities. Despite these indications of their profound ecological and societal value, megafauna face increasing anthropogenic pressures in coastal ecosystems (*18*). However, a collective, quantitative understanding of megafauna assemblages and their conservation status across different types of coastal ecosystems remains largely unavailable, leaving conservation efforts blind to these species and the unique roles they play.

Here, we provide the most comprehensive synthesis to date of megafauna assemblages, their threatened status, and conservation measures for coastal ecosystems spanning a region-wide scale

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using China as a model system. China is an ideal case study for three reasons. First, with an extremely long coastline (over 18,000 km), China contains nearly all temperate and tropical coastal ecosystems found globally (e.g., salt marsh, mangrove, seagrass bed, and coral reef), and each of these systems potentially supports distinct and diverse communities of megafauna. However, the few existing studies in China, as in other countries, have typically focused on a limited number of charismatic species whose ecological functions have largely diminished because of declining populations (e.g., porpoises, dolphins, and dugong) (*19*), neglecting a large component of functionally important species. Second, over the past few decades, China has undergone a rapid shift from a largely inland agrarian society to a coastal industrial economy (*20*), which is representative of many rapidly developing nations characterized by growing populations, urbanization and marked land-use changes, and evolving patterns of resource exploitation. These pressures can lead to habitat loss, overexploitation, coastal pollution, and human-wildlife conflicts. However, the magnitude and relative importance of key threats to megafauna using coastal ecosystems remain unclear. Third, China is increasingly seen as a leader in some of the world's most ambitious and successful projects in ecosystem conservation [e.g., giant panda (*Ailuropoda melanoleuca*) protection and reforestation] (*21*, *22*) and has been rapidly expanding coastal ecosystem conservation, with ~20% of its coastal areas (<50 m depth) already protected by 2020 (*23*). Identifying and overcoming gaps in China's coastal ecosystem conservation are likely to have global implications and further demonstrate leadership as nations seek to meet their "30 by 30" targets.

To assess whether a "megafauna gap" undermines China's expanding coastal ecosystem conservation, we screened and compiled previously reported data from multiple species distribution databases to form a new dataset: "the China Coastal Megafauna dataset" (Materials and Methods). We defined megafauna as those with a maximum body mass no less than 10 kg, to capture a functionally and taxonomically broad range of relatively large animals (see additional discussions in Materials and Methods) (*24*); considered megafaunal species in terrestrial and marine environments; and included mammals, birds, reptiles, cephalopods, and fishes. We considered coastal ecosystems to be those ranging from supratidal to submerged marine neritic zones and grouped these ecosystems into seven main types: mangrove, salt marsh, seagrass/seaweed bed, coral reef, soft sediment, hard bottom, and coastal waters. Using this dataset, we first identified a diverse assemblage of extant megafaunal species associated with different types of coastal ecosystem. Then, we examined the current threatened statuses of each megafaunal species, as well as the major threats facing them, using information reported on the red lists of the International Union for Conservation of Nature (IUCN) and China, where available. Furthermore, we investigated the extent to which megafauna associated with coastal ecosystems are covered by China's existing conservation measures. After highlighting the presence of a wide megafauna gap, we concluded by offering recommendations for addressing this gap to advance coastal ecosystem conservation.

RESULTS AND DISCUSSION

Megafauna are diverse and dependent on coastal ecosystems

We identified a total of 218 extant megafaunal species associated with coastal ecosystems in China (Fig. 1). Of these species, 165, 37, 6, 5, and 5 are fishes, mammals, reptiles, cephalopods, and birds, respectively. The 165 ray-finned and cartilaginous fishes include 96 and 69 species of Actinopterygii and Chondrichthyes,

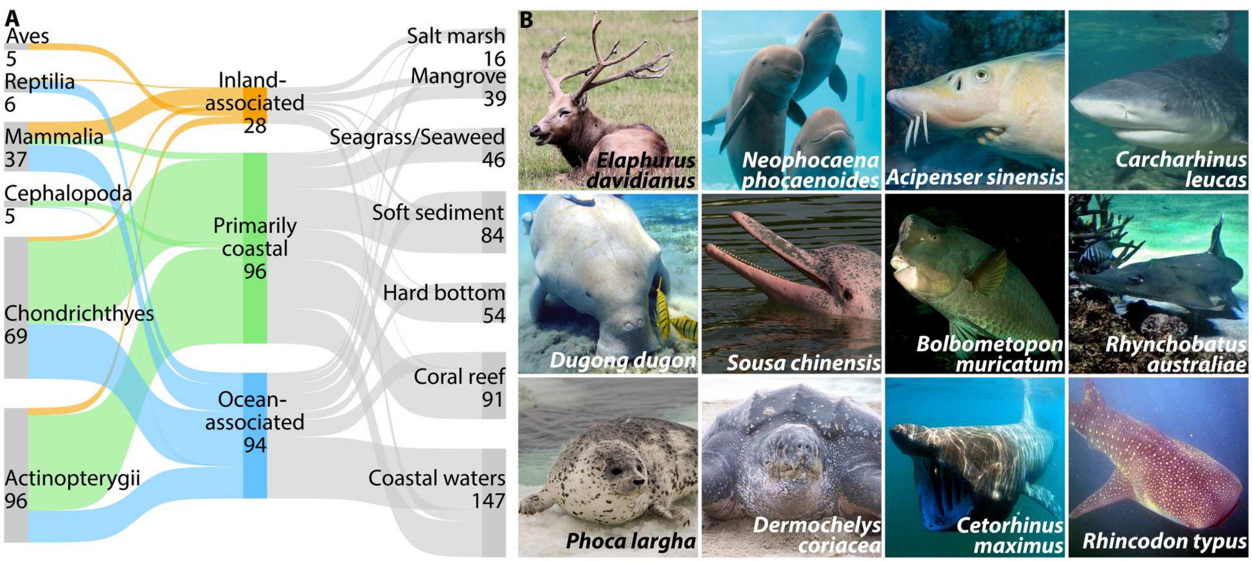

Fig. 1. Many megafaunal species have habitat associations with a variety of coastal ecosystems in China. (**A**) Species richness among taxonomic classes, types of coastal affinity, and associated coastal ecosystems. (**B**) Representative species. Because species often span multiple types of ecosystems, the bar height for types of coastal ecosystem in (A) was rescaled and is not in proportion to that for taxonomic classes. Photo credits (see table S8 for links to licenses): *E. davidianus* (Tim Felce, CC BY-SA 2.0), *Neophocaena phocaenoides* (Huangdan2060, CC BY 3.0), *Acipenser sinensis* (CEphoto, Uwe Aranas, CC BY-SA 3.0), *Carcharhinus leucas* (public domain), *D. dugon* (Julien Willem, GFDL), *S. chinensis* (Chem7, CC BY 2.0), *Bolbometopon muricatum* (Rickard Zerpe, CC BY 2.0), *Rhynchobatus australiae* (rossbennetts, CC BY 2.0), *Phoca largha* (jomilo75, CC BY 2.0), *Dermochelys coriacea* (public domain), *Cetorhinus maximus* (public domain), and *Rhincodon typus* (public domain). Photos were cropped.

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respectively, such as sharks, rays, sturgeons, and tunas. Of all megafaunal species, 42, 8, and 5% have a maximum body mass of no less than 100, 1000, and 10,000 kg, respectively (fig. S1). Megafauna are found along the entire coastline of China, with species richness generally increasing toward lower latitudes but reaching a peak in the Taiwan Strait (Fig. 2). This geographic pattern is mainly attributed to the large variety of marine species using neritic zones and reveals the Strait as a megafauna hot spot.

Most megafaunal species have known habitat associations with multiple ecosystem types. Specifically, according to species' coastal affinity (i.e., whether a species uses inland or oceanic habitats or stays primarily in coastal habitats over their life history), we found that 96 megafaunal species (44%) are primarily coastal dwellers (hereafter, primarily coastal species), including fishes, cephalopods, and two mammals (dugong, *Dugong dugon*; Chinese white dolphin, *Sousa chinensis*). In addition, there are 28 species that use inland habitats (including grassland, forest, and/or freshwater habitats; hereafter, inland-associated species) and 94 species use oceanic habitats (hereafter, ocean-associated species; Fig. 1). Among different types of coastal ecosystems, those defined by structured biogenic habitats including coral reefs, seagrass/seaweed beds, mangrove forests, and salt marshes support a diversity of megafauna (91, 46, 39, and 16 species, respectively; Fig. 1), consistent with studies showing that coastal habitats serve unique functions as nursery areas, refuges, stopovers, and/or foraging sites for such species (*5*, *12*, *25*). Notably, nonvegetated coastal ecosystems such as coastal waters, soft sediments and hard bottoms also support a high diversity of megafauna (147, 84, and 54 species, respectively; Fig. 1). Coastal waters here include multiple separate and mutually exclusive subtypes such as estuaries, coastal lakes/lagoons, and other marine neritic zones (table S1). Furthermore, we found two Chinese endemic species: the Milu deer (*Elaphurus davidianus*) and the Yangtze sturgeon (*Acipenser dabryanus*). Together, these results highlight the importance of coastal ecosystems in China as habitat for megafaunal species.

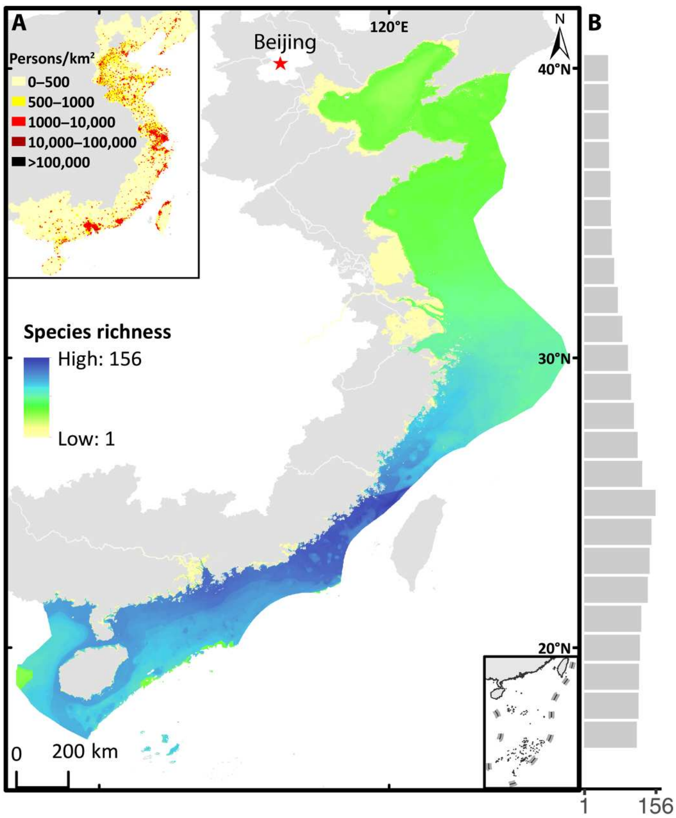

Fig. 2. Species richness of megafauna across China's coast. (**A**) Heatmap of species richness for megafauna associated with China's coastal ecosystems. The inset in (A) illustrates human population density (*59*) in China's coastal provinces in 2020. (**B**) The maximum species richness of megafauna in 1 km–by–1 km grids across latitude. We constrained our analysis to coastal areas ranging from supratidal, intertidal, to submerged marine neritic zones, with elevations between 5 and −200 m, all within mainland China's coastal terrestrial areas and marine areas.

Megafauna in coastal ecosystems are highly threatened

At present, ~44% of these megafaunal species (41 and 47% for lower and upper estimates, respectively) are globally threatened on the basis of the extinction risk assessment by IUCN. We posit that this global-level assessment underestimates the rate megafaunal species are threatened in China for several reasons. First, 78% (170 of 218) of these species are not evaluated or data deficient on China's Red List, most of which are primarily coastal and ocean-associated species (Fig. 3, A and B). Second, the extinction risks for megafaunal species that have been assessed within China, as indicated by Red List categories, are generally skewed worse in China than they are globally ($\chi^2 = 16.02$, df = 1, $P < 0.001$; Fig. 3A). This pattern is consistent among inland-associated ($\chi^2 = 8.52$, df = 1, $P = 0.004$), primarily coastal ($\chi^2 = 4.44$, df = 1, $P = 0.035$), and ocean-associated species ($\chi^2 = 5.73$, df = 1, $P = 0.017$; Fig. 3B).

Analyzing the types of threats to megafauna as reported by IUCN, we found that the average number of threats facing megafaunal species differed among types of coastal affinity ($\chi^2 = 29.32$, df = 2, $P < 0.001$) and taxonomic classes ($\chi^2 = 58.01$, df = 5, $P < 0.001$). The number of threats was significantly higher for inland-associated species than for primarily coastal and ocean-associated species (Fig. 4A) and for Aves, Reptilia, and Mammalia than for Actinopterygii, Chondrichthyes, and Cephalopoda (Fig. 4B). Among different types of threat, direct exploitation is most commonly reported and affects 100% of all megafauna assessed, which corroborates a review of threats to 162 globally threatened megafaunal species (*26*). Habitat disturbance is reported more often for inland-associated (85%) than for primarily coastal (35%) and ocean-associated (28%) species (Fig. 4C). Other pervasive types of threat include pollution (affecting 42, 15, and 21% of inland-associated, primarily coastal, and ocean-associated species, respectively), climate change (affecting 27, 21, and 16% of inland-associated, primarily coastal, and ocean-associated species, respectively), and invasive species and diseases (affecting 15, 1, and 12% of inland-associated, primarily coastal, and ocean-associated species, respectively). Inland-associated species are typically threatened by multiple types of threat, whereas a majority of ocean-associated (64%) and primarily coastal species (56%) are typically threatened by a single type of threat (mostly by fishing; Fig. 4D).

It is highly likely that threats to primarily coastal and ocean-associated megafauna will increase in pace and impact, for several reasons. First, considering that both human populations and corresponding anthropogenic threats are expected to increase with ocean development (*7*), additional types of threats will likely grow to affect

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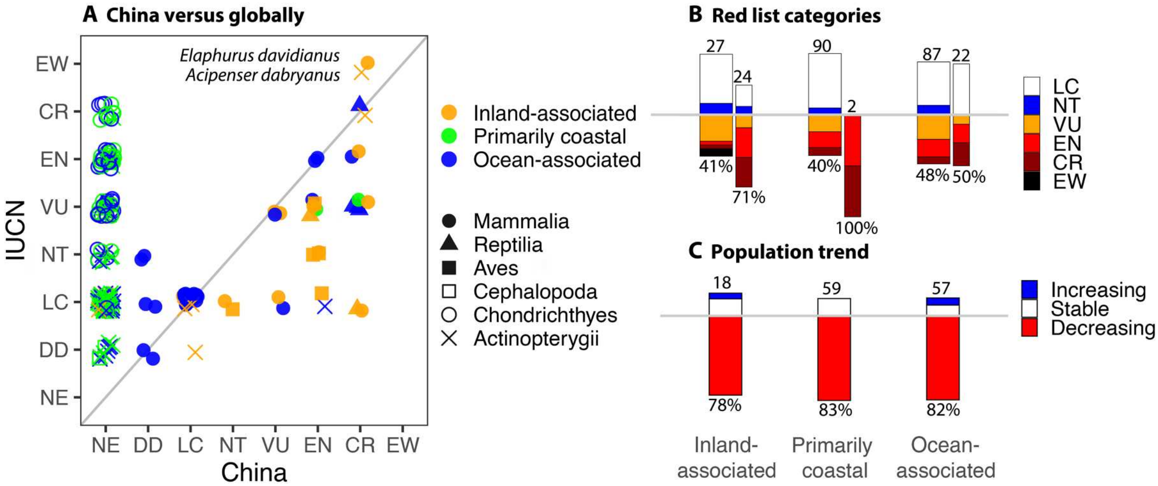

Fig. 3. Threatened status of megafauna. (**A**) Comparison of species extinction risk categories between the red lists of China and IUCN. (**B**) Proportion of species in different extinction risk categories according to the red lists of IUCN (wide bars) and China (narrow bars). (**C**) Proportion of species with population trends reported by IUCN. In (B) and (C), the numbers above each bar represent the total number of species assessed (B and C), the numbers below each bar indicate the percentage of threatened species [including EW (extinct in the wild) species] (B), or the percentage of species with a decreasing population (C), respectively. Categories: EW, CR (critically endangered), EN (endangered), VU (vulnerable), NT (near threatened), LC (least concern), DD (data deficient), and NE (not evaluated).

primarily coastal and ocean-associated megafauna in the future. Second, given the relative difficulty of monitoring species and assessing their threats in inaccessible and expansive coastal marine habitats (*27*), the actual situation for megafauna is likely worse than currently indicated. For example, the indirect impact of bycatch (incidental capture of nontarget species) has increasingly become a major threat to coastal and oceanic species globally (*28*) yet are usually underestimated and underreported in China (*29*). Third, multiple threats increase the likelihood of compounded or synergistic stressors affecting a given species. The synergistic effects of climate change and other human impacts are particularly pervasive in coastal zones (*30*) and are likely to exacerbate threats to megafauna associated with coastal ecosystems. We found that >80% of primarily coastal and ocean-associated megafauna with known population trends at the global level exhibit a decreasing population (Fig. 3C), implying that the proportion of threatened species is likely to increase in the future.

Megafauna are largely omitted in current conservation efforts

Despite the presence of a rich but highly threatened assemblage of megafaunal species, China's current coastal ecosystem conservation measures including legislations, protected areas (PAs), and restoration efforts have largely omitted megafauna. Regarding legislations, we found that 73% (159 of 218) of megafauna have not yet been included on any of China's national protected species lists (tables S2 and S3). Critically, most of those omitted megafauna are primarily coastal and ocean-associated species (89 and 63 species, respectively; table S2). Similarly, on the list of China's recently issued ban on wildlife trade and consumption (table S3), primarily coastal and ocean-associated species were mostly neglected. They are also not systematically included in any protection framework of fisheries management in China except for general fishing bans (e.g., annual summer fishing bans in China's major seas, which may provide blanket protection; table S3). Identifying endangered species of particular importance for functional diversity using the FUSE (functionally unique, specialized, and endangered) index (*31*), we found that only 17 of the top 50 FUSE species are nationally protected species (table S2). Even for protected species, illegal harvest might still happen because of insufficient enforcement, especially in relatively remote areas, although enforcement of legislations is increasingly enhanced (*32*). Thus, despite substantial progress in China's wildlife protection legislation in recent decades (e.g., the Wildlife Protection Law) (*21*), our analyses reveal that megafauna in coastal ecosystems are largely neglected.

Regarding PAs, we found that the spatial protections provided by PAs often do not match the conservation needs for megafaunal species. By 2021, China had established over 326 sites of marine PAs (*23*), most of which cover coastal ecosystems. We first found that although the known ranges of megafauna have overlap with all coastal PAs (Fig. 5A), only ~10% of PAs with known conservation objectives explicitly included megafauna as their conservation targets (*23*), which still focused on a limited number of charismatic species such as cranes, spotted seals, sea turtles, dugongs, dolphins, and porpoises. Second, most established coastal PAs are small and lack connectivity (79% of the coastal PAs are <100 km^2; Fig. 5B), likely compromising their effectiveness as refuges for megafauna with large range sizes and their ability to provide associated conservation values (*33*, *34*). As megafauna, ocean-associated species in particular, often have large geographic ranges; their conservation requires interlocal governance or transnational collaborative actions. Whether established PAs are properly enforced is uncertain. Because many PAs are partially protected (Fig. 5C) and have no boundary information openly available to the public, it is likely that they are poorly enforced (i.e., paper parks). Third, we found that <10% of the most important habitats for megafauna conservation (measured by a FUSE-based habitat importance index; see Materials and Methods) were protected (Fig. 5D), which is far short of the 30% goal for 2030. Although ~20% of shallow habitats (0 to −50 m) in China, often in temperate areas, were fully or highly protected (*23*), we found that 71% of the most important habitats for megafauna conservation is distributed in areas with medium depths (−10

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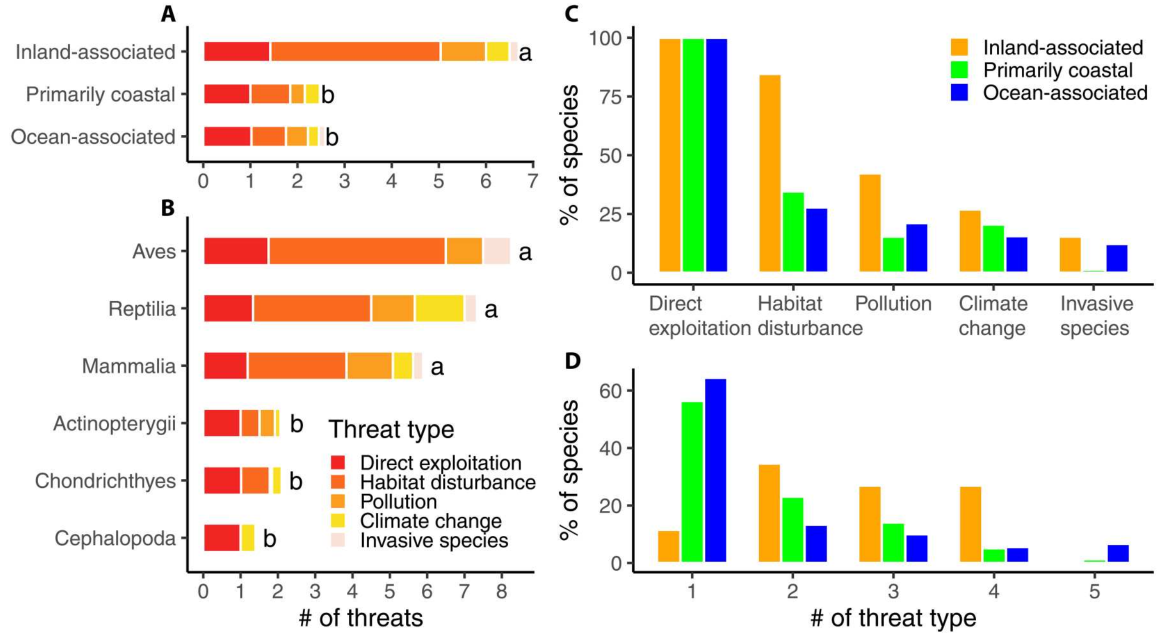

Fig. 4. Anthropogenic threats to megafauna. Average number of threats affecting megafauna per species by (**A**) coastal affinity and (**B**) taxonomic class. (**C**) Percent of species affected by each of the five threat types. (**D**) Percent of species facing a combination of threat types. Threats to species were extracted from the IUCN Red List database, and we grouped them into five threat types indicated by colors (table S6). In (A) and (B), bar length represents the average number of threats within each type of coastal affinity or taxonomic class (error bars were omitted for conciseness). Within each bar, the average number of threats per threat type across all related species is indicated using different colors. Different letters to the right of each bar indicate significant differences in the average number of threats among types of coastal affinity or taxonomic classes (alpha = 0.05).

to −50 m), especially in tropical and subtropical China (Fig. 5A and fig. S2). These results indicate a considerable gap between critical habitats for megafauna and currently established coastal PAs in China.

Regarding restoration efforts, it remains uncertain whether coastal restoration efforts in China are helping to reverse the extinction risk of megafaunal species. As of 2020, China had set up a commendable 250 breeding centers (*21*), but efforts to restore megafauna in coastal ecosystems remain rare in this initiative, and many of these efforts have performed poorly. Previous population reinforcement programs of red-crowned cranes (*Grus japonensis*) and Chinese sturgeon (*Acipenser sinensis*), for example, have not been successful (*35*, *36*), although the restoration of the Milu deer in coastal wetlands is a rare exception (*37*). The lack of success in species restoration is not exclusive to China but rather a result of the fact that megafauna need larger habitats and have long gestation periods, low reproductive rates, and low population growth rates, which increase rearing costs considerably. Furthermore, habitat restoration projects have been rapidly increasing in China (*38*), but whether the restored areas will function as habitats for megafauna is unknown. For instance, China has strictly regulated massive reclamation projects since 2013 (*39*) and has initiated a series of national projects, including 58 Blue Bay improvement projects and 24 coastal zone protection and restoration projects, which have shown signs of success with coastal wetlands displaying a slight to moderate recovery since 2012 (*40*). However, many coastal restoration projects have limited value for addressing the habitat needs of megafauna because they are small or isolated from one another (*38*), making it difficult for megafauna to access and use the necessary habitat types.

Filling the megafauna gap transforms coastal ecosystem conservation

The presence of a rich assemblage of highly threatened, but largely unprotected, megafaunal species in China's coastal ecosystems argues for immediate and systematic incorporation of megafauna into the nation's expanding coastal ecosystem conservation strategy. Given the profound role that megafauna can play in shaping the functions and services of ecosystems that underlie sustainable development goals, their inclusion has the potential to transform several current key measures in coastal ecosystem conservation, potentially amplifying conservation performance. Here, we show this for three main categories of conservation measures: legislative and incentive measures, PA design and management, and restoration design and management, with recommendations provided (table S4).

First, incorporating megafauna will alter legislative and incentive measures for effective coastal ecosystem conservation. (i) Lists of national protected species should be amended to include more primarily coastal and ocean-associated megafauna, especially those with a high FUSE score (table S2 and fig. S3). (ii) Precautionary measures are required to reduce the ecological impacts of nonselective fisheries on coastal megafauna because many coastal megafauna are vulnerable to fisheries bycatch and protection by species lists alone may not be sufficient. Such precautionary measures include promoting the use of gears with fewer collateral impacts (*41*) or dynamic management tools that align megafaunal species movement with fisheries practices (*42*). (iii) More megafauna, top

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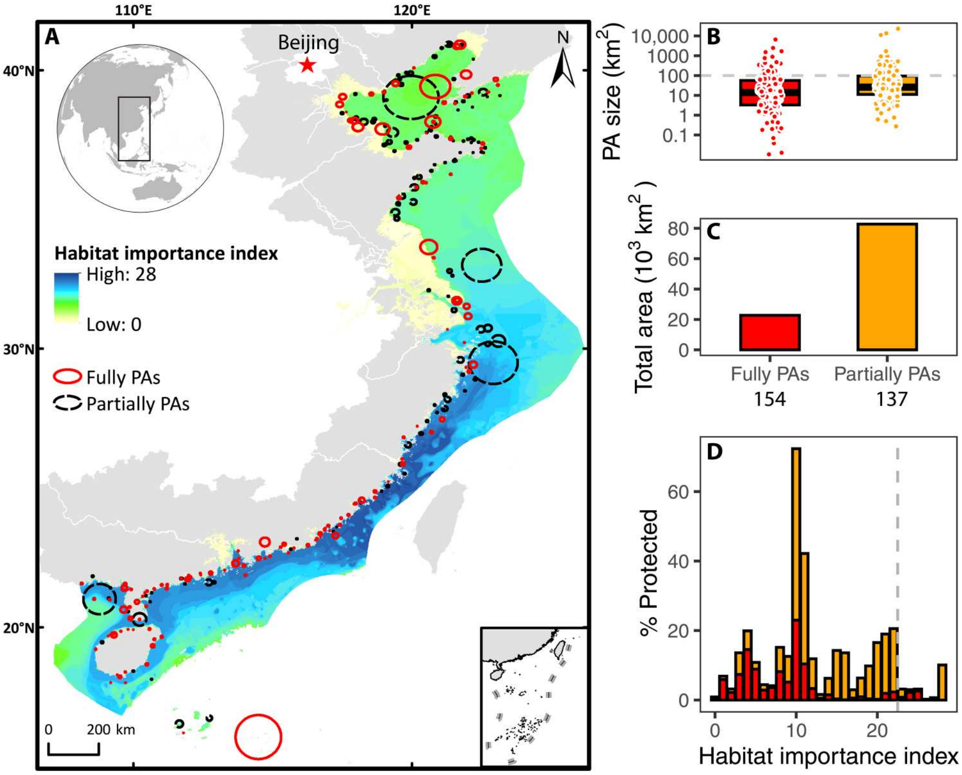

Fig. 5. Spatial mismatch between existing coastal PAs and important habitats for megafauna conservation. (**A**) Spatial distribution of PAs and the habitat importance index for megafauna conservation. The habitat importance index was calculated on the basis of the species FUSE index. (**B**) Summary of the individual sizes of PAs. The box indicates the interquartile range (IQR) of 25th, 50th, and 75th percentiles. (**C**) Total areas of PAs. Also given is the total number of each type of PAs. (**D**) Proportion of PA coverage within each level of the habitat importance index for megafauna conservation (interval = 1). The dashed line indicates the top 20% quantile of the index. PAs are grouped into two categories: fully PAs (shown in red) and partially PAs (shown in orange). As boundaries are unavailable for many PAs, PAs are shown as circles of the same size instead of polygons for their actual shape.

FUSE species (e.g., sharks and sawfish) in particular, should be included as flagship species to raise awareness and funding for coastal ecosystem conservation efforts (*3*). Flagship species conservation has worked in China in terrestrial ecosystems (e.g., pandas) (*21*) and is also likely to work in coastal ecosystems. Taking the "Mazu" belief in the southeastern coastal region of China as an example, the Chinese white dolphin is considered a sacred marine creature and an important representative of marine resources and is therefore highly regarded by the fishers (*43*).

Second, accounting for megafauna will greatly change the design and management of PAs. (i) To incorporate megafauna, PAs must be selected by systematically accounting for the distribution of key megafauna habitats and be scaled in proportion to the required habitat size of megafauna to recover to functionally relevant densities (*44*). Many coastal PAs prioritize criteria related to value for human use rather than value for wildlife conservation and apply minimal habitat size or the abundance of a limited number of taxonomic groups of animals as their primary design criteria (*23*, *45*). However, China has the potential to become a leader in this conservation approach due to its extensive coastlines and growing investments in coastal ecosystem conservation and has recently adopted a strategy to protecting 30% of coastal waters and 35% of coastlines (the "Ecological Conservation Redlines") (*46*). (ii) Alternatively, recognizing the challenge of conserving large areas, corridors can be set aside to promote movement among a series of smaller PAs. This, in turn, requires a deeper understanding of the biology and ecology of megafauna in coastal ecosystems. For example, tracking data of megafauna movements should be used for quantifying the range of megafauna migration corridors and determining critical habitat requirements across their life histories, which can then be used to develop dynamic PA networks (*34*). (iii) PAs that integrate land and sea areas may be prioritized, partly to reduce the exposure of megafauna to pollution, which is a conservation measure China is beginning to adopt (*47*). PAs may not be effective to mitigate pollution from land-based runoff, especially in areas close to human population centers (*48*). Integrated land-sea management in coastal regions, as well as catchment management for estuaries, would not only allow the protection of more types of megafauna habitats but also facilitate pollution control measures, including regulation and supervision of wastewater effluents (*47*).

Third, incorporating megafauna ecological functions will reshape the design and assessment of coastal ecosystem restoration. Coastal ecosystem restoration has traditionally adopted a bottom-up approach (i.e., the Field of Dreams hypothesis) (*49*), emphasizing approaches to restore plants and other habitat-forming foundation species (e.g., corals), which often occur over a small spatial footprint (*50*). Incorporating megafauna would require shifting the approach of coastal ecosystem restoration at least in three ways. (i) The habitat requirements (e.g., site, size, and migration corridors) of megafauna should be accounted for in site selection

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or restoration implementation. (ii) The successful recovery of megafauna should be used as a critical metric of restoration success. (iii) The ecological function of megafauna, including their top-down control of intermediate trophic levels, and associated positive feedbacks for habitat benefit should be harnessed as a tool in the design of restoration projects (*51*). This type of coastal ecosystem restoration has been successful in the eastern North Pacific, where the managed recovery of sea otter populations enhanced the restoration of kelp forests and seagrass beds (*52*, *53*), but has yet to be widely adopted in China and globally.

Incorporating megafauna into coastal ecosystem conservation efforts could yield a variety of local and regional benefits including economic gains from ecotourism, opportunities for enhanced carbon sequestration, increased coastal habitat productivity and ecological stability, and enhanced fishery and nutritional yields (*14*, *17*, *54*). As most of these megafaunal species have not gone extinct globally and there have been cases of successful rewilding (e.g., Milu deer, *E. davidianus*), the windows of opportunity to incorporate megafauna into coastal ecosystem conservation are still open. Therefore, a comprehensive, coordinated national strategy with swift conservation actions and full support of the international conservation community is urgently needed to seize this opportunity before it is too late. This can be facilitated by enhancing basic scientific research, improving the precision of megafaunal data with greater monitoring efforts, and making data open for global assessments. Our findings from a coastal nation with intense development pressures can inform other coastal nations during this UN Decade of Ecosystem Restoration and Decade of Ocean Science for Sustainable Development, leading to greater opportunities to incorporate megafauna to enhance coastal ecosystem conservation and helping achieve sustainable development goals.

MATERIALS AND METHODS

Megafaunal species richness and distributions

To compile a dataset of extant megafaunal species associated with coastal ecosystems in China (we focused on mainland China throughout this work), we used three criteria to screen species: The species has (i) a maximum body mass no less than 10 kg, (ii) habitat association with coastal ecosystems, and (iii) geographic ranges encompassing China. We screened species in the following databases: the IUCN Red List of Threatened Species (ver. 2022-2; www.iucnredlist.org), FishBase (ver. 2023-2; www.fishbase.org), and SeaLifeBase (ver. 2022-12; www.sealifebase.org), including all Mammalia, Aves, Reptilia, Chondrichthyes, Actinopterygii, and Cephalopoda [see (*14*)]. We uniformly used the scientific names of species in the IUCN database and, if needed, renamed species in FishBase and SeaLifeBase by referring to the synonym table given by the IUCN. Note that the concept of megafauna is often context dependent in different studies, with thresholds ranging from 10 kg to 2 tons (*24*). We selected a 10-kg threshold to capture a broad range of relatively large animals. Using the more widely used threshold of 45 kg would yield 120 megafaunal species in total. Rerunning our main analyses using these 120 megafauna did not change our key conclusion that most megafauna and their critical habitats in China's coastal ecosystems remain unprotected (see table S5 and figs. S4 to S8).

Body mass

To determine maximum body masses for mammals, reptiles, and birds, we obtained data from the Amniote life-history database (*55*), PHYLACINE 1.2 (the Phylogenetic Atlas of Mammal Macroecology) (*56*), and the Animal Diversity Web (https://animaldiversity.org). For fishes and other aquatic species, we acquired the maximum published weight from FishBase and SeaLifeBase. For those without weight but with a maximum length, we estimated their weight using length-weight models for each species in those databases; when species-specific models were not available, we used the average model of all species in the most closely related taxonomic grouping.

Habitat association

To determine whether a species has habitat associations with coastal ecosystems, we used species habitat information in the IUCN Red List, FishBase, SeaLifeBase, and review papers (*3*, *11*, *12*). On the basis of the IUCN Habitats Classification Scheme (ver. 3.1), coastal habitats are referred to as those ranging from supratidal to submerged marine neritic zones. We grouped these coastal habitats into seven ecosystem types: mangrove, salt marsh, seagrass/seaweed bed, coral reef, soft sediment, hard bottom, and coastal waters (table S1). Habitat data, as well as geographic range data described below, were collected from IUCN and FishBase/SeaLifeBase using the packages rredlist and rfishbase, respectively, in R 4.2.1.

Geographic range

To determine whether a species' geographic range encompasses mainland China, we used expert-generated species range maps from IUCN or occurrence point data from the Ocean Biodiversity Information System (https://obis.org/) when range maps were unavailable. We considered a species' geographic range to encompass China when either its range map or records of occurrence in any contemporary period included China. This means that species that have become extirpated from China's coastal ecosystems or have become regionally extinct because of range contractions were included in our dataset. We included such species, as they still have the potential to repopulate coastal ecosystems in China if appropriate conservation measures are taken in the future. We excluded species that are globally extinct (e.g., the Chinese paddlefish) and migratory species whose geographic range encompasses only inland regions in China (e.g., many catadromous fishes).

On the basis of the range of their habitat across different systems, we classified megafauna into three types of coastal affinity: inland-associated, primarily coastal, and ocean-associated. Inland-associated species are those whose habitats extend to inland areas such as grassland, forest, and/or freshwater. Primarily coastal species are those that primarily inhabit coastal habitats, including supratidal, intertidal, or marine neritic zones classified by the IUCN (table S1), throughout their entire life cycle. Ocean-associated species are those whose habitats extend to marine oceanic zones. To create a heatmap of megafaunal species richness across China's coastal ecosystems, we obtained IUCN range maps outlining the potential extent of distribution for a total of 203 megafaunal species available [excluding the species that are either EW (extinct in the wild) or extirpated in China's coastal areas; data were last updated on 9 December 2022]. We first merged each species range map data into a single layer and converted it to a raster layer with a spatial resolution of 1 km–by–1 km grid cell in ArcMap 10.8. We then used the Cell Statistics function to calculate the number of species in each grid cell.

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Species threatened status and threats

The population statuses of species, including assigned Red List categories and population trends, were downloaded from IUCN Red List (accessed on 20 May 2023) and China's Red List (2023). The Red List of China is similar to the IUCN's, but it determines the threatened status of species at a country level. Red List categories include EW, critically endangered (CR), endangered (EN), vulnerable (VU), near threatened (NT), least concern (LC), and data deficient (DD) (note that our analysis did not involve globally extinct species or unevaluated species). Species assessed as CR, EN, and VU are referred to as "threatened" species. Following the IUCN approach (www.iucnredlist.org/resources/summary-statistics), the proportion of threatened species was calculated as a best estimate: (EW + CR + EN + VU)/(total − DD), in which DD species were assumed to be threatened at the same rate as data sufficient species. We also calculated the lower and upper estimates of the proportion of threatened species, assuming that none of the DD species were threatened or all were threatened, respectively. Note that in the above calculations, we included EW species (only two, *E. davidianus* and *A. dabryanus*, both of which have been undergoing reintroduction efforts), as they can move into a threatened category following successful reintroduction (www.iucnredlist.org/resources/summary-statistics). To compare the threatened statuses of species between the red lists of China and IUCN for all assessed species and for species within each type of coastal affinity, Kruskal-Wallis rank sum tests were used, in which threatened status was coded as an ordinal level from LC, NT, VU, EN, CR, to EW.

To identify the primary threats contributing to the extinction risk of megafaunal species, we compiled the threats to 194 species with threat data available from IUCN Red List (23 Actinopterygii and 1 Aves species without threat data were excluded). The IUCN threat classification scheme (ver. 3.2) contains almost 50 threats, which we grouped into five broad types: habitat disturbance, direct exploitation, invasive species and diseases, climate change, and pollution (table S6). Threats to EW species were included in our analysis because the two EW species have been reintroduced to the wild. To compare the average number of threats per species across types of coastal affinity and across taxonomic classes, we used Kruskal-Wallis tests due to unequal sample sizes and non-normal distributions of the data. Wilcoxon rank sum tests with continuity correction for multiple testing (the Benjamini-Hochberg method for *P* value adjustment) were then used for pairwise comparisons among different types of coastal affinity and taxonomic classes.

Conservation coverage and critical habitats

To map important coastal habitats for megafauna conservation, we calculated a habitat importance index on the basis of the species FUSE index (*31*, *57*). The FUSE index links traditional measures of species' threatened status with their contribution to functional diversity. We calculated the FUSE index for each species as (*57*): $\ln[1 + (\mathrm{FUn} + \mathrm{FSp}) \times \mathrm{GE}]$, where FUn is the score of species' functional uniqueness and measures mean distance to a set of neighbors, FSp is the score of species specialization and measures relative distance to the centroid of a functional space, and GE is their corresponding IUCN Red List category. To calculate FUn and FSp, we selected seven functional traits to characterize the ecological roles of each megafaunal species in coastal ecosystems (table S7). Trait scores were assigned mainly on the basis of the species information available on FishBase, SeaLifeBase, and IUCN Red List. Then, we created a species trait distance matrix using a modified version of Gower's distance ("gawdis" function of the gawdis package), which allows the treatment of various types of variables (e.g., quantitative, ordinal, nominal, and multichoice binary; see table S7). From this functional dissimilarity matrix, we built a multidimensional Euclidean space based on principal components analysis. On the basis of the multidimensional trait space, we calculated mean FUn considering the five nearest neighbors and FSp as the Euclidean distance of each species to the center of the multidimensional trait space. GE was valued corresponding to its category of threatened status (LC = 0, NT = 1, VU = 2, EN = 3, CR = 4, and EW = 5; DD species were excluded). FUn, FSp, and GE were scaled between 0 and 1 to ensure equal contributions to the index. Last, to identify important areas for megafauna conservation, we calculated a habitat importance index by assigning a FUSE score to the 191 IUCN species range maps available (excluding species that are DD, EW, or extirpated in China's coastal areas) and summing them up. A map of habitat importance was then created using ArcMap 10.8.

To assess the coverage of existing coastal PAs for important habitats for megafauna conservation, we calculated the total percent coverage of PAs by different levels of the habitat importance index. Areas with the top 20% habitat importance index were considered the most important areas for megafauna (*58*). We obtained the location and size of 326 PAs from (*23*) (note that 35 PAs without location and size information or outside the study coastal area were excluded) and then grouped them into fully PAs (marine nature reserves) and partially PAs (special marine PAs, marine parks, and aquatic germplasm reserves, conservation areas that promote recruitment of commercially important, rare, or endangered fish species; table S3) (*23*). As the boundaries of many PAs are unavailable, the boundaries of PAs were assumed to be a perfect, equally sized circle. Sensitivity analysis using 41 PAs with actual boundaries showed that using assumed circle boundaries provided an overall reasonable estimate of the actual coverage of PAs across different levels of habitat importance (fig. S9). We constrained our analysis to habitats ranging from supratidal, intertidal, to submerged marine neritic zones, with elevations between 5 and −200 m, all within mainland China's coastal terrestrial areas and marine areas (*23*). We used 5-m elevation to delimit the upper boundary of supratidal zones, as there was no map of the historical distribution of supratidal zones before strong human alteration in the 1980s (maps are often available only for the recent two or three decades) (*20*). Terrain data were derived from 2022 gridded bathymetric datasets of the General Bathymetric Chart of the Oceans (www.gebco.net). We then calculated spatial overlap between coastal PAs and area of each level of the habitat importance index for both fully and partially PAs (intervals were set to be 1). In addition, we calculated the percentage of total PAs within each level of the habitat importance index and the percentage of areas of each level of the habitat importance index across different elevation zones (5 to 0 m, 0 to −10 m, −10 to −50 m, and −50 to −200 m).

Supplementary Materials

This PDF file includes:

Supplementary Text
Figs. S1 to S9
Tables S1 to S8
References

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REFERENCES AND NOTES

1. C. M. Duarte, S. Agusti, E. Barbier, G. L. Britten, J. C. Castilla, J.-P. Gattuso, R. W. Fulweiler, T. P. Hughes, N. Knowlton, C. E. Lovelock, H. K. Lotze, M. Predragovic, E. Poloczanska, C. Roberts, B. Worm, Rebuilding marine life. *Nature* **580**, 39–51 (2020).
2. J. A. Estes, J. W. 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).
3. B. S. Thompson, S. M. Rog, Beyond ecosystem services: Using charismatic megafauna as flagship species for mangrove forest conservation. *Environ. Sci. Policy* **102**, 9–17 (2019).
4. J. Pittman, D. Armitage, Governance across the land-sea interface: A systematic review. *Environ. Sci. Policy* **64**, 9–17 (2016).
5. J. T. Carlton, J. Hodder, Maritime mammals: Terrestrial mammals as consumers in marine intertidal communities. *Mar. Ecol. Prog. Ser.* **256**, 271–286 (2003).
6. C. Small, R. J. Nicholls, A global analysis of human settlement in coastal zones. *J. Coast. Res.* **19**, 584–599 (2003).
7. 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 (2015).
8. H. K. Lotze, H. S. Lenihan, B. J. Bourque, R. H. Bradbury, R. G. Cooke, M. C. Kay, S. M. Kidwell, M. X. Kirby, C. H. Peterson, J. B. C. Jackson, Depletion, degradation, and recovery potential of estuaries and coastal seas. *Science* **312**, 1806–1809 (2006).
9. B. R. Silliman, B. B. Hughes, L. C. Gaskins, Q. He, M. T. Tinker, A. J. Read, J. C. Nifong, R. Stepp, Are the ghosts of nature's past haunting ecology today? *Curr. Biol.* **28**, R532–R537 (2018).
10. S. M. Rog, R. H. Clarke, C. N. Cook, More than marine: Revealing the critical importance of mangrove ecosystems for terrestrial vertebrates. *Divers. Distrib.* **23**, 221–230 (2017).
11. L. C. Gaskins, A. B. Paxton, B. R. Silliman, Megafauna in salt marshes. *Front. Mar. Sci.* **7**, 561476 (2020).
12. M. Sievers, C. J. Brown, V. J. Tulloch, R. M. Pearson, J. A. Haig, M. P. Turschwell, R. M. Connolly, The role of vegetated coastal wetlands for marine megafauna conservation. *Trends Ecol. Evol.* **34**, 807–817 (2019).
13. D. B. Rasher, R. S. Steneck, J. Halfar, K. J. Kroeker, J. B. Ries, M. T. Tinker, P. T. W. Chan, J. Fietzke, N. A. Kamenos, B. H. Konar, J. S. Lefcheck, C. J. D. Norley, B. P. Weitzman, I. T. Westfield, J. A. Estes, Keystone predators govern the pathway and pace of climate impacts in a subarctic marine ecosystem. *Science* **369**, 1351–1354 (2020).
14. 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).
15. 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).
16. G. L. Britten, M. Dowd, C. Minto, F. Ferretti, F. Boero, H. K. Lotze, Predator decline leads to decreased stability in a coastal fish community. *Ecol. Lett.* **17**, 1518–1525 (2014).
17. A. M. Cisneros-Montemayor, U. R. Sumaila, K. Kaschner, D. Pauly, The global potential for whale watching. *Mar. Policy* **34**, 1273–1278 (2010).
18. B. S. Halpern, M. Frazier, J. Afflerbach, J. S. Lowndes, F. Micheli, C. O'Hara, C. Scarborough, K. A. Selkoe, Recent pace of change in human impact on the world's ocean. *Sci. Rep.* **9**, 11609 (2019).
19. M. Lin, S. T. Turvey, C. Han, X. Huang, A. D. Mazaris, M. Liu, H. Ma, Z. Yang, X. Tang, S. Li, Functional extinction of dugongs in China. *R. Soc. Open Sci.* **9**, 211994 (2022).
20. Q. He, M. D. Bertness, J. F. Bruno, B. Li, G. Chen, T. C. Coverdale, A. H. Altieri, J. Bai, T. Sun, S. C. Pennings, J. Liu, P. R. Ehrlich, B. Cui, Economic development and coastal ecosystem change in China. *Sci. Rep.* **4**, 5995 (2014).
21. G. Huang, X. Ping, W. Xu, Y. Hu, J. Chang, R. R. Swaisgood, J. Zhou, X. Zhan, Z. Zhang, Y. Nie, J. Cui, M. Bruford, Z. Zhang, B. Li, L. Zhang, Z. Lv, F. Wei, Wildlife conservation and management in China: Achievements, challenges and perspectives. *Natl. Sci. Rev.* **8**, nwab042 (2021).
22. F. Hua, X. Wang, X. Zheng, B. Fisher, L. Wang, J. Zhu, Y. Tang, D. W. Yu, D. S. Wilcove, Opportunities for biodiversity gains under the world's largest reforestation programme. *Nat. Commun.* **7**, 12717 (2016).
23. J. J. Bohorquez, G. Xue, T. Frankstone, M. M. Grima, K. Kleinhaus, Y. Zhao, E. K. Pikitch, China's little-known efforts to protect its marine ecosystems safeguard some habitats but omit others. *Sci. Adv.* **7**, eabj1569 (2021).
24. M. Moleón, J. A. Sánchez-Zapata, J. A. Donázar, E. Revilla, B. Martín-López, C. Gutiérrez-Cánovas, W. M. Getz, Z. Morales-Reyes, A. Campos-Arceiz, L. B. Crowder, M. Galetti, M. González-Suárez, F. He, P. Jordano, R. Lewison, R. Naidoo, N. Owen-Smith, N. Selva, J.-C. Svenning, J. L. Tella, C. Zarfl, S. C. Jähnig, M. W. Hayward, S. Faurby, N. García, A. D. Barnosky, K. Tockner, Rethinking megafauna. *Proc. Biol. Sci.* **287**, 20192643 (2020).
25. J. S. Lefcheck, B. B. Hughes, A. J. Johnson, B. W. Pfirrmann, D. B. Rasher, A. R. Smyth, B. L. Williams, M. W. Beck, R. J. Orth, Are coastal habitats important nurseries? A meta-analysis. *Conserv. Lett.* **12**, e12645 (2019).
26. W. J. Ripple, C. Wolf, T. M. Newsome, M. G. Betts, G. Ceballos, F. Courchamp, M. W. Hayward, B. Valkenburgh, A. D. Wallach, B. Worm, Are we eating the world's megafauna to extinction? *Conserv. Lett.* **12**, e12627 (2019).
27. C. E. Sanderson, K. A. Alexander, Unchartered waters: Climate change likely to intensify infectious disease outbreaks causing mass mortality events in marine mammals. *Glob. Chang. Biol.* **26**, 4284–4301 (2020).
28. R. L. Lewison, L. B. Crowder, B. P. Wallace, J. E. Moore, T. Cox, R. Zydelis, S. McDonald, A. DiMatteo, D. C. Dunn, C. Y. Kot, R. Bjorkland, S. Kelez, C. Soykan, K. R. Stewart, M. Sims, A. Boustany, A. J. Read, P. Halpin, W. J. Nichols, C. Safina, Global patterns of marine mammal, seabird, and sea turtle bycatch reveal taxa-specific and cumulative megafauna hotspots. *Proc. Natl. Acad. Sci. U.S.A.* **111**, 5271–5276 (2014).
29. Y. Wang, W. Li, K. van Waerebeek, Strandings, bycatches and injuries of aquatic mammals in China, 2000–2006, as reviewed from official documents: A compelling argument for a nationwide strandings programme. *Mar. Policy* **51**, 242–250 (2015).
30. Q. He, B. R. Silliman, Climate change, human impacts, and coastal ecosystems in the Anthropocene. *Curr. Biol.* **29**, R1021–R1035 (2019).
31. 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).
32. M. 't Sas-Rolfes, D. W. Challender, A. Hinsley, D. Veríssimo, E. J. Milner-Gulland, Illegal wildlife trade: Scale, processes, and governance. *Annu. Rev. Env. Resour.* **44**, 201–228 (2019).
33. S. K. Hooker, L. R. Gerber, Marine reserves as a tool for ecosystem-based management: The potential importance of megafauna. *Bioscience* **54**, 27 (2004).
34. G. J. Edgar, R. D. Stuart-Smith, T. J. Willis, S. Kininmonth, S. C. Baker, S. Banks, N. S. Barrett, M. A. Becerro, A. T. F. Bernard, J. Berkhout, C. D. Buxton, S. J. Campbell, A. T. Cooper, M. Davey, S. C. Edgar, G. Försterra, D. E. Galván, A. J. Irigoyen, D. J. Kushner, R. Moura, P. E. Parnell, N. T. Shears, G. Soler, E. M. A. Strain, R. J. Thomson, Global conservation outcomes depend on marine protected areas with five key features. *Nature* **506**, 216–220 (2014).
35. E. Boscari, J. Wu, T. Jiang, S. Zhang, S. Cattelan, C. Wang, H. Du, C. Li, J. Li, R. Ruan, J. Xu, Y. Zheng, S. D. Palle, J. Yang, L. Congiu, Q. Wei, The last giants of the Yangtze River: A multidisciplinary picture of what remains of the endemic Chinese sturgeon. *Sci. Total Environ.* **843**, 157011 (2022).
36. Y. Lin, P. Xu, W. Zhang, P. Cui, X. Li, C. Lu, Status of red-crowned cranes (*Grus japonensis*) in captivity in zoos and nature reserves in China. *J. Ecol. Rural Environ.* **37**, 668–673 (2021).
37. Z. Cheng, X. Tian, Z. Zhong, P. Li, D. Sun, J. Bai, Y. Meng, S. Zhang, Y. Zhang, L. Wang, D. Liu, Reintroduction, distribution, population dynamics and conservation of a species formerly extinct in the wild: A review of thirty-five years of successful Milu (*Elaphurus davidianus*) reintroduction in China. *Global Ecol. Conserv.* **31**, e01860 (2021).
38. Z. Liu, B. Cui, Q. He, Shifting paradigms in coastal restoration: Six decades' lessons from China. *Sci. Total Environ.* **566-567**, 205–214 (2016).
39. F. Li, D. Ding, Z. Chen, H. Chen, T. Shen, Q. Wu, C. Zhang, Change of sea reclamation and the sea-use management policy system in China. *Mar. Policy* **115**, 103861 (2020).
40. X. Wang, X. Xiao, X. Xu, Z. Zou, B. Chen, Y. Qin, X. Zhang, J. Dong, D. Liu, L. Pan, B. Li, Rebound in China's coastal wetlands following conservation and restoration. *Nat. Sustain.* **4**, 1076–1083 (2021).
41. R. Chuenpagdee, L. E. Morgan, S. M. Maxwell, E. A. Norse, D. Pauly, Shifting gears: Assessing collateral impacts of fishing methods in US waters. *Front. Ecol. Environ.* **1**, 517–524 (2003).
42. E. L. Hazen, K. L. Scales, S. M. Maxwell, D. K. Briscoe, H. Welch, S. J. Bograd, H. Bailey, S. R. Benson, T. Eguchi, H. Dewar, S. Kohin, D. P. Costa, L. B. Crowder, R. L. Lewison, A dynamic ocean management tool to reduce bycatch and support sustainable fisheries. *Sci. Adv.* **4**, eaar3001 (2018).
43. P. S. Ross, S. Z. Dungan, S. K. Hung, T. A. Jefferson, C. Macfarquhar, W. F. Perrin, K. N. Riehl, E. Slooten, J. Tsai, J. Y. Wang, B. N. White, B. Würsig, S. C. Yang, R. R. Reeves, Averting the baiji syndrome: conserving habitat for critically endangered dolphins in Eastern Taiwan Strait. *Aquatic Conserv. Mar. Freshw. Ecosyst.* **20**, 685–694 (2010).
44. K. Norris, A. Terry, J. P. Hansford, S. T. Turvey, Biodiversity conservation and the Earth system: Mind the gap. *Trends Ecol. Evol.* **35**, 919–926 (2020).
45. W. Hu, J. Liu, Z. Ma, Y. Wang, D. Zhang, W. Yu, B. Chen, China's marine protected area system: Evolution, challenges, and new prospects. *Mar. Policy* **115**, 103780 (2020).
46. P. He, J. Gao, W. Zhang, S. Rao, C. Zou, J. Du, W. Liu, China integrating conservation areas into red lines for stricter and unified management. *Land Use Policy* **71**, 245–248 (2018).
47. W. Yue, B. Hou, G. Ye, Z. Wang, China's land-sea coordination practice in territorial spatial planning. *Ocean Coast. Manag.* **237**, 106545 (2023).

Downloaded from https://www.science.org at University of Florida Health Science Center on December 05, 2023

48. Y. Lu, P. Wang, C. Wang, M. Zhang, X. Cao, C. Chen, C. Wang, C. Xiu, D. Du, H. Cui, X. Li, W. Qin, Y. Zhang, Y. Wang, A. Zhang, M. Yu, R. Mao, S. Song, A. C. Johnson, X. Shao, X. Zhou, T. Wang, R. Liang, C. Su, X. Zheng, S. Zhang, X. Lu, Y. Chen, Y. Zhang, Q. Li, K. Ono, N. C. Stenseth, M. Visbeck, V. Ittekkot, Multiple pollutants stress the coastal ecosystem with climate and anthropogenic drivers. *J. Hazard. Mater.* **424**, 127570 (2022).
49. M. A. Palmer, R. F. Ambrose, N. L. Poff, Ecological theory and community restoration ecology. *Restor. Ecol.* **5**, 291–300 (1997).
50. E. Bayraktarov, M. I. Saunders, S. Abdullah, M. Mills, J. Beher, H. P. Possingham, P. J. Mumby, C. E. Lovelock, The cost and feasibility of marine coastal restoration. *Ecol. Appl.* **26**, 1055–1074 (2016).
51. M. Sievers, C. J. Brown, C. A. Buelow, R. Hale, A. Ostrowski, M. I. Saunders, B. R. Silliman, S. E. Swearer, M. P. Turschwell, S. R. Valdez, R. M. Connolly, Greater consideration of animals will enhance coastal restoration outcomes. *Bioscience* **72**, 1088–1098 (2022).
52. E. J. Gregr, V. Christensen, L. Nichol, R. G. Martone, R. W. Markel, J. C. Watson, C. D. G. Harley, E. A. Pakhomov, J. B. Shurin, K. M. A. Chan, Cascading social-ecological costs and benefits triggered by a recovering keystone predator. *Science* **368**, 1243–1247 (2020).
53. B. B. Hughes, R. Eby, E. van Dyke, M. T. Tinker, C. I. Marks, K. S. Johnson, K. Wasson, Recovery of a top predator mediates negative eutrophic effects on seagrass. *Proc. Natl. Acad. Sci. U.S.A.* **110**, 15313–15318 (2013).
54. C. C. Wilmers, J. A. Estes, M. Edwards, K. L. Laidre, B. Konar, Do trophic cascades affect the storage and flux of atmospheric carbon? An analysis of sea otters and kelp forests. *Front. Ecol. Environ.* **10**, 409–415 (2012).
55. N. P. Myhrvold, E. Baldridge, B. Chan, D. Sivam, D. L. Freeman, S. K. M. Ernest, An amniote life-history database to perform comparative analyses with birds, mammals, and reptiles. *Ecology* **96**, 3109–3000 (2015).
56. S. Faurby, M. Davis, R. Ø. Pedersen, S. D. Schowanek, A. Antonelli, J.-C. Svenning, PHYLACINE 1.2: The phylogenetic atlas of mammal macroecology. *Ecology* **99**, 2626–2626 (2018).
57. T. C. Gouhier, P. Pillai, Avoiding conceptual and mathematical pitfalls when developing indices to inform conservation. *Front. Ecol. Evol.* **8**, 263 (2020). 10.3389/fevo.2020.00263.
58. W. Xu, Y. Xiao, J. Zhang, W. Yang, L. Zhang, V. Hull, Z. Wang, H. Zheng, J. Liu, S. Polasky, L. Jiang, Y. Xiao, X. Shi, E. Rao, F. Lu, X. Wang, G. C. Daily, Z. Ouyang, Strengthening protected areas for biodiversity and ecosystem services in China. *Proc. Natl. Acad. Sci. U.S.A.* **114**, 1601–1606 (2017).
59. Center for International Earth Science Information Network (CIESIN) Columbia University, *Gridded Population of the World, Version 4 (GPWv4): Population Density Adjusted to Match 2015 Revision UN WPP Country Totals, Revision 11* (NASA Socioeconomic Data and Applications Center, 2018). [accessed 10 April 2023].
60. H. Wilman, J. Belmaker, J. Simpson, C. de La Rosa, M. M. Rivadeneira, W. Jetz, EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. *Ecology* **95**, 2027–2027 (2014).

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A wide megafauna gap undermines China’s expanding coastal ecosystem conservation

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