RESEARCH ARTICLE CONSERVATION

# Widespread diversity deficits of coral reef sharks and rays

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*SCIENCE* 15 Jun 2023 Vol 380, Issue 6650 pp. 1155-1160 DOI: 10.1126/science.ade4884



## Editor's summary

In recent years, much attention has been given to catastrophic declines in sharks. Most of this attention has focused on large pelagic species that are highly threatened by direct and indirect harvest. Simpfendorfer *et al*. looked globally at the smaller, coral reef–associated species of sharks and rays and found steep declines in shark species (see the Perspective by Shiffman). Five of the most common reef shark species have experienced a decline of up to 73%. As shark species decline on coral reefs, ray species increase, indicating a community-wide shift. Species are best protected when active protections are in place, suggesting routes for better conservation. —Sacha Vignieri

## Abstract

A global survey of coral reefs reveals that overfishing is driving resident shark species toward extinction, causing diversity deficits in reef elasmobranch (shark and ray) assemblages. Our species-level analysis revealed global declines of 60 to 73% for five common resident reef shark species and that individual shark species were not detected at 34 to 47% of surveyed reefs. As reefs become more shark-depleted, rays begin to dominate assemblages. Shark-dominated assemblages persist in wealthy nations with strong governance and in highly protected areas, whereas poverty, weak governance, and a lack of shark management are associated with depauperate assemblages mainly composed of rays. Without action to address these diversity deficits, loss of ecological function and ecosystem services will increasingly affect human communities.



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Coral reef ecosystems are under increasing pressure from human activities—including intense fishing, degraded water quality, and climate change (*1*, *2*)—that threaten species supporting a wide range of ecosystem functions (*3*). Sharks and rays (hereafter "elasmobranchs") have diverse roles on coral reefs as predators and prey across multiple trophic levels and in the cycling and movement of nutrients (*3*–*5*). Recent evidence indicates that overfishing has driven sharks toward functional extinction on many reefs. In a global survey, sharks were not observed on nearly 20% of reefs surveyed (*6*). Yet until recently, reef shark species were listed in lower risk extinction categories by the International Union for the Conservation of Nature (IUCN). With ~37% of all elasmobranch species threatened with extinction (*7*), a key question for coral reef ecosystems lies in understanding the global extent of species loss in elasmobranch assemblages. We characterized elasmobranch assemblage structure on coral reefs across a gradient of human pressures to estimate the local depletion and global extinction risk of the most common reef species, revealing the human and environmental factors that influence assemblage structure and that lead to a deficit in predator diversity that could affect reef ecological functioning.

To understand the extent of the reef elasmobranch diversity deficit, we surveyed 391 coral reefs in 67 nations and territories using 22,756 baited remote underwater video stations (BRUVS). We examined reef-level species richness, species composition of elasmobranch assemblages, and species relative abundance (MaxN; the maximum number of each species observed in a single frame of each 60-min deployment then averaged across all deployments on one reef) (*8*). We examined how elasmobranch species assemblages changed in response to human pressures, using unweighted pair group with arithmetic mean (UPGMA) clustering to identify reefs with the most similar assemblages (*8*). We then compared these clusters with estimated depletion of key resident elasmobranch species at the reef level and examined whether socioeconomic, management, or environmental factors could predict cluster membership, using linear discriminant analysis. Reef-level depletion was estimated by dividing the observed mean MaxN of a species at individual reefs by a model-estimated baseline abundance (without human pressures) for each sampling site (a small group of closely associated reefs) and subtracting this value from 1. Baseline abundance (also expressed as MaxN) was estimated from a general linear model relating observed MaxN to sampling site, human pressure [represented by total market gravity, the size and travel time to human markets (*2*)], and marine protected area (MPA) status [closed to all fishing, open to fishing, or restricted (some fishing but with restrictions)]. The baseline was estimated by setting all parameters to those expected at a site with no human pressure (gravity to the minimum for an ocean basin and protection status to closed) (*8*).

Sampling identified 104 distinct elasmobranch species or species complexes (table S1), representing more than 77% of elasmobranch species known to occur on coral reefs at some point during their lives (*9*). More than half ($n$ = 53) of the species were rarely observed, with 10 or fewer sightings. We estimated reef-level depletion for the nine most commonly occurring species of shark [$n$ = 5; Caribbean reef sharks (*Carcharhinus perezi*) and nurse sharks (*Ginglymostoma cirratum*) in the Atlantic; grey reef sharks (*Carcharhinus amblyrhynchos*), blacktip reef sharks (*Carcharhinus melanopterus*), and whitetip reef sharks (*Triaenodon obesus*) in the Indo-Pacific] and rays [$n$ = 4; yellow stingrays (*Urobatis jamaicensis*) and southern stingrays (*Hypanus americanus*) in the Atlantic; blue spotted mask rays (*Neotrygon* spp.) and blue spotted ribbontail rays (*Taeniura lymma* and *Taeniura lessoni*) in the Indo-Pacific]. The Galapagos shark was excluded from estimates of global depletion because sampling only covered a relatively small proportion of its range, but the results for this species were broadly similar. The nine key resident species represented 77.7% of all elasmobranchs observed in the study and are those that serve important ecological roles (*10*) and contribute the most to, and underpin, livelihoods through fishing (*11*) and dive tourism (*12*).

We found that mean depletion of five key resident reef sharks on individual reefs ranged from 100% depletion (none observed) to 0% (no depletion), averaging 62.8% (Fig. 1A). Mean depletion of key resident reef sharks followed the overall decline in elasmobranch abundance as measured with MaxN (Fig. 1B), decreased as the fraction of the elasmobranch assemblage comprised of sharks decreased (Fig. 1C), and showed little change across a range of elasmobranch species richness (Fig. 1D); these patterns were generally consistent between ocean basins. Across the range of depletion, five main clusters of reefs were

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identified in the Atlantic, and eight were identified in the Indo-Pacific (Figs. 2 and 3), including at least one cluster in each ocean basin (cluster 1 in the Atlantic and cluster 2 in the Indo-Pacific) having shark populations in a relatively intact state, with low levels of depletion of the five main resident reef shark species (Caribbean reef and nurse sharks in the Atlantic; grey reef, blacktip reef, and whitetip reef sharks in the Indo-Pacific) (8). Remaining clusters represented assemblages with increasing depletion of resident shark species and greater proportions of the overall elasmobranch assemblage represented by rays (Figs. 2C and 3B). Both ocean basins show a similar transition through these assemblages as key resident shark species became depleted. The four key ray species (yellow and southern stingrays in the Atlantic; blue spotted mask and blue spotted ribbontail rays in the Indo-Pacific) increased only with depletion of one or more resident reef shark species, with rays dominating in the most shark-depleted areas. These predictable changes in assemblage provide the ability to infer the status of reef shark populations, and the level of human pressure they are experiencing, in future surveys.

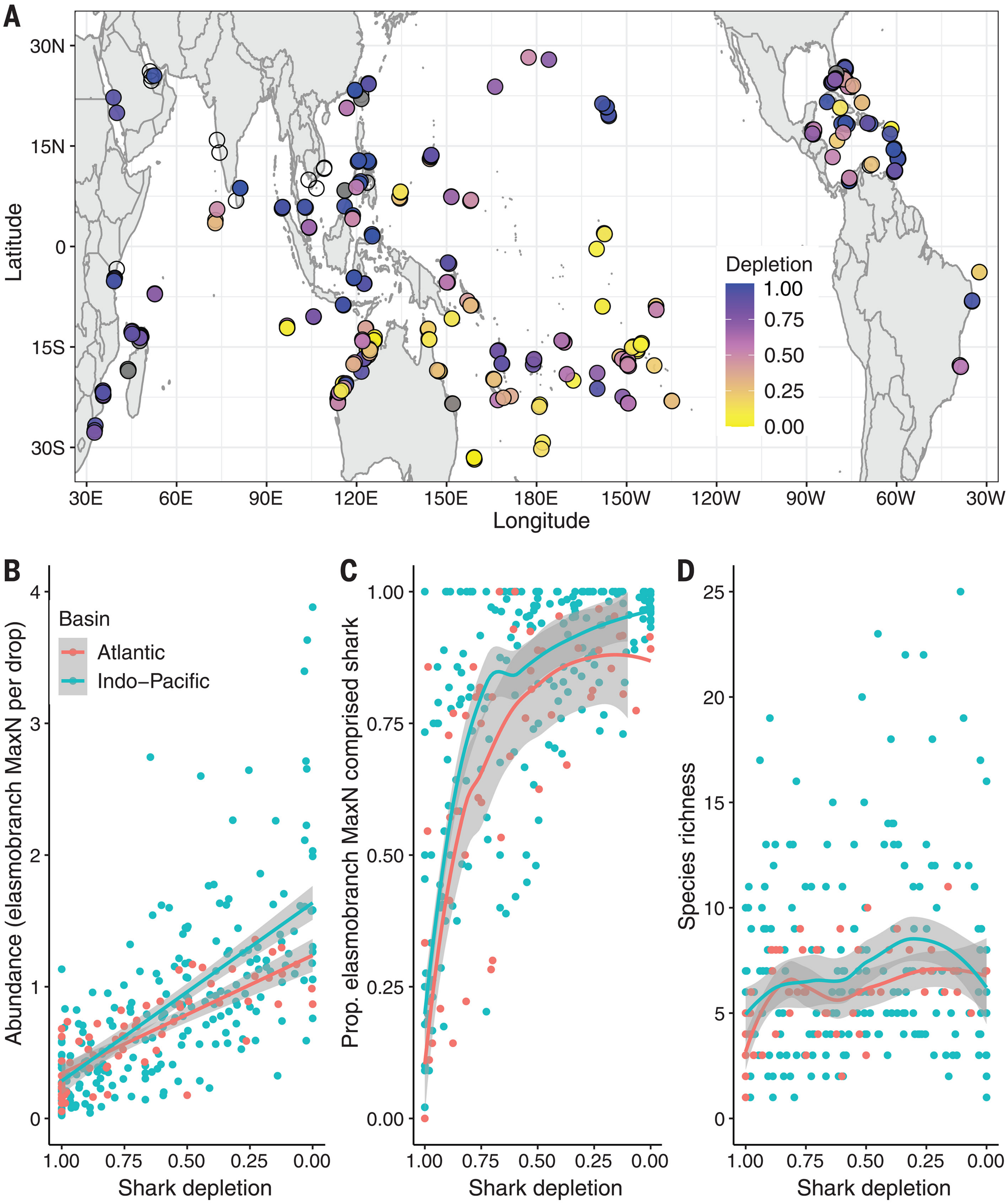


**Fig. 1. The global decline of coral reef elasmobranchs.**

(**A**) Reef-scale estimates of depletion of resident coral reef shark species. Depletion is proportion of unfished population lost, represented as the measured MaxN as a proportion of MaxN in an unfished state (gravity, lowest in basin; MPA status, closed) (8). Open circles indicate no sharks or rays were observed; gray circles indicate none of the resident shark species used to calculate mean depletion were present. (**B**) Relationship between depletion of resident shark species and MaxN by ocean basin. (**C**) Relationship between depletion of resident shark species and the proportion of elasmobranch MaxN that comprised shark,

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demonstrating the transition from shark- to ray-dominated assemblages. (**D**) Relationship between depletion of resident shark species and species richness.

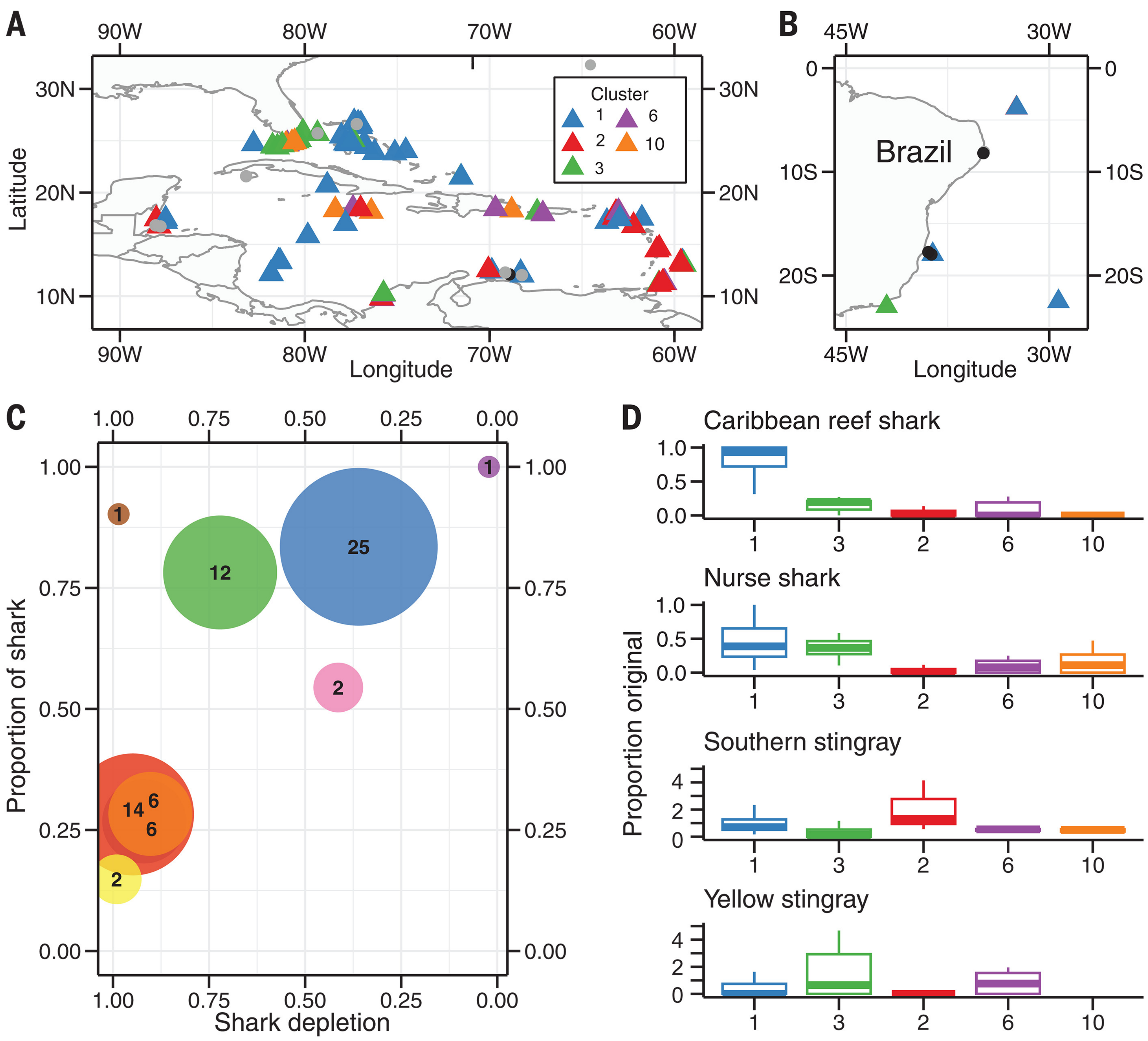


**Fig. 2. Structure of shark and ray assemblages on Atlantic coral reefs.**

(**A** and **B**) Clusters of reefs with similar species composition from UPGMA clustering of 106 reefs in the Atlantic basin based on a global set of 31 coral reef–associated species. Five main clusters, representing 87.0% of reefs, were identified. Their locations are indicated with colored triangles. Reefs with minor clusters are indicated with gray dots ($n$ = 7). Reefs where no elasmobranchs were observed are indicated with black dots ($n$ = 5). (**C**) Regime plot showing all species assemblage clusters as a function of the mean depletion of the resident reef shark species (Caribbean reef and nurse sharks) and the proportion of all observed elasmobranchs that were sharks. Size of points (and numbers) indicate the number of reefs in each cluster, and colors indicate cluster identity as per (A). (**D**) Population level relative to original levels of four resident reef species in each of the five main clusters. Proportion of original level = 1 – depletion. Horizontal lines indicate mean, boxes indicates 25 to 75 percentile, and whiskers indicate 95% confidence interval.

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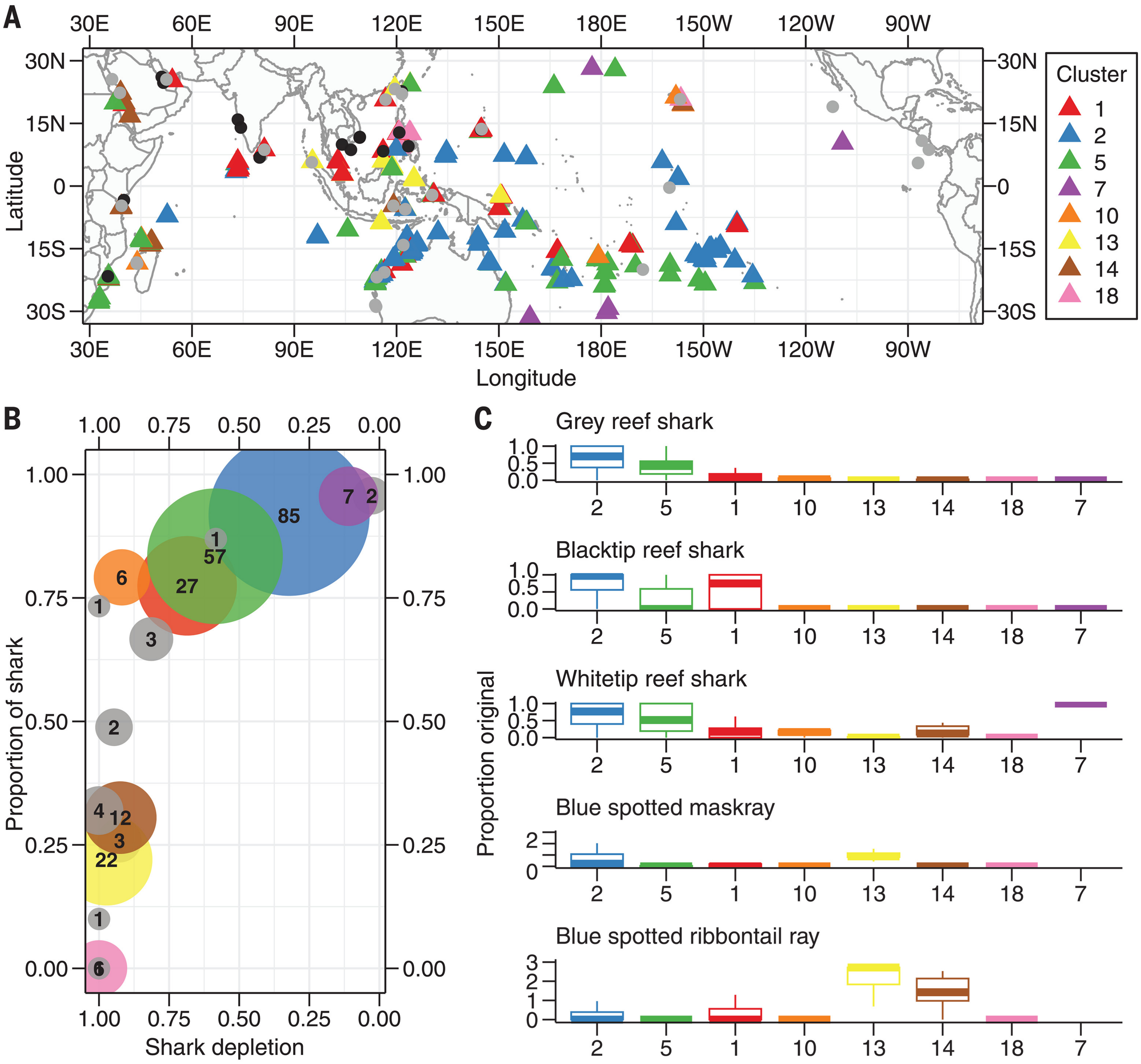


**Fig. 3. Structure of shark and ray assemblages on Indo-Pacific coral reefs.**
(**A**) Clusters of reefs with similar species composition from UPGMA clustering of 285 reefs in the Indo-Pacific basin based on a global set of 31 coral reef-associated species. Eight main clusters, representing 82.1% of reefs, were identified. Their locations are indicated with colored triangles. Reefs with minor clusters are indicated with gray dots ($n$ = 30). Reefs where no elasmobranchs were observed are indicated with black dots ($n$ = 21). (**B**) Regime plot showing all species assemblage clusters as a function of the mean depletion of the resident species of reef shark (grey reef, blacktip reef, whitetip reef, and Galapagos sharks) and the proportion of all observed elasmobranchs that were sharks. Size of points (and numbers) indicate the number of reefs in each cluster, and colors indicate cluster identity as per (A); minor clusters are indicated in gray. (**C**) Population level relative to original levels of five core shark and ray species in each of the eight main species assemblage clusters. Proportion of original level = 1 − depletion. Horizontal lines indicate mean, boxes indicate 25 to 75 percentile, and whiskers indicate 95% confidence interval.

Elasmobranch species assemblage clusters on reefs in both basins were significantly related to certain socioeconomic and management factors, with linear discriminant analysis (LDA) accounting for ~85% of variance between clusters (tables S2 and S3). Important socioeconomic factors included the Human Development Index (an index of a nation’s level of education, life expectancy and standard of living) and Voice and Accountability Index (an index of the extent to which people in each nation can participate in governance, free expression, free media, and free association). Important management factors were whether the reef occurred in a marine protected area (MPA) or whether a reef was within a nation where all targeted shark fishing and trade is prohibited, known as a “shark sanctuary.” Given that shark sanctuaries have largely been implemented in nations in which fishing for sharks was limited for economic or cultural reasons (*6*), their effectiveness as tools for recovering reef shark populations remains an open question. Total market gravity was more important in the Indo-Pacific than the Atlantic, possibly because remote reefs (>4 hours travel time from human settlements) are relatively rare in the Atlantic compared with the Indo-Pacific (fig. S1) (*13*). Environmental factors (coral cover and relief) had little influence in predicting cluster membership. Elasmobranch assemblage structure on coral reefs in both the Atlantic and Indo-Pacific are therefore mainly driven by management and socioeconomic factors, with shark-dominated assemblages more likely to occur in wealthy, well-governed nations and in highly protected

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areas or shark sanctuaries, whereas poverty, limited governance, and a lack of shark protection are associated with assemblages mainly composed of rays.

To further characterize the diversity deficits that underpin these assemblage differences, we compared species observations in our BRUVS with their historical ranges drawn from published literature, including historical accounts, and found that sharks were not detected at 13.6% of reefs (19 Atlantic and 34 Indo-Pacific), whereas rays were not detected at 21.5% of reefs (10 Atlantic and 74 Indo-Pacific); both groups were not detected at 6.6% of reefs surveyed (5 Atlantic and 19 Indo-Pacific). At the species level, absences were severe. On the basis of their known historic distribution, deficits were 46.9% of reefs (112 of 246) for blacktip reef sharks, 41.3% (31 of 75) for Caribbean reef sharks, 40.8% (102 of 250) for grey reef sharks, 36.2% (89 of 246) for whitetip reef sharks, and 34.7% ($n$ = 26 of 75) for nurse sharks (fig. S2). Among rays, deficits were even more stark: 78.9% (75 of 95) for yellow stingray, 62.8% (81 of 129) for blue spotted ribbontail rays, and 55.6% (79 of 142) for blue spotted maskrays. An exception was the southern stingray, which was not detected at only 19.8% ($n$ = 20 of 101) of expected reefs in the Atlantic. A failure to detect rays may not always indicate absence because they are often cryptic and therefore missed on BRUVS, especially when sharks are present (*14*). Collectively, these diversity deficits show that elasmobranch loss on coral reefs is more extensive than previously demonstrated, with widespread losses of key species across many of the world's coral reefs, especially in Asia, eastern Africa, continental South America, and the central-eastern Caribbean.

Previous estimates of the status of reef shark and ray species have been geographically limited, varying among surveyed reefs from very high abundances (*15*) to local extinction (*16*). This disparity has made it difficult to assess the global status of individual species. Therefore, we used our estimates of reef-level depletion to estimate the global depletion and extinction risk of the most common resident reef sharks (five species) and rays (four species). Mean and standard error reef-level depletion was calculated within jurisdictions (nations or remote territories) and used to produce confidence intervals for jurisdictional depletion levels. To estimate an overall global depletion level by species, we weighted the jurisdictional depletion by the percentage of the world's coral reefs in their waters and produced a weighted global mean depletion (*8*). Extinction risk was estimated by comparing proportional global depletion to the criteria for the IUCN Red List A2 (population decline) category (*17*), assuming that the decline had occurred in the past three generations (29 to 90 years). In IUCN assessments before the availability of this global survey, all reef-resident shark species were considered at lower risk of extinction (Near Threatened) (*18*). Grey reef shark had the highest level of global decline [69.8% ± 1 standard error (SE) 62.6 to 77.1], followed by nurse shark (68.6% ± 49.7 to 87.4), Caribbean reef shark (64.8% ± 42.0 to 87.5), blacktip reef shark (64.5% ± 58.7 to 70.4), and whitetip reef shark (60.4% ± 51.2 to 70.2) (Fig. 4). The estimated declines of resident species of reef sharks met the IUCN Red List criteria for Endangered. Population changes of rays were more variable, with increasing populations in some nations and declines in others (fig. S3), reflecting the compositional changes seen across our gradient of human pressures. When examined at the global level, no ray species examined met criteria for elevated extinction risk, which is consistent with current nonthreatened status of these species on the Red List.

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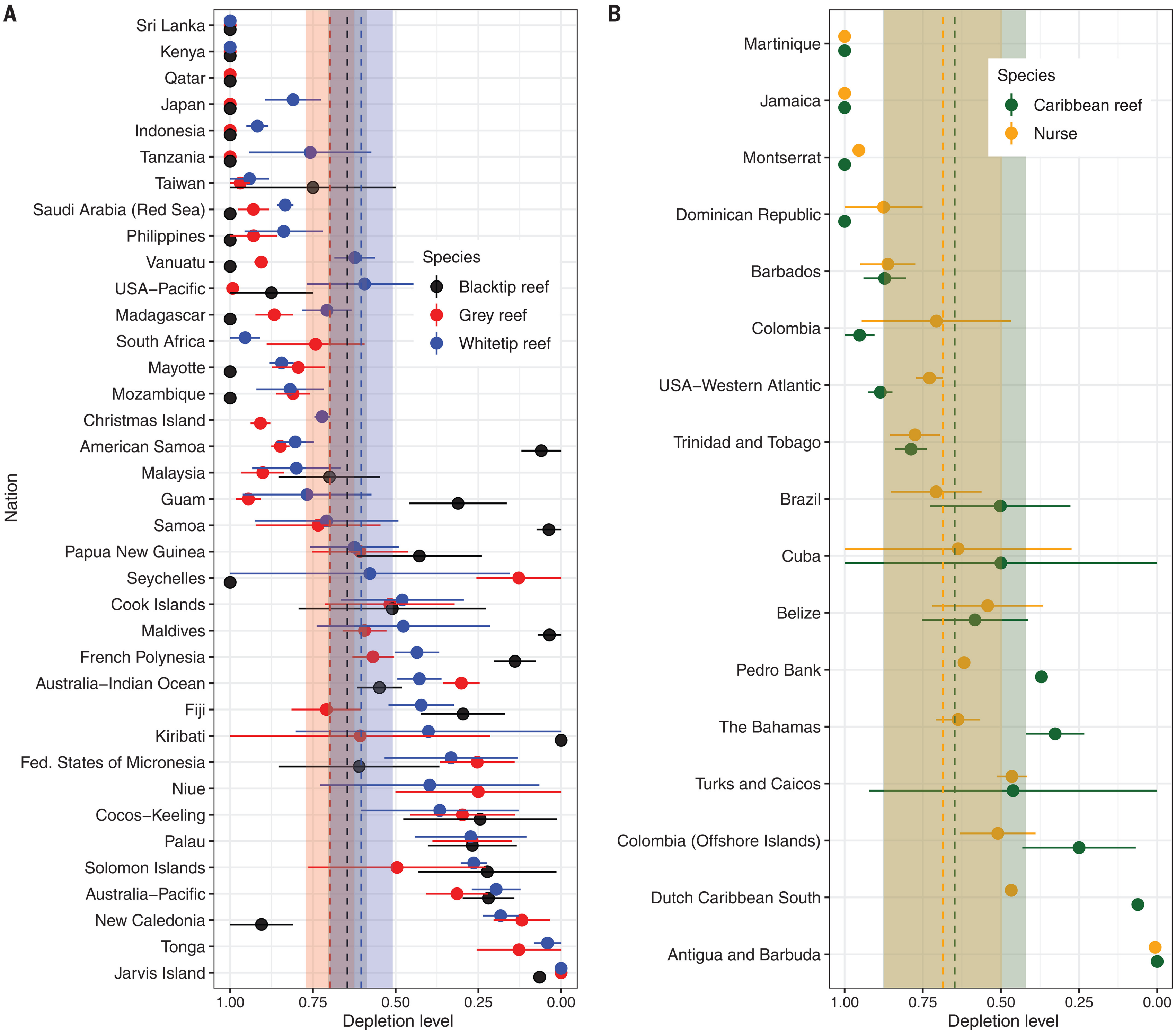


Fig. 4. **Depletion of core coral reef shark species in the Indo-Pacific and Atlantic basins at national or near-national scale.** (**A**) Indo-Pacific basin. (**B**) Atlantic basin. Depletion was calculated by comparing reef-level species MaxN values to unfished, estimated by using a linear model in which market gravity (a measure of the human pressure from population and access to reefs) was set to the ocean basin minimum and reef protected status was "closed" (no take MPA) (8). Reef-level depletion scores were modeled by nation and used to estimate a global level of depletion (vertical dashed lines) ± 1 standard error (shaded area) calculated by weighting national-level depletion by coral reef area (as a percent of global total coral reef area that occurs within the range of each shark species).

Our study of nations hosting ~90% of global reefs reveals that resident reef shark species are at much higher risk of extinction than previously thought. Local declines, shaped by human pressures that vary across ocean basins, have led to consistent changes in the structure of coral reef elasmobranch assemblages that may have profound effects on the broader ecosystem. The direct and indirect effects of fishing have driven shifts in species composition from shark-dominated to ray-dominated assemblages and ultimately the complete loss of sharks and rays at a small proportion (~ 7%) of reefs surveyed. In addition to changes in the structure of assemblages, all major resident shark species have declined to such levels that they qualify as Endangered by the IUCN Red List Criteria. These changes wrought on coral reef elasmobranch assemblages demonstrate the pervasiveness of fishing on coral reefs (19) and the substantial risks to reef-dependent human communities of continued overfishing. Elasmobranch species vary widely in their economic value, with some fished for subsistence, others fished for local or export markets, and others valued alive as tourism resources (12, 20). Thus, understanding threats and conservation options for rebuilding populations at a species level will assist in developing effective management of coral reef elasmobranchs as part of a sustainable social-ecological system.

Although reef sharks are at considerable risk over broad spatial scales, our results show that declines at one reef will have little effect on reefs tens to hundreds of kilometers distant. Thus, despite populations being functionally extinct at the reef level, the potential to rebuild abundances remains relatively high if there are protected areas or strong fisheries management within a region (6). These source populations are present among many small oceanic islands where low human populations and the high cultural value of sharks has resulted in fishing levels that are below those seen elsewhere (21). MPAs also provide the opportunity to act as source populations; however, their designation alone is insufficient to deliver benefits. As others have observed (22), high compliance is required. We show that there are reefs in regions with widespread depletion of reef shark species that had metrics indicating that they are in a relatively healthy state compared with those around them. These included Tubbataha (Philippines), Sipidan (Island Malaysia), Glover's Reef and Lighthouse Reef (Belize), and Misool (Indonesia); in all of these locations, there are programs to actively manage and enforce MPA regulations that are likely to account for these successes (23–25).

Multiple nations have strong management measures (such as spatial protections and/or fishing restrictions) in place that benefit reef species. This study builds the case that species-specific reef shark management provides the best way forward for conservation and rebuilding of reef sharks in places where they have declined, among nations with the desire and capacity to do so (7, 8). Recent studies show that populations of reef sharks can rebound in under a decade if appropriate management strategies that reduce fishing pressure are in place (26). Although direct management is critical, local and national socioeconomic factors that affect the ability of nations to develop, implement, and enforce regulations, and the likelihood that fishers comply with regulations, will be critical to maintaining or rebuilding populations and diverse elasmobranch assemblages. If not addressed, pressures causing the shark and ray diversity deficits we outline will continue to result in a loss of species, ecological functions, and ecosystem services that support sustainable livelihoods for millions of people worldwide.

## Acknowledgments

We thank our individual funders for country-specific deployments, whose contributions greatly enhanced the sampling coverage of the projects; all of the government permitting agencies that allowed us to work in their waters; and the Global FinPrint volunteers from Stony Brook University, Florida International University, James Cook University, the Aquarium of the Pacific, and Shedd Aquarium who watched the BRUVS footage.

**Funding:** Core funding for Global FinPrint was provided by the Paul G. Allen Family Foundation (to D.D.C. and M.R.Hei.).

**Author contributions:** Conceptualization: D.D.C., M.R.Hei., C.A.S., M.R.Heu., M.A.M., M.M., and E.H. Methodology: D.D.C., M.R.Hei., C.A.S., M.R.Heu., M.A.M., M.M., and E.H. Investigation: All authors. Visualization: C.A.S. Funding acquisition: D.D.C. and M.R.Hei. Project administration: D.D.C., M.R.Hei., C.A.S., M.R.Heu., M.A.M., M.M., and E.H. Writing – original draft: C.A.S., D.D.C., M.R.Hei., M.R.Heu., M.A.M., M.M., E.H., and C.S.S. Writing – review and editing: All authors.

**Competing interests:** The authors declare that they have no competing interests

**Data and materials availability:** Data files have been deposited in Dryad (27), and R script has been deposited in Zenodo (28).



## Supplementary Materials

### This PDF file includes:

Materials and Methods

Figs. S1 to S8

Tables S1 to S9

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