

**Title:** Multinational coordination required for conservation of over 90% of marine species

## Authors

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## Abstract

Marine species are declining at an unprecedented rate, catalyzing many nations to adopt conservation and management targets within their jurisdictions. However, marine species are naive to international borders and an understanding of cross-border species distributions is important for informing high-level conservation strategies, such as bilateral or regional agreements. Here, we examined 28,252 distribution maps to determine the number and locations of marine transboundary species. Over 90% of species have ranges spanning at least two jurisdictions, with 58% covering over ten jurisdictions. The highest concentrations of transboundary species are in the USA, Australia, and Indonesia. To effectively protect marine biodiversity, international governance mechanisms—particularly those related to the Convention on Biological Diversity, the Convention on Migratory Species, and Regional Seas Organizations—must be expanded to promote multinational conservation planning, and complimented by a holistic governance framework for biodiversity beyond national jurisdiction.

**Keywords:** Transboundary management, biodiversity, species distributions, Exclusive Economic Zones, marine conservation, collaboration

## One Sentence Summary:

Biodiversity is far more transboundary in the ocean than on land, with most marine species' ranges crossing many international borders.

## MAIN TEXT

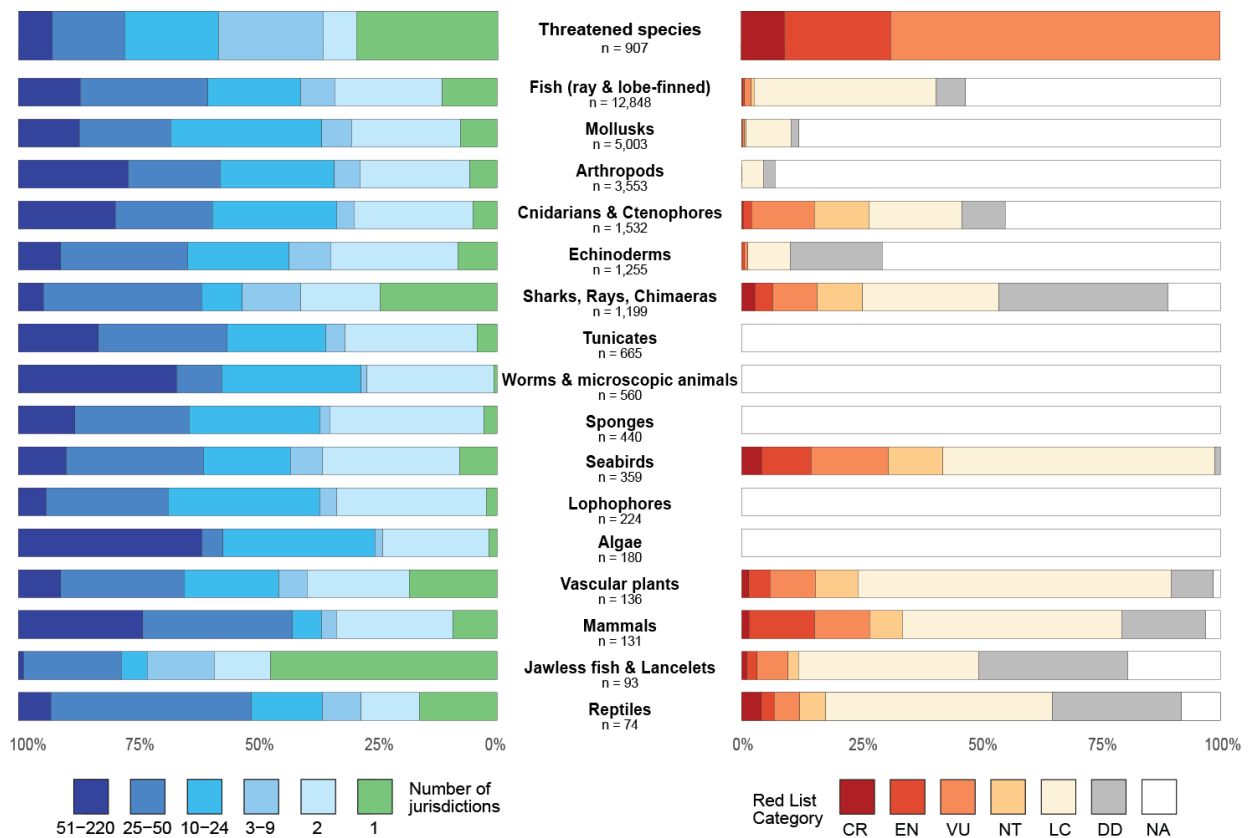
### Introduction

Political jurisdictions have significant economic and cultural implications for humans and can also have a strong influence on regulation and management regimes that affect many marine species. However, species ranges and movement cross administrative boundaries, especially in the marine environment where boundaries are permeable and connectivity is high. For example, larvae can disperse hundreds of kilometres (1) and many marine mammals, sea turtles, seabirds and fish annually migrate across hemispheres. Yet, global initiatives aimed at promoting the conservation and sustainable use of marine biodiversity, such as the Sustainable Development Goals (SDGs) and the Aichi Biodiversity Targets under the United Nations Convention on Biological Diversity (CBD), are implemented by individual countries within their borders with no explicit requirements for international coordination (2). Environmental policy built around administrative jurisdictions and structures risks perverse or ineffective outcomes for species because effective management within one jurisdiction may be undermined by inadequate management in other jurisdictions. Examples include protection of only a fraction of a species' life cycle or migration route (3,4), intense harvesting pressure of particular species along arbitrarily located management boundaries (5), and relaxation of conservation policy in neighbouring jurisdictions (6). To guard against these unintended outcomes, future policy mechanisms must more explicitly address transboundary management. The fundamental disconnect between geopolitical jurisdictions and ecological domains constitutes a major threat to effective long-term conservation, a problem which is exacerbated by projected shifts in species ranges resulting from climate change (7,8).

While there are some existing initiatives that actively address transboundary management, these are almost exclusively focused on charismatic megafauna (e.g., the International Whaling Convention, instruments under the Convention on Migratory Species) or commercially valuable species (e.g. the five regional fisheries organizations that manage tuna). This leaves a key gap in transboundary management for the vast majority of marine biodiversity. There is consensus that effective management of many marine species requires new conservation goals that foster multinational coordination (4,6,9,10), but little is known about the magnitude and extent of transboundary marine biodiversity. Using species distribution data on 28,252 marine species to determine how marine biodiversity is distributed across ocean jurisdictions, we identify priorities for coordinating better protection of marine species.

## Results

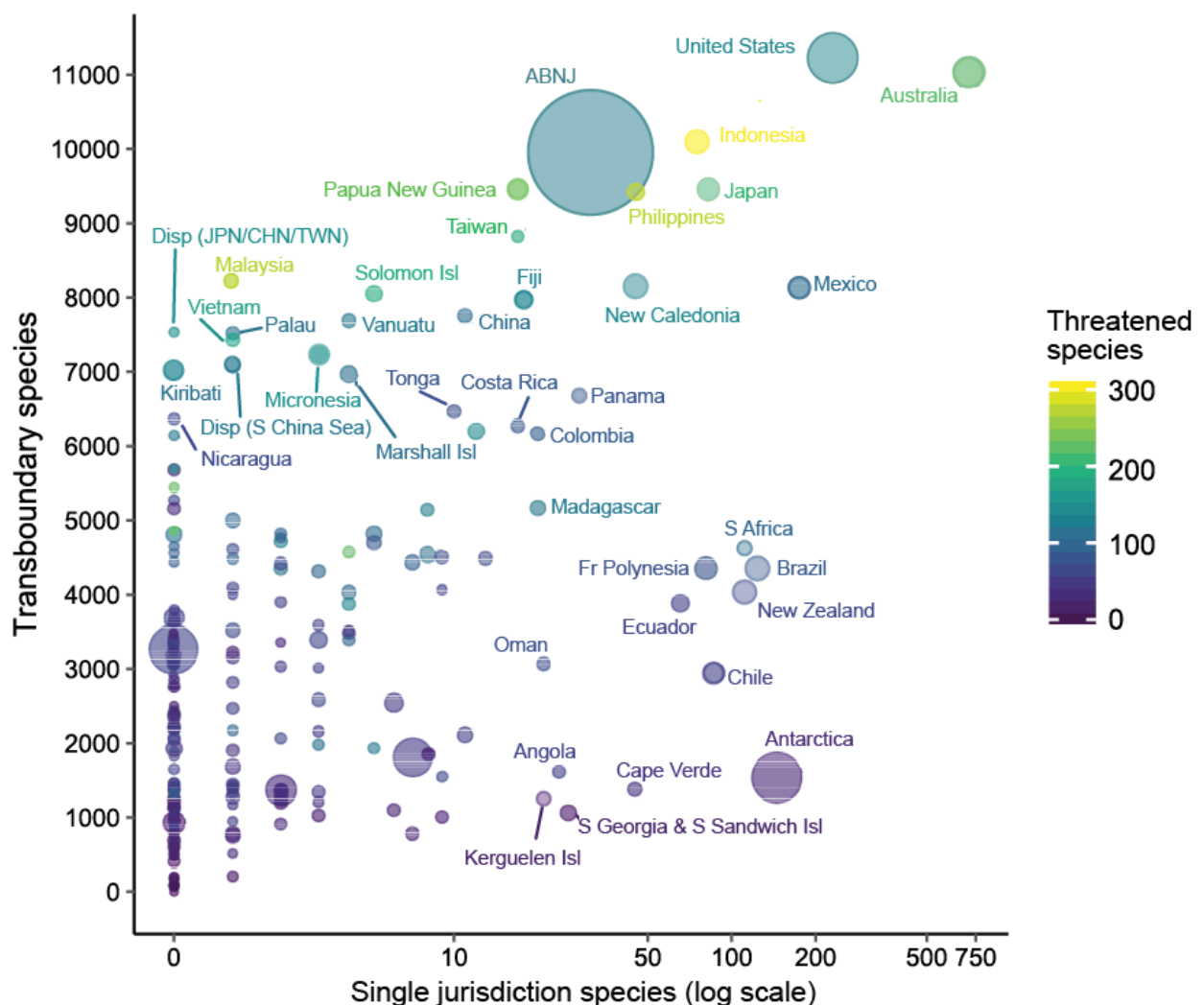
Only 10% of all marine species assessed occupied a single jurisdiction (i.e. endemics, Fig. 1), but half of the 228 jurisdictions have endemic species, with Australia (n=706), the USA (n=231), and Mexico (n=174) hosting 41% of the 2,691 endemics (Fig. 2). Jurisdictions that host species solely within their marine territories are the primary stewards of those species and thus hold sole responsibility for implementing effective conservation actions to ensure their persistence. The other 90% of species (n=25,561) considered in this analysis are found in multiple jurisdictions. Six percent of species occur in exactly two jurisdictions; the country pairs that share the most dual-jurisdiction species are the USA and Mexico (n=240), the USA and Canada (n=224), and Australia and New Zealand (n=193). These countries clearly present important opportunities for conservation partnerships. However, the majority (84%) of transboundary species occupy more than two jurisdictions: 58% occupy more than ten jurisdictions and 15% occupy more than 50 jurisdictions. This presents a significant governance challenge as it requires coordination among approximately a quarter of the nations on Earth to manage these species effectively.



**Fig. 1. Species' conservation statuses and number of jurisdictions overlapping their distributions.** Colored bars show the proportions of each taxonomic group in each IUCN threat category (CR = Critically Endangered, EN = Endangered, VU = Vulnerable, NT = Near Threatened, LC = Least Concern, DD = Data Deficient, NA = not assessed) and range of jurisdictions. Taxonomic groups are ordered by descending number of species. Threatened (CR, EN, VU) species are shown at the top.

The taxonomic groups with the highest proportions of transboundary species represent poorly studied phyla of worms and microscopic animals, algae (red and green), lophophores (small sessile filter feeders), and sponges (Fig. 1). Most of the species with distributions spanning the highest number of jurisdictions are charismatic vertebrates (e.g., cetaceans, sea turtles) and commercially valuable fish (e.g., tunas and billfish, pelagic sharks) (Table S1). Orca whales (*Orcinus orca*) occur in the most jurisdictions (n=220), followed by minke whales (*Balaenoptera acutorostrata*, n=211) and common bottlenose dolphins (*Tursiops truncatus*, n=211). However, several species of deep-water fish and cephalopods are also found in hundreds of jurisdictions; for example, short-rod anglerfish (*Microlophichthys microlophus*, n = 200) and jewel enope squid (*Pyroteuthis margaritifera*), which occurs in the largest number of jurisdictions (n=199) of any invertebrate.

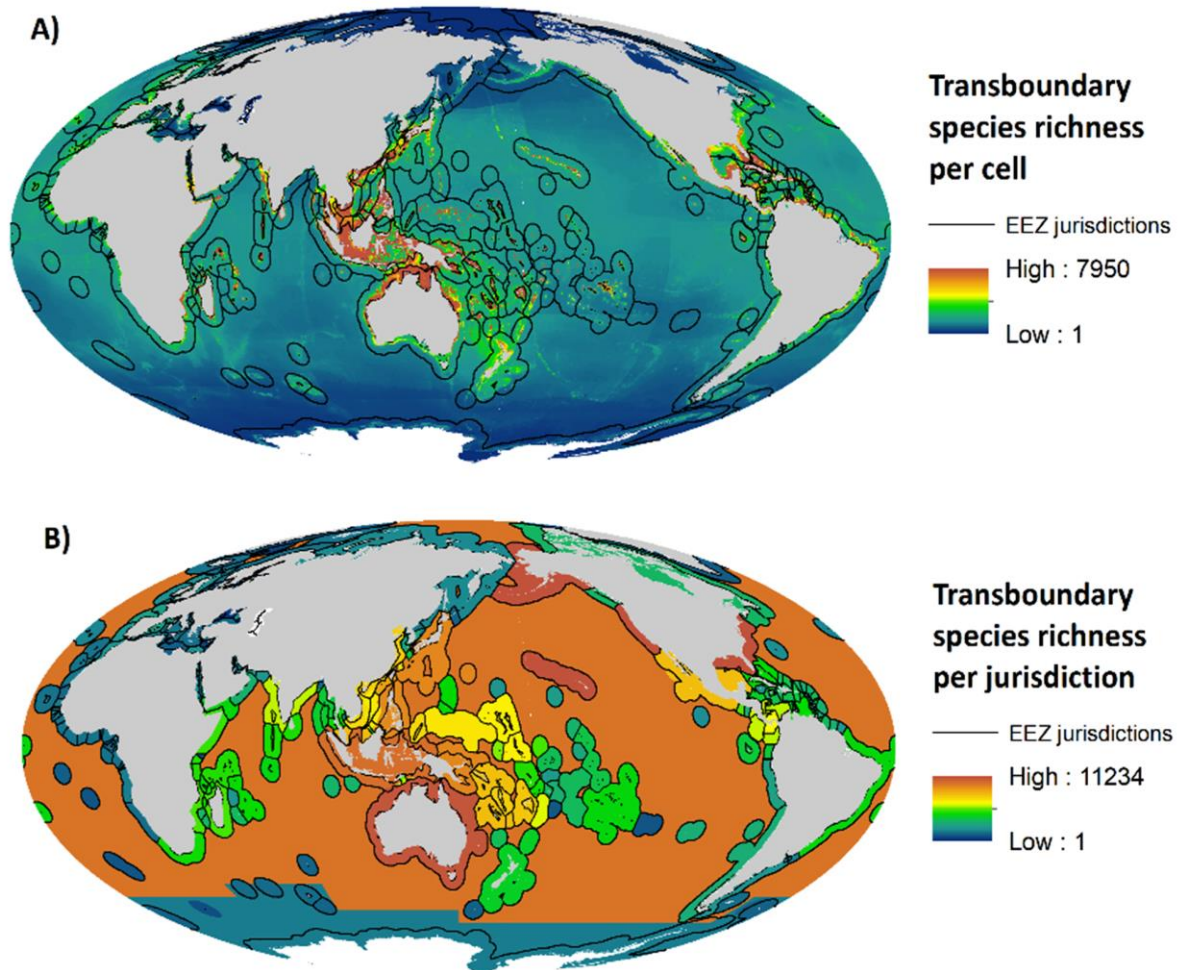
Over one-third (35%) of the marine species included have been assigned a threat status by the IUCN, but most (78%) assessed species are vertebrates and 7% are listed as Data Deficient. Consistent with the expected pattern of greater extinction risk for species with smaller ranges (11,12), we find that 71% of species listed as threatened (i.e. classified as Critically Endangered, Endangered, Vulnerable) on the IUCN Red List (n=907) occur in only one jurisdiction compared to 10% of non-threatened species. This provides more opportunities for individual nations with threatened endemics (e.g., Australia, Ecuador, Mexico) to abate the marine extinction crisis.



**Fig. 2. Number of species per jurisdiction.** Color corresponds to the number of threatened (Critically Endangered, Endangered, or Vulnerable) transboundary species and size corresponds to jurisdiction area (larger dots represent larger areas). All 228 jurisdictions are shown, with labels for jurisdictions ranking in the top 25 for number of transboundary or single jurisdiction species

Transboundary species are concentrated in three biodiversity hotspots in the tropics that have high densities of small island states: East Asia and Oceania, Central America and the Caribbean, and the Western Indian Ocean (Figs. 2, 3). Our results indicate that transboundary species richness is more closely correlated with latitude than with area; large jurisdictions in temperate latitudes have fewer species than many small tropical jurisdictions (Fig. S1), although uneven research effort across countries and regions biases our knowledge of marine biodiversity. As the vast majority of mapped marine species are distributed across multiple jurisdictions, patterns of transboundary species richness are similar to previous species richness maps with smaller subsets of species (e.g. Fig. 2A (13), Fig. 2A,B (14)), Fig. 1 (15)). Many countries in these regions have limited capacity to manage or report on marine biodiversity, especially island states with many species and large ocean territories (e.g., New Caledonia, Indonesia; See Fig. S1, Table S2). The jurisdictions with the most transboundary species are the USA, Australia, Indonesia, and Areas Beyond National Jurisdiction (ABNJ) (Figs. 2,3), with Australia and Indonesia harboring the greatest richness of threatened transboundary species (Fig. 2). The country pairs that share the most species are Australia and Papua New Guinea, Australia and Indonesia, and Australia and the Philippines. Countries with large numbers of transboundary species all share many species with ABNJ, especially the USA, Australia, and Japan, which all have more than 5,000 species that also occur in ABNJ. It is critical that countries sharing many species with each other collaborate for conservation and management of those species, but any species that is shared with ABNJ presents a significant governance challenge.





**Fig. 3. Transboundary species richness.** Maps of the number of transboundary species richness (A) per grid cell and (B) per jurisdiction.

### Discussion

The transboundary nature of virtually all marine biodiversity exacerbates the complexity of ocean conservation. Small-island nations with vast seascapes face great challenges in effective implementation and enforcement for typical marine conservation strategies, such as marine protected areas (16). Political conflicts between countries present another major obstacle to multi-jurisdictional conservation. In some cases, countries have agreed on conservation measures despite political tensions (e.g., the Coral Triangle Initiative (17), joint management of salmon in the Northeast Pacific (18), but in other cases (e.g., the South China Sea (19), the Southwest Atlantic (20)), multilateral cooperation remains intractable (19).

The nearly half of the planet lying beyond national jurisdictions, where persistent geographic and taxonomic governance gaps have resulted in greater cumulative impacts on species and ecosystems compared to EEZs (21), presents a particular governance challenge (4,20,22,23). Currently, there are few avenues for recourse if agreements are not honored (especially in the ABNJ (22), no set rules regarding how to assess transboundary impacts from activities in ABNJ, and no global mechanism to allow the implementation of marine protected areas in ABNJ. The legal foundation for management and protection of transboundary species stems directly from the UN Convention on the Law of the Sea (UNCLOS). However, management mechanisms and

governance structures have arisen both through implementing agreements to UNCLOS (e.g., for high sea fisheries through the Fish Stocks Agreement and for deep-sea mining through the establishment of the International Seabed Authority) as well as through the proliferation of biodiversity conventions and organizations (the CBD, Convention on Migratory Species, UN Food and Agriculture Organization, and Regional Seas Organizations under the UN Environment Programme) (23–25). The need for more holistic and coordinated governance of marine biodiversity is at the core of the negotiations over a new international legally binding instrument on the conservation and sustainable use of marine biological diversity of areas beyond national jurisdiction (BBNJ) (26). The solutions being offered in the draft BBNJ agreement (27) start to address the gaps described above, and reflect both the need for a global understanding of marine biodiversity (e.g., through a central scientific body) as well as understanding of regional contexts (implementation through regional bodies, and the central role of capacity development and technology transfer).

Best practice for transboundary conservation considers each country's geographic and cultural context, and includes collaboration, cost-sharing, and resource transfer at multiple scales, including both intraregional (e.g., among countries in South East Asia) and interregional (e.g., between Northern European and South East Asian regional management organizations). Better outcomes can be achieved by redistributing the burden of conservation, which currently falls disproportionately on countries with lower management capacity (16,28). International conservation initiatives could encourage countries with greater capacity but fewer species (e.g. Northern European countries) to set higher targets for marine biodiversity in their waters, and create avenues to transfer resources to lower capacity countries.

Potential mechanisms for regional coordination of management of transboundary species could be through the Convention on Migratory Species (29), which already plays this role through its family of sub-instruments including Concerted Action Plans, MoUs and Multilateral Environmental Agreements (e.g., Agreement on the Conservation of Albatrosses and Petrels). While this would seem a logical way forward, the Convention on Migratory Species has limited power to control exploitation, and only applies to species whose movements cross jurisdictions as they undertake regular migrations between habitats. Only a small fraction of the species considered here would fall into that category. Regional Seas Programmes offer another regional approach to transboundary management of marine biodiversity (30). To date these organizations have been largely focused on pollution and management within jurisdictions (6), although discussion about expanding their geographic mandates into ABNJ to better support regional implementation of a new high seas biodiversity agreement affords an opportunity to broaden the role of these organizations to coordinating management of transboundary species.

An example of coordinated management of transboundary species by a Regional Seas Programme is the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR), the governing body for fisheries and biodiversity in Antarctica and the Southern Ocean. Although focused on commercially exploited biodiversity, CCAMLR has effectively facilitated collaboration among individual States to govern a large and remote area with considerable success (31,32). In contrast to terrestrial species (at least terrestrial vertebrates)—of which almost half occur within the borders of individual countries (33)—the highly transboundary distribution of marine biodiversity means that complex management contexts such as CCAMLR and the need for countries to engage with governance of ABNJ are the norm, not the exception.

We collated maps for roughly one-fifth of recorded marine species (34). While this analysis is the first attempt to show the geopolitical distribution of marine biodiversity across international

boundaries, substantial knowledge gaps remain, especially for offshore and deep-sea habitats. In particular, large and remote areas such as ABNJ and Antarctica likely harbor many more transboundary and single-jurisdiction species than indicated by this analysis. Collaboration around research and monitoring is a crucial element of transboundary conservation, as even research institutions in wealthy nations lack the resources required to explore and document marine biodiversity across a typical EEZ.

Holistic assessment of transboundary marine biodiversity requires integrating data across sectors and engagement beyond traditional academic sources of biodiversity data. If we are to provide reasonable baselines to enable meaningful environmental impact assessment and guide sustainable use of the ocean, military, industry and traditional sources of knowledge must be fused with scientific research data streams and fed into ocean observing frameworks (e.g. those provided by the Global Ocean Observing System). This requires increased and structural support for the Global Ocean Observing System and for its Regional Alliances through increased and targeted support for the Intergovernmental Oceanographic Commission of UNESCO. The opportunity to develop these partnerships and implement these structural changes is now, as part of the strategy for delivering on the goals of the UN Decade of Ocean Science for Sustainable Development. While fisheries biodiversity data remain very difficult to access, other industries have been more open to release of such information. After years of work, the International Seabed Authority has developed an MoU with the Intergovernmental Oceanographic Commission and released its database of contractor biodiversity data, which includes surveys of some of the deepest and most remote areas of the ocean floor. If we are to confront the global marine defaunation crisis and more effectively protect species across borders, incentives for engagement in ocean observation from sectors that typically do not participate in biodiversity conservation are critical.

Global maps of the political distribution of marine biodiversity help inform the need for better and broader reporting and governance of the more than 25,000 transboundary marine species. There are examples of successful conservation or management of transboundary biodiversity for some charismatic migratory species (e.g. humpback whales (35), some sea turtle populations (36), and fish stocks (e.g., Pacific halibut, some Northeast Pacific salmon stocks (37)). However, transboundary management of megavertebrates remains a central obstacle to their conservation with virtually all albatross and migratory sharks listed as threatened or near threatened, along with the majority of sea turtle populations (4). Transboundary fish stocks may be the most egregious example, with shared and highly migratory stocks experiencing twice the level of overfishing as those within a single jurisdiction (38).

Cooperative management regimes need to be strengthened and expanded to other marine species. Additionally, the need for conservation policy to address transboundary distributions will only become greater as climate change alters species' ranges, shifting ranges into (and out of) different countries, complicating existing conservation mechanisms for both transboundary and single-country species (7,8,19). We need to conceptualize the biodiversity crisis in the same way we understand climate change, as a truly global problem that requires coordinated global solutions. All countries—even if they are landlocked—are linked to the ocean via the provision of protein, raw materials, and climate regulation, and thus have an interest in protecting marine biodiversity. While persistent political tensions between countries (e.g. South China Sea, Persian Gulf, Baltic Sea) continue to impede conservation efforts, cooperation on biodiversity protection can also serve as a peace-building tool (17,39). Given the rapid declines of many marine species, conservation mechanisms must transcend political conflicts so they are robust to transient political fads. Although international cooperation is foundational to CBD (as it is core to the



founding Rio Principles), nations remain primarily focused on implementing conservation actions within their own borders. Our analysis shows it is imperative that the Strategic Plan for the UN Decade of Ocean Science, the new BBNJ treaty, and the next phase of global biodiversity commitments under the Post-2020 Global Biodiversity Framework incorporate effective mechanisms for transboundary cooperation to improve monitoring, reporting on, protection and governance of marine biodiversity.

## Materials and Methods

### *Experimental Design*

We aimed to advance knowledge of global marine species distributions by combining maps from the IUCN and AquaMaps, which host the two largest global databases of marine species range maps. The IUCN has published range maps for over 31,000 species (40). Experts review the maps and outline the spatial boundaries of each species' distribution, based on observation records and expert knowledge of occurrence and habitat preferences. Polygons are assigned one of six codes for species presence, ranging from extant to extinct in that area. Species are classified by the broad "system" they occur in (e.g. marine, freshwater, freshwater and marine) and then by finer habitat categories within those systems (e.g. Marine Neritic – Subtidal rock and rocky reefs). We used a series of filtering processes to select 9,916 predominantly marine species from the IUCN database. First, we used the systems and habitat information to select marine species, recognizing that these categories are ill-suited to many coastal species that occur in mangroves, estuaries, and intertidal zones and depend heavily on terrestrial, fresh and saltwater ecosystems. We removed all amphibians listed as "marine" (e.g. cane toad, *Rhinella marina*), which can adapt to saline environments but primarily inhabit and depend on freshwater ecosystems (41). We then used two additional filters for taxon groups that are particularly difficult to categorize based on ecosystem and habitat: for birds, we used the expert-reviewed list of seabirds compiled by BirdLife International, and for reptiles, we combined two lists of marine reptiles from peer-reviewed publications (42,43). We used only global range maps for each species, excluding the IUCN maps for subpopulations (most of which are sea turtles or marine mammals).

AquaMaps has generated 22,938 marine species distribution maps using models based on species-specific envelopes of environmental preference, which include variables such as temperature, depth, and salinity (44). The environmental envelopes are based on occurrence records and published databases such as FishBase (45) and OBIS (34), and the model overlays these preferences onto a map of environmental attributes. The result is a global 0.5° grid with a relative probability of occurrence for each species in each grid cell. A small proportion (12%) of the maps have been reviewed by experts. We selected plant and animal species, excluding chromists, protists, and bacteria because there were only 47 species maps available for these three kingdoms combined, indicating they were far from comprehensive.

In total, the two datasets provide range maps for 28,252 unique plant and animal species, with 4,033 occurring in both datasets. For these species, we elected to use the IUCN maps because they are expert reviewed and have a conservation status for each species (although many are listed as Data Deficient). Both mapping approaches make certain assumptions and will introduce errors of commission and omission, especially for poorly studied species and in deep waters where empirical data is lacking (17). Overall, there is strong agreement between IUCN and AquaMaps range maps for well-studied species (e.g. mammals), but both datasets contain discontinuities and errors; for instance, IUCN maps tend to overpredict coral presence in deep waters and the AquaMaps model tends to extrapolate ranges beyond known occurrences to a greater extent than the expert-reviewed IUCN maps (15).

We first created a map of maritime jurisdictions by combining all Antarctic EEZs into one jurisdiction, and all High Seas regions into the Areas Beyond National Jurisdiction (ABNJ). A number of EEZ boundaries are disputed; we identified the 13 contiguous disputed areas and labelled them as separate jurisdictions with the claiming sovereignties (except for the “Disputed South China Sea,” which is claimed by 11 nations) using the global EEZ map from [marineregions.org](http://marineregions.org).

To combine the AquaMaps and IUCN databases, we first created a lookup table of species present in both databases by performing several iterations of matching. We began with exact matches of scientific names, then compared the databases using lists of previous names or synonyms. Spelling is not always consistent even for the same name, so we compared the remaining species by genus name and manually checked similar names in online species databases ([marinespecies.org](http://marinespecies.org), [sealifebase.org](http://sealifebase.org), [fishbase.org](http://fishbase.org)). For the AquaMaps distributions, we first removed all species duplicated in the IUCN dataset, then for the remaining species we selected cells with at least 50% probability of occurrence and did not repeat the analysis with different probability of occurrence thresholds, as results of previous studies have shown that global scale results are robust to these thresholds (13–15). For the IUCN maps, we selected cells where each species is extant (presence = 1) and removed 57 maps of subpopulations from the data, considering only species' global distributions.

We analyzed the AquaMaps and IUCN datasets separately at their respective resolutions, before rasterizing both spatial grids and reprojecting the 0.5° AquaMaps grid to the higher resolution IUCN raster using nearest neighbor assignment to preserve cell values. We then overlaid the grids onto the map of jurisdictions. To analyze the distribution of species across jurisdictions, we first calculated the number of jurisdictions in which each species occurs, and compared patterns across broad taxonomic groupings (vertebrates, invertebrates, plants) and IUCN threat statuses. For a species to occur in a jurisdiction, we used a cut-off of 10 cells (1,000km<sup>2</sup>) or at least 10% of a species' total range falling in that jurisdiction. Ten coastal or semi-aquatic species with small or medium-sized distributions did not meet either criteria; for these species, we included all jurisdictions overlapping their ranges. We then calculated the number of single-jurisdiction (n=1) and transboundary (n>1) species occurring in each jurisdiction. To map the distributions of transboundary species globally, we calculated the number of species occurring in each grid cell. We conducted two sensitivity analyses for occurrence thresholds: one with no cut-off for occurring in a jurisdiction, and a second using a cut-off of five percent of a species' total range or 10 cells in a jurisdiction. Results were similar for the five percent and 10 cell scenarios; we chose the latter for the final analysis because many marine species have extremely large ranges, thus, five percent of their range could encompass an entire jurisdiction, if not multiple jurisdictions.

### ***Statistical Analysis***

Effectively managing large numbers of transboundary marine species is a major governance challenge. We used information on six governance indicators from the World Bank to explore correlations between countries' governance capacity and transboundary species richness in their marine estates. We used the "WDI" package in R to pull the six governance indicators for each country and year (1996-2018). We then filled missing scores with the closest year available, calculated the average score for each country in 2018, and scaled the composite score from 0-1. For overseas territories that do not have individual governance scores, we substituted the sovereign country's score, recognizing this score often does not accurately reflect the actual governance capacity of the territory (e.g. the many French territories in the Indian Ocean). Seventeen jurisdictions do not have governance scores: Antarctica, the ABNJ, Ascension, Western Sahara, and the 13 disputed jurisdictions. We used Pearson's correlation tests and found

no significant correlation between governance score and number of transboundary species for the 209 jurisdictions with WGI scores ( $r = -0.0479$ ,  $p = 0.488$ ), or for the 161 sovereign nations with overseas territories excluded ( $r = 0.0011$ ,  $p = 0.988$ ).

## H2: Supplementary Materials

Materials and Methods

Figure S1

Tables S1-S2

## References and Notes

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## Acknowledgments

**General:** We thank Cristina Garilao and Kristin Kaschner for providing access to the AquaMaps database, and Scott Atkinson for assistance with processing spatial data.



**Funding:** CJK was funded by a University of Queensland Fellowship and the Australian Research Council.

**Author contributions:** Authors are listed in order of contribution, apart from the senior author (RKR). LAR, BSH, CJK, CDK, BW, HSG, JCM, RKR, JEMW and MRF conceptualized the study. LAR analysed the data. CO made substantial contributions to the code and assisted with data access and preparation. LAR, BSH, CJK, JEMW, CO, MRF, and RKR conceptualised and designed the figures. LAR produced the figures, with help from BW in the preparation of Figure 3. LAR wrote the text, with substantial editorial input from BSH, JEMW, DCD, and RKR. All authors made editorial contributions to the final text.

**Competing interests:** Authors declare no competing interests.

**Data and materials availability:** Two primary databases were used in this study: The publicly available IUCN Redlist of Threatened Species (<https://www.iucnredlist.org>; link provided in the manuscript text) and the AquaMaps database (Kaschner, K. et al. AquaMaps: Predicted range maps for aquatic species. World wide web electronic publication Version 08/2016 (2016). Available upon request at: [www.aquamaps.org](http://www.aquamaps.org)). All figures and tables in the text and supplementary material have associated raw data. These data will be made available as csv files on a publicly accessible repository ([figshare.com](http://figshare.com)). We used two additional public and freely available databases: maps of global maritime boundaries ([marineregions.org](http://marineregions.org)) and World Governance Indicators from the World Bank, accessed via the R packages "WDI" and "wbstats." All analyses were conducted in the free software R (version 3.6.0). The code used to produce the figures and tables will be provided as R Markdown files in the public figshare repository.

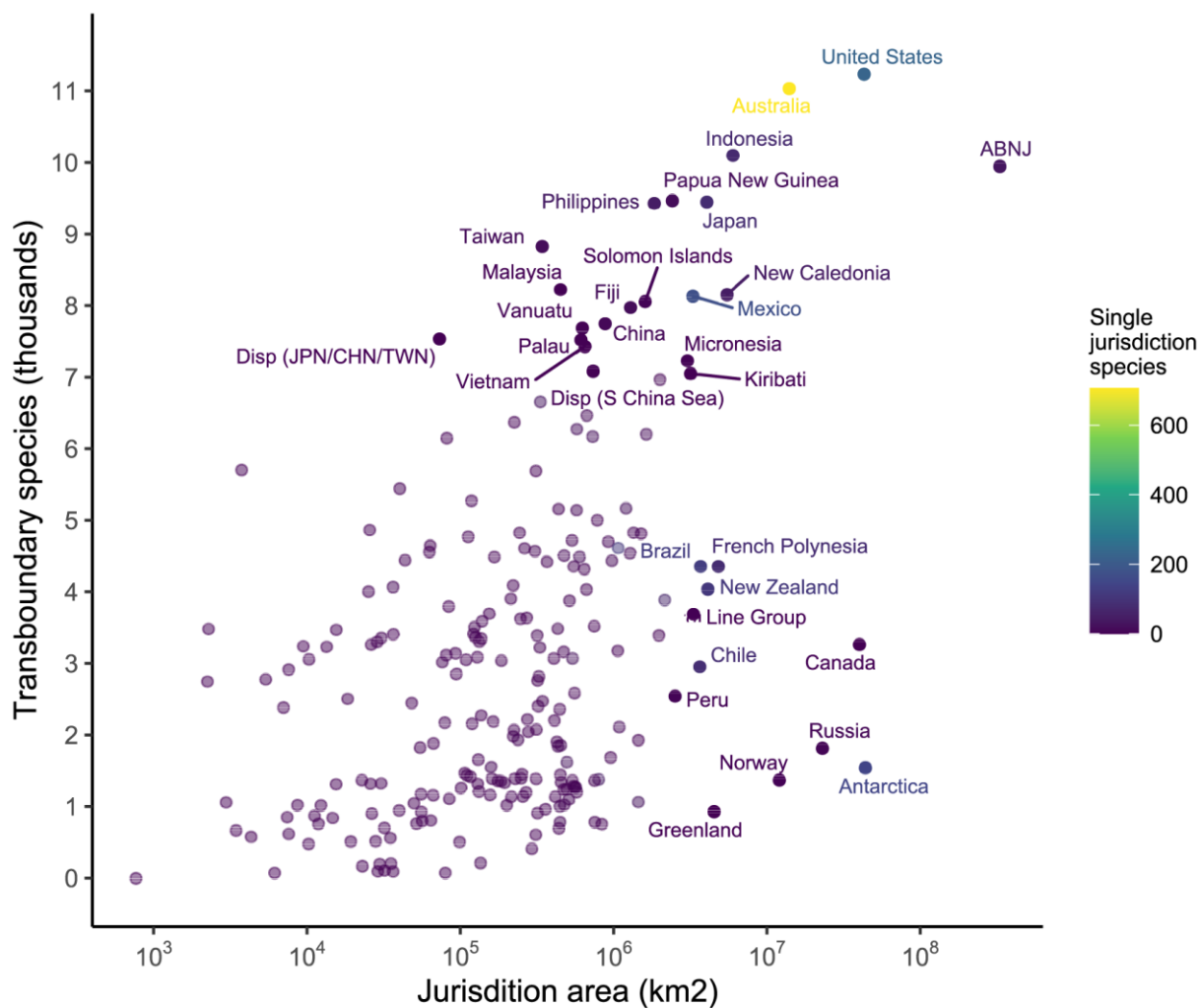
## Figures and Tables

**Fig. 1. Species' conservation statuses and number of jurisdictions overlapping their distributions.** Colored bars show the proportions of each taxonomic group in each IUCN threat category (CR = Critically Endangered, EN = Endangered, VU = Vulnerable, NT = Near Threatened, LC = Least Concern, DD = Data Deficient, NA = not assessed) and range of jurisdictions. Taxonomic groups are ordered by descending number of species. Threatened (CR, EN, VU) species are shown at the top.

**Fig. 2. Number of species per jurisdiction.** Color corresponds to the number of threatened (Critically Endangered, Endangered, or Vulnerable) transboundary species and size corresponds to jurisdiction area (larger dots represent larger areas). All 228 jurisdictions are shown, with labels for jurisdictions ranking in the top 25 for number of transboundary or single jurisdiction species.

**Fig. 3. Transboundary species richness.** Maps of the number of transboundary species richness (A) per grid cell and (B) per jurisdiction.

## Supplementary Materials



**Fig. S1: Transboundary species per area.** Number of transboundary species compared to area of jurisdiction (km<sup>2</sup>), shown on a log<sub>10</sub> transformed scale. Labels show jurisdictions ranking in the top 20 for number of transboundary species or for area of jurisdiction. Dis = Disputed territory.

**Table S1.**

**Species conservation status and taxonomic information.** The top 100 species are shown, ranked by number of jurisdictions (Jur.) they occur in. Red List categories (Cat.) are CR = Critically Endangered, EN = Endangered, VU = Vulnerable, NT = Near Threatened, LC = Least Concern, DD = Data Deficient, None = Not assessed.

Rank	Species name	Jur.	Cat.	Species group	Class
1	<i>Orcinus orca</i>	220	DD	Mammals	Mammalia
2	<i>Balaenoptera acutorostrata</i>	211	LC	Mammals	Mammalia
3	<i>Tursiops truncatus</i>	211	LC	Mammals	Mammalia
4	<i>Physeter macrocephalus</i>	210	VU	Mammals	Mammalia
5	<i>Alopias vulpinus</i>	205	VU	Sharks, Rays, Chimaeras	Chondrichthyes
6	<i>Ziphius cavirostris</i>	204	LC	Mammals	Mammalia
7	<i>Eretmochelys imbricata</i>	203	CR	Reptiles	Reptilia
8	<i>Grampus griseus</i>	202	LC	Mammals	Mammalia
9	<i>Megaptera novaeangliae</i>	201	LC	Mammals	Mammalia
10	<i>Xiphias gladius</i>	201	LC	Fish (ray & lobe-finned)	Actinopterygii
11	<i>Pseudorca crassidens</i>	200	NT	Mammals	Mammalia
12	<i>Microlophichthys microlophus</i>	200	LC	Fish (ray & lobe-finned)	Actinopterygii
13	<i>Pyroteuthis margaritifera</i>	199	None	Mollusks	Cephalopoda
14	<i>Argyropelecus hemigymnus</i>	198	LC	Fish (ray & lobe-finned)	Actinopterygii
15	<i>Carcharodon carcharias</i>	197	VU	Sharks, Rays, Chimaeras	Chondrichthyes
16	<i>Pteroplatytrygon violacea</i>	197	LC	Sharks, Rays, Chimaeras	Chondrichthyes
17	<i>Remora remora</i>	197	LC	Fish (ray & lobe-finned)	Actinopterygii
18	<i>Balaenoptera musculus</i>	196	EN	Mammals	Mammalia
19	<i>Prionace glauca</i>	196	NT	Sharks, Rays, Chimaeras	Chondrichthyes
20	<i>Isurus oxyrinchus</i>	195	EN	Sharks, Rays, Chimaeras	Chondrichthyes
21	<i>Katsuwonus pelamis</i>	195	LC	Fish (ray & lobe-finned)	Actinopterygii
22	<i>Istiophorus platypterus</i>	195	LC	Fish (ray & lobe-finned)	Actinopterygii
23	<i>Stenella coeruleoalba</i>	194	LC	Mammals	Mammalia
24	<i>Steno bredanensis</i>	192	LC	Mammals	Mammalia
25	<i>Cyclothone braueri</i>	192	LC	Fish (ray & lobe-finned)	Actinopterygii
26	<i>Ctenopteryx sicula</i>	190	None	Mollusks	Cephalopoda
27	<i>Haliphron atlanticus</i>	189	None	Mollusks	Cephalopoda
28	<i>Walvisteuthis virilis</i>	189	None	Mollusks	Cephalopoda
29	<i>Lucifer typus</i>	187	None	Arthropods	Malacostraca
30	<i>Ulva lactuca</i>	187	None	Algae	Ulvophyceae
31	<i>Vitreledonella richardi</i>	187	None	Mollusks	Cephalopoda
32	<i>Anoplogaster cornuta</i>	187	LC	Fish (ray & lobe-finned)	Actinopterygii

**Table S1 continued**

33	<i>Cyclothone pseudopallida</i>	187	LC	Fish (ray & lobe-finned)	Actinopterygii
34	<i>Onychoteuthis banksii</i>	186	None	Mollusks	Cephalopoda
35	<i>Chauliodus sloani</i>	186	LC	Fish (ray & lobe-finned)	Actinopterygii
36	<i>Cranchia scabra</i>	185	None	Mollusks	Cephalopoda
37	<i>Lagocephalus lagocephalus</i>	185	LC	Fish (ray & lobe-finned)	Actinopterygii
38	<i>Melanocetus johnsonii</i>	185	LC	Fish (ray & lobe-finned)	Actinopterygii
39	<i>Sigmops elongatus</i>	184	None	Fish (ray & lobe-finned)	Actinopterygii
40	<i>Cryptopsaras couesii</i>	184	LC	Fish (ray & lobe-finned)	Actinopterygii
41	<i>Balaenoptera borealis</i>	183	EN	Mammals	Mammalia
42	<i>Ulva clathrata</i>	182	None	Algae	Ulvophyceae
43	<i>Octopoteuthis sicula</i>	182	None	Mollusks	Cephalopoda
44	<i>Kogia breviceps</i>	182	DD	Mammals	Mammalia
45	<i>Carcharhinus longimanus</i>	182	VU	Sharks, Rays, Chimaeras	Chondrichthyes
46	<i>Cyclothone pallida</i>	182	LC	Fish (ray & lobe-finned)	Actinopterygii
47	<i>Chaenophryne ramifera</i>	182	LC	Fish (ray & lobe-finned)	Actinopterygii
48	<i>Vampyroteuthis infernalis</i>	181	None	Mollusks	Cephalopoda
49	<i>Sternoptyx diaphana</i>	180	None	Fish (ray & lobe-finned)	Actinopterygii
50	<i>Scopeloberyx opisthopterus</i>	179	None	Fish (ray & lobe-finned)	Actinopterygii
51	<i>Melamphaes polylepis</i>	179	None	Fish (ray & lobe-finned)	Actinopterygii
52	<i>Bolitaena pygmaea</i>	179	None	Mollusks	Cephalopoda
53	<i>Kogia sima</i>	179	DD	Mammals	Mammalia
54	<i>Chaenophryne longiceps</i>	179	LC	Fish (ray & lobe-finned)	Actinopterygii
55	<i>Ceratias holboelli</i>	179	LC	Fish (ray & lobe-finned)	Actinopterygii
56	<i>Liguriella podophthalma</i>	178	None	Mollusks	Cephalopoda
57	<i>Cunina octonaria</i>	178	None	Cnidarians & Ctenophores	Hydrozoa
58	<i>Coryphaena hippurus</i>	178	LC	Fish (ray & lobe-finned)	Actinopterygii
59	<i>Alopias superciliosus</i>	178	VU	Sharks, Rays, Chimaeras	Chondrichthyes
60	<i>Notolychnus valdiviae</i>	178	LC	Fish (ray & lobe-finned)	Actinopterygii
61	<i>Melanostomias niger</i>	177	None	Fish (ray & lobe-finned)	Actinopterygii
62	<i>Phyllodoce madeirensis</i>	177	None	Worms & microscopic animals	Polychaeta
63	<i>Mesoplodon densirostris</i>	177	DD	Mammals	Mammalia
64	<i>Cyclothone acclinidens</i>	177	LC	Fish (ray & lobe-finned)	Actinopterygii
65	<i>Valenciennellus tripunctulatus</i>	176	None	Fish (ray & lobe-finned)	Actinopterygii
66	<i>Gennadas scutatus</i>	176	None	Arthropods	Malacostraca
67	<i>Thysanoteuthis rhombus</i>	176	None	Mollusks	Cephalopoda
68	<i>Liocranchia reinhardti</i>	176	None	Mollusks	Cephalopoda
69	<i>Polycheles typhlops</i>	176	LC	Arthropods	Malacostraca
70	<i>Eurypharynx pelecanooides</i>	176	LC	Fish (ray & lobe-finned)	Actinopterygii

**Table S1 continued**

71	<i>Eustomias dendriticus</i>	175	None	Fish (ray & lobe-finned)	Actinopterygii
72	<i>Echeneis naucrates</i>	175	LC	Fish (ray & lobe-finned)	Actinopterygii
73	<i>Bentheogennema intermedia</i>	174	None	Arthropods	Malacostraca
74	<i>Gelidium pusillum</i>	174	None	Algae	Florideophyceae
75	<i>Didemnum candidum</i>	174	None	Tunicates	Ascidacea
76	<i>Ommastrephes bartramii</i>	174	None	Mollusks	Cephalopoda
77	<i>Glycera tessellata</i>	174	None	Worms & microscopic animals	Polychaeta
78	<i>Cyclothone alba</i>	174	LC	Fish (ray & lobe-finned)	Actinopterygii
79	<i>Lobianchia gemellarii</i>	174	LC	Fish (ray & lobe-finned)	Actinopterygii
80	<i>Nemichthys scolopaceus</i>	173	None	Fish (ray & lobe-finned)	Actinopterygii
81	<i>Systellaspis debilis</i>	173	None	Arthropods	Malacostraca
82	<i>Japetella diaphana</i>	173	None	Mollusks	Cephalopoda
83	<i>Remora osteochir</i>	173	LC	Fish (ray & lobe-finned)	Actinopterygii
84	<i>Sergia japonica</i>	172	None	Arthropods	Malacostraca
85	<i>Sandalops melancholicus</i>	172	None	Mollusks	Cephalopoda
86	<i>Lysidice collaris</i>	172	None	Worms & microscopic animals	Polychaeta
87	<i>Globicephala macrorhynchus</i>	172	LC	Mammals	Mammalia
88	<i>Euprotomicrus bispinatus</i>	172	LC	Sharks, Rays, Chimaeras	Chondrichthyes
89	<i>Taaningichthys bathyphilus</i>	172	LC	Fish (ray & lobe-finned)	Actinopterygii
90	<i>Scopelarchus analis</i>	172	LC	Fish (ray & lobe-finned)	Actinopterygii
91	<i>Ranzania laevis</i>	171	None	Fish (ray & lobe-finned)	Actinopterygii
92	<i>Gnathophausia zoea</i>	171	None	Arthropods	Malacostraca
93	<i>Stenella attenuata</i>	171	LC	Mammals	Mammalia
94	<i>Mobula birostris</i>	171	VU	Sharks, Rays, Chimaeras	Chondrichthyes
95	<i>Malacosteus niger</i>	170	None	Fish (ray & lobe-finned)	Actinopterygii
96	<i>Bathothauma lyromma</i>	170	None	Mollusks	Cephalopoda
97	<i>Pterygioteuthis giardi</i>	170	None	Mollusks	Cephalopoda
98	<i>Manta birostris</i>	169	None	Sharks, Rays, Chimaeras	Elasmobranchii
99	<i>Systellaspis pellucida</i>	169	None	Arthropods	Malacostraca
100	<i>Balaenoptera brydei</i>	169	None	Mammals	Mammalia



**Table S2.**

**Transboundary species per jurisdiction.** The top 100 jurisdictions are shown, ranked by number of transboundary (TB) species. TB Thr = Threatened (Critically Endangered, Endangered, Vulnerable) species, Single Jur = single jurisdiction species, Rank spp/area = rank out of all 228 jurisdictions for number of transboundary species per km<sup>2</sup>. Composite World Governance Indicator score is scaled 0-1 (1 = best governance score)

Jurisdiction	Number of species			Rank TB	Rank spp/km <sup>2</sup>	Area (km <sup>2</sup> )	WGI score
	TB	TB Thr	Single Jur				
United States	11234	141	231	1	222	42,956,219	0.748
Australia	11033	222	706	2	220	13,913,692	0.815
Indonesia	10099	305	75	3	204	5,947,885	0.473
ABNJ	9946	125	31	4	228	329,586,795	NA
Papua New Guinea	9469	237	17	5	166	2,407,382	0.384
Japan	9450	207	82	6	188	4,040,612	0.768
Philippines	9431	276	45	7	151	1,835,028	0.433
Taiwan	8827	193	17	8	60	342,997	0.723
Malaysia	8226	274	1	9	75	451,797	0.595
New Caledonia	8154	142	45	10	207	5,487,212	0.723
Mexico	8133	107	174	11	185	3,284,660	0.429
Solomon Isl	8058	189	5	12	154	1,609,757	0.457
Fiji	7974	135	18	13	140	1,293,036	0.542
China	7750	106	11	14	115	878,364	0.439
Vanuatu	7689	123	4	15	97	622,073	0.519
Disp (JPN/CHN/TWN)	7538	151	0	16	24	73,343	NA
Palau	7524	116	1	17	96	608,167	0.558
Vietnam	7429	173	1	18	101	647,232	0.429
Micronesia	7229	153	3	19	186	3,011,912	0.568
Disp (S China Sea)	7084	120	1	20	108	736,364	NA
Kiribati	7051	114	0	21	192	3,165,351	0.565
Marshall Isl	6969	110	4	22	170	2,004,593	0.473
Panama	6655	80	28	23	69	332,644	0.520
Tonga	6465	78	10	24	107	668,054	0.552
Nicaragua	6369	68	0	25	50	223,935	0.317
Costa Rica	6274	82	17	26	102	576,132	0.617
India	6204	144	12	27	167	1,637,706	0.479
Colombia	6172	89	20	28	119	730,703	0.464
Disp (AUS/IND/TLS)	6148	123	0	29	31	81,421	NA
Disp (AUS/PNG)	5702	145	0	30	2	3,740	NA

**Table S2 continued**

Nauru	5689	31	0	31	74	310,565	0.494
East Timor	5444	227	0	32	16	40,226	0.409
Guatemala	5276	66	0	33	41	118,336	0.379
Madagascar	5169	122	20	34	163	1,205,825	0.349
Howland Isl & Baker Isl	5160	33	0	35	100	437,862	0.748
Mozambique	5144	130	8	36	113	574,410	0.344
Somalia	5003	102	1	37	139	784,502	0.077
Brunei	4866	230	0	38	13	25,698	0.624
Seychelles	4827	105	5	39	168	1,340,839	0.572
Tanzania	4826	94	2	40	70	243,130	0.390
Tuvalu	4815	115	0	41	175	1,502,551	0.562
Kenya	4771	95	2	42	43	112,400	0.386
Sri Lanka	4720	133	2	43	114	534,085	0.471
Maldives	4701	84	5	44	152	922,110	0.401
Mayotte	4648	93	0	45	32	63,362	0.723
South Africa	4613	98	111	46	162	1,069,378	0.526
Wallis & Futuna	4609	72	1	47	77	262,864	0.723
Thailand	4571	226	4	48	83	306,891	0.445
Juan de Nova Isl	4558	89	0	49	33	62,551	0.723
Mauritius	4542	110	8	50	169	1,280,068	0.653
Venezuela	4509	68	9	51	109	473,325	0.151
Bahamas	4491	69	13	52	127	597,705	0.620
Comoro Isl	4488	95	1	53	56	165,505	NA
Glorioso Isls	4443	87	0	54	25	43,699	0.723
NMariana Isls & Guam	4435	90	7	55	157	976,203	0.748
Cuba	4421	62	2	56	99	365,756	0.408
Yemen	4357	120	2	57	123	548,014	0.101
Brazil	4356	83	123	58	211	3,672,584	0.452
French Polynesia	4355	77	81	59	217	4,795,468	0.723
British Indian Ocean Territory	4319	102	3	60	136	642,745	0.767
Honduras	4091	56	1	61	72	219,971	0.374
Belize	4069	57	9	62	22	36,250	0.442
New Zealand	4039	64	111	63	215	4,106,954	0.862
Andaman & Nicobar	4035	102	4	64	142	663,520	0.479
Aruba	4005	60	1	65	14	25,214	0.738
Puerto Rico & Virgin Isl	3906	60	2	66	73	212,193	0.748
Ecuador	3889	58	65	67	199	2,159,837	0.420
Myanmar	3880	136	4	68	126	514,147	0.312

**Table S2 continued**

Disp (JPN/KOR)	3798	49	0	69	40	83,761	NA
Turks & Caicos Isl	3699	57	0	70	64	154,242	0.767
Line Group	3690	58	0	71	212	3,311,931	0.565
Dominican Republic	3640	55	0	72	88	270,774	0.452
Jamaica	3627	52	0	73	85	246,488	0.549
Guadeloupe & Martinique	3593	56	3	74	59	138,683	0.723
Phoenix Group	3522	71	1	75	155	748,009	0.565
Haiti	3510	54	4	76	51	123,867	0.273
Norfolk Isl	3488	52	4	77	122	432,638	0.815
Oecussi Ambeno	3485	28	0	78	1	2,276	0.409
St Lucia	3473	50	0	79	11	15,560	0.615
Bassas da India	3414	26	0	80	54	122,177	0.723
St Vincent & Grenadines	3410	51	0	81	26	36,511	0.613
Cook Isls	3395	65	3	82	203	1,972,843	0.516
Reunion	3394	94	4	83	103	316,499	0.685
Ile Europa	3369	28	0	84	57	125,624	0.723
Curacao	3359	32	2	85	23	30,535	0.663
Guyana	3351	40	0	86	62	136,910	0.458
Samoa	3307	92	0	87	61	132,306	0.630
Dominica	3303	53	0	88	20	28,749	0.596
Canada	3266	60	0	89	225	39,886,598	0.818
Grenada	3265	54	0	90	18	26,282	0.556
Saba	3243	52	0	91	7	9,484	0.663
Bonaire	3235	31	0	92	10	13,391	0.663
Christmas Isl	3225	28	1	93	106	330,036	0.815
Palmyra Atoll	3179	41	0	94	176	1,059,726	0.748
Cocos Isl	3166	49	1	95	135	470,117	0.815
Anguilla	3145	56	0	96	47	92,654	0.669
British Virgin Isl	3120	59	0	97	45	80,529	0.767
Suriname	3089	42	0	98	63	128,363	0.461
Oman	3072	73	21	99	145	538,980	0.528
American Samoa	3071	93	0	100	125	406,816	0.685