

1 Title: Multinational coordination required for conservation of at least 90% of marine species**2 Abstract**

3 Marine species are declining at an unprecedented rate, catalyzing many nations to adopt conservation and
4 management targets within their jurisdictions. However, marine species and the biophysical processes that
5 sustain them are naive to international borders. An understanding of the prevalence of cross-border species
6 distributions is important for informing high-level conservation strategies, such as bilateral or regional
7 agreements. Here, we examined 28,252 distribution maps to determine the number and locations of
8 transboundary marine plants and animals. Over 90% of species have ranges spanning at least two
9 jurisdictions, with 58% covering more than ten jurisdictions. All jurisdictions have at least one
10 transboundary species, with the highest concentrations of transboundary species in the USA, Australia,
11 Indonesia, and the Areas Beyond National Jurisdiction. Distributions of mapped biodiversity indicate that
12 overcoming the challenges of multinational governance is critical for a much wider suite of species than
13 migratory megavertebrates and commercially exploited fish stocks—the groups that have received the
14 vast majority of multinational management attention. To effectively protect marine biodiversity,
15 international governance mechanisms (particularly those related to the Convention on Biological
16 Diversity, the Convention on Migratory Species, and Regional Seas Organizations) must be expanded to
17 promote multinational conservation planning, and complimented by a holistic governance framework for
18 biodiversity beyond national jurisdiction.

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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 movements cross administrative boundaries, especially in the marine environment where boundaries are permeable and connectivity is high. For example, larvae can disperse hundreds of kilometers (Ramesh et al., 2019) 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 (CBD, 2011). 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 (Dunn et al., 2019; Studds et al., 2017), intense harvesting pressure of particular species along arbitrarily located management boundaries (Song et al., 2017), and relaxation of conservation policy in neighboring jurisdictions (Gjerde, 2012). 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 (Burden & Fujita, 2019; Hobday et al., 2015).

Transboundary natural resource management ("transboundary management") is defined as any process of collaboration across boundaries that increases the effectiveness of attaining natural resource management or biodiversity conservation goals (van der Linde et al., 2002). Many forms of transboundary management already exist in the marine space. Usually, individual countries respond to

some sort of multilateral body, as is the case with the CBD, governance of World Heritage Sites, the Coral Triangle Initiative, management of straddling fish stocks) (Crespo et al., 2019; P. Mackelworth, 2012; Morrison et al., 2020). The legal foundation for transboundary management 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 (such as the CBD, Convention on Migratory Species, UN Food and Agriculture Organization, and Regional Seas Organizations under the UN Environment Programme) (Ardron et al., 2014; Cullis-Suzuki & Pauly, 2010; Warner, 2014).

So far, these mechanisms have focused on particular threats to the marine environment or small subsets of marine biodiversity. For example, Regional Seas Programmes offer a regional approach to transboundary management of marine biodiversity (*Regional Seas Programmes*, 2020), but have been largely focused on pollution and management within jurisdictions (Gjerde, 2012). Most other initiatives focus on highly migratory or mobile species (e.g., instruments under the Convention on Migratory Species), charismatic megafauna (e.g., the International Whaling Convention), or commercially valuable species (e.g., the five regional fisheries organizations that manage tuna). Many charismatic megafauna and commercially valuable species are also highly migratory, and the need for multi-national management of these species is clear (Harrison et al., 2018). However, only a small fraction of marine biodiversity falls into these categories. Migrations are not the only way in which species are connected across their distributions; even sessile or non-migratory species can be impacted by threats such as overexploitation, noise, debris, or coastal runoff that occur in another part of their distribution (Gregory, 2009; Ramesh et al., 2019; Slabbeekoor et al., 2010).

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) (United Nations, 2020). The

solutions being offered in the draft BBNJ agreement 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) (Vierros & Harden-Davies, 2020). Thus, while there is consensus that effective management of many marine species requires new conservation goals that foster multinational coordination among sovereign nations (Crespo et al., 2019; Dunn et al., 2019; Gjerde, 2012; Kark et al., 2015), 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.

Materials and Methods

Species maps

We combined maps from the IUCN and AquaMaps, which host the two largest global databases of marine species range maps and represent approximately one-fifth of the marine species listed in the Ocean Biogeographic Information System (OBIS) database (OBIS, 2020). The IUCN has published range maps for over 31,000 terrestrial, aquatic, and marine species (IUCN, 2019). 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. This analysis focuses on predominantly marine species, although we recognize that the marine and terrestrial 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 used a series of automated and manual filtering processes to select 9,916 predominantly marine species from the IUCN database. The IUCN classifies species 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). First, we used the systems and habitat information

to select marine species. 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 (Hopkins & Brodie, 2015). 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 peer-reviewed lists of marine reptiles (Elfes et al., 2013; Rasmussen et al., 2011). We considered only species' global distributions, removing 57 maps of subpopulations from the data (most of which are sea turtles or mammals), and then selected cells where each species is extant (presence = 1).

AquaMaps has 22,938 marine species distribution maps in 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 excluded chromatists, protists, and bacteria because there were only 47 species maps available for these three kingdoms combined. For the plant and animal species, we selected cells with at least 50% probability of occurrence as a moderate threshold for species' occurrence in a cell, recognizing that thresholding can introduce inflated estimates of species richness (Guillera-Arroita et al., 2015). Results of previous studies have shown that global scale results are robust to different probability of occurrence thresholds (Jones et al., 2018; O’Hara et al., 2017; Selig et al., 2014).

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, sealifebase.org, fishbase.org). 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). Our final dataset included 18,352 (65.0%) AquaMaps and 9,900 (35.0%) IUCN maps (Supplementary Figure 1).

Both mapping approaches make assumptions and will introduce errors of commission and omission, especially for poorly studied species where empirical data is lacking (Supplementary Information 1). 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 (O’Hara et al., 2017). However, overall there is strong agreement between IUCN and AquaMaps range maps especially for well-studied species (e.g. mammals) (O’Hara et al., 2017).

Ocean jurisdictions

To analyze the distribution of species across jurisdictions, 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. Next, we overlaid the combined species map onto a map of maritime jurisdictions from marineregions.org, which we adjusted 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).

We then 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 ($1,000\text{km}^2$) 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 (10 cells or 10% of their range in a jurisdiction); 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.

Sensitivity analyses

We tested six alternate scenarios to explore the sensitivity of the results to different cutoffs for whether a species occurs in a cell and whether it occurs in a jurisdiction. First, we considered two alternate scenarios for occurrence in a jurisdiction: one with no cut-off, and a second using a cut-off of five percent of a species' total range or 10 cells in a jurisdiction. Results for the proportion of species that are transboundary differed by less than 1% between 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. The 10 cell cut-off was the most conservative threshold for determining if a species was transboundary, but compared to the no-cutoff scenario, the proportion of species considered to be transboundary only decreased by 1.9%. Next, we explored the sensitivity of the results to different probability of occurrences for species in the AquaMaps database. We tested 10, 40, 60, and 90% probability of occurrence thresholds, maintaining the 10 cell jurisdictional cutoff. Moving from the most conservative (90%) threshold to the least conservative (10%) threshold only increased the total proportion of transboundary species by 2.0%.

Country governance scores

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 where the greatest transboundary species richness occurs compared to countries' potential capacity to monitor and manage biodiversity, recognizing that wealth and governance capacity does not indicate whether there is political will to implement conservation actions (Morrison et al., 2020). We used the "WDI" and "wbstats" packages in R (version 3.6.0) 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 ($r = -0.0479, p = 0.488, 95\% \text{ CI } [-0.1819, 0.0877]$), or for the 161 sovereign nations with overseas territories excluded ($r = 0.0011, p = 0.988, 95\% \text{ CI } [-0.1526, 0.1548]$).

Results

We used 28,252 available species maps from the two largest global databases of marine plant and animal distributions, recognizing that coverage is geographically and taxonomically uneven. Large vertebrates have the best representation, with range maps available for close to 100% of chondrichthyans, vascular plants (mangroves and seagrasses), mammals, reptiles, and seabirds (Figure 1). Compared to vertebrates and vascular plants, coverage is much poorer for invertebrate chordates (jawless fish, lancelets, and tunicates), invertebrates, and red and green algae (Supplementary Table 1). Many of the invertebrate groupings are polyphyletic (for example, worms and microscopic animals includes approximately 16 phyla). The polyphyletic groups encompass a wide variety of species that are genetically disparate compared to the well-studied classes of vertebrates. Many of these group classifications are under debate even at high taxonomic levels, such as a phylum.

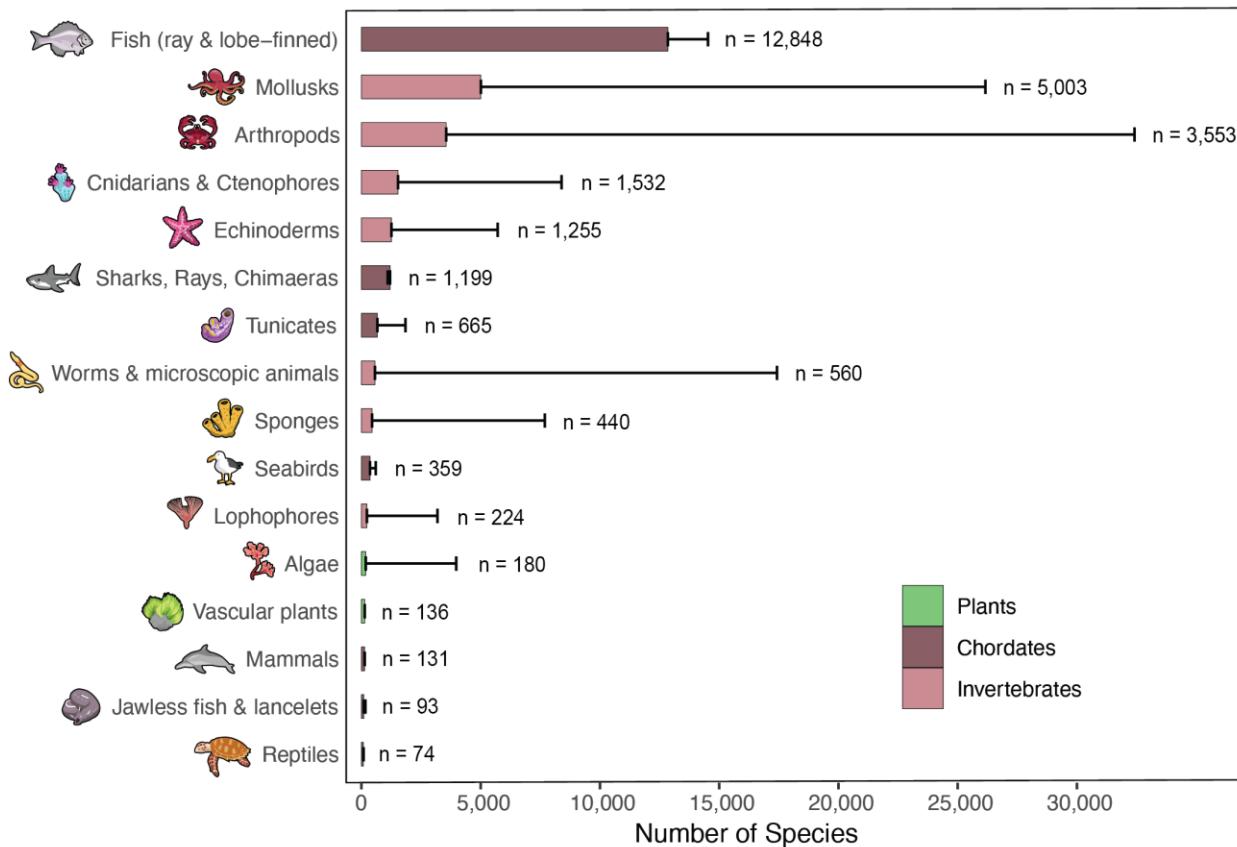


Figure 1: Number of species range maps in the combined IUCN and AquaMaps databases (bars)

compared to the number of confirmed species listed in the OBIS database (lines). Color indicates whether species are plants, chordates, or invertebrates. Bars are labeled with the number of range maps included in the analysis. Species groups are ordered by descending proportion of recorded species that have range maps.

Only 10% of all mapped marine species assessed occupied a single jurisdiction (i.e. endemics, Figure 2), 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 (Figure 3). 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 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.

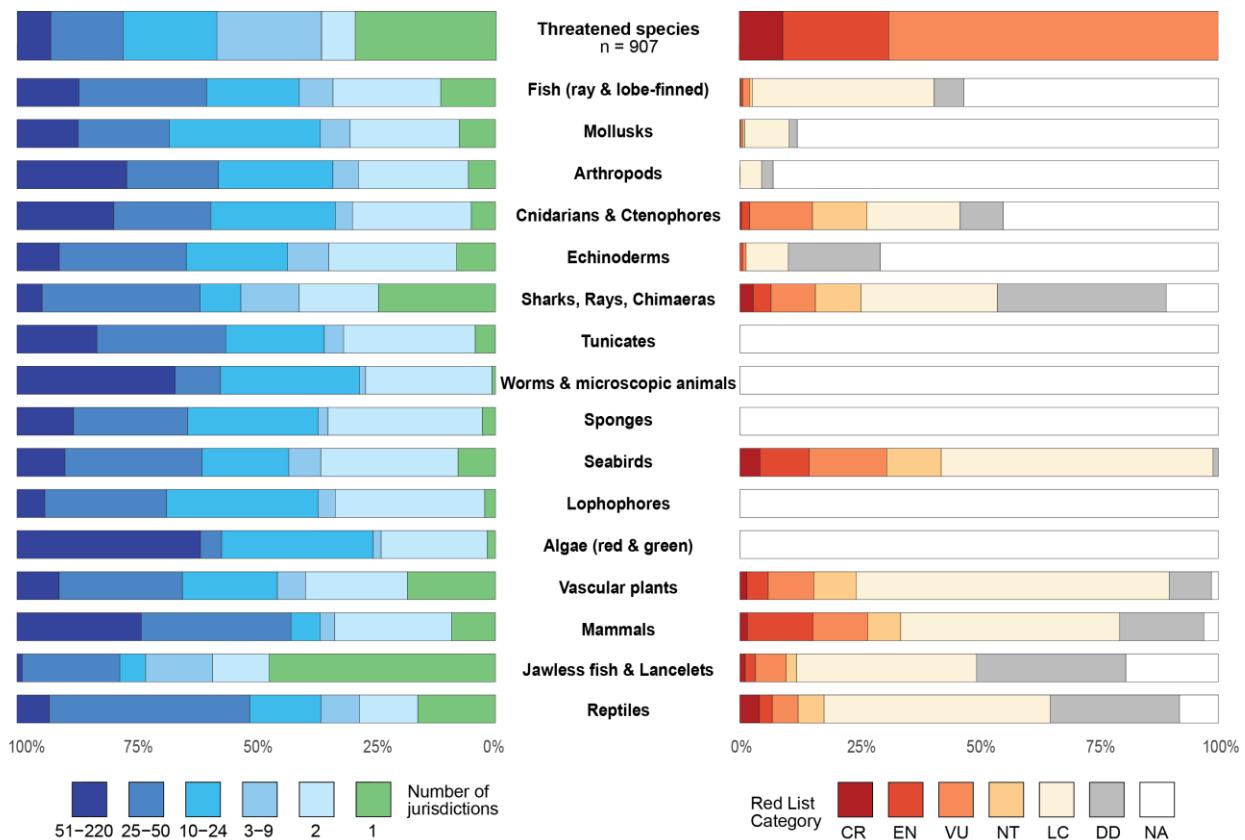


Figure 2: Species' conservation statuses and number of jurisdictions overlapping their distributions.

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 mapped 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 (Figure 2). A species with sessile or small-ranged individuals can still be highly transboundary if the species is cosmopolitan or occurs in an area with many smaller jurisdictions. Likewise, mobile individuals can be endemic to a jurisdiction that covers a large area. For example, a comparatively high proportion of chondrichthyans (sharks, rays, chimaeras) are endemic to large (and relatively well-studied) EEZs such as Australia, South Africa, and the US (Derrick et al., 2020). Other taxonomic groups with proportionally fewer transboundary species are jawless fish and lancelets, vascular plants (seagrasses and mangroves), and reptiles. These groups have few species, often occur in large EEZs (e.g., most of the reptiles are marine snakes that are endemic to Australia, Indonesia, and the Philippines), and many do not have a pelagic larval stage, which is the dominant propagation strategy for marine species (Cavalcanti & Gallo, 2008; Elfes et al., 2013; Kon et al., 2006; Spalding, 2010; Spalding et al., 2003).

In contrast, most of the species with distributions spanning the highest number of jurisdictions are large-bodied, highly mobile or migratory vertebrates (e.g., cetaceans, sea turtles) and commercially valuable fish (e.g., tunas and billfish, pelagic sharks) (Supplementary Table 2). 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 (Purvis et al., 2000; Reynolds et al., 2005), 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.

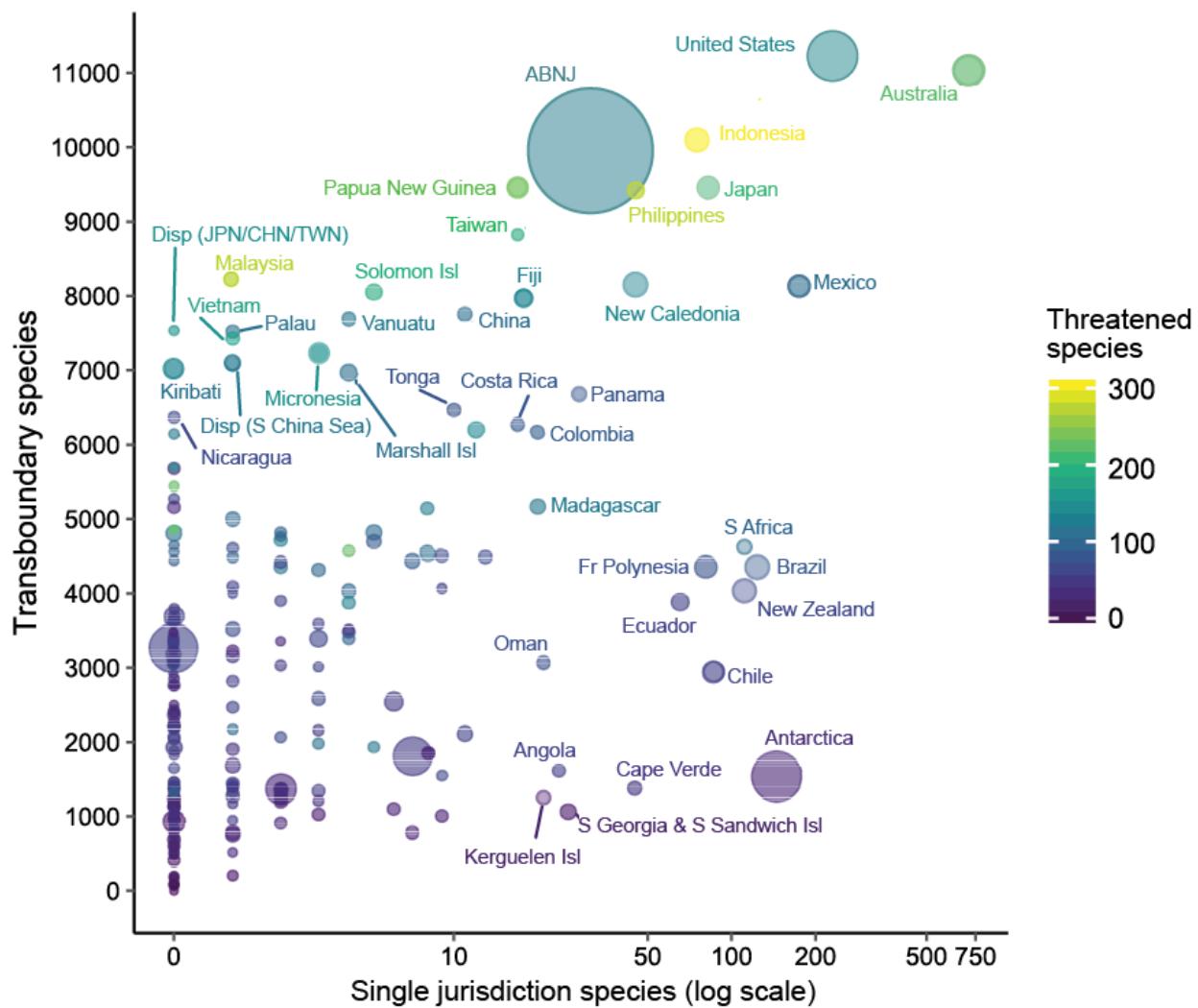


Figure 3: Number of species per jurisdiction. Color corresponds to the number of threatened (Critically Endangered, Endangered, or Vulnerable) transboundary species and size corresponds to jurisdiction area (larger dots represent larger areas). All 228 jurisdictions are shown, with labels for jurisdictions 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 (Figures 3, 4). 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., Selig et al. 2014, Tittensor et al. 2010, O’Hara et al. 2017). 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 (Supplementary Figure 2), even though the tropics are the most under-sampled region. Thus, we expect that tropical jurisdictions will have proportionally more species than our results show (Menegotto & Rangel, 2018). However, our estimate is likely a universal under-representation of transboundary species because rare or cryptic species are typically under-sampled across all geographic areas (Coddington et al., 2009).

Sampling bias affects what species are recorded in databases such as OBIS (due to uneven research effort across geographic or taxonomic domains), and what species have enough observations to build a range map (Supplementary Information 1). Interestingly, the Mediterranean does not include any of the highest ranking countries for transboundary species richness, even though it has many jurisdictions in a fairly small area, is relatively well-studied, and is considered a hotspot of marine biodiversity (Bianchi & Morri, 2000). Our approach likely reduces this sampling bias towards areas such as the Mediterranean because it is most pronounced for large vertebrates (Donaldson et al., 2016), whereas we include all mapped plants and animals. Regions such as the Mediterranean and parts of the Arctic are notable for other aspects of biodiversity, for instance, species’ range rarity, but are less prominent areas for known species richness (Selig et al., 2014).

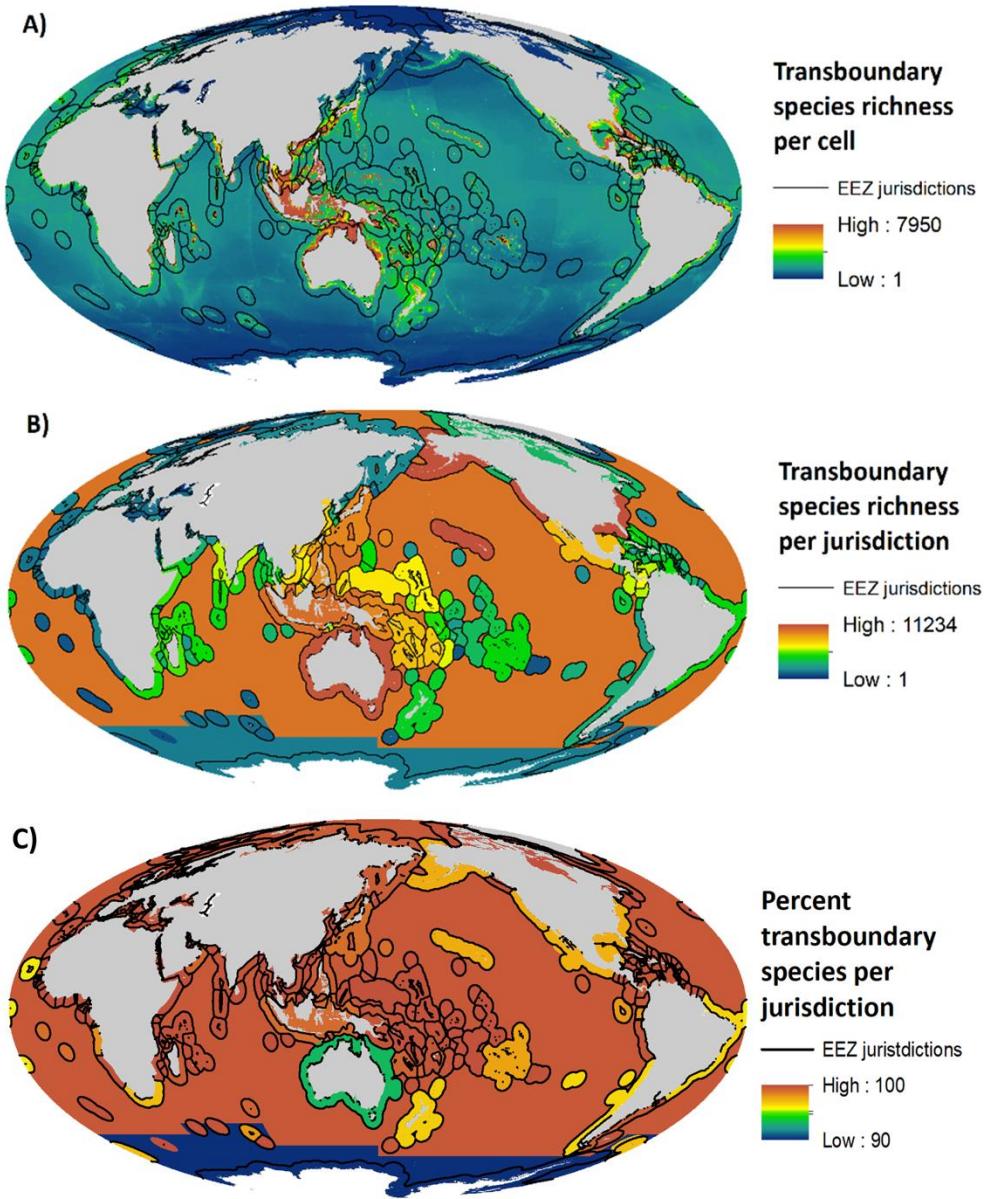


Figure 4: Transboundary species richness. Maps of the number of transboundary species (A) per grid cell, (B) per jurisdiction, and (C) as a proportion of the total number of mapped species in each jurisdiction

The jurisdictions with the most transboundary species are the USA, Australia, Indonesia, and Areas Beyond National Jurisdiction (ABNJ), which all have large areas in the tropics (the USA mainly due to Hawaii and its overseas territories) (Figures 3,4). Australia and Indonesia have the greatest

richness of threatened transboundary species. Half (114) of the 228 jurisdictions share 100% of their mapped species with at least one other jurisdiction, and all jurisdictions have more than 97% transboundary species except for Antarctica (91.3%), Australia (94.0%), and Cabo Verde (96.8%) (Figure 4C). 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.

Pearson's correlation tests showed no significant correlation between governance score and number of transboundary species for the 209 jurisdictions with WGI scores ($r = -0.0479, p = 0.488$, 95% CI [-0.1819, 0.0877]), or for the 161 sovereign nations with overseas territories excluded ($r = 0.0011, p=0.988$, 95% CI [-0.1526, 0.1548]). However, it is notable that many of the tropical countries with large numbers of transboundary species are island states with large ocean territories to govern, and limited capacity to manage or report on marine biodiversity (e.g., New Caledonia, Indonesia; See Supplementary Figure 2, Supplementary Table 3) (Failler et al., 2019). At the same time, many countries responsible for managing large numbers of transboundary species are not the countries most in need of outside funding (although funding is only one element of transboundary collaboration, it is an important one). For example, Australia and France (which has many biodiversity rich overseas territories) both have high governance scores, yet they rank among the top 40 countries with the most underfunded conservation and have by far the largest difference between expected and observed spending on the top 40 list (Waldron et al., 2013).

Discussion

The transboundary nature of marine species

This work establishes that the vast majority of marine biodiversity is extremely transboundary. The frequency of transboundary distributions is similar among a broad range of taxonomic groups, and is robust to different thresholds for species occurrence. Many marine species are distributed among large

numbers of jurisdictions (more than 50 and up to 220). We find that small, sessile, or non-migratory species have similar transboundary patterns to larger and better-known vertebrates, such as commercially exploited fish stocks (Maureaud et al., 2020). Although there is sampling bias across countries and regions, overall, both understudied and well-studied countries share the vast majority of their marine biodiversity with other jurisdictions.

The transboundary nature of virtually all marine biodiversity exacerbates the complexity of marine conservation. Whereas most land belongs to a single country, over 60% of the ocean's surface—and nearly 95% of its volume—lies beyond national jurisdictions. In the ABNJ, persistent geographic and taxonomic governance gaps have resulted in greater cumulative impacts on species and ecosystems compared to EEZs (O'Hara et al., 2019). ABNJ present a significant governance challenge because there are few avenues for recourse if agreements are not honored (Friedman, 2019), no set rules regarding how to assess transboundary impacts from activities in ABNJ, and no global mechanism to allow the implementation of protected areas in ABNJ. Another key challenge for transboundary marine species conservation is that many biodiversity-rich countries lack governance capacity—a pattern that is also true on land (Mason et al., 2020)—but face additional obstacles when they are small-island nations with vast EEZs to govern (and are often surrounded by the ABNJ). This geography makes effective implementation and enforcement for typical marine conservation strategies, such as marine protected areas, even more difficult (Faille et al., 2019; Marinesque et al., 2012).

Effective transboundary management

Equitable and effective transboundary conservation would consider each country's geographic and cultural context, and include collaboration, cost-sharing, and resource transfer at multiple scales. This includes both intra (e.g., among countries in South East Asia) and interregional (e.g., between Northern European and South East Asian regional management organizations) scales, as well as between individual nations (e.g., Australia and Papua New Guinea). Better outcomes can be achieved by redistributing the burden of conservation, which currently falls on government institutions, and disproportionately on governments with lower management capacity (Hanich et al., 2015; Marinesque et al., 2012).

Importantly, many wealthier countries have large numbers of transboundary species in their EEZs (e.g., USA, Australia, French and British Overseas Territories). These countries—Australia being the most egregious example—often dedicate relatively little of their wealth and resources to conservation, especially when their economies are largely dependent on natural resource industries (Morrison et al., 2020; Ward et al., 2021). In these cases, transboundary collaboration might include increased pressure from other States and non-state actors to catalyze political will. International conservation initiatives could encourage countries with greater capacity (e.g., Australia, Northern European countries) to set higher targets for marine biodiversity in their waters, as well as create avenues to transfer resources to the high biodiversity but lower capacity countries. Multilateral conservation funds are one such avenue; for example, the US-Canada Pacific Salmon Treaty that involved contributions to a conservation fund (albeit between two well-resourced countries) (Pinsky et al., 2018).

An example of coordinated regional management of transboundary species 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 and technically not occurring across multiple jurisdictions, CCAMLR has effectively facilitated collaboration among individual States to govern a large and remote area with considerable success (Maguire et al., 2006; Pons et al., 2018). In contrast to terrestrial species (at least terrestrial vertebrates)—of which almost half occur within the borders of individual countries (Mason et al., 2020)—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.

Currently, most transboundary conservation occurs at the government level, often supported by intergovernmental organizations and non-state actors such as regional bodies, foundations, academic institutions, and environmental NGOs (Gallo-Cajiao et al., 2019; P. Mackelworth, 2012; P. C. Mackelworth et al., 2019; Morrison et al., 2020). This framework does not actively engage industry actors, which are sometimes more powerful than individual nation-states (Morrison 2020) and are often

already operating under a transboundary framework (e.g., shipping, mining, or fishing corporations).

Other types of legal instruments beyond UNCLOS—such as trade agreements, which often include environmental provisions—are an opportunity to expand biodiversity protection across borders (Brandi et al., 2019).

Knowledge gaps and collaboration

We collated maps for roughly one-fifth of recorded marine species (OBIS, 2020). While this analysis is the first attempt to show the geopolitical distribution of marine biodiversity across international boundaries, substantial taxonomic and geographic knowledge gaps remain, especially for invertebrates and algae and for offshore and deep-sea habitats. In particular, large and remote areas such as ABNJ and Antarctica likely harbor many more species than indicated by this analysis. However, we also know surprisingly little about some large, visible species. We limited this study to the plant and animal kingdoms, omitting the chromists (which include kelp) because only a few dozen maps exist in these databases. Giant kelps are keystone species that provide critical habitats, but only recently have comprehensive mapping efforts begun (Mora-Soto et al., 2020). Collaboration around research and monitoring—including data sharing—is a crucial element of transboundary conservation (Maureaud et al., 2020), as even research institutions in wealthy nations lack the resources required to explore and document marine biodiversity across a typical EEZ.

Thus, 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, then military, industry and traditional sources of knowledge must be fused with scientific research data streams and fed into open-access ocean observing frameworks (e.g., those provided by the Global Ocean Observing System). This requires increased 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 slightly 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. Long-term engagement will be critical for convincing industry stakeholders to share biodiversity data (Maureaud et al., 2020). 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.

Future challenges

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 mapped transboundary marine species. There are examples of successful conservation or management of transboundary biodiversity for some charismatic migratory species; for example, humpback whales (Bejder et al., 2016), some sea turtle populations (Mazaris et al., 2017), and a few fish stocks, notably Pacific halibut and some Northeast Pacific salmon stocks (Dankel et al., 2008). 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 (Dunn et al., 2019). Transboundary fish stocks may be the most egregious example, with shared and highly migratory stocks experiencing twice the level of overfishing and declining more quickly than those within a single jurisdiction (FAO, 2014; Palacios-Abrantes et al., 2020).

The need for conservation policy to address transboundary distributions will only become greater as climate change phenomena such as warming, acidification, and sea-level rise alter species ranges, shifting ranges into (and out of) different countries, complicating existing conservation mechanisms for both transboundary and single-country species (Burden & Fujita, 2019; Hobday et al., 2015; Kapsenberg & Cyronak, 2019; Spijkers et al., 2019). Climate change effects on marine biodiversity also extend

beyond shifting species ranges; for example, altering the location of key habitat areas and biological processes (e.g., migration routes, spawning, nesting, and feeding grounds), species' interactions (e.g. invasive species), and ecosystem function (e.g., primary productivity, nutrient processing and exchange) (Doney et al., 2012; Hewitt et al., 2016). Therefore, we urgently need to create flexible and cooperative transboundary management frameworks so that conservation can keep pace with rapid changes in marine biodiversity (Maureaud et al., 2020). 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 at many different scales (Gattuso et al., 2018).

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 ocean conservation efforts, cooperation on biodiversity protection can also serve as a peace-building tool (P. Mackelworth, 2012; Roulin et al., 2017). 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 without coordinating actions with their adjacent or regional neighbors. 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.

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Data Availability

Two primary databases were used in this study: The publicly available IUCN Red List of Threatened Species (<https://www.iucnredlist.org>; link provided in the manuscript text) and the AquaMaps database (Available upon request at: www.aquamaps.org). The code used to produce the figures and tables are provided as R Markdown files in a public GitHub repository (https://github.com/lroberson/transboundary_spp_pub).

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