

**Hotspots in the marine realm:
The where and why of shark and ray biodiversity**

**by
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Abstract

Understanding the spatial distributional patterns of species is critical for determining the mechanisms behind marine biodiversity and appropriating conservation efforts. We used the distribution maps of all known marine species in the class Chondrichthyes to explore the degree of spatial congruency across three measures of species richness hotspot, as well as their threatened counterparts. Overall, spatial congruency was low, suggesting that conservation attention should not focus solely on areas of high species richness. We then investigated the abiotic and biotic drivers of global species richness. Sea surface temperature, productivity, and oceanic upwellings were some of the strongest abiotic predictors for richness. Areas of high richness also comprised many small ranging, younger species, indicative of species diversification occurring in the tropics. This work predominantly highlights the importance of considering which measure of richness we use when approaching conservation and advances our understanding of the biogeography of sharks and rays in the marine realm.

Keywords: endemism; evolutionarily distinct; threatened; spatial patterning; sharks and rays; latitudinal biodiversity gradient

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List of Acronyms

| | |
|------|--|
| AIC | Akaike Information Criterion |
| ED | Evolutionarily Distinct |
| ESRI | Environmental Systems Research Institute |
| IUCN | International Union for the Conservation of Nature |
| NOAA | National Oceanic and Atmospheric Administration |
| SD | Standard Deviation |
| SST | Sea Surface Temperature |

Chapter 1. Introduction

The world is a beautiful array of life that is constantly changing and adapting. To date, we have discovered that almost all animal phyla occur in the oceans, while fewer than half exist on land (May 1988). Yet our knowledge of the aquatic world and the species that inhabit it remains in large part a mystery. This lends to one of the most peculiar challenges in life to date, attempting to identify and explain the near endless biodiversity perpetually being discovered on Earth. Aside from the vast number of organisms on land and in the ocean, there is inherent spatial patterning in species distributions that many are familiar with. These patterns of distributions tend to peak in the tropics and gradually decrease as we move away from the equator and towards the poles, and is known as the latitudinal biodiversity gradient. However, some taxa go against our well-known biodiversity patterning. For example, pelagic species, such as marine mammals and zooplankton, display a stronger subtropical or temperate pattern (Tittensor et al. 2010), while deep sea species have their richness peak in higher latitudes (Woolley et al. 2016). Explaining the distributional patterns of species in the marine realm and understanding why they may differ from our current knowledge of the terrestrial environment has become a fundamental quest to ecologists to help guide our understanding of the world and the diversity we live in today. The concept of modern biodiversity was most likely given its limelight from Gene Evelyn Hutchinson's "Homage to Santa Rosalia", where he pondered how it was possible that many different species could coexist in a given environment while competing for limiting resources (Hutchinson 1959). An example being the vast number of plankton species that can not only exist, but thrive in a single drop of water (Worm and Tittensor 2018). Recently completed is the First Global Census of Marine Life (2000 – 2010) that systematically charted and attempted to understand the patterns and distribution of marine taxa. With the study of marine biodiversity being a relatively fresh concept still in its early stages of understanding, there are numerous ways in which we can go about exploring the mechanisms which have led to the vastness of species who are currently present in the oceans today.

Even though there is an incredible amount work researching the diversity of the world's oceans, most rarely deviate from looking at biodiversity in a singular tone, most

commonly known as total species richness. This measure involves characterizing the total number of different species found in a given area. Species richness is usually greatest, both terrestrially and aquatically, at tropical latitudes (Chaudhary, Saeedi, and Costello 2016; Lucifora, Garcia, and Worm 2011; Tittensor et al. 2010), with a few taxa deviating from the norm such as deep sea species or marine mammals (Tittensor et al. 2010; Woolley et al. 2016). Species richness measures can also be extended to measure the number of highly evolutionarily distinct (ED) taxa. ED taxa are defined as the species that encompass the greatest share of evolutionary history, usually measured from the branch lengths of a phylogenetic tree (Mace, Gittleman, and Purvis 2003). A third common method for measuring richness is counting the presence of endemic species. Endemics are those species that typically only exist within defined environmental and ecological conditions, and as a result are usually characterized by having small range sizes (Myers et al. 2000). Lastly, we can measure richness by tallying the number of threatened species (Vulnerable, Endangered, or Critically Endangered) as defined by the International Union for the Conservation of Nature's (IUCN) Red List of Threatened Species within each of the aforementioned measures of richness (total, ED, endemic). This type of measure is important because threatened species have a more imminent conservation value due to their high risk of extinction usually due to anthropogenic effects such as overfishing, habitat loss, and pollution.

Exploring the inherent spatial patterning of different measures of species richness is only one aspect of understanding biodiversity. Another direction is to aim at understanding the drivers behind biodiversity. Most work exploring and developing hypotheses for the drivers behind the biodiversity gradient have focused on the terrestrial realm. However, these hypotheses have also been applied, albeit more sparingly, in the marine realm. The five major hypotheses include the (1) kinetic energy (Clarke and Gaston 2006; Wright 1983), (2) productivity (Wright 1983), (3) climate stability (Sanders 1968), habitat availability (Worm et al. 2005), and (5) the tropics-as-a-cradle hypothesis of evolutionary age and range size (Chown and Gaston 2000). The kinetic energy hypothesis states that there will be more species in warmer waters because of increased metabolic rates near the equator leading to higher rates of species diversification (Rohde 1992; Worm and Tittensor 2018). The primary productivity hypothesis postulates that when production, usually measured in the form of phytoplankton, is abundant, there will be more species because of the greater availability

of resources (Evans, Warren, and Gaston 2005; Jetz et al. 2009). Climate stability relates to the seasonal variations in climate, where high latitudinal regions experience more seasonal differences, therefore, selecting for species with broad climatic niches and better dispersal abilities (Sandel et al. 2011; Sunday, Bates, and Dulvy 2011). High seasonality in the temperate regions means that the tropics are hypothesized to have higher species richness because they contain both the wide-ranging, broad niche species, as well as the small-ranging, habitat specialists. Habitat availability describes the physical complexity and/or quantity of a given habitat (e.g. elevation, shelf area, coastline etc.), where increases of complexity or quantity have the potential to increase diversity by providing a range of niches for organisms to exploit (Worm et al. 2005). The final hypothesis is the tropics-as-a-cradle hypothesis that explores the characteristics of species lineages themselves. The hypothesis revolves around the concept that the tropics act as an evolutionary cradle by having more recently evolved species with smaller geographic range sizes (Chown and Gaston 2000; Jablonski, Kaustuv, and Valentine 2006; Rohde 1992).

While most of the development in understanding biodiversity has relied on terrestrial datasets, the marine realm provides an independent test of both the latitudinal biodiversity gradient in the ocean and the drivers behind marine species richness. This thesis aims at exploring the spatial distributional patterning and the abiotic and biotic drivers of biodiversity for all marine Chondrichthyans (sharks, rays, and chimaeras, hereafter referred “sharks and rays”). One quarter of all sharks and rays are categorized as threatened by the IUCN, or are predicted to be threatened based on their large body size and exposure to fisheries (Dulvy et al. 2014; Walls and Dulvy 2020). They have survived through every mass extinction over the last 400 million years and are among the most evolutionarily distinct vertebrate radiations of marine predators (Carrier, Musick, and Heithaus 2012; Stein et al. 2017). Further, sharks and rays occur in all the world’s oceans from the deep-sea, oceanic, neritic, and estuarine habitats, to freshwater rivers and lakes connected to the ocean (Carrier et al. 2012). The availability of fully developed Red List Assessments and geographic distribution maps make sharks and rays a good case study to understanding the patterns that have structured diversity in the oceans and can provide critical information on the ecology, evolution, and conservation for entire ecosystems and species lineages.

In Chapter 2 we investigate the degree of spatial congruency (or overlap) between three species richness metrics: total richness, endemic richness, and evolutionarily distinct species richness, as well as their threatened counterparts. We explore how their level of combined and pairwise spatial congruencies change as the definition of hotspot (richest 2.5%, 5% and 10% cells) and resolution (1°, 4°, and 8°) change. Overall, we found low spatial congruency between the three richness measures irrespective of the definition of hotspot, with the threatened species comprising an even smaller subset of the species distributional patterns. Coarsening the resolution (i.e. 1° to 8°) caused the geographic locations of congruency to change, however, overall spatial congruency between the three richness measures still remained low. The identified areas of congruency contained over half (64%) of all sharks and rays and occurred off major continental coastlines. Lastly, in pairwise comparisons of species richness measures, evolutionarily distinct species richness had the highest overlap with total species richness. These results highlight that focusing conservation efforts on total species richness will not inevitably contribute efforts to species that are at a higher risk, nor will it protect other dimensions of species richness like endemism. Further, the lack of spatial congruency between species richness measures infers that they are largely affected by different ecological and evolutionary entities.

In the second data chapter (Chapter 3), we explore both the abiotic and biotic correlates that are proposed to explain species richness for all marine sharks and rays. Overall, species richness was highest at lower latitudes and was supported by three of the five hypotheses. Species richness was greater where waters were warmer, and where there was an increase in both productivity and frontal systems. The tropics-as-a-cradle hypothesis was also supported where species rich areas comprised both smaller-ranging, and younger species, indicative of species diversification. While species rich areas at lower latitudes had smaller-ranging and younger species, the tropics as a whole was dominated by wide-ranging, older species, ultimately questioning whether regions of high species richness are true areas of diversification or are just an accumulation of small-ranging, young species, such as endemics. Overall, these results help affirm some of the terrestrial developed hypotheses on what influences biodiversity and opens the doors to further exploring the biogeography of sharks and rays through their evolutionary history.

I wrap up this thesis with a summary chapter (Chapter 4) reviewing the key findings from previous chapters, their implications, as well as their pitfalls and directions for future research. In summary, this research provides one of the first works done analyzing the spatial patterning of biodiversity hotspots among (1) different metrics of species richness (i.e. total species richness, endemism etc.), and (2) across varying spatial resolutions. My research also independently analyzes how abiotic and biotic variables drive species distributions across the globe. There has been a tremendous amount of work on understanding the drivers of species richness in the terrestrial world and even less so in the marine environment. This in turn makes my research all the more paramount as sharks and rays are globally distributed and are one of the oldest vertebrate lineages alive to date. This research also provides an example of how our understanding of the spatial patterning of biodiversity can depend quite drastically on our choice of biodiversity metric and spatial resolution. Lastly, this work can (1) be used to further explore both the spatial congruency and the abiotic and biotic drivers of biodiversity between for the entire ocean, including coastal, shelf, and deep water sharks and rays, and (2) provide a comparative baseline for future marine research that focuses on exploring the evolutionary attributes that are involved in shark and ray biodiversity patterns through mechanisms such as metabolic rate and speciation.

“When we no longer look at an organic being as a savage looks at a ship, as at something wholly beyond this comprehension; when we regard every production of nature as one which has had a history; when we contemplate every complex structure and instinct as the summing up of many contrivances, each useful to the possessor, nearly in the same way as when we look at any great mechanical invention as the summing up of the labour, the experience, the reason, and even the blunders of numerous workmen; when we thus view each organic being, how far more interesting, I speak from experience, will the study of natural history become!”

Charles Darwin (1859),
The Origin of Species

Chapter 2. Spatially congruent sites of importance for global shark and ray biodiversity¹

2.1. Abstract

Many important areas identified for conservation priorities focus on areas of high species richness, however, it is unclear whether these areas change depending on what aspect of richness is considered (e.g. evolutionary distinctiveness, endemism, or threatened species). Furthermore, little is known of the extent of spatial congruency between biodiversity measures in the marine realm. Here, we used the distribution maps of all known marine sharks, rays, and chimaeras (class Chondrichthyes) to examine the extent of spatial congruency across the hotspots of three measures of species richness: total number of species, evolutionarily distinct species, and endemic species. We assessed the spatial congruency between hotspots considering all species, as well as on the subset of the threatened species only. We consider three definitions of hotspot (2.5%, 5%, and 10% of cells with the highest numbers of species) and three levels of spatial resolution (1°, 4°, and 8° grid cells). Overall, we found low congruency among all three measures of species richness, with the threatened species comprising a smaller subset of the overall species patterns irrespective of hotspot definition. Areas of congruency at 1° and 5% richest cells contain over half (64%) of all sharks and rays and occurred off the coasts of: (1) Northern Mexico Gulf of California, (2) USA Gulf of Mexico, (3) Ecuador, (4) Uruguay and southern Brazil, (5) South Africa, southern Mozambique, and southern Namibia, (6) Japan, Taiwan, and parts of southern China, and (7) eastern and western Australia. Coarsening resolution increases congruency two-fold for all species but remains relatively low for threatened measures, and geographic locations of congruent areas also change. Finally, for pairwise comparisons of biodiversity measures, evolutionarily distinct species richness had the highest overlap with total species richness regardless of resolution or definition of hotspot. We suggest that focusing conservation attention solely on areas of high total species richness will not

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necessarily contribute efforts towards species that are most at risk, nor will it protect other important dimensions of species richness.

2.2. Introduction

Species distributions are widely used to characterise and explain the patterns seen in biodiversity throughout the world and can be used to help identify places of conservation priority (Gaston 1996; Gaston and Blackburn 1996a; Lucifora et al. 2012). Species richness, defined as the number of different species in a given area, is generally greatest in the tropical latitudes (Chaudhary et al. 2016; Lucifora et al. 2011; Tittensor et al. 2010). Although this pattern is dominant in terrestrial systems, hotspots of species richness in the ocean can occur along productive frontal systems and subtropical boundary zones (Chaudhary et al. 2016; Gagne et al. 2020; Worm and Tittensor 2018), many of which tend to result from the overlap of wider-ranging species (Lennon et al. 2004). Global assessments of biodiversity have previously focused on identifying priority areas based on total number of species alone (Roberts et al. 2002), however there are other interpretations of species richness that have not yet been explored, such as evolutionary distinctiveness or endemism.

Evolutionarily distinct (ED) species, defined as species that encompass the greatest share of evolutionary history, usually measured from the branch lengths of a phylogenetic tree (Mace et al. 2003), are also of conservation value (Vane-Wright, Humphries, and Williams 1991). Areas of high evolutionary distinctiveness are important to conservation because they can capture those species who embody unique forms, functions, and genomes (Jetz et al. 2014). For example, any one species of echidna embodies a greater fraction of the morphological, physiological, and ecological diversity of class Mammalia than any one species of the 2,000 or so species of rodents (Collen et al. 2011; Vane-Wright et al. 1991). In some lineages, especially sharks and rays, extinction risk is greatest in the species that embody the largest share of this evolutionary history because they exhibit traits, such as large body size, that render them intrinsically sensitive to threats such as hunting or overfishing (Jetz et al. 2014; Purvis et al. 2000; Rosauer and Mooers 2013; Waldron et al. 2013). Endemism is defined as those species that exist only in a defined geographic region (Myers et al. 2000). Endemic species tend to merit high conservation priority because of their small geographical range sizes and low population numbers (Hughes, Bellwood, and Connolly

2002). An influential analysis of threatened terrestrial endemics revealed that 44% of all endemic plants and 35% of endemic vertebrates occurred in only 2% of the global land area (Myers et al. 2000), demonstrating how an endemism-centric approach can be incredibly spatially efficient in identifying areas for conservation. Identifying the geographical areas that harbor congregations for different richness metrics, such as total species, evolutionarily distinct species, or endemic species, have resulted in becoming a significant component of the terrestrial conservation agenda (Myers et al. 2000). While there are numerous values that could be used to drive conservation, there is an urgency to conserve those threatened species that are at risk of extinction.

The 2020 Aichi biodiversity target to conserve 10% of coastal and marine areas drove a rapid expansion of marine protected areas, with the area covered rising from 0.67% of the world's oceans in 2000 to 6.4% in 2017 (UNEP-WCMC and IUCN 2020). Within the newly drafted 2030 Kunming biodiversity framework, target 2 aims to “protect 30% of sites of particular interest on both land and sea” (Anon 2020). Now is the time to shape the rapidly developing 2030 agenda of biodiversity conservation by identifying areas that harbour the combination of the greatest richness, endemism, and evolutionary distinctiveness (Grenyer et al. 2006; Hughes et al. 2002; Orme et al. 2005), amongst the many other dimensions of biodiversity, as well as their threatened counterparts. In addition to shedding light on the distribution of species diversity (and across the different measures with which diversity can be defined), these identified areas can be used to inform regions of focus for subsequent systematic conservation planning exercises (Pressey et al. 2007).

One quarter of all sharks, rays, and chimaeras (class Chondrichthyes; hereafter referred to as “sharks and rays”) are categorized as threatened (Vulnerable, Endangered, or Critically Endangered) on the International Union for the Conservation of Nature's (IUCN) Red List of Threatened Species, or are predicted to be threatened based on their large body size and exposure to fisheries (Dulvy et al. 2014; Walls and Dulvy 2020). Sharks and rays are among the most evolutionarily distinct vertebrate radiation of marine predators (Stein et al. 2017), and their slow life histories result in low population growth rates (Hutchings et al. 2012; Pardo, Kindsvater, Cuevas-Zimbrón, et al. 2016; Pardo, Kindsvater, Reynolds, et al. 2016). These features combine to render them highly sensitive to overfishing (Davidson, Krawchuk, and Dulvy 2016; Dulvy et al. 2014). The availability of comprehensive Red List Assessments and geographic

distribution maps make sharks and rays a good case study to understand how marine species richness measures are spatially distributed and can be conserved most efficiently. There are few analyses that explore the spatial distribution and overlap of different biodiversity measures in the terrestrial realm and even fewer in the ocean. The terrestrial studies have all found a lack of spatial overlap occurring throughout a variety of different taxa (i.e. birds, insects, plants) (Orme et al. 2005; Prendergas et al. 1993; Williams et al. 1996). While marine studies yield comparable patterns to the terrestrial realm, most focus on relatively sessile species (i.e. coral reefs) or on other dimensions of biodiversity (i.e. functional diversity) (Lucifora et al. 2011; Roberts et al. 2002).

Here, we use a global database of all known shark and ray distributions to explore the spatial congruency among three species richness measures: total number of species, ED species richness, and endemic species richness. Spatial congruence is defined here as the spatial overlap between hotspot areas. We also explore the level of spatial congruency of the species richness measures for threatened shark and ray species only because of their greater conservation urgency. Specifically, we examine the (1) overall spatial congruency among all species richness measures and the subset of threatened species, and (2) changes in spatial congruency according to different definitions of hotspot used, as well as different levels of spatial resolution.

2.3. Methods

We obtained distribution maps for all known sharks, rays, and chimaeras in the class Chondrichthyes from the IUCN (Davidson and Dulvy 2017; Dulvy et al. 2014). All maps were projected with Lambert equal area for analysis. A global grid map was overlain at a cell resolution of 1° by 1°, equating to an approximate distance at the equator of 110 km. The global grid contains 44,181 cells after excluding terrestrial land masses, which are any cells containing land from the Environmental Systems Research Institute (ESRI) vector map of the world (Natural Earth 2018). Across all species richness measures evaluated, each species is scored as present within a grid cell if any part of their distribution range falls within the grid cell boundaries. Total species richness ($n = 1,083$ spp.) was calculated as the total number of unique species within each grid cell. We consider all marine species together rather than separate coastal and pelagic species because many pelagic species are also neritic – occurring on the continental shelf. Hence, we have retained the pelagic species to capture the true richness and

evolutionary distinctness of shelf seas. Evolutionary distinctiveness scores were calculated as the sum of the branch lengths of a species down to the root of the phylogenetic tree, with each branch inversely weighted by the number of species that it subtends (Redding et al. 2008; Redding and Mooers 2006). Species with longer branches and fewer relatives have higher evolutionary distinctiveness scores. ED species richness ($n = 264$ spp.) was defined as those species with the highest quartile of evolutionary distinctiveness scores (represented as age in millions of years) and is calculated as the total number of unique species per cell that are within the evolutionarily distinct upper quartile. Endemic species richness ($n = 527$ spp.) was calculated as the total number of unique species within each grid cell that have range sizes below the median of the range sizes of all species (i.e. 419,659 km²) (Davidson et al. 2012; Pompa, Ehrlich, and Ceballos 2011; Roberts et al. 2002). To quantify total threatened species richness ($n = 178$ spp.), we counted the number of species within each grid cell that are currently listed as Vulnerable, Endangered, or Critically Endangered (i.e. threatened) according to the IUCN Red List Categories and Criteria (IUCN 2018). Threatened endemic richness ($n = 70$ spp.) was calculated in the same way as endemic species richness, but subset to the IUCN threatened species only. Finally, threatened ED species are those ED species that have been classified by the IUCN as threatened ($n = 49$ spp.).

We defined richness hotspots as those containing the top 5% of richest cells for each of the biodiversity measures. Previous research has shown that the richest 1-5% of total land area can capture a substantial proportion of species (Bibby et al. 1992; Myers 1990; Myers et al. 2000). We tested the extent of spatial congruency between shark and ray hotspots derived for all three species richness measures (i.e. total species, ED species, and endemic species), and between all three threatened subsets of the biodiversity measures. Extent of spatial overlap between hotspots was calculated using the following equation (Orme et al. 2005):

$$\text{Total proportion of overlap} = \frac{\sum C_n}{\sum A_n}$$

Where C is equal to the areas of congruence for each species richness measure, A the total distributional area of species richness measure hotspots, and n the number of species richness measures used to calculate congruence. To explore our original choice

of hotspot (5%) or choice of spatial resolution (1°), we also calculated spatial overlap for two different definitions of hotspot (richest 2.5% and 10% of cells), and two levels of coarser spatial resolution (4° and 8° grid cells). All analyses were carried out using ArcGIS Pro 2.4.3 (ESRI 2019) and R v.3.6.1 (R Studio Team 2018; Team 2019).

2.4. Results

In general, the distributional patterns of total and ED species richness spanned the global ocean environment while endemic species were confined to the coastlines (Figures 2.1, and A1 – A2). We focus our presentation of results and discussion of overall biodiversity patterns and congruency on the 5% definition criterion over all three resolutions (1°, 4°, and 8°). The results did not greatly differ between the three definitions of species richness hotspot (Figures 2.2, and A3 – A11; A1 Table). Biodiversity hotspots for all shark and ray species were greatest near the equatorial coastlines for all measures except endemic species richness (Figure 2.3). There are clear deviations from the well-known latitude-richness relationship, with no species richness hotspots present around equatorial coastlines (i.e. East Africa, Central Brazil, and Central America) and some richness hotspots occurring in high latitude locations, particularly in the southern hemisphere (notably South Africa, Atlantic South America, and Australia; Figure 2.3A). These biodiversity patterns are more apparent for the subset of threatened species only (Figure 2.3D-F). The distribution of ED species is broadly similar to the total richness pattern, but with a notable deficit along the northern coast of South America, particularly the Northwest Atlantic and eastern Pacific coastlines (Figure 2.3A-B). The anti-tropical distribution of endemism hotspots is most strongly present in the southern hemisphere (Figure 2.3C and 2.3F).

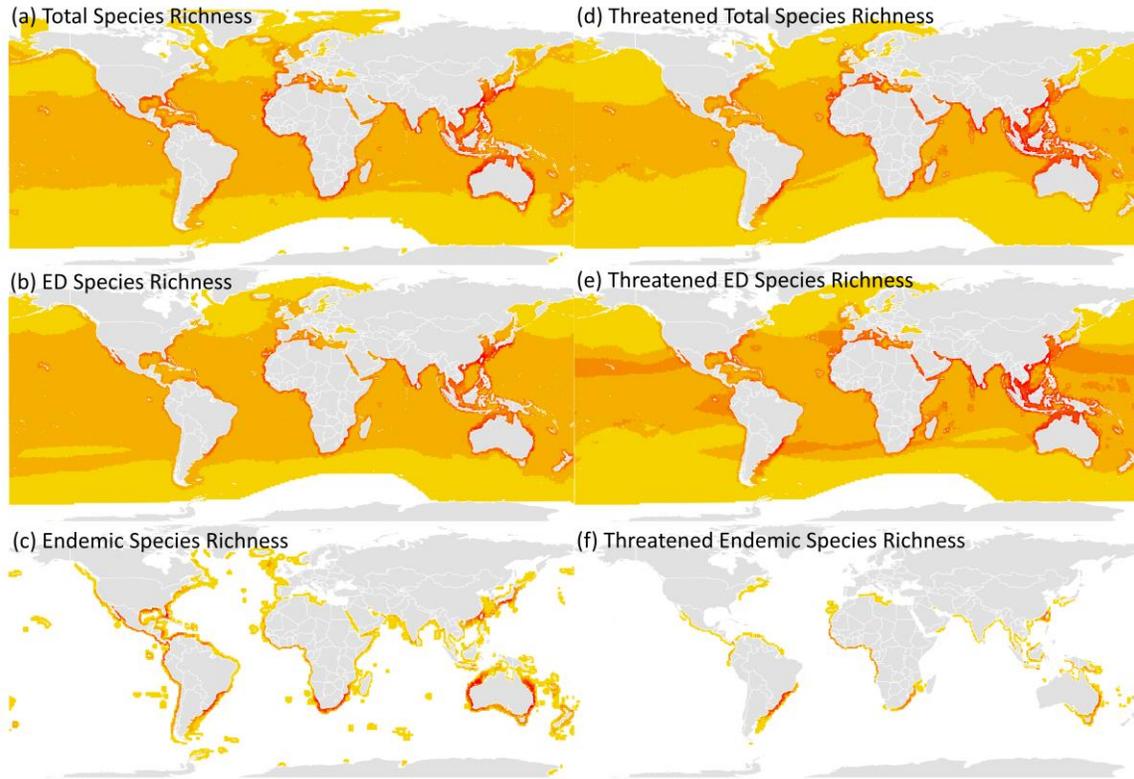


Figure 2.1 Global biodiversity patterns for three measures of species richness at 1° resolution. General richness for (a) total species, (b) evolutionarily distinct (ED) species, and (c) endemic species. (d-f) Threatened subsets of richness patterns for (d) total species, (e) evolutionarily distinct (ED) species, and (f) endemic species. Geographic coordinate system is in NAD83, projected coordinate system is Lambert equal area. The data used for this figure under CC BY license is granted permission from the International Union for the Conservation of Nature (IUCN), original copyright 2011.

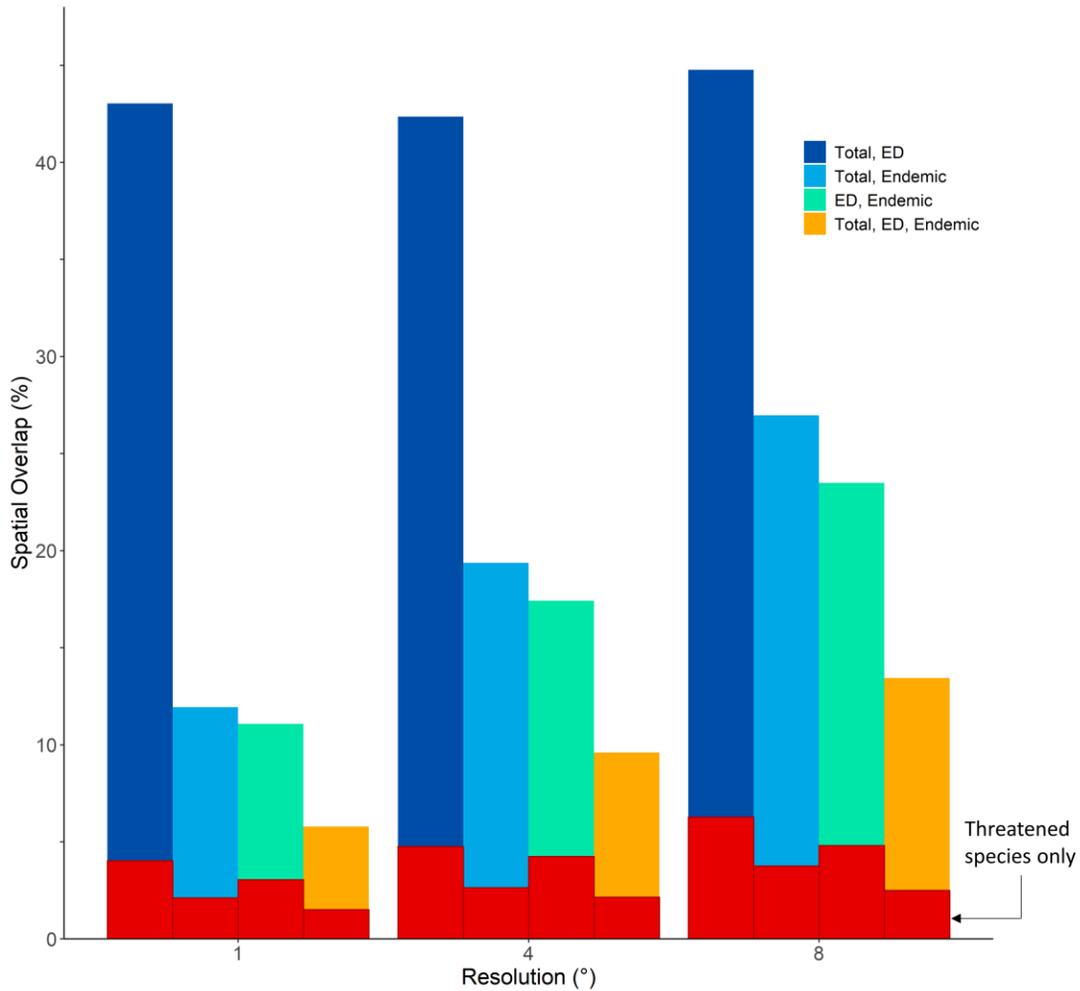


Figure 2.2 Spatial congruency (measured as percent overlap) of shark hotspots between three species richness measures: total species, evolutionary distinct (ED) species, and endemic species. Congruency shown for hotspot definition of the richest 5% of cells and three levels of spatial resolution: 1°, 4°, and 8°. The subsets of threatened species across species richness measures are indicated in red.

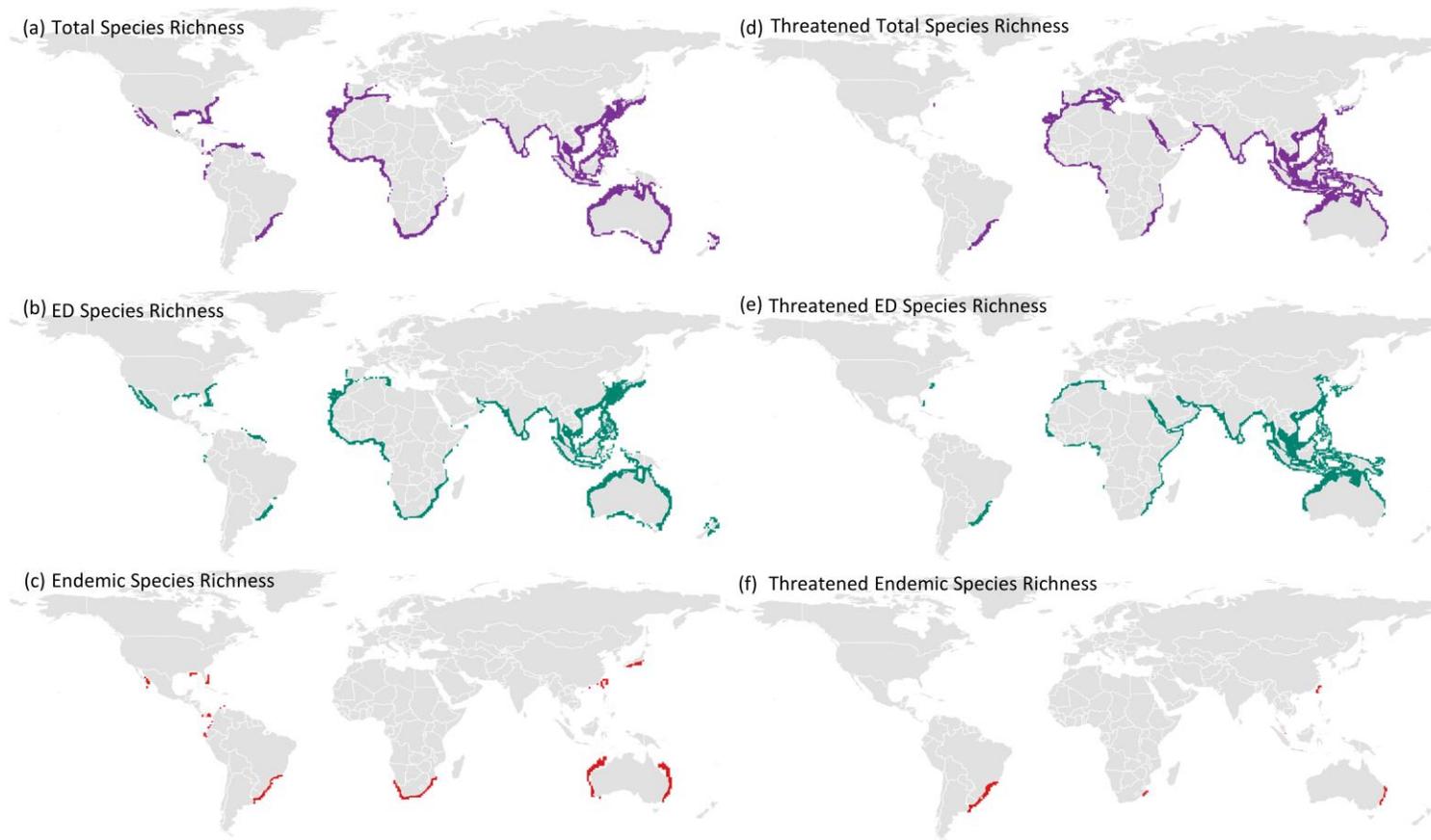


Figure 2.3 Biodiversity hotspots derived for three measures of species richness. General richness hotspots of (a) total species, (b) evolutionarily distinct (ED) species, and (c) endemic species. Richness hotspots of the threatened subset for (d) total species, (e) evolutionarily distinct (ED) species, and (f) endemic species. For each species richness measures, hotspots are defined as the richest 5% of grid all cells. Geographic coordinate system is in NAD83, projected coordinate system is Lambert equal area, grid cell resolution is 1°. The data used for this figure under CC BY license is granted permission from the International Union for the Conservation of Nature (IUCN), original copyright 2011.

In general, there was very low spatial congruence when comparing the hotspots of all three species richness measures (total species, ED species, endemic species; A2.1 Table). Cumulatively, all three biodiversity hotspots (for 1° resolution at 5% richest cells) occupied an area of 32,162,358 km², of which only 5.78% (1,859,971 km²) were spatially congruent between all three hotspots (orange cells; Figure 2.4A). These eight areas of congruency occurred off the coasts of: (1) Northern Mexico Gulf of California, (2) USA Gulf of Mexico, (3) Ecuador, (4) Uruguay and southern Brazil, (5) South Africa, southern Mozambique, and southern Namibia, (6) Japan, Taiwan, and parts of southern China, and (7) eastern and western (Figure 2.4B-E), and in total contain over half (64%) of all marine sharks and rays. The hotspots calculated for the subset of threatened species followed a similar pattern, albeit with considerably lower spatial congruency. The hotspots derived from all biodiversity measures (at 1° resolution) for threatened species only covered a cumulative area of 28,839,224 km² with a mere 1.51% (436,506 km²) of overlap between the three biodiversity hotspots (Figure 2.5A). The 1.51% of overlap occurred off the coasts of: (1) Brazil and Uruguay (making up nearly two thirds of the total area; 286,767 km²), (2) South Africa, (3) Taiwan, and (4) eastern Australia (Figure 2.5B-E). In total, these areas of overlap comprise 37% of all marine shark and ray species.

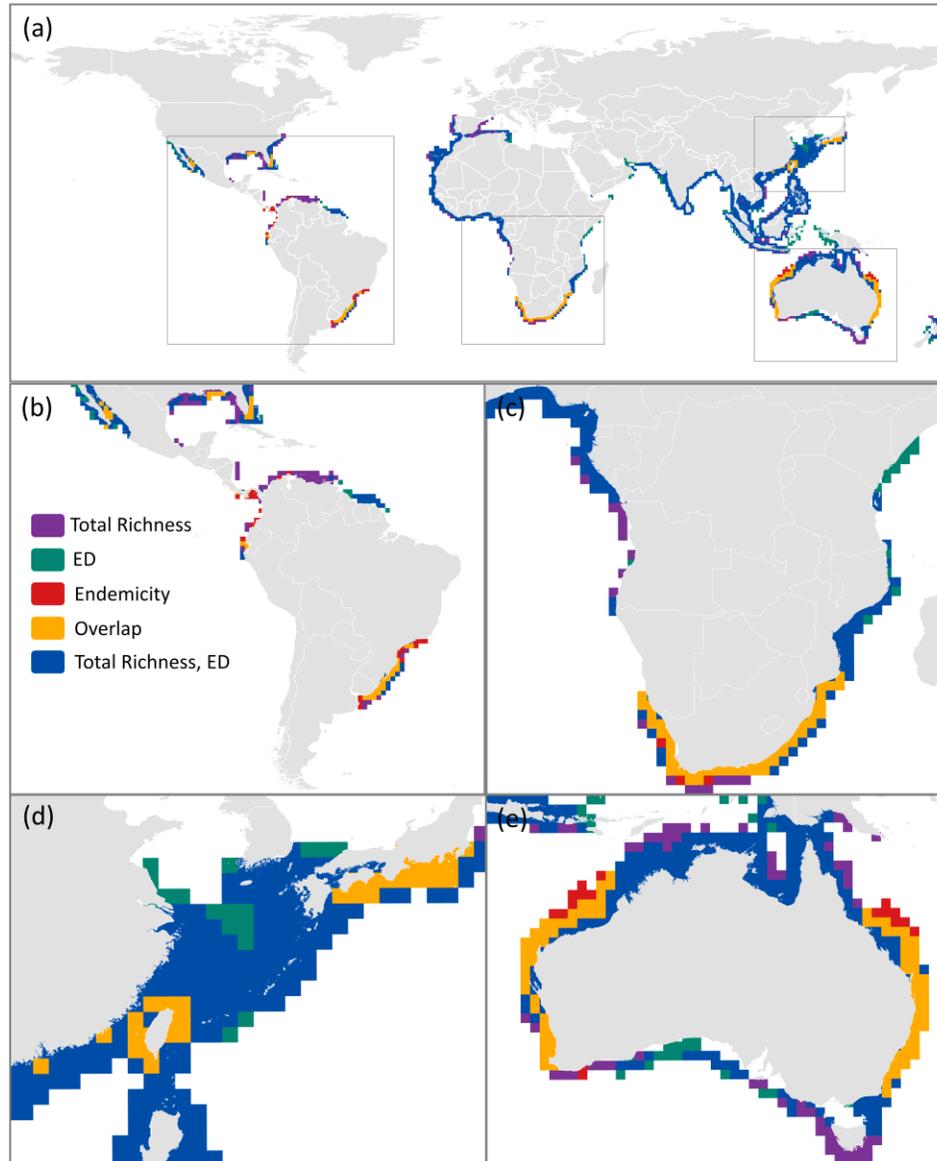


Figure 2.4 (a) Spatial congruence between global hotspots (defined at richest 5% of all grid cells) of three species richness measures: total species (purple), evolutionarily distinct (ED) species (green), and endemic species (red). Spatial congruence between hotspots derived for all three measures are represented by orange cells. Map insets highlighting specific areas of overlap: (b) North and South America, (c) southern Namibia, South Africa, and southern Mozambique, (d) Japan, Taiwan, and parts of southern China, and (e) Australia. Areas of congruence between total species richness and ED species richness are in blue. Grid cell resolution is 1°. The data used for this figure under CC BY license is granted permission from the International Union for the Conservation of Nature (IUCN), original copyright 2011.

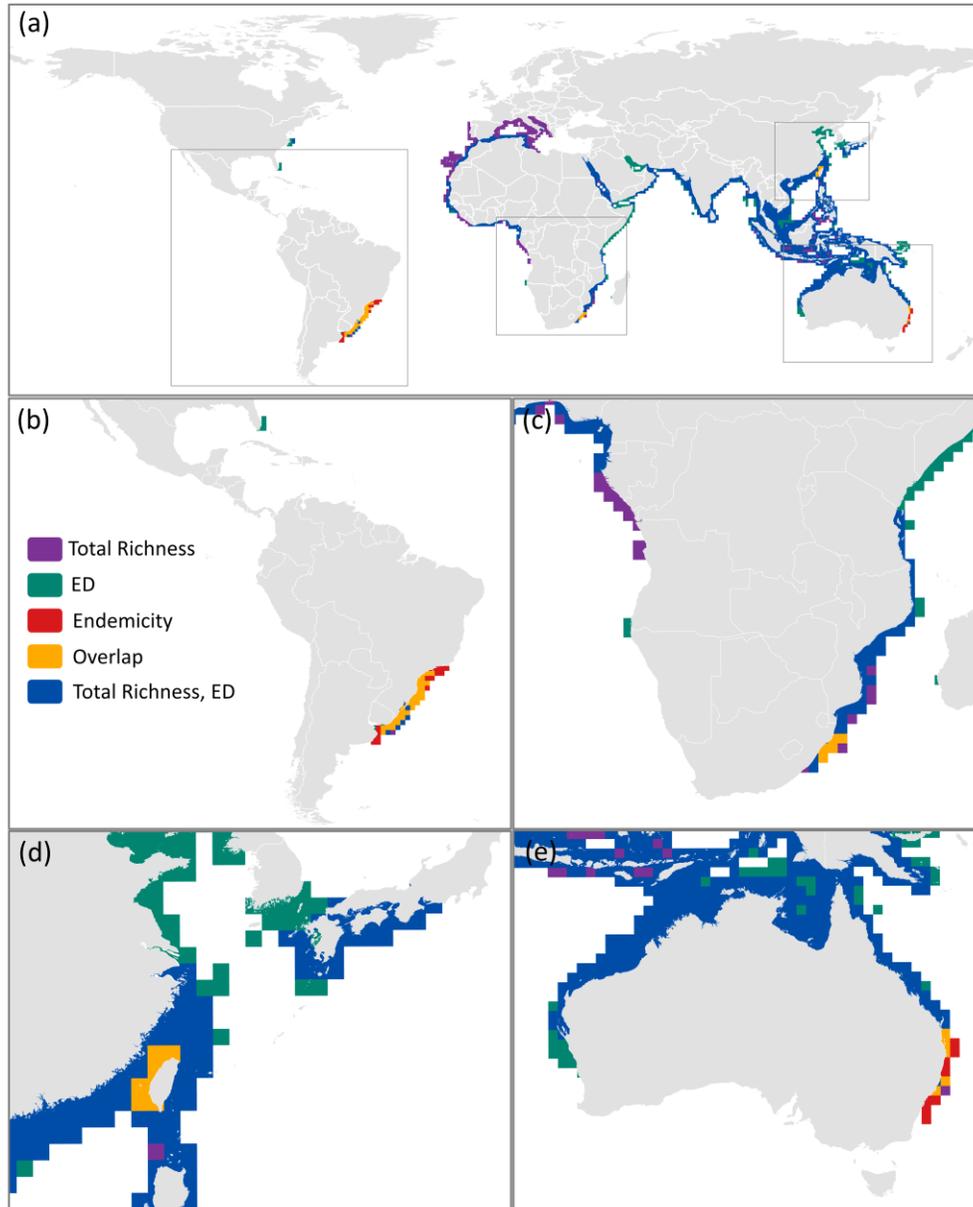


Figure 2.5 (a) Spatial congruence between threatened global hotspots (defined at richest 5% of grid all cells) of three species richness measures: total species (purple), evolutionarily distinct (ED) species (green), and endemic species (red). Spatial congruence between hotspots derived for all three measures are represented by orange cells. Map insets highlighting specific areas of overlap (b) southern Brazil and Uruguay, (c) parts of South Africa, (d) Taiwan, and (e) eastern Australia. Areas of overlap between total species richness and ED species richness are in blue. Grid cell resolution is 1°. The data used for this figure under CC BY license is granted permission from the International Union for the Conservation of Nature (IUCN), original copyright 2011.

Of all pairwise comparisons of spatial overlap, congruency between total number of species and ED species of all shark and ray species was consistently the highest (average of ~43%), and this remained true across all definitions of hotspot, as well as levels of spatial resolution (Figures 2.2, and A3; A1 Table). Conversely, spatial overlap between total number of species and endemic species of all shark and ray species remained at approximately half (average of ~20%) of the total species and ED species overlap across all definitions and resolutions of hotspot (Figures 2.2, and A3; A1 Table). ED species and endemic species overlap followed similar low congruency trends (average of ~17%) to that of total species and endemic species (Figures 2.2, and A3; A1 Table). The threatened species subset had similar results where ED hotspots had the highest percent of overlap with total species richness, averaging ~6% across all definitions of hotspot and levels of spatial resolution (Figures 2.2, and A3; A1 Table). Correspondingly, spatial overlap of total species and endemic species as well as ED species and endemic species of threatened shark and ray species only, were consistently lower than congruency of total species and ED species, averaging ~4% and ~4.5% across all definitions of hotspot and levels of spatial resolutions (Figures 2.2, and A3; A1 Table). Similar to the total species results, the highest degree of overlap for the threatened species richness subset was between total species and ED species (Figures 2.2, and A3; A1 Table).

Our results showed that changing the definition of hotspot resulted in a minor increase in congruency between all three species richness measures, with the extent of spatial overlap still remaining relatively low (Figures 2.6A-C, A12A-C, and A13A-C). For example, when redefining hotspots as the richest 10% of cells, the overlap increased slightly from 5.78 to 6.38% (A1 Table). Spatial overlap for the subset of threatened species reflected similar results between hotspot definition, again displaying a minor increase when the definition of hotspot was increased (Figures 2.6D-F, A12D-F, and A13D-F). For example, at 1° resolution, increases in spatial overlap between the 2.5% of richest cells, 5% of richest cells, and 10% of richest cells were minor (1.04%, 1.51%, and 1.93% overlap, respectively; A1 Table).

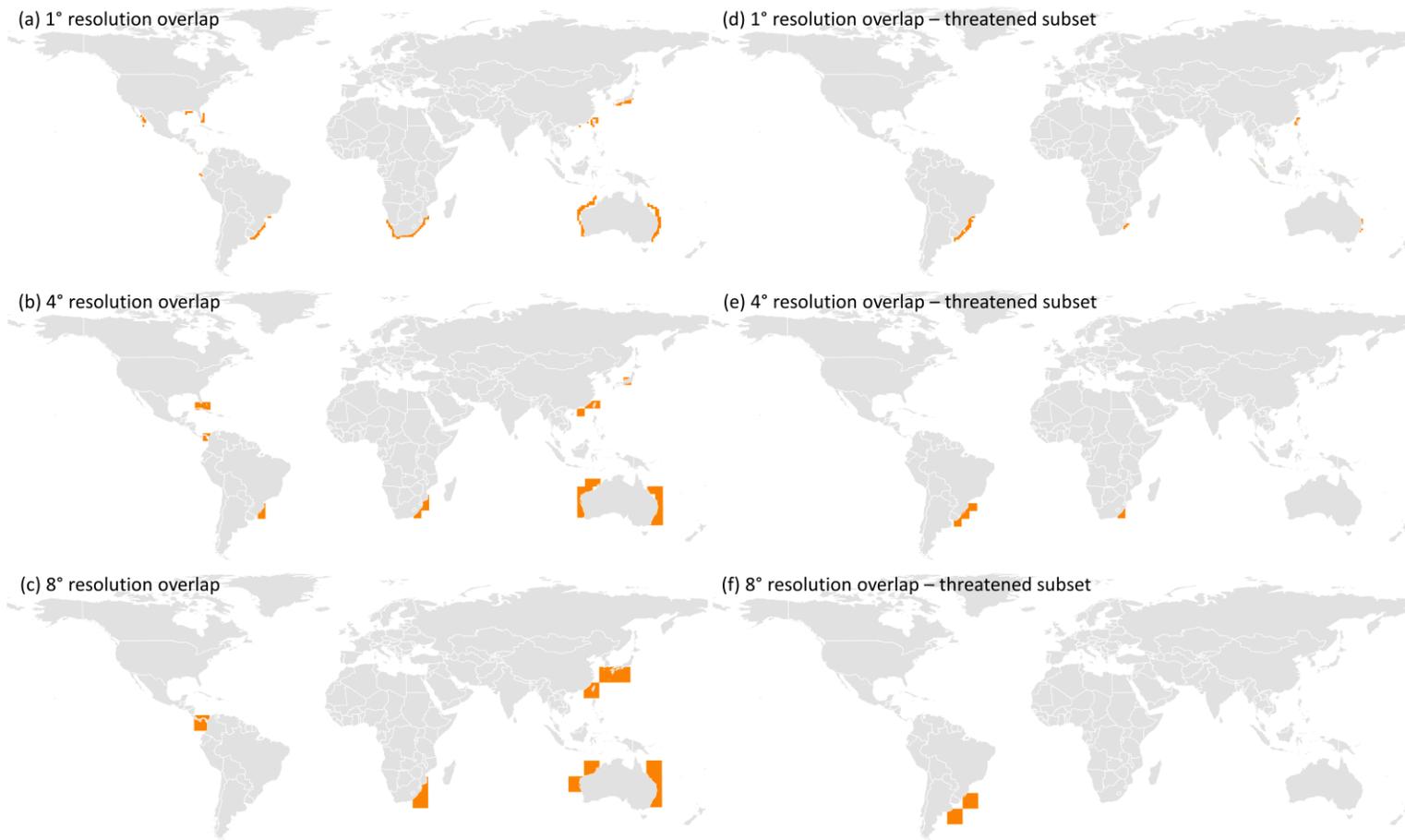


Figure 2.6 Spatially congruent areas between biodiversity hotspots derived from different species richness measures represented as the richest 5% of grid all cells. Spatially congruent areas between total species, evolutionarily distinct (ED) species, and endemic species at resolution levels of (a) 1°, (b) 4°, and (c) 8°, and (d-f) congruent areas for the threatened species subsets at each corresponding resolution level. The data used for this figure under CC BY license is granted permission from the International Union for the Conservation of Nature (IUCN), original copyright 2011.

Increasing the cell size from 1° to 8° led to 13.42% of hotspots being congruent, resulting in a greater than two-fold increase in congruency for all species (5.78% at 1° resolution), and the largest percentage of coverage contained within the country boundaries of Australia (44%), South Africa (21%), and southern Brazil and Uruguay (9.5%; Figure 2.6A; A1 Table). This increase in cell size also shifted the dominant locations of hotspot overlap (Figure 2.6A-C). At a 4° resolution, areas of congruence disappeared from the coasts of Mexico and Ecuador, shifting to more representation in the USA, Colombia, and Panama (Figure 2.6B). At an 8° resolution, the spatial congruence disappeared altogether from the coasts of Brazil (Figure 2.6C). Similar results were seen in the threatened species subsets; despite overall low spatial overlap between levels of resolution, overlap increased marginally between 1°, 4°, and 8° cell size (1.51%, 2.15%, and 2.50% overlap, respectively; A1 Table). Spatially congruent areas between the threatened subsets were predominantly found off the coasts of southern Brazil and Uruguay (66%), which was consistent across all levels of spatial resolution examined (Figure 2.6D – F). Contrastingly, these congruent areas of threatened species were present in Taiwan and Australia at 1° resolution, and South Africa at 1° and 4° (Figure 2.6D-F). At 8° resolution, congruency locations for threatened species no longer corresponded at all with the areas of congruency identified for all shark and ray species (Figure 2.6C and F).

2.5. Discussion

We describe four major findings. First, there was low overall spatial congruency when comparing the hotspots of all three measures of species richness (total species, ED species, and endemic species), offering a small area of focus for future conservation planning exercises. Even though those areas of spatial congruency are small in extent, they comprise approximately two thirds (64%) of all shark and ray species. Second, when comparing congruency pairwise between different species richness measures, ED species richness had the highest percent of overlap with total species richness, irrespective of spatial resolution or hotspot definition. These two findings were consistent for all shark and ray species, as well as for the subset of threatened species only. Third, congruency across the three richness measures for all threatened species is relatively insensitive to hotspot definitions (from 2.5% to 10% of richest cells) and was consistently low across these definitions. Fourth, increasing cell size (from 1° to 8°) lead to a two-fold increase in congruency between all species richness measures generally. These results have implications for shark and ray biodiversity, our knowledge of the different dimensions of biodiversity and how they can differ through space, and the effect of resolution in understanding spatial congruency.

In contrast to Küper et al. 2004, who demonstrated that there was a higher congruence of plant biodiversity when hotspot was redefined, we found that the extent of spatial congruency identified was low overall for the three measures of richness (total species, ED, endemic species) for all shark and ray species and the threatened species only. These results highlight considerable differences in the spatial distribution patterns of some biodiversity hotspots for sharks and rays, depending on the species richness measure used. The low congruency we have found between different measures of richness caution that it might be inappropriate to use total species richness as the sole feature of biodiversity to focus conservation attention towards. Our findings highlight that hotspots identified with other desirable species richness measures can be lost if there is a sole focus on total species richness, which has been a common strategy in identifying important areas for conservation (Roberts et al. 2002; Trebilco et al. 2011). If congruency among these hotspots identified with the different richness measures were high, then it would be reasonable to assume that relying on any one measure would be adequate to determine important areas for conservation that represented all three

richness measures. However, our results demonstrate that this is not the case, and that not considering certain species richness measures can result in the exclusion of important features of biodiversity for conservation attention (e.g. endemic, threatened, evolutionarily distinct species). The low level of spatial congruency between the species richness measures also means that a relatively small fraction of the world's ocean area could provide a tractable focal point for global shark and ray conservation. However, we caution that this kind of focal conservation strategy would still need to account for the opportunities and challenges presented by differing social, economic and cultural contexts (MacKeracher, Diedrich, and Simpfendorfer 2018; Mizrahi et al. 2019), in addition to the abundance, dispersal abilities, and activity patterns of the wide range of shark and ray species (Dwyer et al. 2020).

Interestingly, there was a relatively high spatial overlap of 43% between the hotspots identified for ED species richness and total species richness, when considering all shark and ray species. For the threatened species however, this overlap was considerably lower, at 4.02%. This finding of high congruency is supported by the suggestion that areas of high total species richness tend to be made-up of wide-ranging species, a characteristic commonly found in evolutionarily distinct species (Lennon et al. 2004). It is also potentially of little surprise that ED species overlap highly with total species richness because sharks and rays are one of the most evolutionarily diverse species groups with the average species embodying over 26 million years of shared unique evolutionary history (Stein et al. 2017). Furthermore, until the last decade, it was believed that areas of high total species richness harboured both a high number of endemic and threatened species for two reasons: (1) those areas experience greater levels of threatening processes such habitat transformation and exploitation, and (2) they are likely to be inhabited by species that are on average at a greater risk to these threatening processes (Gaston and Blackburn 1996a; Jetz, Rahbek, and Colwell 2004). More recently however, Orme et al. (Orme et al. 2005) demonstrated weak relationships of congruence between threat and total species richness from terrestrial avian fauna, further highlighting the necessity of using different types of species richness measures to identify important areas for biodiversity conservation (Orme et al. 2005). Our study is one of the first to demonstrate a relatively high degree of spatial congruence between hotspots of ED species richness and total species richness of all shark and ray species, as compared to the overlap of endemic species and total species.

The areas of spatial congruence for total and threatened shark and ray species cluster around coastal waters, while endemic species are primarily found at the convergent boundaries of tropical and temperate ecosystems. These warm reef environments at the convergent boundaries have been known to serve as hotspots for species evolution due to their high productivity and habitat complexity (Kieffer, Simpson, and Foote 2010; Siqueira et al. 2016). In most cases, these areas of overlap are also found within the bounds of a country's exclusive economic zone (EEZ), which have also been flagged as hotspots of functional diversity in sharks (Lucifora et al. 2011). The species richness measures examined in this paper only represent a small aspect of biodiversity and do not take into account other measures, such as functional diversity. Functional diversity is known to be crucial in maintaining the structure and function of marine ecosystems (Ferretti et al. 2010) and would likely also yield similarly incongruent hotspots. Ultimately, a future study could expand on our findings by exploring the extent of spatial congruency between other biodiversity metrics, such as functional diversity in all sharks and rays.

Studies that consider different levels of spatial resolutions have considered only one level of resolution that are either smaller (e.g. $\leq 1^\circ$) (Grenyer et al. 2006; Jetz and Rahbek 2001; Lucifora et al. 2011) or larger (e.g. $\geq 8^\circ$) (Tittensor et al. 2010) than those assessed in our study, missing the potential differences that could occur between the two. Our findings demonstrate that there are differences between these two levels of spatial resolution. We found that a reduction in resolution (i.e. larger sampling units, such as grid cells here) influenced global patterns of species richness hotspots for all sharks and rays. For example, at a coarse resolution (here, 8° cells), if an individual species' range slightly crossed the boundary of an 8° grid cell, its distribution would now be considered to encompass the entirety of that 8° cell as opposed to its true smaller fraction. The coarsening of hotspots and shifting of congruency locations resulting from coarser resolutions causes congruency locations to disappear where they were otherwise present at finer resolutions (i.e. Brazil and Uruguay; Fig 2.6). Previous work on riparian weeds also found that coarser resolutions were unable to model fine-scale distributions successfully and were also poor predictors of national species' distributions (Collingham et al. 2000). Overall, our results support the well-known finding that changes in spatial resolution can influence results in spatial analyses. Different areas of congruency identified at various spatial resolutions can make it difficult for conservation

management to direct focus to any particular area but demonstrates the importance of explicitly considering spatial resolution when determining important areas to further investigate for conservation priority. Furthermore, there are now numerous studies that examine how to integrate conservation planning across multiple levels of resolution (Arponen et al. 2012; Larsen and Rahbek 2005; Shriner, Wilson, and Flather 2006).

It is important to note the caveats of the distributional dataset used for this study. The IUCN species distribution map database was created from peer-reviewed, expert-generated maps around known locations of species distributions (Dulvy et al. 2014). Experts from the IUCN Shark Specialist Group (SSG) created a shapefile of the geographic distribution for each chondrichthyan species based on the original maps provided to the Food and Agriculture Organisation of the United Nations, using the standard mapping protocol for marine species devised by the IUCN Global Marine Species Assessment team (<https://sites.wp.odu.edu/GMSA/>). The maps show the Extent of Occurrence of the species cut to one of several standardized basemaps depending on the ecology of the species (i.e. coastal and continental shelf, pelagic, and deepwater). The original maps were updated, corrected, or verified by experts at the Red List workshops or by out-of-session assessors and SSG staff (Dulvy et al. 2014). These maps are likely to contain commission rather than omission errors such that a species is shown to be present in an area when in fact it is not (Rondinini and Chiozza 2010). Commission errors can be problematic for hotspot identification because they risk identifying areas that are not true hotspots and directing valuable and limited conservation resources to those untrue hotspot areas (Di Marco et al. 2017). Omission errors risk missing true hotspot areas of richness and therefore true areas of congruency between the different species richness metrics. Omission errors can also result in a reduction of spatial options available when it comes to systematic conservation planning (Rondinini et al. 2006). Aqua-maps can be used as an alternative or complementary data source to the IUCN distribution maps, they are created using habitat suitability models based on point distribution data and thus give an indication of probabilities of species occurrence across the distribution ranges (Kesner-Reyes et al. 2012). However, these models are rarely vetted by taxonomists that understand the biology and geographical distribution and veracity of point records. Although the IUCN distributional data are not without limitations, they are currently the most comprehensive datasets for studying shark and ray biodiversity patterns in the ocean. While we recognize there have

been range contractions, our approach is to identify the historic pattern of richness for each species and demonstrate a baseline understanding of global shark and ray biodiversity (Dulvy et al. 2016; Lawson et al. 2020). These maps are continually refined with routine updates of global species catalogues and field guides, lending scope to conduct more refined global analyses in future studies (Ebert et al. 2013; Ebert and Stahlman 2013; Last et al. 2016; White et al. 2006).

Although this was in essence a global analysis, the low richness and wide ranging nature of species inevitably means no hotspots were found in the pelagic ecosystem. Furthermore, endemic species richness tends to be strictly coastal, unless defined differently than the one used in this study. Therefore, future work can examine the identification of hotspot areas of species richness measures and their corresponding areas of spatial congruency when coastal and pelagic ecosystems are analyzed independently. A lack of spatial congruency among the three species richness measures also opens up future work to explore the potential differences in environmental and evolutionary drivers of individual species richness measures, at varying spatial extents. For example, at smaller extents (e.g. local) species have been known to be influenced by local attributes like competition, and habitat availability, whereas at large extents (e.g. global) it is hypothesized that environmental variables have a stronger relationship with global species patterns (Belmaker and Jetz 2011; van Rensburg, Chown, and Gaston 2002; Worm and Tittensor 2018). In conclusion, the lack of spatial congruency between different species richness measures (and likely other biodiversity measures) could provide a global informative perspective on areas that merit further attention where management could focus their efforts for the conservation of shark and ray biodiversity, especially in preparation for the 2030 Kunming Targets. The low level of spatial congruency means that the eight places with spatial overlap in all three measures of species richness might provide a useful starting point to direct conservation planning, Marine Protected Area designation, and improved fisheries management and secure a future for sharks and rays.

“The most striking feature of Earth is the existence of life, and the most striking feature of life is its diversity.”

David Tilman

Chapter 3. Shark and ray biodiversity driven by tropical cradles of young, narrow-ranging species²

3.1. Abstract

Understanding global biodiversity gradients is a long standing question in ecology and evolution. Often environmental covariates are used to explain richness gradients whereas the interplay of ecological and evolutionary explanatory variables are not typically considered together. Therefore, we describe marine richness patterns across the world's coastal seas and test five macroecological hypotheses: (1) kinetic energy, (2) productivity, (3) climate stability, (4) habitat availability, and (5) tropics-as-a-cradle hypotheses. We have a unique opportunity to evaluate hypotheses underlying global species richness using the most basal vertebrate radiations: class Chondrichthyes (sharks, rays, and chimaeras, hereafter "sharks and rays"). We used the IUCN Red List species distribution maps for nearly all marine sharks and rays ($n = 1,054$ species) overlaid on a 4° global grid system. We used generalized linear models to evaluate the strength of support for each of the five classes of hypotheses. The results support three of the five hypotheses. First, species richness is highest at warmer temperatures found in the tropics, consistent with the kinetic energy hypothesis. Second, there is a strong positive relationship between richness and both primary productivity and oceanic fronts, supporting the productivity hypothesis. Lastly, areas of high species richness found at lower latitudes comprise narrower-ranging and younger species, providing support for the tropics-as-a-cradle hypothesis. However, while species rich areas support the tropics-as-a-cradle hypothesis, northern latitudes have younger and smaller ranging species than the tropics regardless of species richness. Ultimately, these results increase our understanding of the multi-dimensional effects of abiotic and biotic variables on species distributions and numbers and opens the door to further exploring whether the tropics are a true cradle of diversity for sharks and rays, or are just acting as an area of accumulation for small ranging, young species, such as endemics.

² A version of this chapter is in preparation for journal submission with coauthors Nicholas K. Dulvy, and Lindsay N.K. Davidson.

Keywords: spatial heterogeneity, biogeography, latitudinal biodiversity gradients, cradle-museum hypotheses, Rapoport's Rule, geographical range, hotspots, conservation

3.2. Introduction

One of the most profound challenges to date is to understand the spatial patterning of the diversity of life on Earth. The quantity, variety, and distribution of biodiversity scales across species and populations, and a range of habitats and ecosystem characteristics (Mace et al. 2005). One of the most prevalent patterns is the latitudinal gradient in species richness, defined as the number of different species in a given area, and which tends to be greatest at tropical latitudes and decreases towards the poles (Chaudhary et al. 2016; Lucifora et al. 2011; Tittensor et al. 2010). The latitudinal biodiversity gradient was first described on land, but is also prevalent in the coastal seas, albeit with some important differences, such as nutrient upwellings at frontal systems in mid-latitudes (Worm, Lotze, and Myers 2003). There are five major hypotheses that underlie the well-known latitudinal richness pattern. These five hypotheses include the (1) kinetic energy (Clarke and Gaston 2006; Wright 1983), (2) productivity (Wright 1983), (3) climate stability (Sanders 1968), (4) habitat availability (Worm et al. 2005) and (5) the tropics-as-a-cradle hypothesis of evolutionary age and range size (Chown and Gaston 2000).

The kinetic energy hypothesis postulates more species in warmer waters due to increased metabolic rates resulting in higher rates of net diversification (speciation rate minus the extinction rate) (Rohde 1992; Worm and Tittensor 2018). The primary productivity hypothesis explains that greater primary productivity supports more species, and therefore higher species richness, as primary production increases the availability of resources, which allows for larger population sizes and niche specialization (Evans et al. 2005; Jetz et al. 2009). Climate stability describes seasonal and longer-term variations in climate, with high latitude temperate and polar regions experiencing strong seasonal differences (high seasonality) that may select and retain mainly wide-ranging migratory species with better dispersal abilities, lower extinction rates, and broader climatic niches (Sandel et al. 2011; Sunday et al. 2011). Conversely, the tropics have a greater number of species most likely due to a seasonally stable climate, that suits not only the over-wintering populations of wide-ranging, broader niche species, but also the small-ranging,

habitat-specialists (Rangel et al. 2018; Somveille et al. 2013). Habitat availability can be described by the physical quantity and/or complexity of a given environment (e.g. elevation, shelf area, coastline, etc.). Increases in the physical complexity of a habitat have the potential to increase diversity by providing a range of habitat niches for organisms to exploit, both at small and large scales (Worm et al. 2005). Most research that seeks to disentangle the correlates of biodiversity gradients have focused mainly on the abiotic drivers and ecological hypotheses (Costello and Chaudhary 2017; Gagne et al. 2020; Tittensor et al. 2010), leaving few analyses that have sought to understand the differential importance of both abiotic and biotic processes. The final hypothesis we present, explores the biotic processes through the ‘tropics-as-a-cradle’ characteristics of species lineages themselves, where the tropics are thought to be a cradle of evolutionary innovation having a disproportionate number of more recently evolved species with smaller geographic range sizes (Chown and Gaston 2000; Jablonski et al. 2006; Rohde 1992).

While most of the theory and conceptual development has relied on terrestrial datasets, understanding biodiversity patterns in the oceans provides an independent test of the mechanisms underlying species richness not least because of the phytoplankton dominance of primary production and the prevalence of size-based species interactions (Reuman et al. 2014; Webb 2012). Here, we focus on sharks and rays, one of the three lineages of fishes, that are one of the largest and most successful vertebrate radiations to date (Kriwet, Kiessling, and Klug 2009; Stein et al. 2017). Sharks and rays have survived through every mass extinction over the last 400 million years, and they predate much of the development of biodiversity on land. Further, sharks and rays occur in all the world’s waters from the deep-sea, oceanic, neritic, and estuarine habitats, to freshwater rivers and lakes connected to the ocean (Carrier et al. 2012). They are also one of the few basal vertebrate lineages with comprehensive species distribution maps and a complete phylogeny, making them an excellent group of fishes to study the mechanisms underlying marine biodiversity patterns (Davidson and Dulvy 2017; Maisey, Naylor, and Ward 2004; Stein et al. 2017).

Here, we use a global database of all known marine shark and ray distributions to test abiotic and biotic hypotheses to explain the broad-scale spatial patterning of biodiversity in the ocean. Specifically, we test the (1) kinetic energy, (2) productivity, (3) climate stability, (4) habitat availability, and (5) tropics-as-a-cradle hypotheses to

examine how the age and range size of species contributes to our understanding of the marine latitudinal richness gradient.

3.3. Methods

3.3.1. Species distributions

We used global distributions maps of all marine shark and ray species (~1,086 species) obtained from the IUCN (Davidson and Dulvy 2017; Dulvy et al. 2014; IUCN 2018). These maps used the original shark and ray distributions from the Food and Agriculture Organisation of the United Nations where experts from the IUCN Shark Specialist Group (SSG) developed a shapefile of the geographic distribution of each shark and ray species. The distributions used standard mapping protocols for marine species devised by the IUCN Global Marine Species Assessment team (<https://sites.wp.odu.edu/GMSA/>). Distribution maps were projected in a Lambert Equal Area projection to preserve area across the extent of the analysis, and the geographic coordinate system was in NAD83. Freshwater obligates including species from the Families Carcharhinidae, Potamotrygonidae, and Dasyatidae (totalling 32 species) were excluded from analyses.

3.3.2. Spatial resolution and extent

We created a global grid across the entire marine environment and determined the number of species per grid cell. The global grid was adapted from the spatial resolution presented in Tittensor et al., 2010 to a cell resolution of 4° by 4°, equating to a distance of approximately 440 km at the equator. This resolution should be sufficient to identify underlying patterns of global drivers of species richness (Sandel et al. 2011; Tittensor et al. 2010). The global grid contained 3,078 cells after excluding terrestrial land masses which were defined as any cells whose area contained strictly land; as obtained from the Environmental Systems Research Institute (ESRI) vector map of the world (Natural Earth 2018). A grid cell was classified as coastal if the cell intersected with a land mass and a country's exclusive economic zone (EEZ, $n = 898$).

3.3.3. Measuring species richness gradients

We determined species richness gradients across the global grid. A species is scored as present if any part of their distribution range fell within the grid cell boundaries. Species richness was calculated as the number of unique species within each grid cell ($n = 1,054$ spp.). The global grid was restricted to coastal cells only to minimize problems with zero- and one-inflated data due to low richness in the pelagic oceans and excluded any grid cells that contained no species ($n = 749$).

3.3.4. Collation of the five biodiversity hypotheses

We compiled eight variables relating to the kinetic, productivity, climate stability, habitat availability, and the tropics-as-a-cradle hypotheses (Table 3.1). The data were averaged on the 4° global grid from their original resolutions, unless otherwise noted.

- (1) **Kinetic Energy Hypothesis:** To represent available energy (Clarke and Gaston 2006), we used sea surface temperature (hereafter termed “SST”) at a 1° resolution provided by the National Oceanic Atmospheric Administration. We calculated the mean monthly sea surface temperature within each 1° grid cell across 35 years from 1981 – 2016. We then averaged between all 1° grid cells contained in each of our 4° grid cells to get an overall mean sea surface temperature.
- (2) **Productivity Hypothesis:** The productivity hypothesis was tested using both primary production and SST slope as an index of frontal zones. First, primary productivity ($\text{g}\cdot\text{m}^{-3}\cdot\text{day}^{-1}$) was calculated as the mean primary productivity per grid cell (downloaded from Bio-ORACLE’s databank; Reynolds et al. 2002). Second, steep gradients of SST slope values can capture frontal oceanic areas and was calculated as the absolute difference in SST between each cell and its eight neighbouring cells using the NOAA temperature data, then averaged for each 4° grid cell (Reynolds et al. 2002).
- (3) **Climate Stability Hypothesis:** Climate stability is calculated as seasonality by first taking the mean standard deviation for each year between 1981 to 2018, resulting in 35 values per 1° grid cell. At the 4° resolution, this totalled

560 values per grid cell. Then, per 4° grid cell, we took the average between each yearly standard deviation.

- (4) **Habitat Availability Hypothesis:** Coastline length (km) was used to represent habitat availability and was derived from 1:10m land vector shapefiles provided by Natural Earth (Natural Earth 2018). Coastline length is calculated as the total length of coast in kilometers available within each grid cell. This is particularly useful for capturing small-scale heterogeneity, such as the presence of peninsulas and islands in grid cells.
- (5) **Tropics-as-a-cradle Hypothesis:** Three variables were used to test the tropics-as-a-cradle hypothesis. First, the average age of species per grid cell was calculated using a measure of species-level evolutionary distinctiveness (ED), represented in millions of years (Stein et al. 2017). Within every 4° grid cell, the mean ED was then calculated across all species present in that cell. Second, the standard deviation of mean age of species (SD Age) was calculated to represent the heterogeneity in species age on a grid cell by grid cell basis. Here, a null hypothesis would be that the variation in standard deviation of mean age of species would increase as species richness increases because we innately have more species, and therefore, more room for a wider spread of evolutionary ages. Lastly, geographic range size was defined on a per species basis as the total number of grid cells a single species occupied, ranging from 1 to a maximum of 3,078, if a species occupied the entire ocean. Range size for that grid cell is then averaged across all species categorized as present within each 4° grid cell. For example, grid cells with a lower overall value (i.e. range size), would, on average, represent areas of species with smaller range sizes, and vice versa.

3.3.5. Statistical analyses

3.3.5.1 Data Preparation

To prepare the dataset for statistical analyses we removed any rows of data where (1) grid cells did not contain any predictor variables, and (2) any truncated grid cells where area was less than 10% of the total area of a regular-sized grid cell (192,730km²) (Tittensor et al. 2010). To test for covariation in the abiotic and biotic

variables we ran a Spearman's Rank-order pairwise correlation across all variables, and removed one of the two variables when they had an absolute value greater than ± 0.70 to prevent problems with model identifiability (i.e. dissolved oxygen was dropped because it covaried with sea surface temperature and tests the stress hypothesis as opposed to the kinetic energy hypothesis; $r = -0.95$; Supplementary Figure S1). Abiotic variables were log transformed to help normalize the data. All abiotic and biotic variables were then scaled and standardized by dividing by two standard deviations to make model coefficients comparable. Species counts remained untransformed as transforming count data is less effective in model performance and more difficult to interpret than selecting the appropriate distribution term in statistical models (O'Hara and Kotze 2010). We used an interaction term of latitudinal region to help explain the non-linearity of mean age of species. All other predictor variables did not have an interaction term because biologically speaking, there is no inherent interaction between latitudinal region and the other predictor variables. For example, it is already well established that sea surface temperature increases with decreasing latitude and therefore does not require an interaction term to explain the already known pattern. Furthermore, primary production is also not expected to directly coincide with latitude because it is largely driven by nutrient upwellings and agricultural run-off. Latitudinal region was created as a categorical variable where regions were made into four groups of being either the Tropics (0° to $\pm 23.5^\circ$), Sub-Tropics ($\pm 23.5^\circ$ to $\pm 40^\circ$), Temperate ($\pm 40^\circ$ to $\pm 60^\circ$), or Polar ($\pm 60^\circ$ to $\pm 90^\circ$) regions.

3.3.5.2 Spatial autocorrelation

Spatial autocorrelation occurs when adjacent regions are inherently more similar to one another than distant regions (Tobler 1970). We tested for spatial autocorrelation as it violates one of the key assumptions of traditional statistical approaches - residuals are independent and identically distributed (Kuhn and Dormann 2012). Violating this assumption can result in spatial pseudoreplication and deflated estimates of variance and have corresponding impacts on model inference (Dormann 2007; Dormann et al. 2007). Spatial patterning was present in both the response variables and most ($n = 10$ of 11) of the covariates. Therefore, to help account for spatial variation in geographic proximity, we created one categorical variable describing ocean basin. We used a four-level unordered factor to describe geography: Atlantic Ocean (including the Mediterranean Sea), Pacific Ocean, Indian Ocean, and the Poles (encompassing both

the Arctic and Southern Oceans). The inclusion of a categorical variable helped explain the structure in the data resulting from geographically similar conditions such as temperature. Lastly, spatial autocorrelation patterning was not found in the residuals of any of the models. However, the addition of an autocovariate spatial autocorrelation term estimates how much the response variable at any one location reflects response values at surrounding locations and improves model fit (Dormann et al. 2007). The autocovariate is calculated from a distance-weighted function of neighboring response values to the model's explanatory variable (Dormann et al. 2007). The inclusion of a spatial autocorrelation autocovariate in our models, although not inherently necessary, improved both model performance and model residuals.

3.3.5.3 Covariates of species richness

To evaluate the five hypotheses, we ran a series of generalized linear models with a zero-truncated negative binomial distribution and log-link family ($n = 749$) using all variables except dissolved oxygen. Mean range size of species and mean age of species were highly collinear ($r = 0.78$; Figure B4) and caused problems with model identifiability. However, we were still interested in their individual effects on species richness, and therefore ran two global models with all abiotic variables where mean range size and mean age of species were considered independently from one another;

$$\begin{aligned}
 \text{Richness} \sim & \text{Mean SST} + \text{Mean Primary Productivity} + \text{SST Slope} + \text{Seasonality} \\
 & + \text{Coastline Length} + \text{Range Size} + \text{Ocean Basin} \\
 & + \text{Spatial Autocovariate}
 \end{aligned}
 \tag{eqn 1}$$

$$\begin{aligned}
 \text{Richness} \sim & \text{Mean SST} + \text{Mean Primary Productivity} + \text{SST Slope} + \text{Seasonality} \\
 & + \text{Coastline Length} + \text{Mean Age of Species}(\text{LatRegion}) + \text{SD Age} \\
 & + \text{Ocean Basin} + \text{Spatial Autocovariate}
 \end{aligned}
 \tag{eqn 2}$$

where richness represents the number of species (range 1-179). The variables represent the abiotic and biotic predictors used in the models, where eqn1 include mean range size, and eqn2 has both mean age of species with the interaction term of latitudinal

region (LatRegion) and SD age. Both models included a categorical variable of ocean basin and a spatial autocovariate term.

We used a model selection approach and model AIC comparison to independently test the strength of each of the five hypotheses that explains shark and ray species richness (Table 3.1). Multicollinearity was tested by running a variance inflation factor on model variables without the interaction. Model assumptions were evaluated by plotting residuals versus fitted values, and the residuals were assessed for spatial dependency by plotting them against latitude-longitude and running Moran's I diagnostics.

All spatial analyses were performed using ArcGIS Pro version 2.3.3 (ESRI 2019) and statistical analyses were performed in R V.1.2.1335 and R V.3.6.1 (R Studio Team 2018; Team 2019). We used the `glmmTMB` package (Brooks et al. 2017) and `spdep` package (Bivand, Pebesma, and Gomez-Rubio 2013; Bivand and Wong 2018).

3.4. Results

Overall, species richness is highest in the tropics and decreases gradually approaching the polar regions. There is a latitudinal gradient in richness with more species in the tropics and fewer at higher latitudes (Figure 3.1). The equatorial regions with high species richness (~179 species per grid cell) include central America surrounding Panama, and the central Indo-Pacific Ocean encompassing southeast Asia including Malaysia, the Philippines, Indonesia, and Cambodia (Figure 3.1). However, species richness follows more broadly a sub-tropical latitudinal distributional pattern with high richness primarily occurring not only at the equator but also closer to the Tropics of Capricorn (23.5° S) and Cancer (23.5° N). The regions with high species richness near the Tropic boundaries include eastern South Africa and Mozambique, eastern and western Australia, and the Northwest Pacific surrounding Taiwan, southern Japan, and the east coast of China (Figure 3.1).

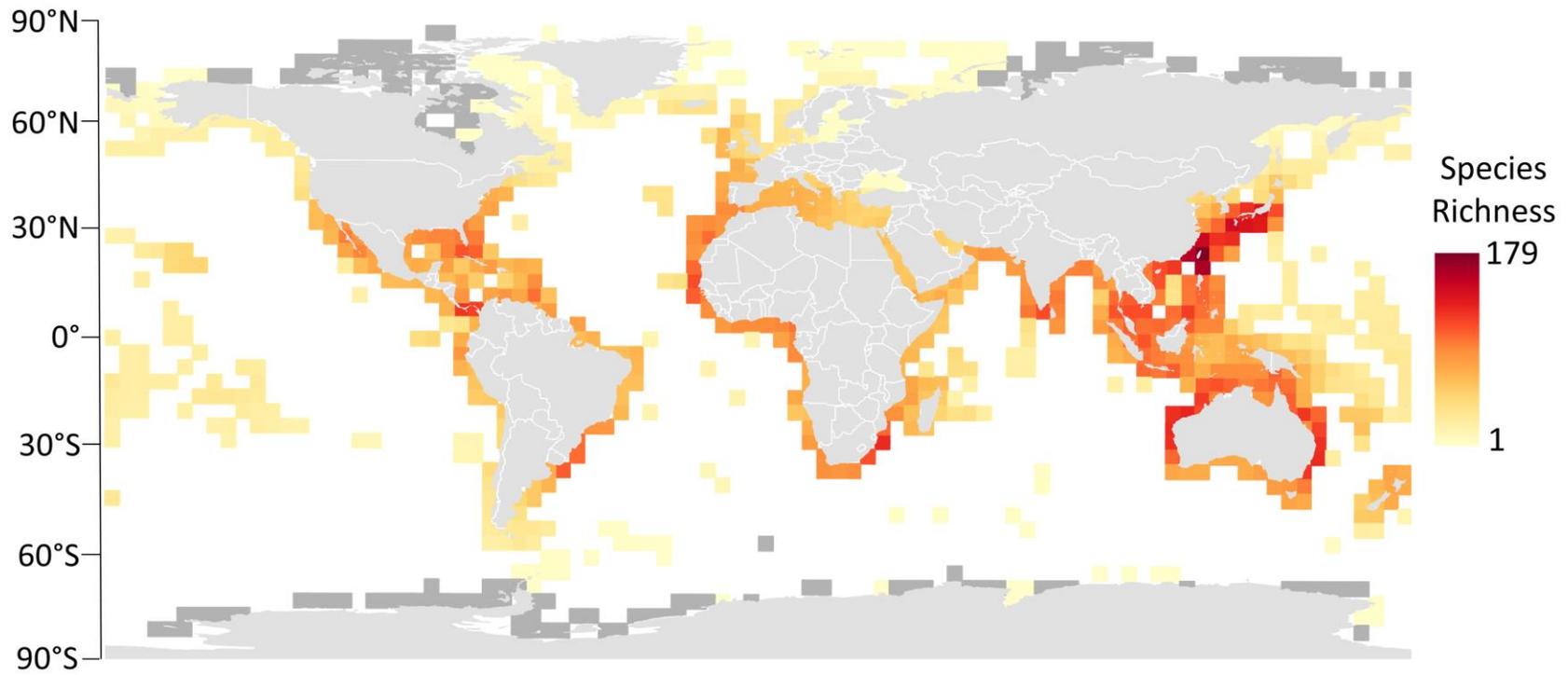


Figure 3.1 Global biodiversity patterns of shark and ray species richness at 4° resolution. Colour-scaling is represented as a colour gradient where grey cells represent coastal grid cells with no species present.

The best supported model included all abiotic variables and the biotic variable of range size in the global model and a spatial autocovariate term (AICc = 5034; Table 3.1), demonstrating that no single hypothesis explains species richness. The best supported hypotheses were the kinetic energy, productivity, and tropics-as-a-cradle hypotheses. There was a positive relationship between SST and species richness (Figure 3.2A) whereby more species are found in warmer waters closer to the equator than at the poles, consistent with the abiotic hypothesis of kinetic energy ($b = 0.77$ [0.718, 0.83]; Figure 3.3; Table 1). There was also a positive relationship between species richness and both primary productivity ($b = 0.02$ [0.01, 0.04]; Figure 3.2B) and frontal upwelling and downwelling systems (SST Slope; $b = 0.04$ [0.01, 0.05]; Figure 3.2C), providing support for the productivity hypothesis that more species are found in regions with greater productivity and that contain more frontal systems carrying nutrients (Figure 3.3; Table 1).

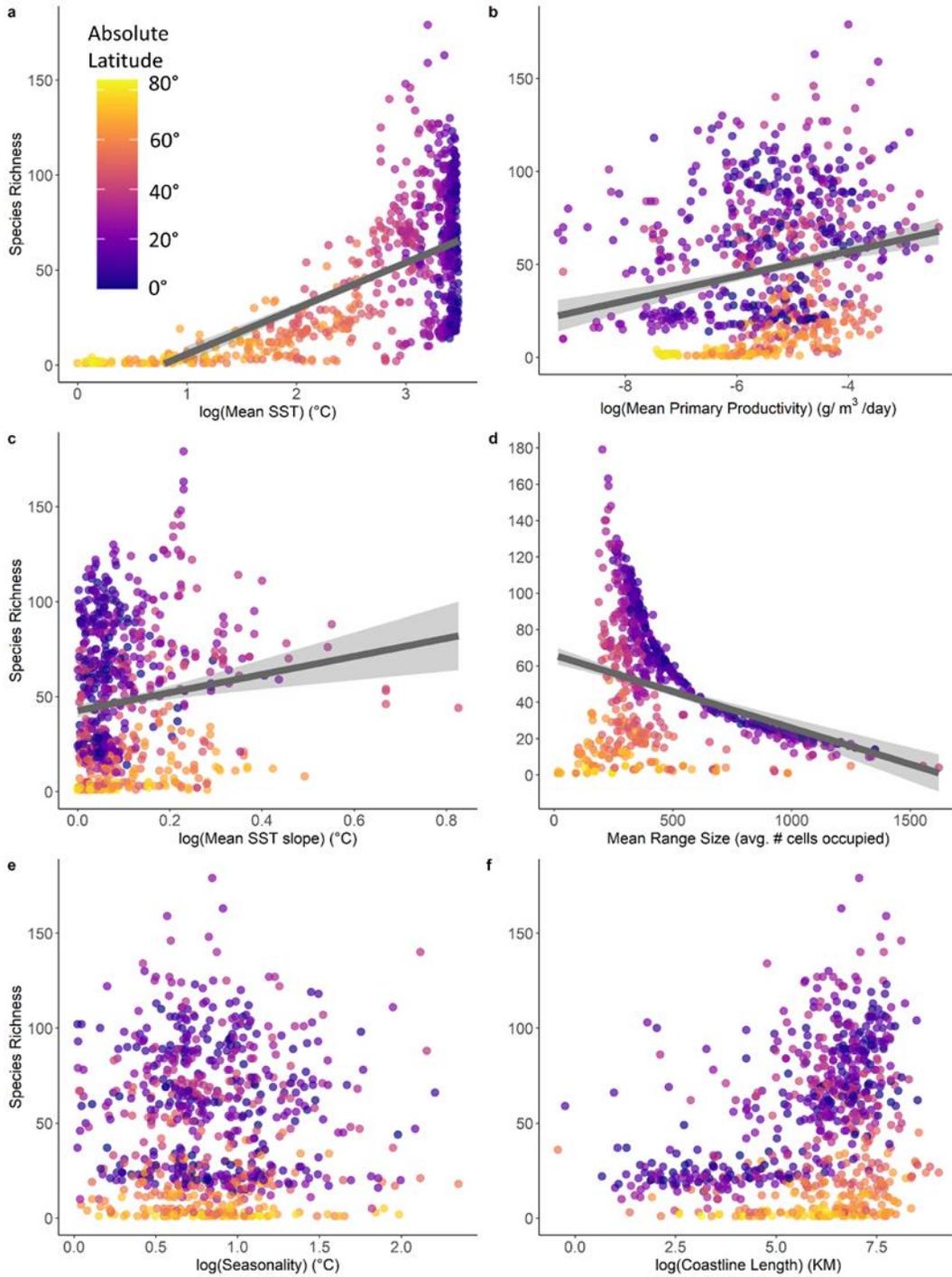


Figure 3.2 Abiotic and biotic trend plots for shark and ray species richness. Panels represent relationships between species richness and (a) mean sea surface temperature (SST), (b) primary productivity, (c) slope of mean SST, (d) mean range size of species, (e) seasonality (standard deviation of SST), and (f) coastline length. Panels a-c and e-f have log-transformed predictor variables, and all panels are unstandardized. Points are colored using the absolute latitude.

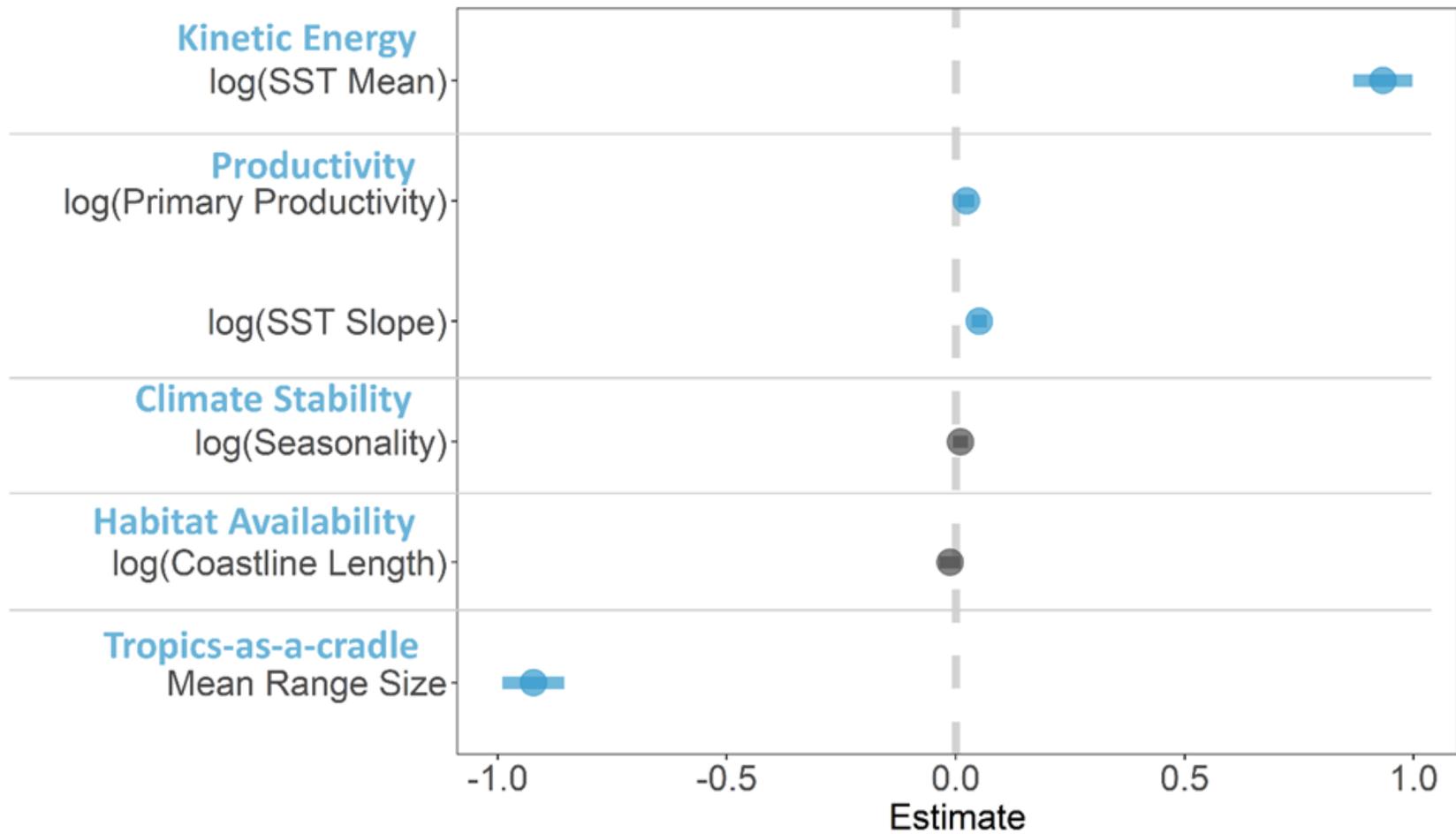


Figure 3.3 Coefficient plot of the best supported model of each of the five associated abiotic hypotheses and the biotic hypothesis using range size for shark and ray species.

The biotic tropics-as-a-cradle hypothesis relies upon high richness places being composed of species with small ranges and young ages. First, we find that species range was negatively related with species richness ($b = -0.92 [-0.98, -0.85]$; Figure 3.3; Table 1), but the pattern was wedge-shaped such that regions with small ranging species have a large spread in species richness (Figure 3.2D). The wedge arises because there are small range species found near the poles, generally, in areas of low richness. However, there are some exceptions, such as the high richness of the southern Indian Oceans islands of the Kerguelan biogeographic province and the Falklands/South Sandwich Islands of the South Georgian province, which comprised mainly wide-ranging regionally endemic skates that are Gondwanaland relicts (Figure 3.4A). Range size is highly bimodal at the tropics, with the largest tropical ranges comprising wide-ranging pelagic sharks occurring around oceanic islands with low richness and smaller ranges occurring along species rich tropical and subtropical continental shelves (Figure 3.4A-B). Consequently, while the range-richness pattern is wedge-shaped the dominant pattern is a negative relationship between range size and richness, such that the most species rich places on continental shelves are dominated by small-ranging species (Figure 3.3). By comparison, the climate stability and habitat availability hypotheses had relatively less explanatory power on species richness (Figure 3.2E-F; Figure 3.3).

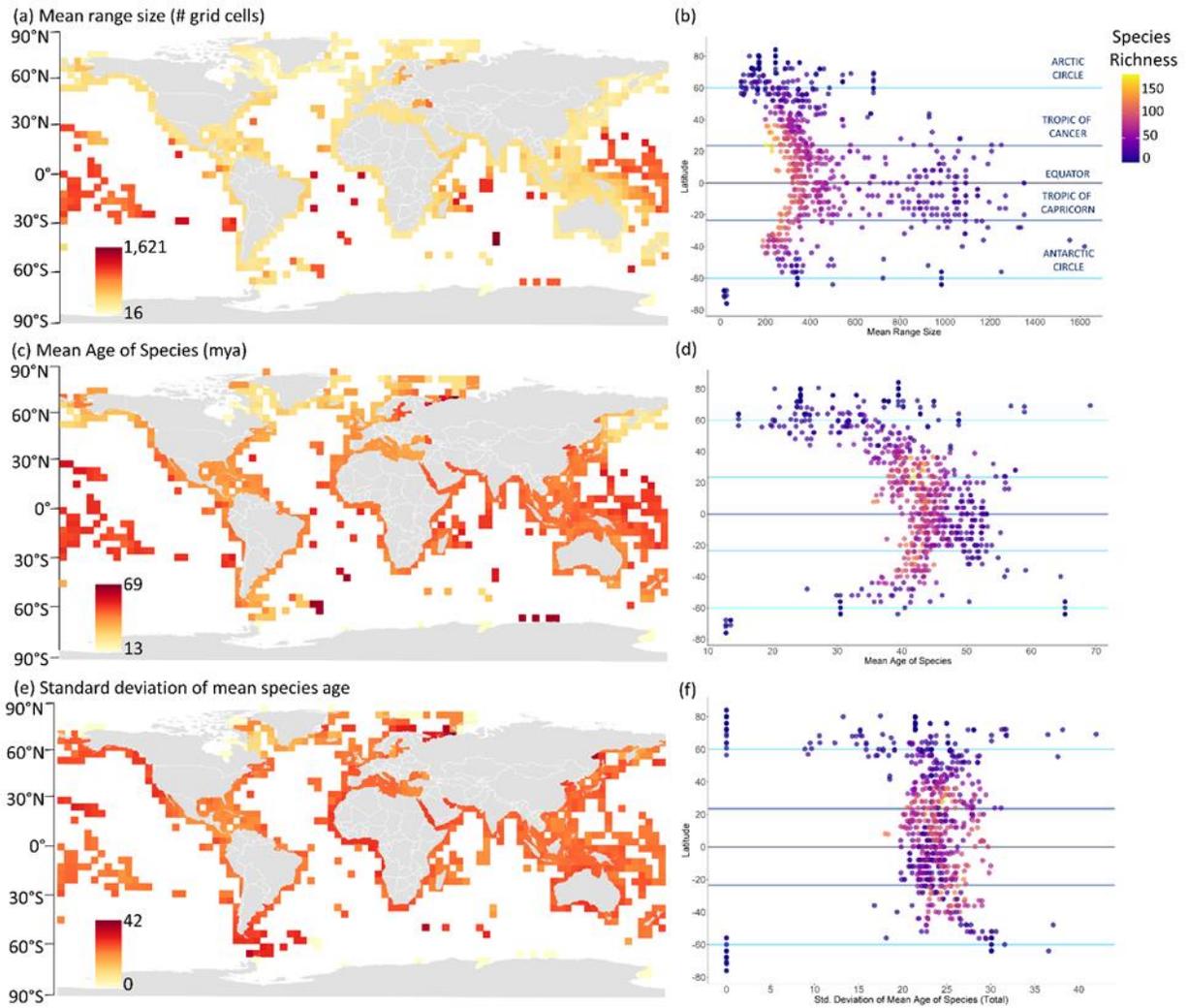


Figure 3.4 Biotic variables of the tropics-as-a-cradle hypothesis. Panels on the left-hand side (a,c,e) represent the geographic distribution on a grid cell level of (a) mean range size, (c) mean age of species, and (e) SD age of species. Panels on the right-hand side (b,d,f) represent the biotic variables' corresponding relationship with latitude for (b) range size, (d) mean age of species, and (f) SD age of species, whereby points are colored by species richness.

Second, the tropics-as-a-cradle hypothesis also suggests we would expect high species richness areas in the tropics to be mostly composed of young species. To explore the effects of age on species richness, the second best supported global model included all abiotic variables and the biotic variable of mean age of species and SD age. Species age had a “peaked” pattern with latitude such that polar and temperate regions were made up of a wide range of young and old species while subtropical and tropical regions contained primarily older species (Figure 3.5A). Furthermore, while the tropics contained the majority of the oldest species, a few regions in the poles also displayed some older relics, specifically at the northern end of Russia (Zapolyarny District) and southern ocean islands archipelagoes, such as Falkland/Malvina, Georgia and South Sandwich Island, and Kerguelen plateau (Figure 3.4C-D). The relationship between species richness and age in the tropics and subtropics was much steeper than that in the temperate and polar regions such that species ages in the higher latitudes tended to be more widespread, including both young and old species (Figure 3.5A). Overall, species richness had a negative relationship with age in three of the four latitudinal regions (tropics, subtropics, and polar) such that species rich areas comprised younger species ($b_{Trop} = -0.35 [-0.57, 0.13]$; $b_{SubT} = -0.36 [-0.59, -0.13]$; $b_{Polar} = -0.39 [-0.58, -0.20]$; Figure 3.5A and 3.5C; Table 3.1). The temperate region had a weak positive relationship with species richness and age ($b_{Temp} = 0.04 [-0.18, 0.26]$; Figure 3.5A and 3.5C; Table 3.1), however, this relationship was not significant. Lastly, we would expect a smaller range in SD Age in species rich areas if the tropics-as-a-cradle hypothesis were true. However, species richness had a positive relationship with SD age such that species rich areas comprised a wider range in species ages ($b = 0.38 [0.30, 0.46]$; Figure 3.5B and Figure 3.5C; Table 3.1). Furthermore, the widest ranging species surrounding tropical latitudes (Figure 3.3A-B) tended to comprise some of the oldest species (Figure 3.3C-D) and contained a spread of species ages around 30 – 40 standard deviations (Figure 3.3E-F).

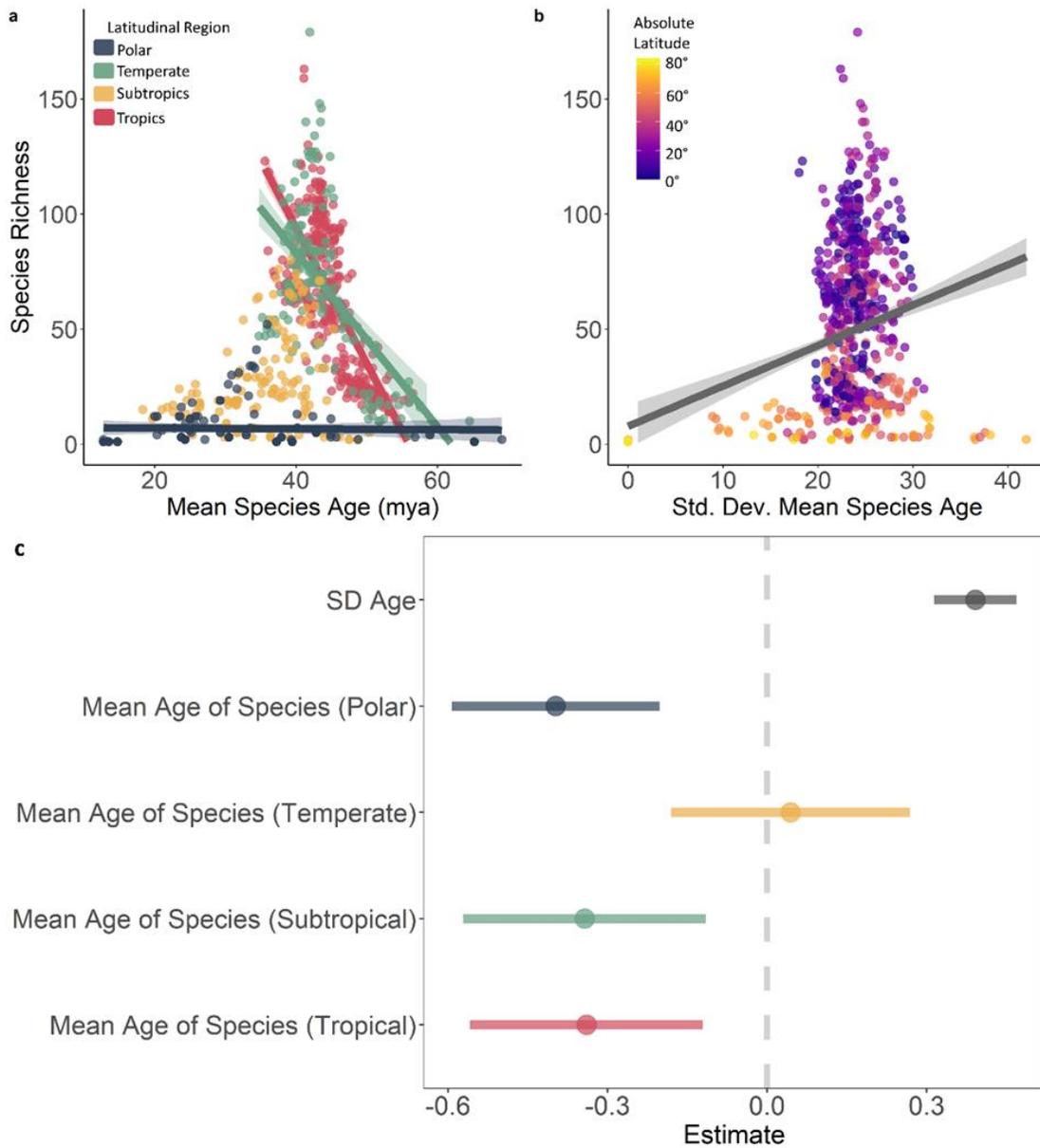


Figure 3.5 Biotic trend plots and coefficient plot for second best supported global model of shark and ray species richness. Panels represent relationships between species richness and (a) mean age of species (mya) and (b) SD age of species. Panel (c) represents the coefficient plot for biotic age variables for the tropics-as-a-cradle hypothesis. Predictor variables are represented as unstandardized. Points are coloured by (a) the interaction variable of latitudinal region and (b) absolute latitude, and trend lines represent linear regression lines from the model output where variable outputs were significant.

Table 3.1 Support of individual hypotheses and full model including all variables on species richness of sharks and rays. All models include the categorical variable of Ocean Basin and a spatial auto-covariate term. “Predicted effect” indicates the direction of the effect of the hypothesized mechanism on a baseline model of species richness where ↑ indicates an increase and ↓ a decrease. All models include the number of parameters used (k), the model coefficient (b) and 95% confidence intervals, AIC, ΔAIC_c, and AIC weights for model comparison.

| Hypothesis | References ^a | Predicted effect | k (# of parameters) | Formula: Species Richness ~ | b (95% CI) | AIC | ΔAIC _c | AIC weights |
|----------------------|-------------------------|------------------|---------------------|---|--|------|-------------------|-------------|
| Habitat Availability | 4 | ↑ | 1 | Coastline Length (km) | 0.15 (0.11, 0.19) | 6209 | 905 | 0 |
| Productivity | 2 | ↑ | 1 | Mean Primary Productivity | 0.06 (0.03, 0.10) | 6118 | 814 | 0 |
| | | ↑ | 1 | SST Slope | 0.06 (0.04, 0.09) | 6116 | 812 | 0 |
| Climate Stability | 1 | ↓ | 1 | Seasonality | -0.004 (-0.03, 0.03) | 6133 | 809 | 0 |
| Kinetic Energy | 2, 3 | ↑ | 1 | Mean SST | 0.27 (0.20, 0.35) | 6083 | 779 | 0 |
| Cradle Hypothesis | 5 | ↑ | 1 | SD Species Age (mya) | 0.20 (0.12, 0.28) | 6110 | 806 | 0 |
| | | ↓ | 1 | Mean Range Size (per grid cell) | -0.43 (-0.49, -0.37) | 5932 | 628 | 0 |
| | | ↓ | 1 | Mean Species Age (mya) | Polar: 0.06 (-0.16, 0.27) Temperate: -0.13 (-0.37, 0.11) Subtropical: -0.76 (-1.02, -0.49) Tropical: -0.75 (-1.00, -0.50) | 5910 | 606 | 0 |
| | | | 7 | Mean SST Mean Primary Productivity SST Slope Seasonality Coastline Length Mean Species Age SD Species Age | 0.88 (0.76, 1.00) 0.05 (0.03, 0.07) 0.05 (0.03, 0.07) 0.01 (-0.01, 0.03) 0.10 (0.07, 0.12) Polar: -0.39 (-0.58, -0.20) Temperate: 0.04 (-0.18, 0.26) Subtropical: -0.36 (-0.59, -0.13) Tropical: -0.35 (-0.57, -0.13) 0.38 (0.30, 0.46) | 5573 | 269 | 0 |
| Full Model with Age | | | | | | | | |

| Hypothesis | References ^a | Predicted effect | <i>k</i> (# of parameters) | Formula: Species Richness ~ | <i>b</i> (95% CI) | AIC | ΔAIC _c | AIC weights |
|----------------------------|-------------------------|------------------|----------------------------|--------------------------------|----------------------|------|-------------------|-------------|
| Full Model with Range Size | | | 6 | Mean SST | 0.93 (0.87, 1.00) | 5304 | 0 | 1 |
| | | | | Mean Primary Productivity | 0.02 (0.01, 0.04) | | | |
| | | | | SST Slope | 0.05 (0.03, 0.07) | | | |
| | | | | Seasonality | 0.01 (-0.01, 0.03) | | | |
| | | | | Coastline Length | -0.01 (-0.03, 0.01) | | | |
| | | | | Mean Range Size | -0.92 (-0.99, -0.85) | | | |

3.5. Discussion

Sharks and rays comprise the oldest radiation of vertebrates and provide a unique alternate opportunity to understand the generality of latitudinal richness hypotheses across vertebrates. We find that three of the five hypotheses have at minimum marginal effects on species richness such that the greatest richness is driven by abiotic features (such as temperature and productivity) and intrinsic biotic attributes (such as species age and range size). The places with the greatest richness tend to be along the tropical and subtropical continental shelves with greater temperature and frontal systems and comprise small-ranging, younger species. Here, we discuss two major findings. First, we examine the richness relationships with the abiotic features (1) temperature, (2) primary productivity, and (3) frontal systems. Second, we examine the biotic richness relationships of (1) range size and (2) age.

Biodiversity both on land and in the marine environment are supported by greater energy availability at the equator, also known as the kinetic energy hypothesis (Clarke and Gaston 2006; Wright 1983). However, it is crucial to note that temperature does not have a direct effect on the diversification of species. For example, on land, energy is usually provided by plants through the evapotranspiration of water from plants and soils, which is a process driven by temperature and solar radiation. In contrast, in the marine environment, temperature and solar radiation are believed to have a direct effect on the production of primary productivity whereby higher temperatures and increased solar radiation increase productivity. Therefore, from an ecological stance, increased solar radiation and temperatures entering at the equator tend to help support more biological primary productivity, sustaining more individuals, and further leading to an increase in the number of species that can coexist in a given area, also known as the productivity and more-individuals hypotheses (Clarke and Gaston 2006; Wright 1983). From a metabolic perspective, increased temperature drives increased metabolic rates in individuals, leading to faster generation times and mutations rates resulting in greater speciation and species turnover (Allen, Brown, and Gillooly 2002; Clarke and Gaston 2006). Thus, temperature's effect on species is indirect such that increases in temperatures can allow for increased primary productivity and species metabolic rates, which in turn promote species diversification.

However, temperature and productivity are not so closely coupled in the ocean as on land. Indeed, the equatorial warm oceans are characterised by very low primary production, which can be reflected in the clarity of water around tropical coral reefs. Generally, equatorial primary production is nutrient-limited rather than light- and temperature-limited. Instead, production ramps up at the subtropical latitudes as a result of the upwelling of nutrients relating to Hadley cells driving trade winds and westerlies. Thus, while temperature might be greatest near the equator, primary production and up- and down-welling may be greater at Tropics of Cancer/Capricorn. This may help explain the bands of high richness around Florida (USA), northwest Africa, the northern Indian Ocean, Taiwan and Japan in the northern hemisphere, as well as the high richness endemicity hotspots of Brazil/Uruguay/Argentina, South Africa/Mozambique and Australia (Davidson and Dulvy 2017; Derrick, Cheok, and Dulvy 2020). Therefore, temperature may itself not be the direct mechanism to the distributional patterns of marine species through metabolic hypotheses but may be acting indirectly by driving primary productivity, and frontal systems. Clearly, there is much scope to investigate the detailed mechanisms underlying direct metabolic and indirect abiotic hypotheses underlying the kinetic temperature latitude hypothesis. Next, we consider the biotic hypotheses of range and age relating to the tropics-as-cradle hypothesis.

The latitudinal pattern of range size is bimodal at the tropics where the widest ranging species occur in pelagic insular habitats surrounding areas like Hawaii and Vanuatu in the Pacific, and the smallest ranges are along continental coastlines where richness is highest. The wide-ranging species in the tropical pelagic oceans can arise from longer persistence times at lower latitudes, allowing species more time to expand their distributions (Gaston and Blackburn 1996b). However, small range sizes were one of the strongest predictors for determining areas of higher total richness, which occurred along tropical continental coastlines. Our findings are consistent with other studies that hypothesize that areas of high richness are made up of small-ranging species because species are more likely to undergo speciation from an increased likelihood of being bisected by a geographic barrier (Chown and Gaston 2000). Overtime the width of the tropics has expanded and contracted with the mean temperature of the Earth, leaving opportunity for formerly wide-ranging species to be bisected on either side of a peninsula, such as the Florida pan handle (Figure 3.1), or isolated in basin seas revealed by shifting sea levels (Carpenter and Springer 2005). Part of this complexity in

shark and ray distributional patterning is driven by the break-up and fragmentation of Gondwanaland which formerly connected South America, South Africa, and Australia (Long 1994). For decades, a ridge of islands connected south America to Australia, which combined with sea level changes, lead to repeated opening and closing of seas enabling speciation, particularly of skates who are unable to cross open oceans, ultimately increasing the number of small-ranging species (Long 1994). Additionally, Rapoport's Rule, which has been flagged more as an effect rather than a rule, states that species range sizes decrease towards the equator (Gaston, Blackburn, and Spicer 1998; Stevens 1989). This pattern has been known to arise due to seasonality, and hence, the production cycle, such that species have broader ranges at intermediate latitudes because they migrate poleward to access the high, but transient productivity (Somveille et al. 2013). Therefore, there is a foraging benefit trade-off with the cost of migration such that if you are small, and in the tropics, the migratory cost is too high to be worth the benefit (Somveille et al. 2013). Tropical species are therefore non-migratory and hence have small ranges, whereas at higher temperate and polar latitudes, populations tend to be migratory. Considering sharks and rays are one of the oldest vertebrate lineages alive to date, their spatial patterns in range size display a complex evolutionary signature of species diversification and biogeography in the marine realm.

High species richness was also driven by younger aged species in the tropics. The combination of both small ranged and young species driving high richness areas could be indicative of two separate processes that can help explain overall shark and ray biodiversity. First, species rich areas are acting as a cradle of diversity because they are composed of smaller ranging and younger species (Table 3.1). Second, when considered independently of species richness, lower latitude regions are indicative of a 'tropics-as-a-museum' pattern because they contain larger ranging species, older species, and a smaller standard deviation in species ages (Figure 3.3B, 3.3D and 3.3F). More research is needed to understand the relationship between range size and age of lineage because the results could be suggestive of the northern latitudes being true areas of diversification. This would mean that species rich areas are not true regions of diversification but are in fact, just an accumulation of small-ranging, young species, such as endemics. Numerous studies have documented conflicting results in relation to the cradle-museum dichotomy (Gaston and Blackburn 1996b; Jetz et al. 2004; Rabosky et al. 2018). For example, speciation rates and turnover have been found to be greater at

cooler latitudes in fishes, pointing more towards the tropics acting as a museum of older species (Rabosky et al. 2018). Our analysis demonstrates that old species dominate the tropical diversity pattern with wide ranging species occurring around small island areas in the pelagic ocean, specifically around Hawaii, Polynesia, and Vanuatu (Figure 3a), where richness is lower. However, visually, the tropics are dominated by a recent radiation of carcharhinids (Sorenson, Santini, and Alfaro 2014). Any further exploration of fish landing sites in the tropics will suggest that the tropics are only dominated by requiem sharks, but the reality is that the numerical dominance of this recent radiation mask the incredible evolutionary history of the wider tropical diversity, including the continental Rhinopristiformes (guitarfishes) and Orectolobiformes (wobbegongs), and pelagic Lamniformes (mackerel sharks), which are among the most evolutionary distinct sharks and rays (Stein et al. 2017). Exploring the speciation rate with latitude could help to further close the current knowledge gap of the cradle-museum dichotomy in the marine realm for sharks and rays.

A key caveat is that we used IUCN distributional data created from peer-reviewed, expert-generated maps based on the taxonomic literature and the original maps from the Food and Agriculture Organisation of the United Nations (Dulvy et al. 2014). The distribution maps have been clipped to best represent the ecology of the species (i.e. coastal and continental shelf, pelagic, and deepwater). As such these maps are more likely to contain commission rather than omission errors such that a species is more likely to be present in an area when in fact it is not (Di Marco et al. 2017). Commission errors can be problematic because they risk identifying high richness areas that are not true areas of high species richness and therefore cause mis-interpretation of results (Rodrigues 2011). However, omission errors act in the opposite manor and risk missing true areas of high species richness, which can result in underrepresentation of species rich regions (Davidson and Dulvy 2017). Although the IUCN maps have their limitations, they are currently the most comprehensive datasets for studying shark and ray biodiversity patterns and drivers in the ocean. Although there have most likely been range contractions of shark and ray species due to overfishing and habitat loss (Dulvy et al. 2016; Lawson et al. 2020; Yan et al. 2020), our approach is to identify the historic pattern of richness for each species to aid in our understanding of shark and ray biodiversity. A lot of strength in these maps comes from the fact that they are constantly

being refined with updates of global species catalogues and field guides (Ebert et al. 2013; Ebert and Stahlman 2013; Last et al. 2016).

Attempting to understand the applicability of the latitudinal biodiversity gradient across taxa in the oceans has been an ever evolving endeavor, and while the central aim of this study was to explore just that, we've highlighted that small-ranging and younger species play a key role in determining regions of high species richness, supporting the tropics-as-a-cradle hypothesis. With the availability of new emerging maps in the near future for all sharks and rays, there will be an opportunity to revise these richness-latitude patterns when the new maps from the global shark trends project become available. The next step is to further delve into the evolutionary mechanisms of shark and ray biodiversity, and tease apart the museum-cradle dichotomy by understanding how various evolutionary mechanisms such as metabolic rate and speciation play a role in determining (1) species richness gradients, and (2) latitudinal patterns in species distributions. By combining the abiotic and biotic mechanisms of species richness together, we have opened the foundation to further understand the historical and present day biogeography of the oceans and the lineages that reside within them. This work helps to build up our current knowledge of biodiversity, have implications on both understanding the biogeography of sharks and rays, and provides a stepping-stone to further explore the evolutionary attributes that have given rise to present day richness patterns for sharks and rays.

Chapter 4. Concluding Summary

This thesis explored the global spatial biodiversity of the world's marine sharks and rays, and how their distributions and numbers are influenced by both ecological and evolutionary mechanisms. Chapter 2 investigated the degree to which three measures of species richness (total, endemic, and evolutionary distinct) were spatially congruent, as well as their threatened counterparts. Chapter 3 tested four abiotic hypotheses and one biotic hypothesis proposed to be mechanisms influencing species distributions and numbers. These hypotheses were explored for global marine shark and ray species richness. Chapter 2 discerned that hotspots of different measures of species richness have low overall spatial congruency while Chapter 3 connected more pieces of the puzzle by revealing that regions high in species richness are found in warmer waters, and in areas with both increased primary productivity and oceanic fronts. Species rich areas also contain smaller ranging, and younger species. In this concluding chapter, I provide an overview of the key findings, their implications, research caveats that come along with all research, and the future directions that the research could take.

There has been a tremendous amount of work on studying biodiversity both terrestrially and aquatically, where the majority of results affirm our current knowledge of the latitudinal biodiversity gradient of species richness decreasing towards the poles (Chaudhary et al. 2016; Lucifora et al. 2011; Tittensor et al. 2010). In this thesis, we approached understanding the global marine biodiversity of sharks and rays through an empirical perspective with the aim of gathering a better fundamental knowledge of (1) the spatial patterning of different measures of biodiversity in sharks and rays, and (2) the abiotic and biotic processes that govern their distributions in the ocean. The results demonstrated that overall spatial congruency remained low between all measures of richness (total, endemic, evolutionarily distinct), as well as their threatened counterparts, regardless of the definition of hotspot or spatial resolution (Chapter 2). Areas of congruency at 1° and 5% richest cells contained over half (64%) of all sharks and rays and occurred off six major continental coastlines (Chapter 2). In Chapter 3 we found that areas of high total richness are supported by the kinetic energy, productivity, and tropics-as-a-cradle hypotheses. Although species richness is highest in the tropics and contains smaller-ranging and younger species, the tropics as a whole, regardless of species richness is dominated by wide-ranging, older species, therefore questioning whether

species rich areas are true areas of diversification, or are simply areas of accumulation of small-ranging, young species, such as endemics.

Developing a thorough understanding of the patterns of biodiversity and the mechanisms driving it are crucial from both a conservation and biogeographic perspective. From a conservation perspective, we see the importance and value of considering multiple metrics of biodiversity when doing conservation planning and spatial prioritization. From a biogeographic standpoint, this research has shed light on how well terrestrial developed hypotheses, when adapted to represent the marine realm, can inform us about the distribution of species throughout the ocean. They have also opened us up to further explore the evolutionary entities of biodiversity in sharks and rays, such as determining true areas of diversification and/or accumulation for sharks and rays.

Given the multi-modal distribution of sharks and rays in the ocean, this research focused solely on coastal regions, however, we recommend that future work encapsulates and compares results across the entire ocean, including coastal, shelf, and pelagic regions. Furthermore, being able to integrate how abiotic and biotic mechanisms determine global biodiversity in the oceans, particularly for sharks and rays, offers up a novel opportunity to explore how humanity further influences species distributions and numbers. While studying the congruency and drivers of biodiversity in the oceans is novel on its own, pairing an analysis that explores the socio-economic effects of human expansion and settlement (i.e., fishing pressure, the state of the economy, and the effectiveness of fishing regulations) could offer up a plethora of knowledge that may be lacking from fully understanding shark and ray distributions in the marine realm. Lastly, this thesis was analyzed on a large spatial scale, and while it is known that the patterns and predictors can change across scales, it is likely that the ecological variables with the strongest effect on biodiversity globally will change at local scales. For example, where temperature and seasonality are important globally, competition and environmental heterogeneity may become more important at local scales (Worm and Tittensor 2018). This means that while understanding the mechanisms of biodiversity at global scales aids us tremendously in understanding what influences biodiversity, exploring the mechanisms at local scales could help illuminate the cross-scale differences in biodiversity for both local and global spatial distributional patterning.

As the status and distribution maps for sharks and rays are constantly being updated and refined, and environmental data consistently collected at finer spatial resolutions, understanding shark and ray biodiversity will only improve with time. Future work could begin to incorporate other measures of biodiversity, such as functional diversity, into the analysis of the overall spatial congruency of shark and ray biodiversity. This would help guide overall spatial prioritization and conservation. Second, it has been previously demonstrated that biodiversity can have reverse latitudinal patterns in the ocean (Rabosky et al. 2018). Since our results demonstrate that species rich areas are acting as a cradle, but spatially, the tropics are dominated by wide-ranging, older species, it would be interesting to explore the tropics-as-a-cradle hypothesis more thoroughly through (1) including the entire marine environment, and (2) exploring other biotic attributes such as metabolic rate and speciation. Including the entirety of the marine environment means we could analyze the spatial patterning of diversity between coastal, shelf, pelagic, and deep-water sharks and rays, potentially identifying a threshold at which the spatial patterning of biodiversity changes. Finally, to tie both chapters together, future research could explore the differences and similarities in the abiotic and biotic mechanisms behind coastal, shelf, pelagic, and deep-water biodiversity patterns, but also across multiple metrics of diversity (i.e. endemic, ED, functional etc.).

4.1. Conclusion

Sharks and rays are one of the oldest vertebrate lineages alive to date (Kriwet et al. 2009; Stein et al. 2017), and are increasingly threatened by overfishing, habitat loss, and climate change (Davidson et al. 2016; Dulvy et al. 2014). Advancing our understanding of their past and current biodiversity throughout the oceans will aid in our ability to implement effective conservation action to protect not just sharks and rays, but other lineages such as coral reef ecosystems, fish, and marine mammals. Increasing our understanding of the innate biodiversity in the ocean can shed light onto how distributions developed and changed over time to be how they are today.

“Pursue something so important that even if you fail, the world is better off with you having tried.”

Tim O'Reilly

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Appendix A. Supplemental information for Chapter 2

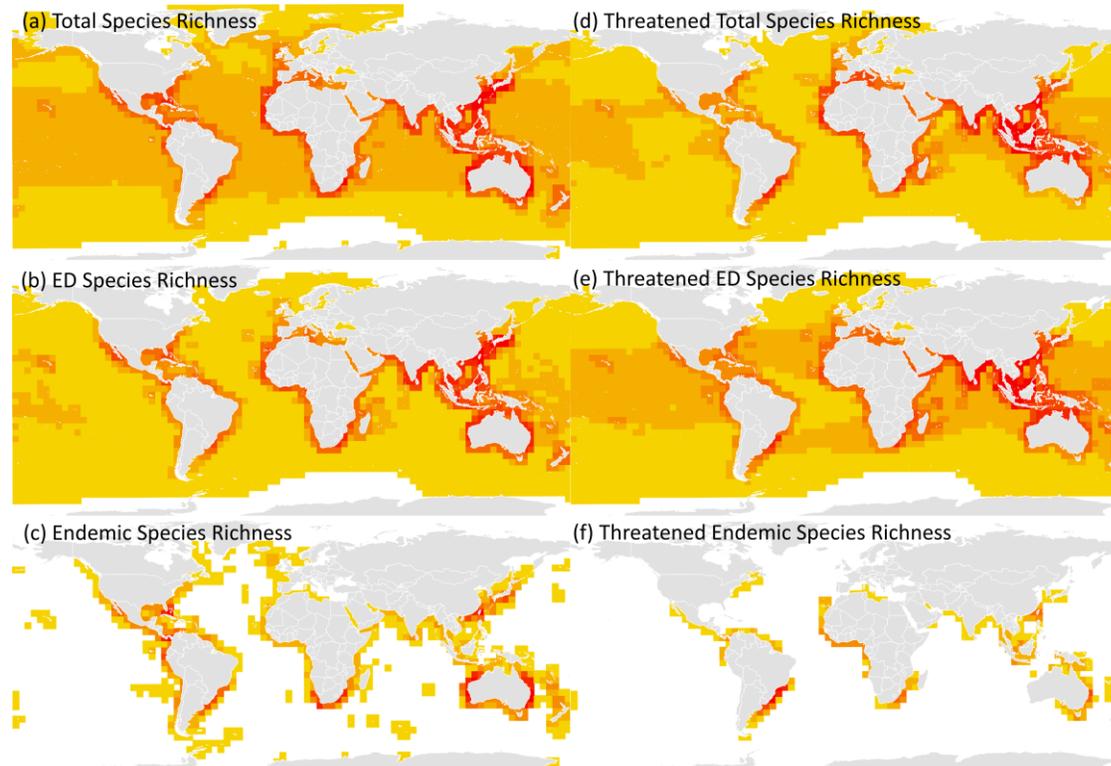


Figure A1 Global biodiversity patterns for three measures of species richness at 4° resolution. General richness for (a) total species, (b) evolutionarily distinct (ED) species, and (c) endemic species. (d-f) Threatened subsets of richness patterns for (d) total species, (e) evolutionarily distinct (ED) species, and (f) endemic species. Geographic coordinate system is in NAD83, projected coordinate system is lambert equal area. The data used for this figure under CC BY license is granted permission from the International Union for the Conservation of Nature (IUCN), original copyright 2011.

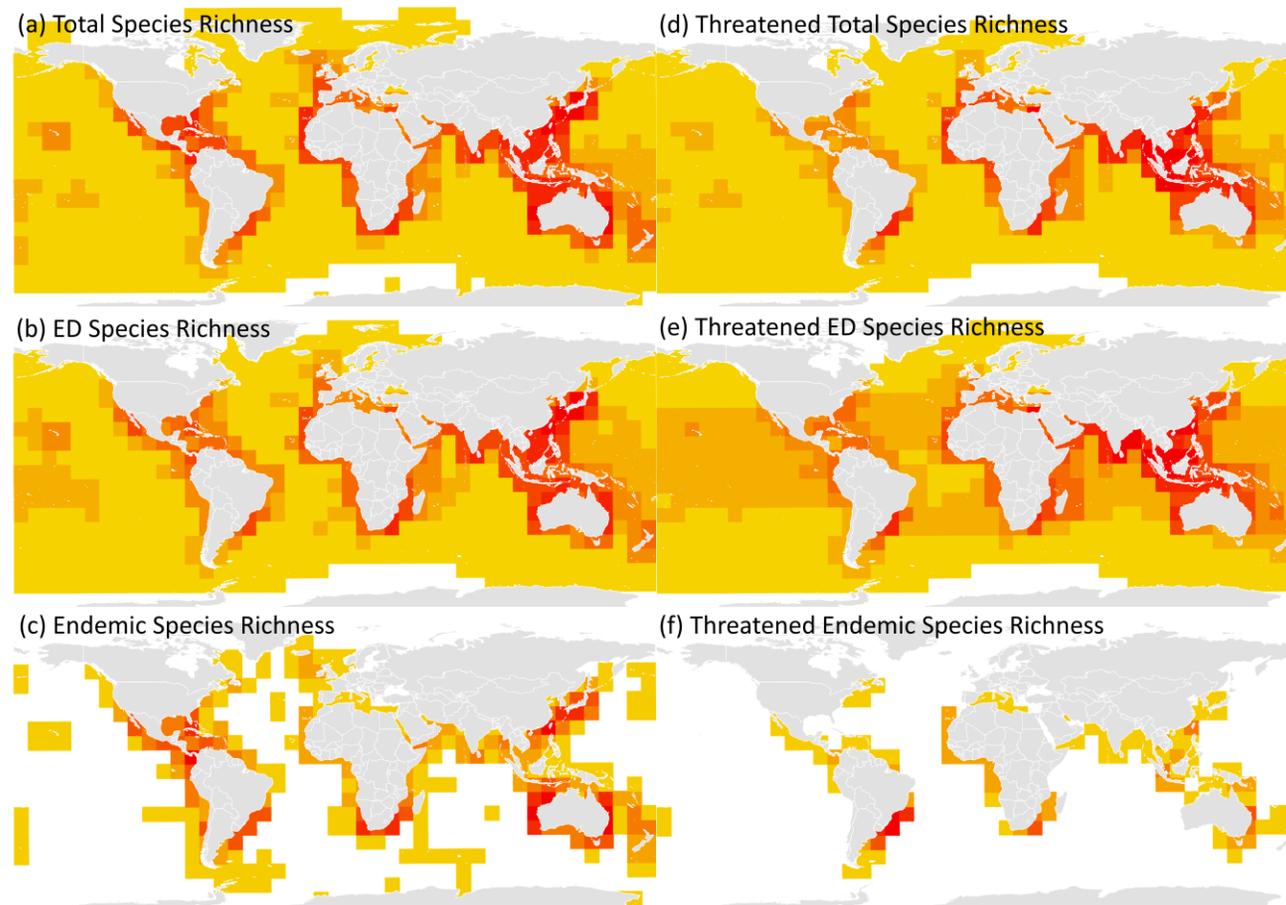


Figure A2 Global biodiversity patterns for three measures of species richness at 8° resolution. General richness for (a) total species, (b) evolutionarily distinct (ED) species, and (c) endemic species. (d-f) Threatened subsets of richness patterns for (d) total species, (e) evolutionarily distinct (ED) species, and (f) endemic species. Geographic coordinate system is in NAD83, projected coordinate system is lambert equal area. The data used for this figure under CC BY license is granted permission from the International Union for the Conservation of Nature (IUCN), original copyright 2011.

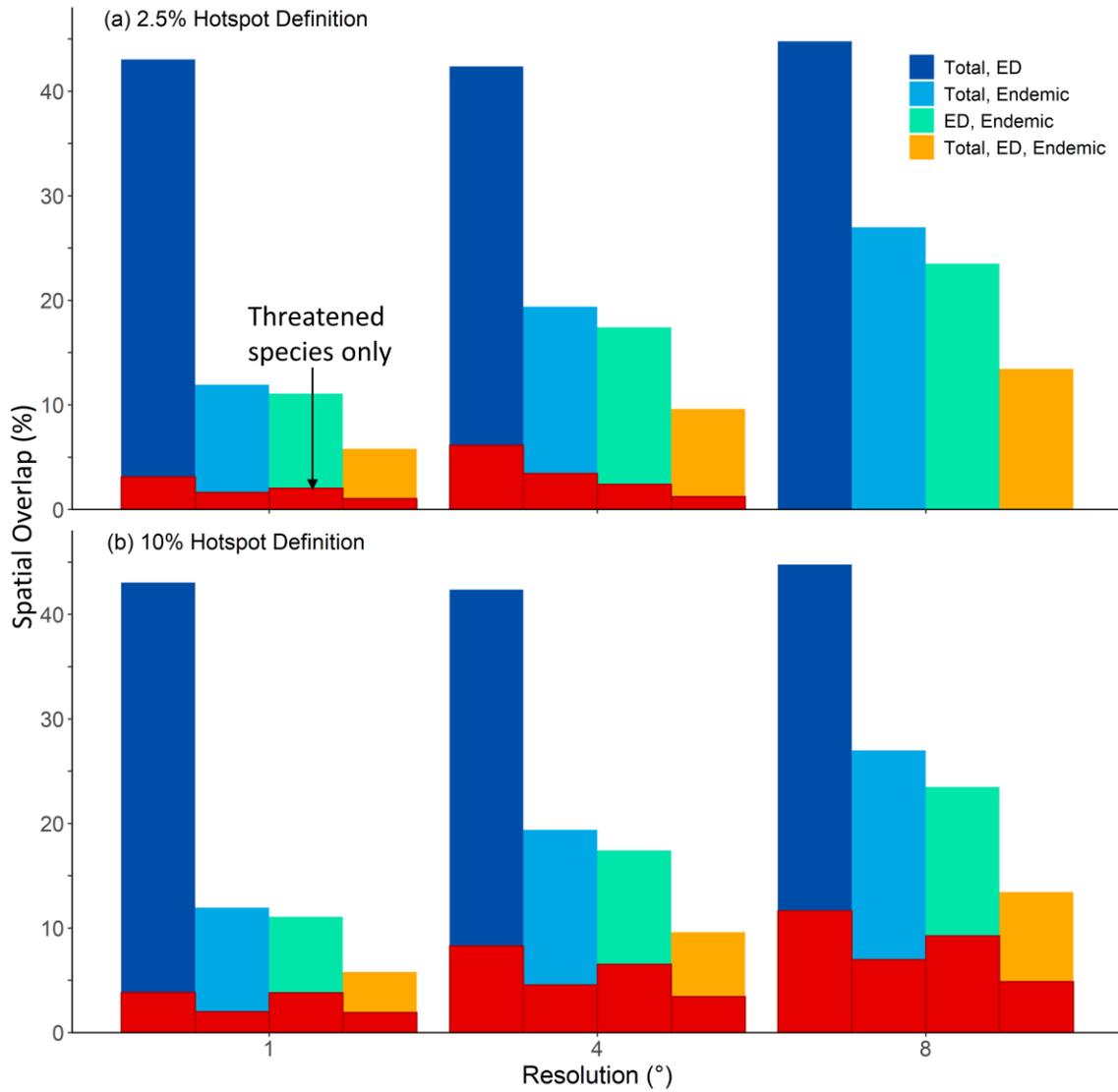


Figure A3 Spatial congruency (measured as percent overlap) of shark hotspots between three species richness measures: total species, evolutionary distinct (ED) species, and endemic species. Congruency is represented at two levels of hotspot definition: (a) 2.5% and (b) 10%, and three levels of spatial resolution: 1°, 4°, and 8°, for total number of species and the subset of threatened species indicated in red.

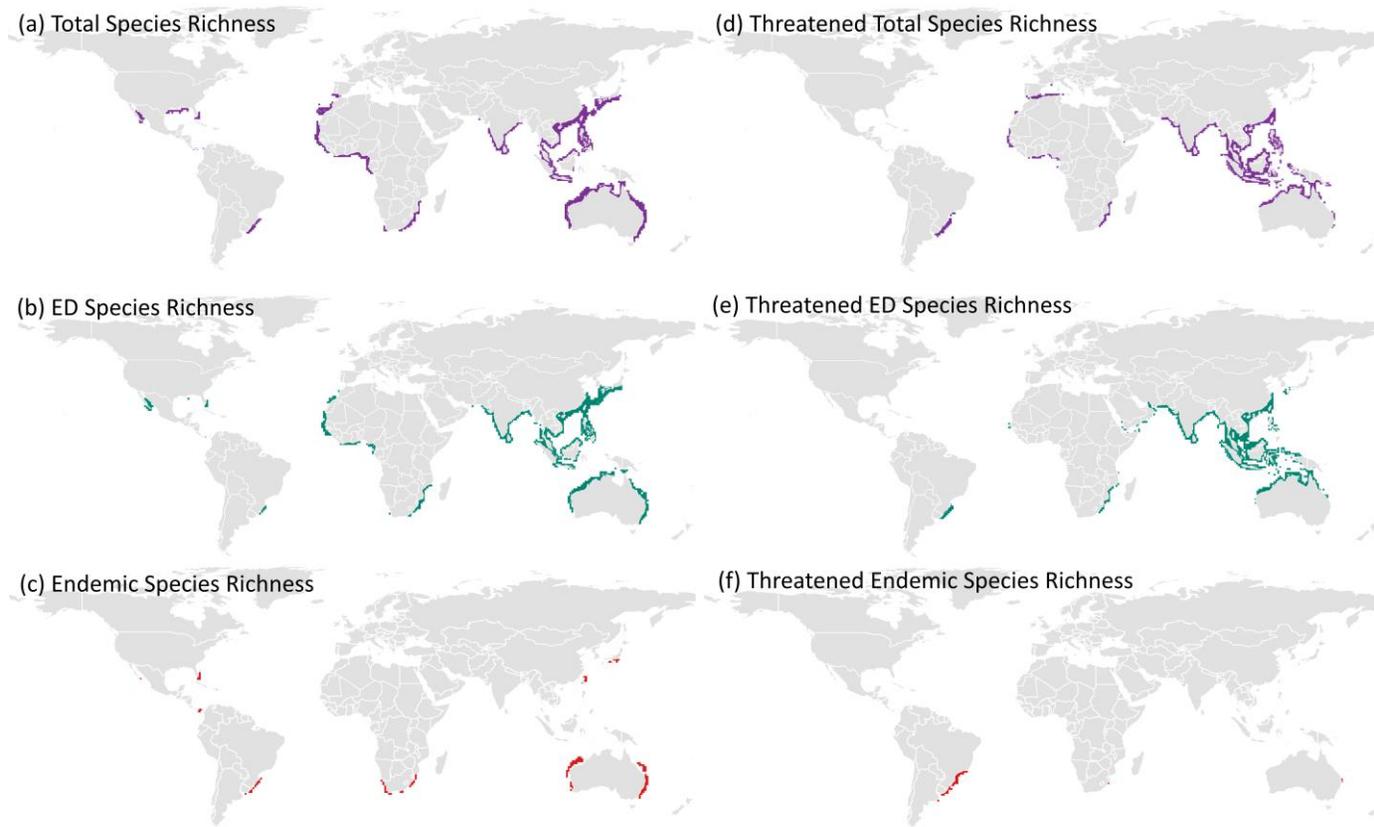


Figure A4 Biodiversity hotspots derived for three measures of species richness. General richness hotspots of (a) total species, (b) evolutionarily distinct (ED) species, and (c) endemic species. (d-f) Threatened subset of richness hotspots for (d) total species, (e) evolutionarily distinct (ED) species, and (f) endemic species. For each species richness measures, hotspots are defined as the richest 2.5% of grid all cells. Geographic coordinate system is in NAD83, projected coordinate system is lambert equal area, grid cell resolution is 1°. The data used for this figure under CC BY license is granted permission from the International Union for the Conservation of Nature (IUCN), original copyright 2011.

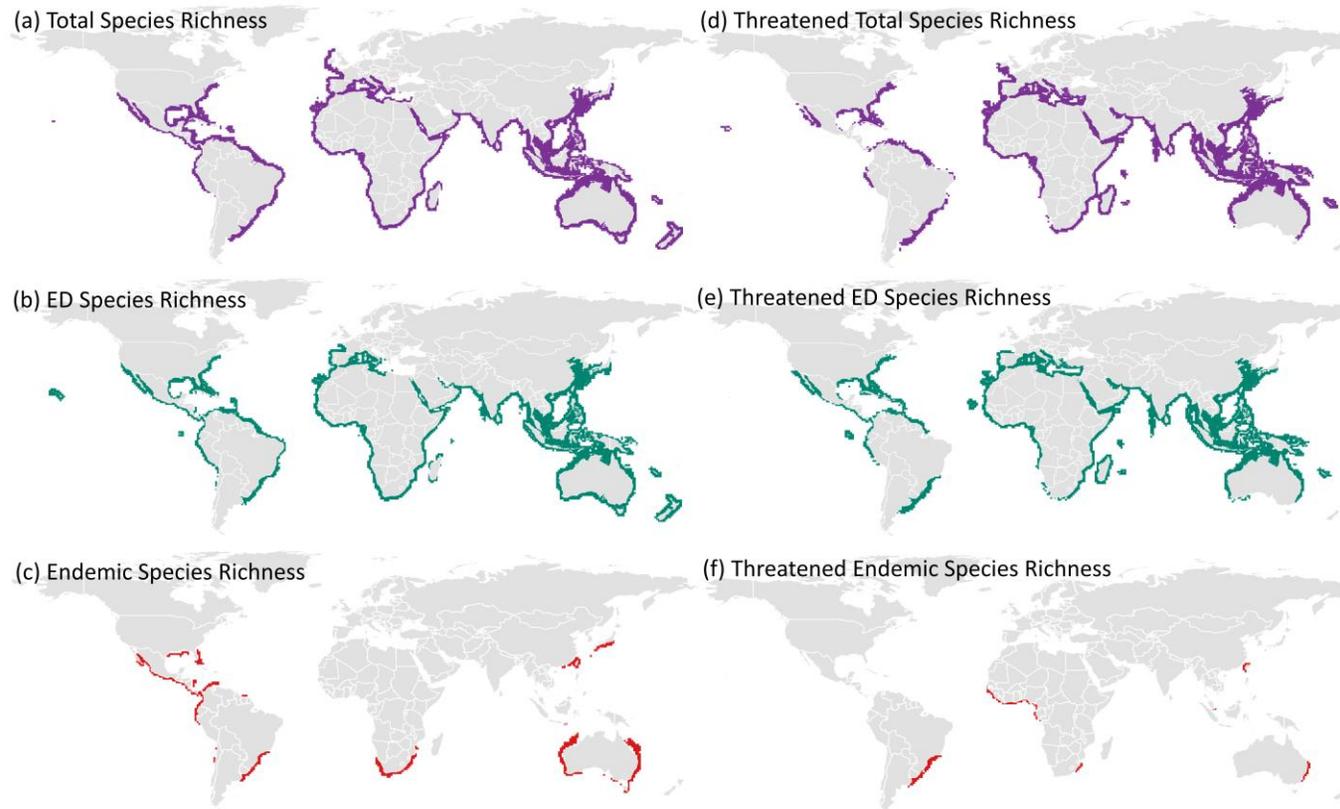


Figure A5 Biodiversity hotspots derived for three measures of species richness. General richness hotspots of (a) total species, (b) evolutionarily distinct (ED) species, and (c) endemic species. (d-f) Threatened subset of richness hotspots for (d) total species, (e) evolutionarily distinct (ED) species, and (f) endemic species. For each species richness measures, hotspots are defined as the richest 10% of grid all cells. Geographic coordinate system is in NAD83, projected coordinate system is lambert equal area, grid cell resolution is 1°. The data used for this figure under CC BY license is granted permission from the International Union for the Conservation of Nature (IUCN), original copyright 2011.

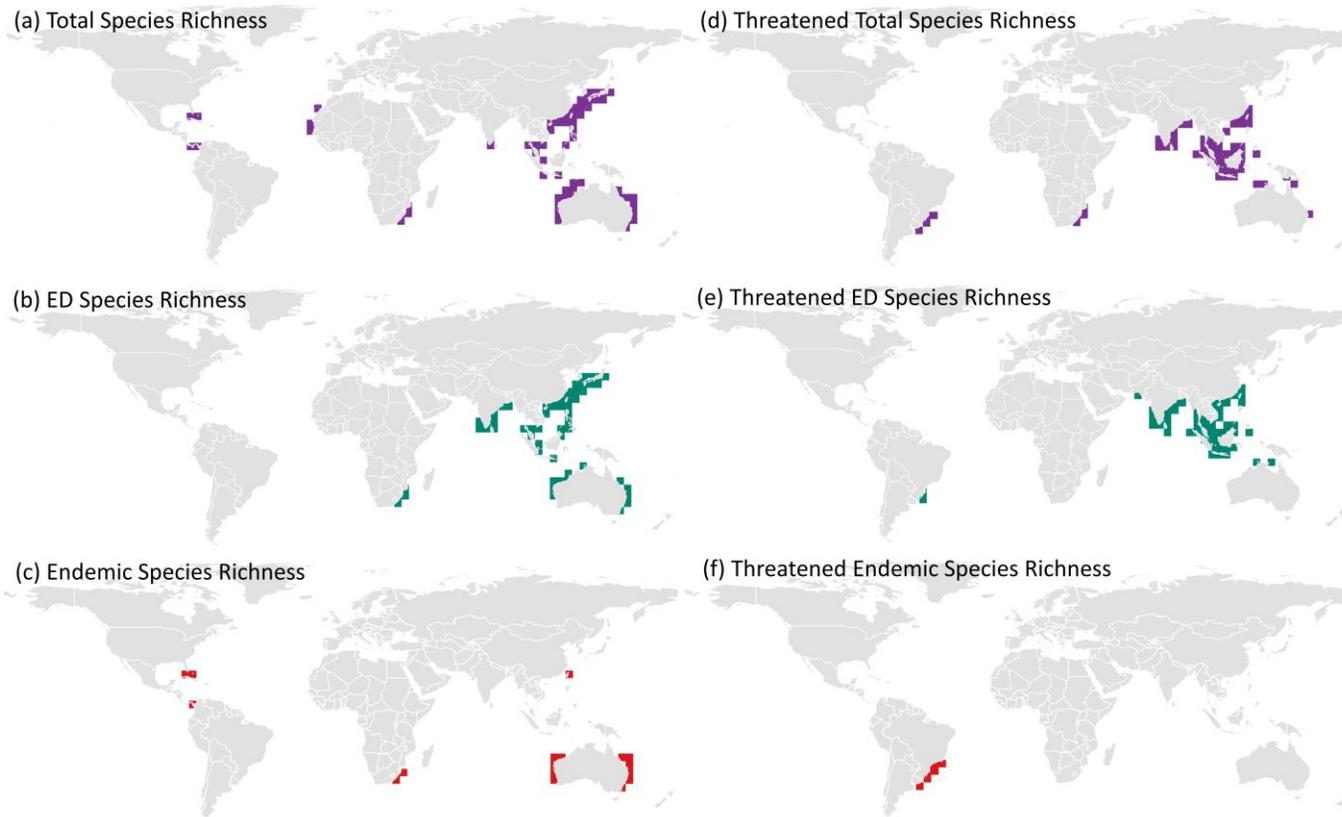


Figure A6

Biodiversity hotspots derived for three measures of species richness. General richness hotspots of (a) total species, (b) evolutionarily distinct (ED) species, and (c) endemic species. (d-f) Threatened subset of richness hotspots for (d) total species, (e) evolutionarily distinct (ED) species, and (f) endemic species. For each species richness measures, hotspots are defined as the richest 2.5% of grid all cells. Geographic coordinate system is in NAD83, projected coordinate system is lambert equal area, grid cell resolution is 4°. The data used for this figure under CC BY license is granted permission from the International Union for the Conservation of Nature (IUCN), original copyright 2011.

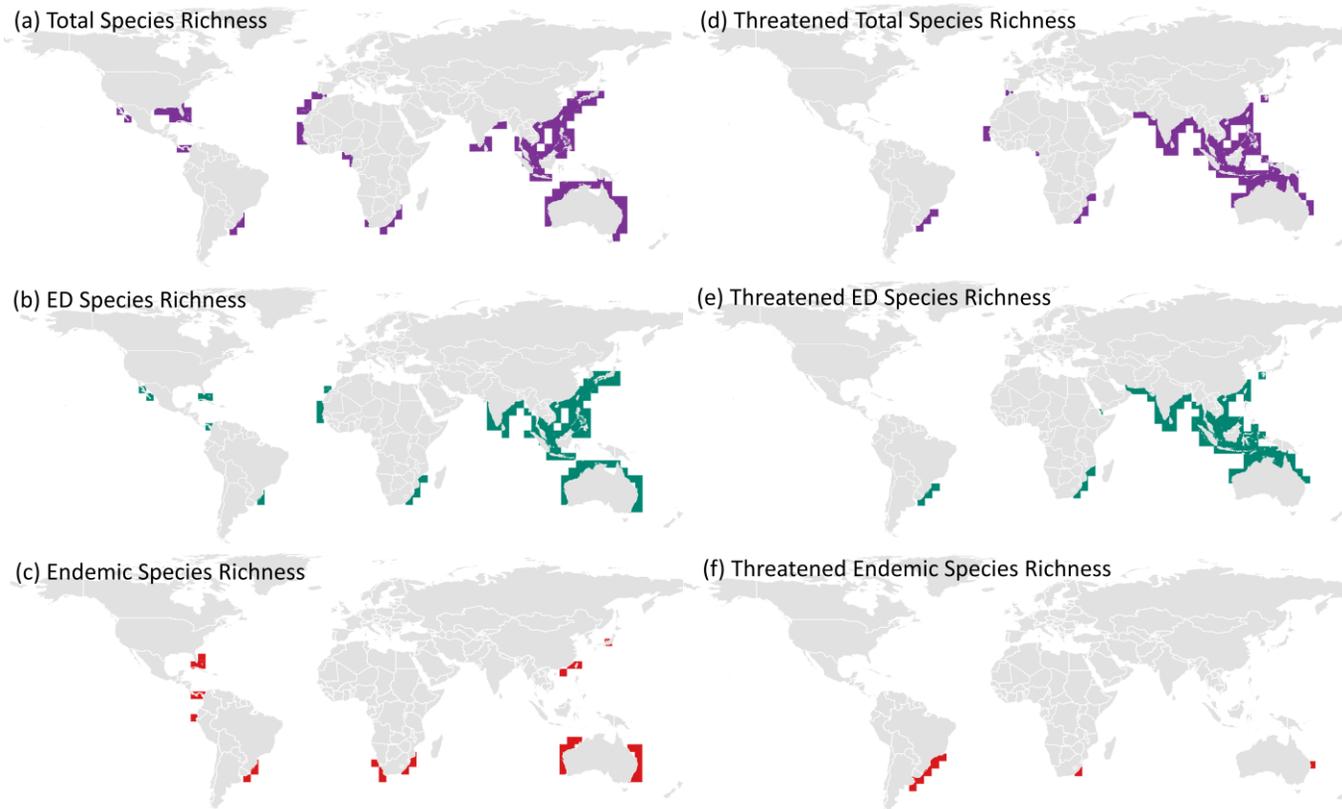


Figure A7 Biodiversity hotspots derived for three measures of species richness. General richness hotspots of (a) total species, (b) evolutionarily distinct (ED) species, and (c) endemic species. (d-f) Threatened subset of richness hotspots for (d) total species, (e) evolutionarily distinct (ED) species, and (f) endemic species. For each species richness measures, hotspots are defined as the richest 5% of grid all cells. Geographic coordinate system is in NAD83, projected coordinate system is lambert equal area, grid cell resolution is 4°. The data used for this figure under CC BY license is granted permission from the International Union for the Conservation of Nature (IUCN), original copyright 2011.

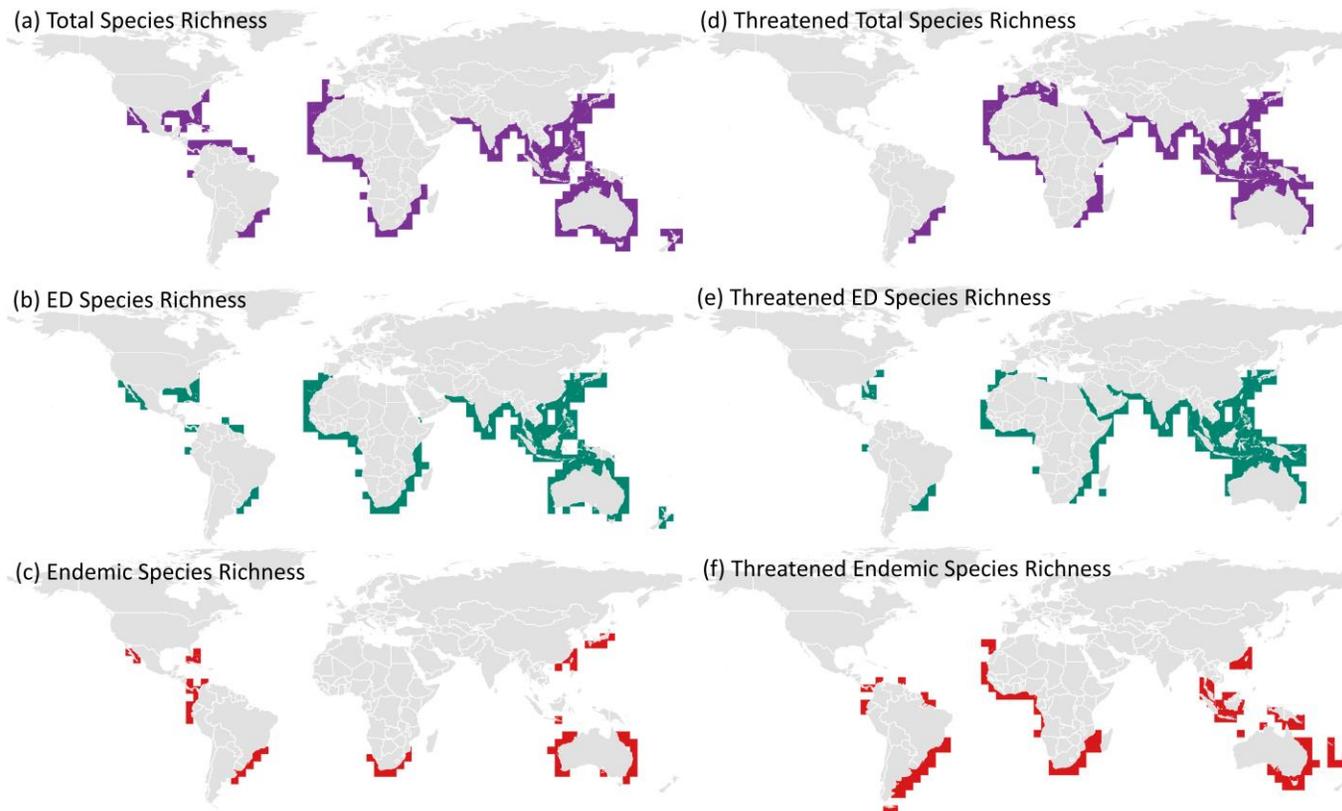


Figure A8

Biodiversity hotspots derived for three measures of species richness. General richness hotspots of (a) total species, (b) evolutionarily distinct (ED) species, and (c) endemic species. (d-f) Threatened subset of richness hotspots for (d) total species, (e) evolutionarily distinct (ED) species, and (f) endemic species. For each species richness measures, hotspots are defined as the richest 10% of grid all cells. Geographic coordinate system is in NAD83, projected coordinate system is lambert equal area, grid cell resolution is 4°. The data used for this figure under CC BY license is granted permission from the International Union for the Conservation of Nature (IUCN), original copyright 2011.

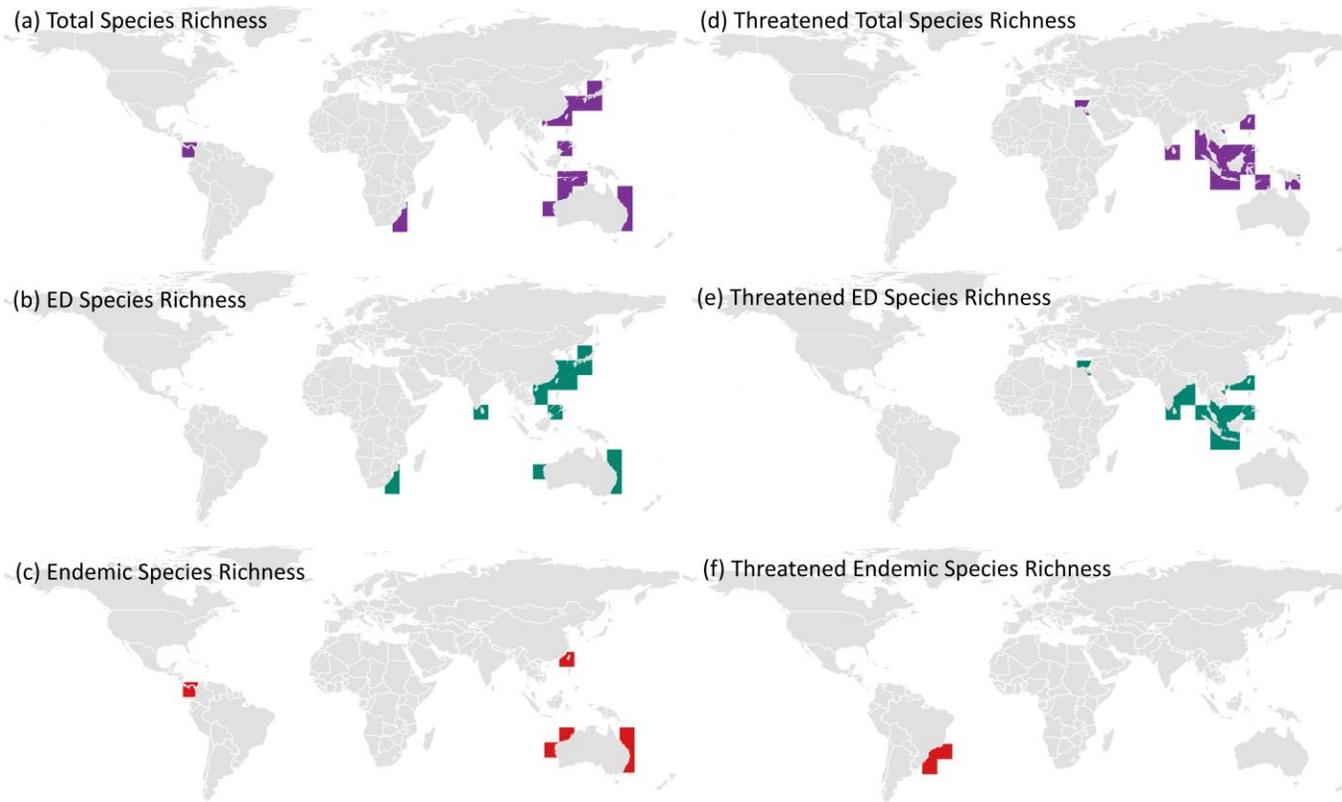


Figure A9 Biodiversity hotspots derived for three measures of species richness. General richness hotspots of (a) total species, (b) evolutionarily distinct (ED) species, and (c) endemic species. (d-f) Threatened subset of richness hotspots for (d) total species, (e) evolutionarily distinct (ED) species, and (f) endemic species. For each species richness measures, hotspots are defined as the richest 2.5% of grid all cells. Geographic coordinate system is in NAD83, projected coordinate system is lambert equal area, grid cell resolution is 8°. The data used for this figure under CC BY license is granted permission from the International Union for the Conservation of Nature (IUCN), original copyright 2011.

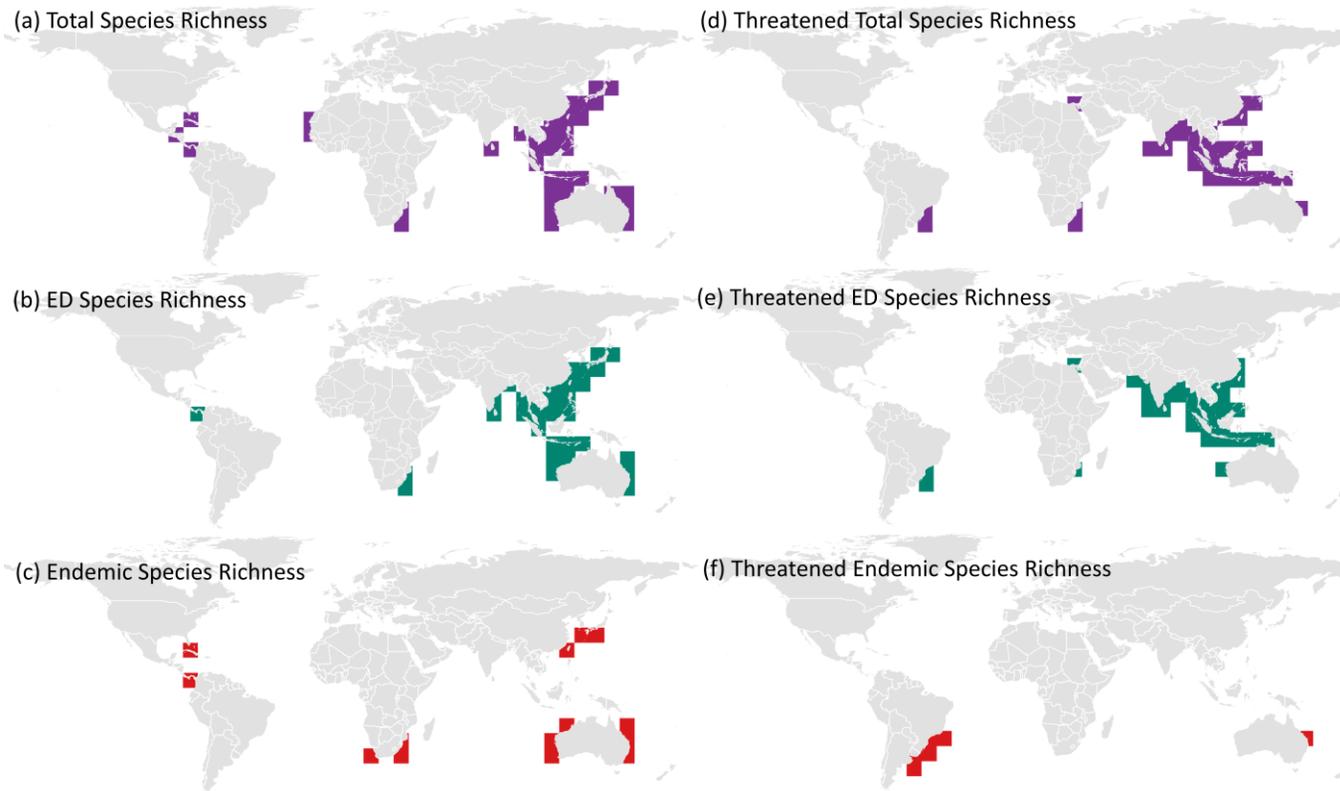


Figure A10 Biodiversity hotspots derived for three measures of species richness. General richness hotspots of (a) total species, (b) evolutionarily distinct (ED) species, and (c) endemic species. (d-f) Threatened subset of richness hotspots for (d) total species, (e) evolutionarily distinct (ED) species, and (f) endemic species. For each species richness measures, hotspots are defined as the richest 5% of grid all cells. Geographic coordinate system is in NAD83, projected coordinate system is lambert equal area, grid cell resolution is 8°. The data used for this figure under CC BY license is granted permission from the International Union for the Conservation of Nature (IUCN), original copyright 2011.

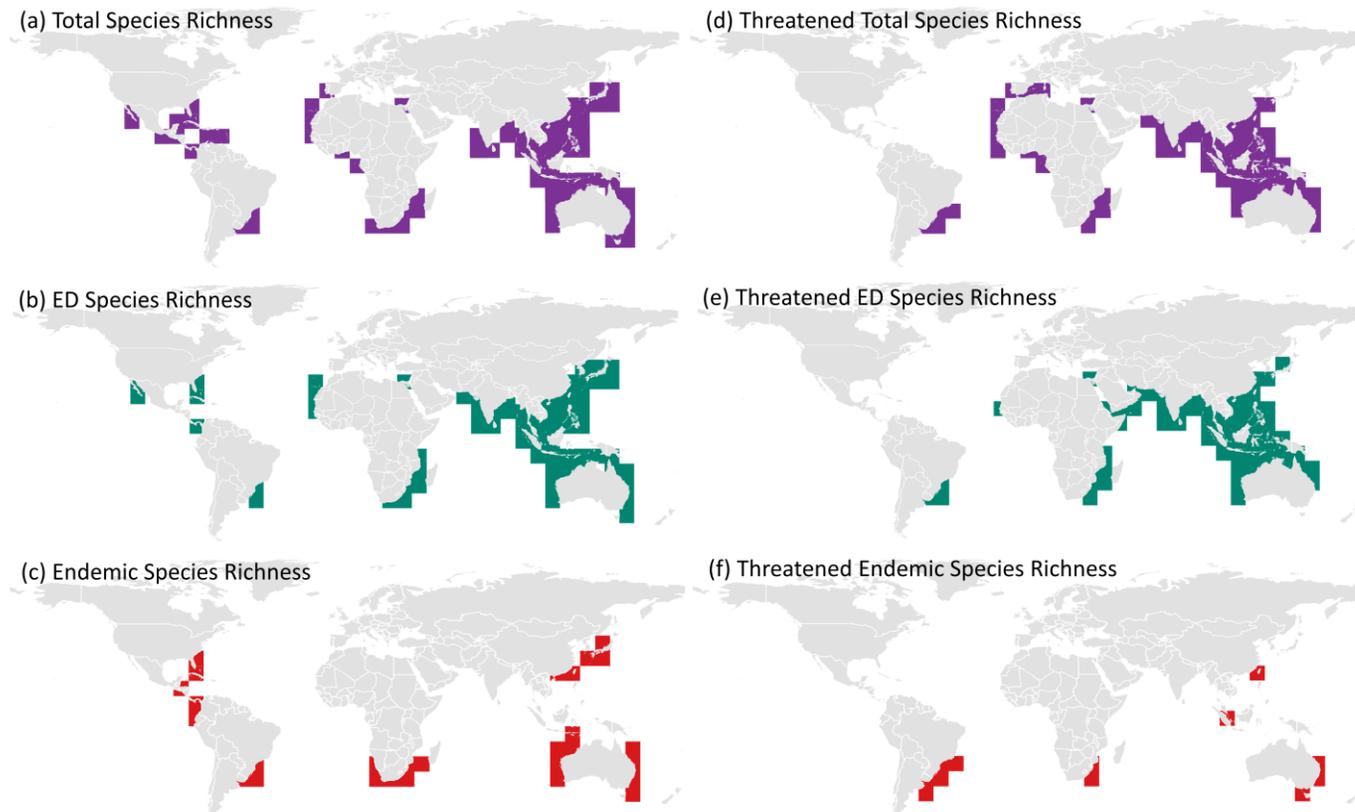


Figure A11 Biodiversity hotspots derived for three measures of species richness. General richness hotspots of (a) total species, (b) evolutionarily distinct (ED) species, and (c) endemic species. (d-f) Threatened subset of richness hotspots for (d) total species, (e) evolutionarily distinct (ED) species, and (f) endemic species. For each species richness measures, hotspots are defined as the richest 10% of grid all cells. Geographic coordinate system is in NAD83, projected coordinate system is lambert equal area, grid cell resolution is 8°. The data used for this figure under CC BY license is granted permission from the International Union for the Conservation of Nature (IUCN), original copyright 2011.

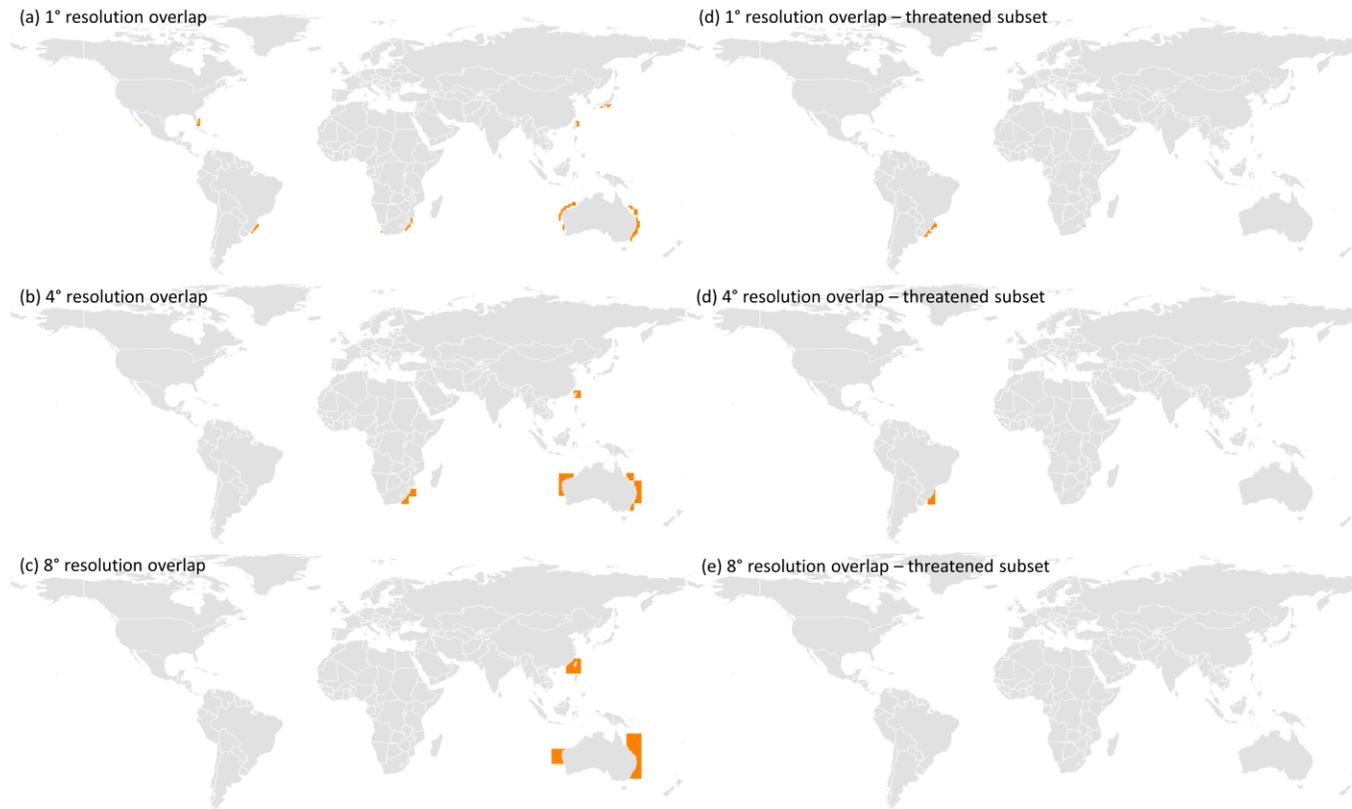


Figure A12 Spatially congruent areas between biodiversity hotspots derived from different species richness measures represented as the richest 2.5% of grid all cells. Spatially congruent areas between total species, ED species, and endemic species at (a) 1° resolution, (b) 4° resolution, and (c) 8° resolution, and (d-f) for the subset of threatened species, corresponding to resolution levels of (a-c). The data used for this figure under CC BY license is granted permission from the International Union for the Conservation of Nature (IUCN), original copyright 2011.

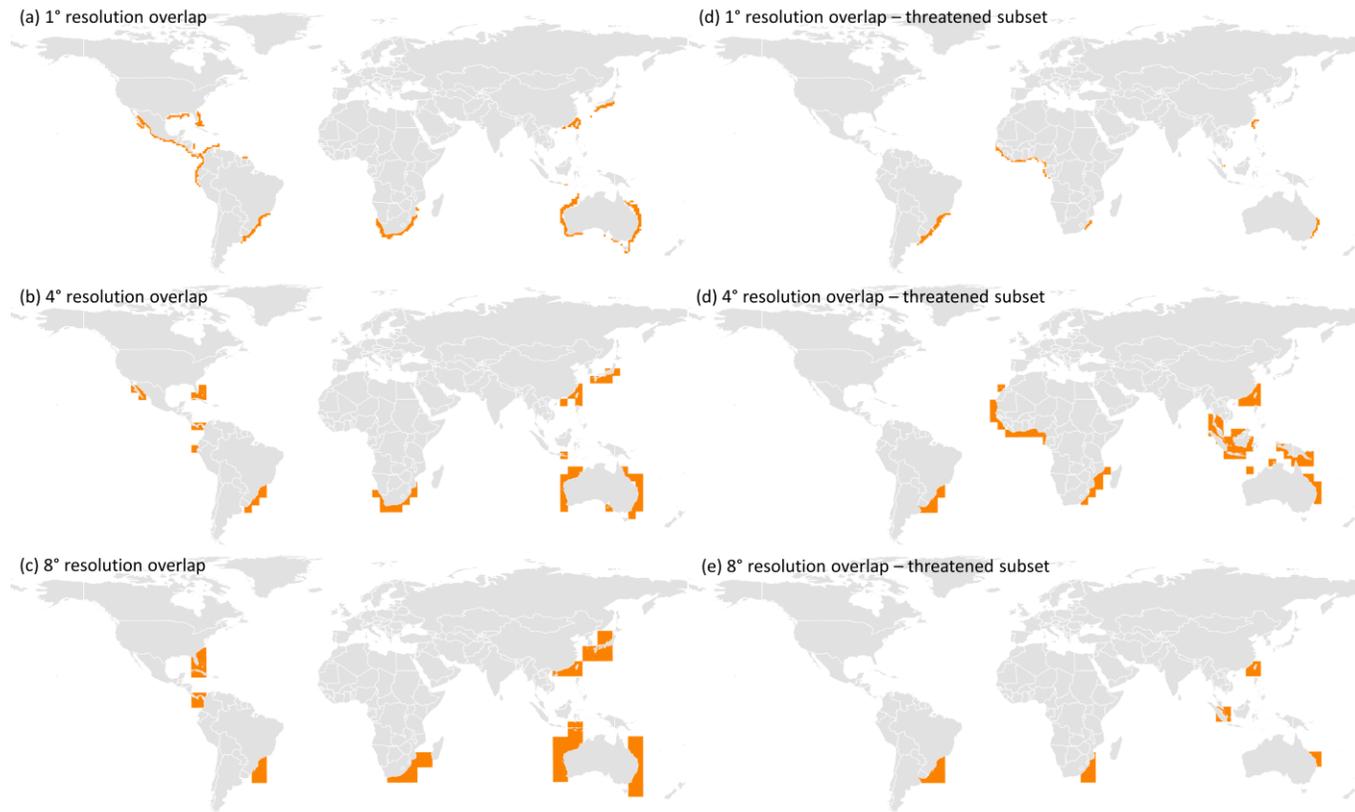


Figure A13 Spatially congruent areas between biodiversity hotspots derived from different species richness measures represented as the richest 10% of grid all cells. Spatially congruent areas between total species, ED species, and endemic species at (a) 1° resolution, (b) 4° resolution, and (c) 8° resolution, and (d-f) for the subset of threatened species, corresponding to resolution levels of (a-c). The data used for this figure under CC BY license is granted permission from the International Union for the Conservation of Nature (IUCN), original copyright 2011.

Table A1 Spatial congruency (measured as percent overlap) of shark hotspots between three species richness metrics: total species, evolutionary distinct (ED) species, and endemic species. Congruency is compared between three levels of spatial resolution: 1°, 4°, and 8°, for total number of species and the subset of threatened species, and at three levels of defining hotspot (2.5%, 5%, and 10% richest cells).

| Cell size | Percent Richest cells (%) | Species category | Spatial congruency between richness measures (% overlap) | | | | | | |
|-----------|---------------------------|------------------|--|----|-------|---------|---------|----|-------|
| | | | Total | ED | Total | Endemic | Endemic | ED | |
| 1° | 2.5 | total | 41.42 | | 11.89 | | 10.77 | | 5.63 |
| | | threatened | 3.12 | | 1.62 | | 2.02 | | 1.04 |
| | 5 | total | 43.03 | | 11.93 | | 11.07 | | 5.78 |
| | | threatened | 4.02 | | 2.11 | | 3.05 | | 1.51 |
| | 10 | total | 45.68 | | 12.47 | | 12.26 | | 6.38 |
| | | threatened | 3.83 | | 2.00 | | 3.81 | | 1.93 |
| 4° | 2.5 | total | 37.81 | | 21.94 | | 15.76 | | 8.61 |
| | | threatened | 6.14 | | 3.44 | | 2.41 | | 1.24 |
| | 5 | total | 42.35 | | 19.37 | | 17.41 | | 9.60 |
| | | threatened | 4.76 | | 2.64 | | 4.24 | | 2.15 |
| | 10 | total | 45.35 | | 19.11 | | 18.46 | | 10.11 |
| | | threatened | 8.28 | | 4.55 | | 6.54 | | 3.43 |
| 8° | 2.5 | total | 36.41 | | 29.71 | | 21.39 | | 12.34 |
| | | threatened | 0 | | 0 | | 0 | | 0 |
| | 5 | total | 44.76 | | 26.97 | | 23.49 | | 13.43 |
| | | threatened | 6.27 | | 3.76 | | 4.81 | | 2.50 |
| | 10 | total | 44.39 | | 26.42 | | 25.74 | | 14.58 |
| | | threatened | 11.64 | | 6.98 | | 9.24 | | 4.87 |

Appendix B. Supplemental information for Chapter 3

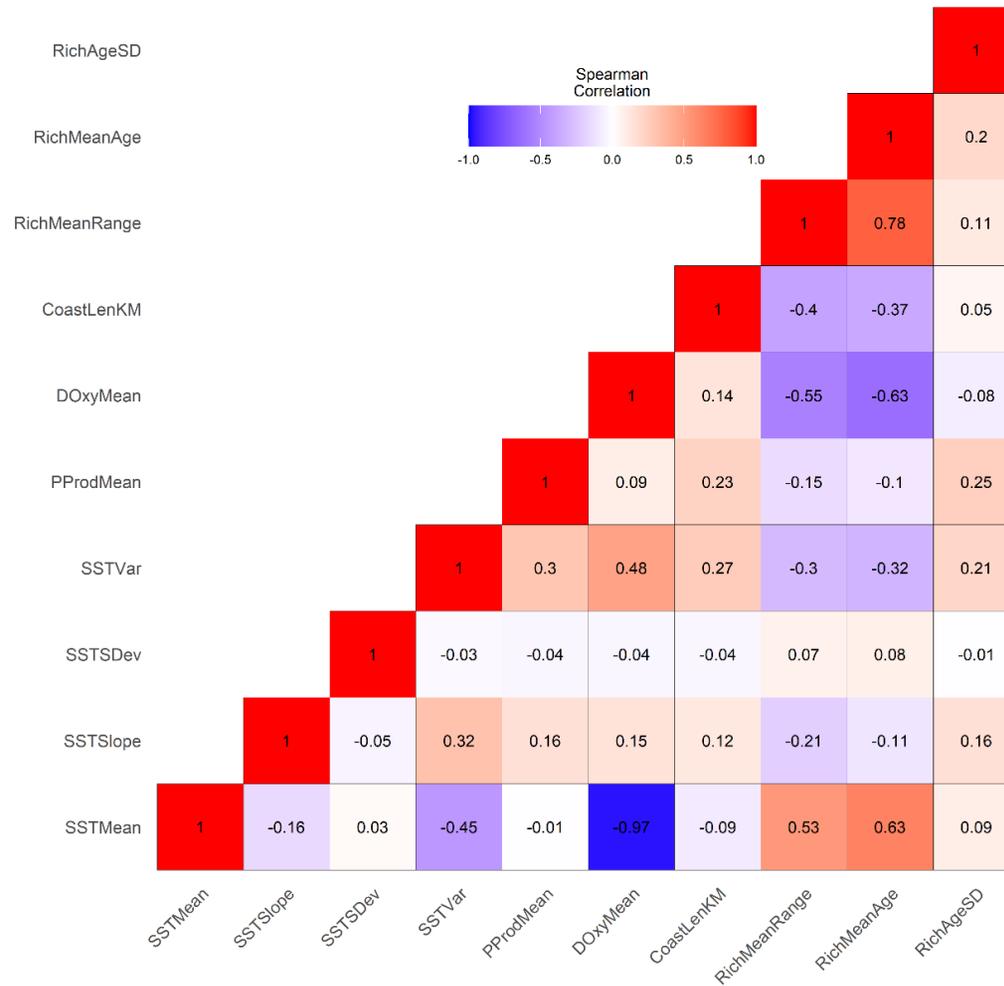


Figure B1 Correlation matrix of abiotic and biotic variables calculated using the Spearman rank correlation coefficient for shark and ray species richness.

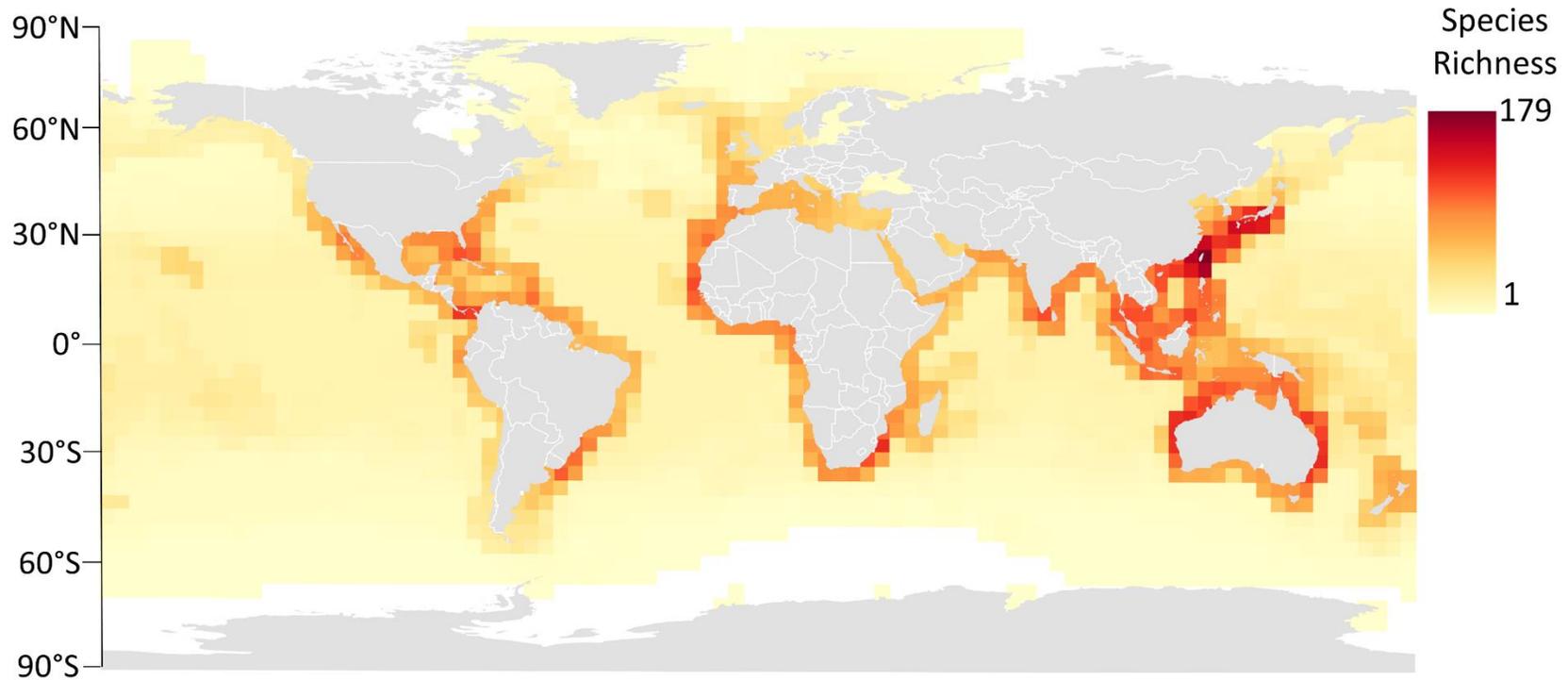


Figure B2 Global richness patterns for sharks and rays. Areas in white indicate no presence of Chondrichthyan species. Geographic coordinate system is in NAD83, projected coordinate system is lambert equal area, and grid cells are at a resolution of 4°.

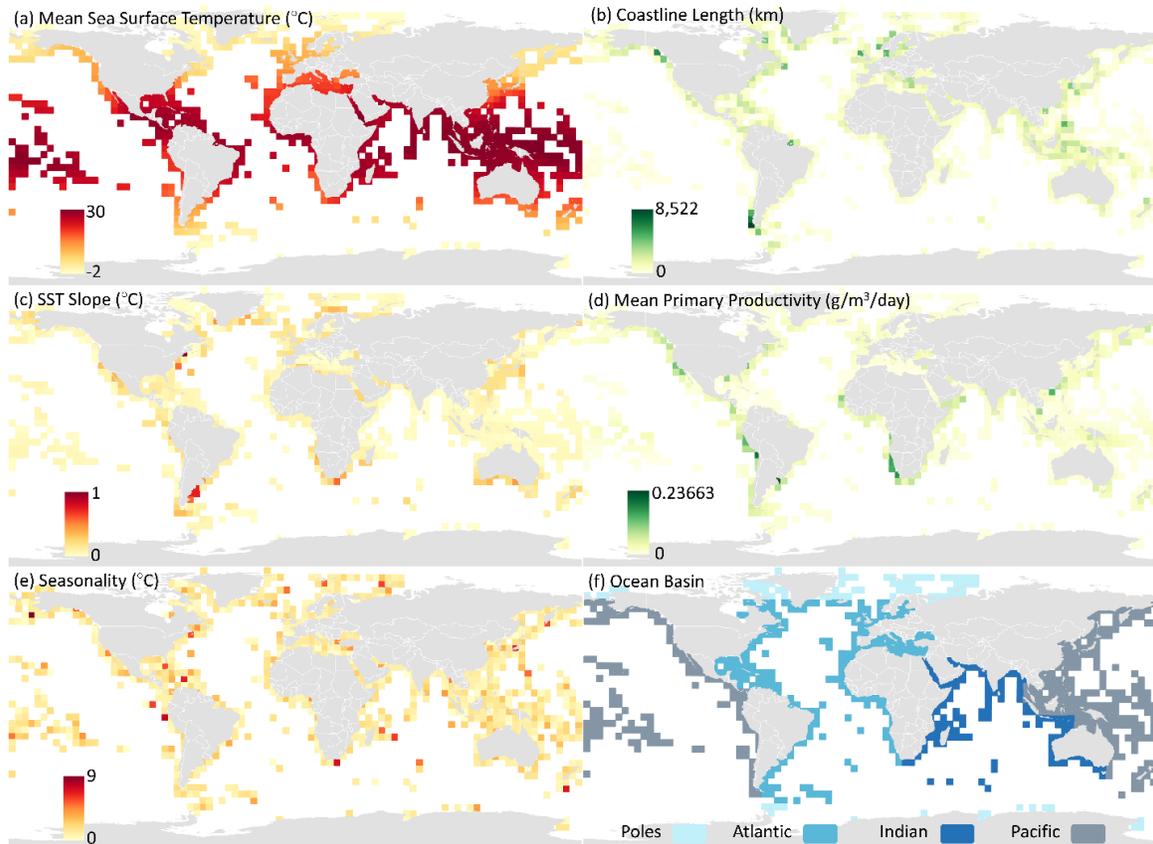


Figure B3 Drivers of total richness representing (a) mean sea surface temperature (SST), (b) coastline length, (c) SST slope, (d) mean primary productivity, (e) seasonality (standard deviation of SST), and (f) ocean basin. Geographic coordinate system is in NAD83, projected coordinate system in Lambert equal area, and grid cell resolution is 4°. Colour-scaling is adjusted per panel to optimize contrast.

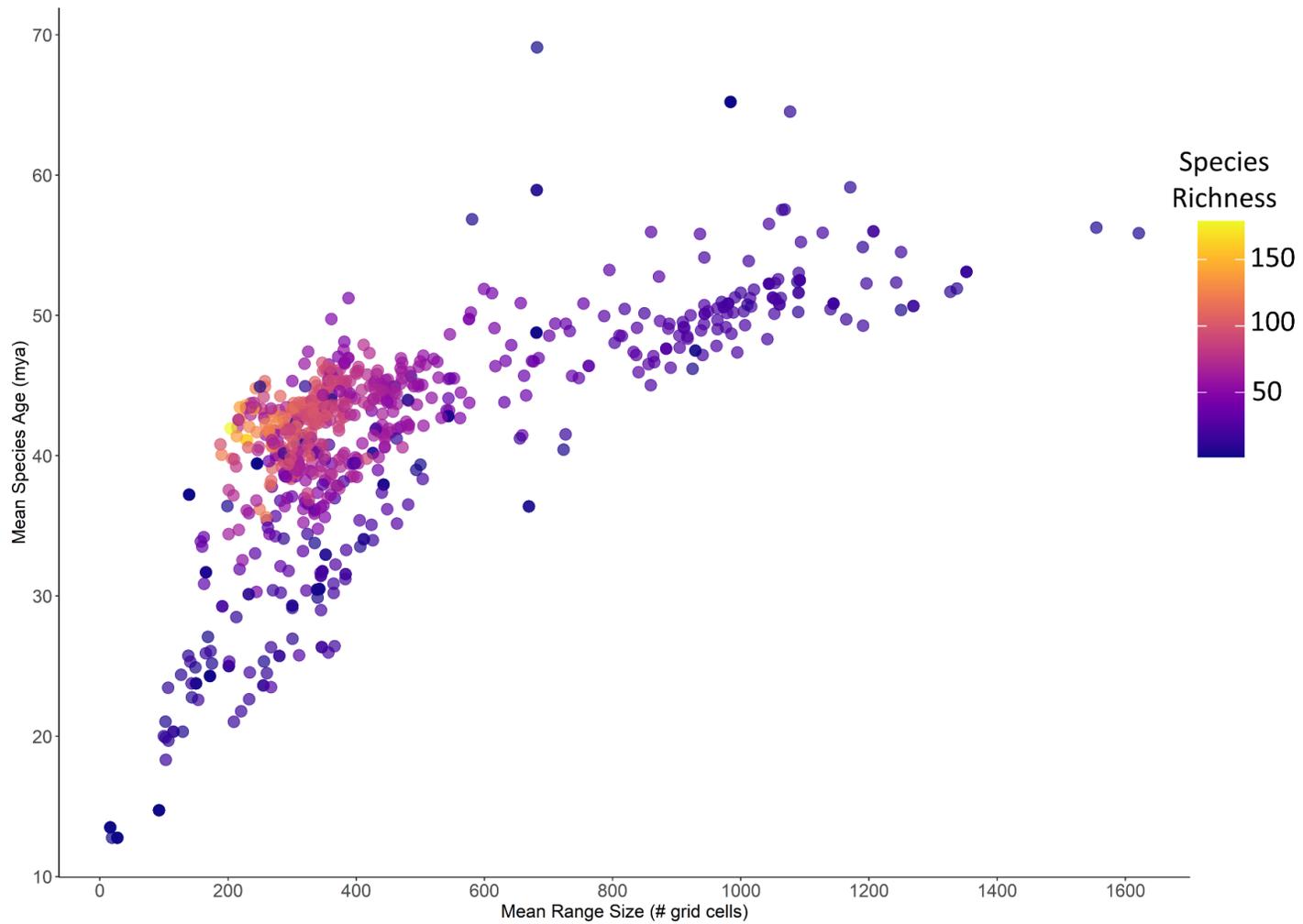


Figure B4 Bivariate plot of mean species age versus mean range size. Points are unstandardized, untransformed, and coloured by species richness visual purposes. Spearman's rank correlation value between the two variables is $r = 0.78$.

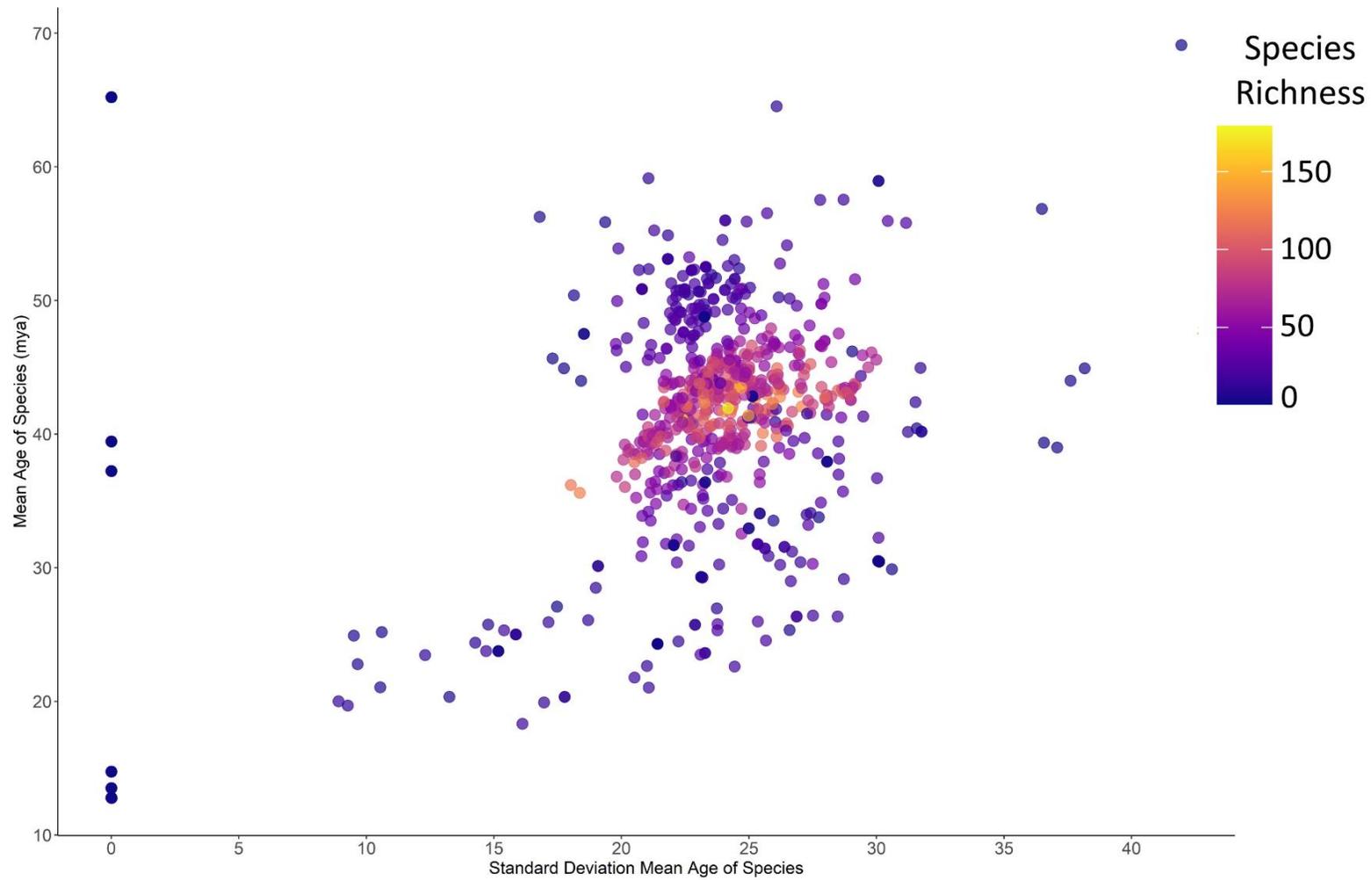


Figure B5 Bivariate plot of mean species age versus the standard deviation of mean age of species to test for Taylor's Power Law. Points are unstandardized and untransformed, and are coloured by species richness for visual purposes. Linear slope between the two variables is equal to 0.3.

Table B1 Environmental and Evolutionary data sources used for GLM analyses of species richness and endemicity.

| Data | Source | Units | Original Resolution | Download Date |
|---------------------------------------|--|-------------------------------------|---------------------|---------------|
| Distribution Maps | Distribution maps of all known Chondrichthyans (https://www.iucnredlist.org/) | NA | NA | 01/2018 |
| Coastline Length | Free vector and raster map data (https://www.naturalearthdata.com) | km | 1:10m | 03/2018 |
| Sea Surface Temperature (SST) | NOAA Optimum Interpolation (OI) Sea Surface Temperature (SST) V2: NOAA_OI_SST_V2 (https://www.esrl.noaa.gov/psd/data/gridded/data.noaa.oisst.v2.html) | °C | 1 degree | 02/2018 |
| Dissolved Oxygen | Bio-Oracle data bank (http://www.biooracle.org/downloads-to-email.php) | mol·m ³ | 1 degree | 03/2018 |
| Primary Productivity | Bio-Oracle data bank (http://www.biooracle.org/downloads-to-email.php) | g·m ³ ·day ⁻¹ | 1 degree | 03/2018 |
| Chondrichthyan Age (level of Species) | Stein, R <i>et al.</i> , (2017). Global priorities for conserving the evolutionary history of sharks, rays, and chimaeras. <i>Nature Ecology and Evolution</i> , 1–11. https://doi.org/10.1038/s41559-017-0448-4 | mya | NA | NA |