Review

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Marine Biodiversity, Biogeography, Deep-Sea Gradients, and Conservation

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The oceans appear ideal for biodiversity — they have unlimited water, a large area, are well connected, have less extreme temperatures than on land, and contain more phyla and classes than land and fresh waters. Yet only 16% of all named species on Earth are marine. Species richness decreases with depth in the ocean, reflecting wider geographic ranges of deep sea than coastal species. Here, we assess how many marine species are named and estimated to exist, paying particular regard to whether discoveries of deep-sea organisms, microbes and parasites will change the proportion of terrestrial to marine species. We then review what factors have led to species diversification, and how this knowledge informs conservation priorities. The implications of this understanding for marine conservation are that the species most vulnerable to extinction will be large and endemic. Unfortunately, these species are also the most threatened by human impacts. Such threats now extend globally, and thus the only refuges for these species will be large, permanent, fully protected marine reserves.

Introduction

There are several reasons to expect there to be more species in the oceans than on land. Life has existed in the sea longer than on land — fossils indicate bacteria existed in the oceans over 3.7 billion years ago [1] and on land by 3.1 billion years ago [2]. The fossil record indicates that marine diversity exceeded that on land for 3.6 billion years [3], but currently only 16% of named living species are marine [4]. According to biogeographic theory, species richness increases with habitat area, and the oceans cover 71% of the Earth's surface [5]. This greater connectivity between ocean populations would have reduced the risk of extinctions, such as may happen on land and in freshwater habitats due to natural catastrophes. If we consider land to provide habitat for species to a combined height (into the air) and depth (into the soil) of 10 m, then the ocean has 900 times more liveable volume than exists on land. Water is essential for life, but is often scarce on land. On land, extreme hot and cold temperatures, and rapid temperature variation, contrast with the generally slow-changing and mild range of temperatures in the ocean.

Previous comparisons of biodiversity on land and in the sea have not challenged that only one-sixth of species living today are marine, despite under-sampling of the deep sea and uncertainties about the diversity of microscopic species and parasites [6–8]. Maybe marine discoveries will catch up with those on land — the rate of discovery of marine species has been higher than terrestrial since the 1950s [9]. The deep sea is less explored than coastal areas, but occupies 60% of the planet (Figure 1) [10,11], and its stability and large area may accommodate a high species richness [12]. The apparent latitudinal gradient in marine species richness has been shown to be biased by sampling effort [13]. Thus, apparent deep-sea gradients are also likely to be biased. Indeed, some experts unreservedly state that deep-sea diversity exceeds that in coastal seas (e.g., [14]).

In this Review, we update knowledge of marine species richness, provide a new assessment of the deep-sea gradient in marine species richness, and summarise recent findings on host specificity and microbial biogeography. This knowledge can help inform conservation of marine biodiversity.

Species Richness

The first comprehensive checklist of how many marine species had been named was in the online database, the World Register of Marine Species (WoRMS) [4]. It now contains 243,000 accepted species. Since its first analysis six years ago [15], the number of accepted species in WoRMS has grown by 4% (Table 1), and two phyla have been lost: Myxozoa are now placed within Cnidaria, and Echiura within Polychaeta. Changes in the number of species are due to the addition of previously omitted domains (Bacteria, Archaea, and Viruses), re-classification of species (as marine, freshwater and terrestrial), recognition of synonyms, and incremental amendments to many taxa. For example, over 1,000 species were added to each of the taxa Chlorophyta, Rhodophyta, Foraminifera, diatoms, Euglenozoa (protozoans), amphipod and copepod crustaceans, and fish. WoRMS still awaits the addition of probably a few thousand species of parasitic nematodes, will inevitably be missing some recently described species, and will include some as yet unrecognised synonyms (multiple names for the same species). Thus, the 243,000-species inventory can be considered to contain 98% of described species. In using this as a baseline to consider how many species may exist, the sources of uncertainty that need to be considered are: significance of unrecognised synonyms; potential hyper-diversity of microbes, parasites, and deep sea species; and relationship of molecular (cryptic) diversity to new species.

Synonyms

A significant problem in estimating how many species are known, and thus extrapolating future discoveries, is to what

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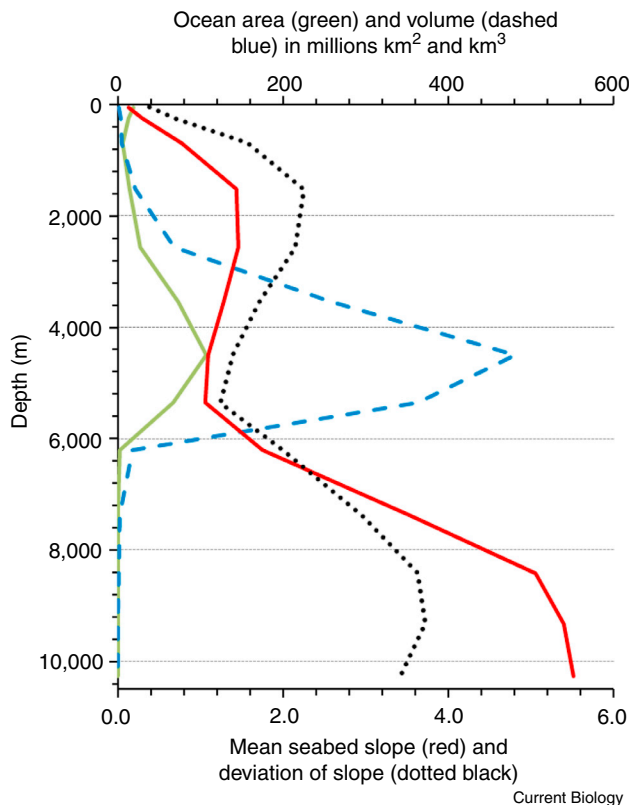Ocean area (green) and volume (dashed blue) in millions km^2 and km^3

Figure 1. Depth gradients of ocean area, volume and seabed slope.
Relationship of ocean depth (m) with sea surface area (green line, millions of km^2), ocean volume (dashed blue line, millions of km^3), seabed slope (red line, degrees), and the standard deviation of slope (dotted line) as an index of topographic variation. Data from Costello *et al*. [5].

extent synonymies have been recognised. Over 40% of marine species names are synonyms [15]. Similar or higher proportions have been found in other studies — 32% of marine mammal fossils [16]; 31% of overall insects and 56% of butterflies [17]; possibly 40% of planktonic protists [18]; 78% of flowering plants [19]; 81% of freshwater fish in Europe [20]; 93% of unionid mussels [21]. Where complete synonymies have been compiled, this can be over 90% (e.g., there are 1,284 names for 89 species of cetaceans in WoRMS). The more popular a taxon, the more scientific names exist for its species. In time, a proportion, perhaps 20% [15,22], of presently accepted names will prove to be synonyms, so both additions of new species and losses due to discovered synonymies occur. There are also species on the list that have not been recorded since their first description in previous centuries. It is likely that some of these species have been better described under a new name and these old names should not be considered valid [18]. Synonyms also arise where the morphology of a species varies in different environmental conditions, or when a species has different life stages such that these are described as distinct species [18]. Resolving these synonyms can take decades [4]. For flowering plants, the present number of species is probably accurate, as future discoveries will be balanced by recognition of synonyms [23]. This may also be the case for many other taxa, and will only be resolved after thorough taxonomic revisions [4,24].

Cryptic Diversity

The term 'cryptic species' has been applied to species that live hidden in crevices among rocks and habitat forming species such as corals, kelp holdfasts, maerl, oyster and mussel beds. However, it has also been used to refer to species that can be differentiated only by molecular analysis and not morphology. Perhaps 99% of previously indentified species have been described using only morphological characters [25,26]. This is still largely the case for newly identified species, for example, only 9% of new mollusc species descriptions include genetic data [27].

The ease of DNA analysis, including in the environment, has led to the discovery of extraordinary genetic richness in water and sediment samples [28,29], leading to suggestions that these techniques will reveal many times more species than presently described. This conflation of cryptic diversity with cryptic species is misleading. In most cases, these taxa have not been and never become described as species [30]. This cryptic diversity indicates genetic diversity, a within-species component of biodiversity, such as described for the Foraminifera [31]. It would be more helpful to characterise the organisms' biology and ecology to enable their formal description as species, and their role in ecosystems [32–39].

Molecular studies may discover some species names to be synonyms, as well as revealing some names to consist of several genotypes that may indicate new species [40–46]. Just as morphology is not perfect for discriminating species, neither are genetic markers. For example, mitochondrial DNA varies in complex ways across taxa [47–51] including being correlated with population size [52,53] and organisms' life-spans [54]. There are also examples of well-established species that cannot be distinguished by standard genetic markers [55–57]. Therefore, it is recommended to treat genetic information with the same circumspection in distinguishing species as morphological and other phenotypic information [58].

There seems no doubt that bacteria and protists have extraordinary genetic diversity [28,59]. However, the most common measure of molecular diversity — 16S rRNA — only indicates molecular variation, and should not be used on its own to characterise species [28,60–62]. In-depth analysis of such data suggests bacterioplankton may consist of only 1,200 phenotypic species (ecospecies) [63]. Too often, analyses of genetic diversity equate this to species diversity. Discoveries of microbial populations with unique molecular markers need to follow through and cultivate the microbes to determine what their biological characteristics are [37,64]. The term 'species' should be reserved for taxa that have been formally described and named according to the Codes of Nomenclature.

Viruses have more genetic diversity than bacteria, and bacteria more than protists [65]. Genetic diversity thus appears to be inversely correlated with species diversity across the domains of life. Similarly, there is no correlation between genetic and species richness among vertebrates [66] and among alpine plants [67]. Individual-based population models show that, while genetic variation arises as a function of population size, it varies with organisms' body size [68]. Below about 1 mm in size, there is less competition to drive speciation and high gene flow, so it is difficult for new species to arise. Above this size, competition for resources increases and leads to specialisation, and small

Table 1. Number of the currently 243,000 accepted marine species in higher taxa (Kingdom, Phylum, Class or Order) in the World Register of Marine Species (WoRMS) on 5th March 2017.

Higher taxon	Species	Note
Plants, fungi, protozoans and prokaryotes		
Bacillariophyceae	9833	Diatoms
Foraminifera	9001	Forams
Rhodophyta	8179	Red algae
Other Chromista	7623	Single-celled photosynthetic eukaryotes
Chlorophyta	3251	Green algae
Phaeophyceae	2642	Brown algae
Other Protozoa	2201	Single-celled flagellated eukaryotes
Bacteria	2142	Bacteria
Fungi	1375	Fungi
Tracheophyta	312	Mangroves, seagrasses
Archaea	118	Archaea bacteria
Viruses	110	Viruses
Cnidaria and relatives		
Hydrozoa	3667	Hydroids
Octocorallia	3610	Soft corals, sea pens
Hexacorallia	3424	Corals, sea anemones
Other Cnidaria	456	Jellyfish
Ctenophora	197	Sea gooseberries
Placozoa	1	Flat animals
Vermiform (worm-like) animals		
Platyhelminthes	12635	Flat worms
Polychaeta	11700	Bristle and paddle worms
Nematoda free-living	6510	Round worms
Nemertea	1376	Ribbon worms
Oligochaeta	902	Earthworms
Gastrotricha	497	Hairy-bellied worms
Acanthocephala	477	Parasitic acorn worms
Xenacoelomorpha	455	Bilateral worms
Cephalorhyncha	236	Horse-hair and other worms
Entoprocta	183	Goblet worms
Hirudinea	156	Leeches
Mesozoa	147	Mesozoan worms
Sipuncula	147	Peanut worms
Chaetognatha	131	Arrow worms
Hemichordata	130	Acorn worms
Gnathostomulida	101	Jaw worms
Phoronida	11	Horseshoe worms
Shelled animals and their relatives		
Gastropoda	35820	Snails, sea slugs
Bivalvia	8340	Clams, mussels
Echinodermata	7294	Starfish, sea urchins, sea cucumbers
Other Mollusca	2840	Chitons, squid, octopus
Brachiopoda	422	Lamp shells

Table 1. Continued

Higher taxon	Species	Note
Arthropoda and relatives		
Peracarida	18456	Amphipods, isopods, cumaceans, mysids
Decapoda	13211	Crabs, lobsters
Copepoda	11290	Copepods
Ostracoda	5957	Seed shrimp
Other Crustacea	2655	Krill, fairy shrimp, water fleas
Hexapoda	1787	Insects, Collembola
Acarina	1470	Mites
Pycnogonida	1345	Sea spiders
Tardigrada	203	Water bears
Other Chelicerata	112	Horseshoe crabs, spiders, pseudoscorpions
Myriapoda	69	Millipedes, centipedes
Other phyla		
Porifera	8600	Sponges
Bryozoa	6186	Moss and mat animals
Rotifera	201	Wheel animals
Cycliophora	2	
Chordata		
Cephalochordata	30	Lancelets, amphioxus
Tunicata	3057	Sea squirts, salps
Pisces	18317	Boney fish, sharks, hagfish
Mammalia	138	Whales, dolphins, seals, manatees
Reptilia	108	Turtles, snakes
Aves	646	Birds

populations mean that some genotypes will go extinct, especially in sexually reproducing organisms. In addition, sexual selection increases genetic distinctiveness (including when related genotypes may go extinct) and incipient speciation, but most microbial reproduction is asexual, reducing the likelihood of new species evolving [69–71].

Biodiversity includes variation within and between species [72]. Thus, the exploration of the role of genetic diversity is key to understanding the evolution and function of life on Earth. However, for the above reasons, it should not be conflated with species diversity. Although descriptions of species often do not explicitly state their species concept [73], most assume that the characters that they use to discriminate species reflect reproductively isolated and evolutionarily distinct lineages. These lineages are likely to contain populations that may be distinguished morphologically, genetically, and geographically, but have the same ecology. Nevertheless, some species may only be practically distinguished using genetic data. These cryptic species may comprise about 20% of undescribed marine species [15]. Thus, the loss of species due to synonymies could be balanced by the gain in species discriminated by molecular methods.

Exploration Effort
The growth of marine science, including new field stations, research ships, and sampling methods (e.g., scuba, underwater

video, acoustics [74]) has shown unprecedented rates of discovery of new species, taxonomic publications, and seven times more authors of new marine species in the past decade than in the 1950s [11,75,76]. The number of marine species described per year exceeded 2,000 three times in the past decade, a rate never before achieved [15]. However, this is only about 11% of the 13,000 living species described annually [24,75]. This proportion is less than the 16% that marine species already comprise of all species, and the number of species described annually per taxon is highly correlated with the number of already named species [76]. Thus, despite unprecedented high rates of description of marine species, and major advances in undersea exploration, the evidence indicates that marine species will not increase their proportion of global species richness. In terms of numbers of new species, authors and publications, marine taxonomy has never been so productive as now. While it therefore seems unlikely that sampling or taxonomic effort explains the relatively lower species richness in the ocean than land, this pattern would change if many rare and endemic species were discovered in the deep sea, and if marine parasites or microbes proved to be far richer in species than presently documented.

Deep-Sea Species

Almost two-thirds of the Earth is deep sea, with 84% of the ocean area and 98% of its volume below 2,000 m [5]. As the least explored environment on Earth the deep sea may harbour many undiscovered species [77,78]. However, their number may not necessarily exceed discoveries in coastal seas, particularly in coral ecosystems. The number of marine species has been found to decline with depth [79–83], peak at depths ranging between 300 and 4,700 m [84–95], or have no significant gradient [96]. However, the 19 studies cited here were both taxonomically and geographically restricted to parts of the Atlantic (50%), Pacific (22%) and Southern oceans, and three studies in the Mediterranean Sea.

As is the case with latitudinal gradients [97], we expect depth gradients to vary geographically and between taxa. Thus, here we compared depth gradients for 32,328 species that had depth information among the 51,670 species from the Ocean Biogeographic Information System, which we previously analysed for latitudinal gradients [13] (Figure 2).

More species have been recorded from coastal than offshore, and tropical than polar regions (Figure 2). This was also the case when over 10,000 marine species' distribution ranges were overlaid [98]. When we mapped the number of species as equal area hexagons ($\sim$50,000 km^2), it was clear that places with a low number of recorded species existed at all depths in the ocean, but that the most species-rich locations occurred at less than 100 m depth (Figure 3A). There was an average of 1,572 ± 145 (95% CI) species shallower than 100 m depth per hexagon, 543 ± 83 between 100 and 200 m, and <157 ± 16 deeper (Figure 3B). There were almost four times more species between 0 and 100 m than 100 and 200 m (i.e., 41,350 and 11,592, respectively). However, there was a similar total number of species in the 200–300 m and 400–500 m depth intervals (8,335 and 8,583, respectively; Figure 3C). Because these data were biased by sampling effort, we calculated ES50, an index of estimated species richness in 50 repeatedly drawn samples from each depth zone. This result confirmed the peak at 400–500 m depth (42 ± 2.5 versus 41 ± 2.6 at 0–100 m; Figure 3D). Nevertheless,

there was a sharp decline in species richness by all these measures of diversity with depth in the ocean.

Our data analyses (Figure 3) support previous observations of large geographic and depth ranges in deep-sea species [99–104]. Thus, there are few species restricted to deeper than 3,500 m [105–109]. These biogeographic patterns reflect habitat homogeneity compared to coastal environments, including low slope (<1°) and topographic variation (Figure 1), and constant dark and cold (Figure 2). Although slope and topographic variation may be greater in the deepest hadal zones, these occupy <1 % of the ocean floor area and volume (Figure 1). Low population densities in the deep sea require good dispersal abilities (and thus high gene flow) to colonise isolated habitats (e.g. hydrothermal vents, whale falls) [99]. Larvae of benthic species may disperse in the plankton for months to over a year [110]. Genetic analyses indicate that biological connectivity [111] and duration of larvae in the plankton [112] increase with depth. These life-history strategies maximise the chance of larvae finding a suitable food supply in a nutrient-poor and enormous habitat. They therefore explain why deep-sea species are relatively widespread and have lower global species richness (gamma diversity) than shelf species.

Microscopic Species

The relatively high number of microscopic species (bacteria, protists, fungi, meiofauna) found in local studies (alpha diversity) has led to expectations that they would comprise most species on Earth. However, at global scales, the taxa with the smallest body size are never the most species-rich, either within higher taxa or across taxa [113–116]. For all species on Earth, 11% of species are in microscopic taxa (<1 mm), 86% macroscopic, and 3% large animals (>10 cm) [76]. In the ocean, these proportions are 25%, 74% and 1%, respectively. These differences in body size may be because of insufficient sampling and species descriptions, or may be because the biogeography of these organisms is fundamentally different from larger taxa.

Microbial biogeography has received increased attention in the past 15 years [117,118]. Studies for a range of microbial eukaryotes have found them to disperse widely and to be more widespread than flowering plants and larger animals. These studies included protists [119–123], phytoplankton [124–126], meiofauna (rotifers, tardigrades, nematodes, microturbellaria, and gastrotrichs) [127], algae and lichens [128,129], as well as ferns [130], bryophtyes [131,132] and fungi [133,134] with abundant and resilient spores. Several studies have found that free-living marine nematodes, like other meiofauna, are relatively cosmopolitan compared with macrofauna [107,135–137], as are harpacticoid copepods [138]. In addition, these taxa and others can be passively transported in water, air, and through attachment to larger animals [139] and drifting materials. Although the composition of aerial plankton remains poorly studied [140–143], it is clear that microbes and arthropods can be transported across oceans and between continents [144–147]. The wind generally travels ten times faster than ocean currents, so this long-distance transport of both terrestrial, freshwater and marine propagules could lead to near cosmopolitan geographic ranges.

The geographic distributions of many protist [148,149] and fungi [150] species are more associated with habitat conditions than geography. Similarly, the distribution of bacteria has been
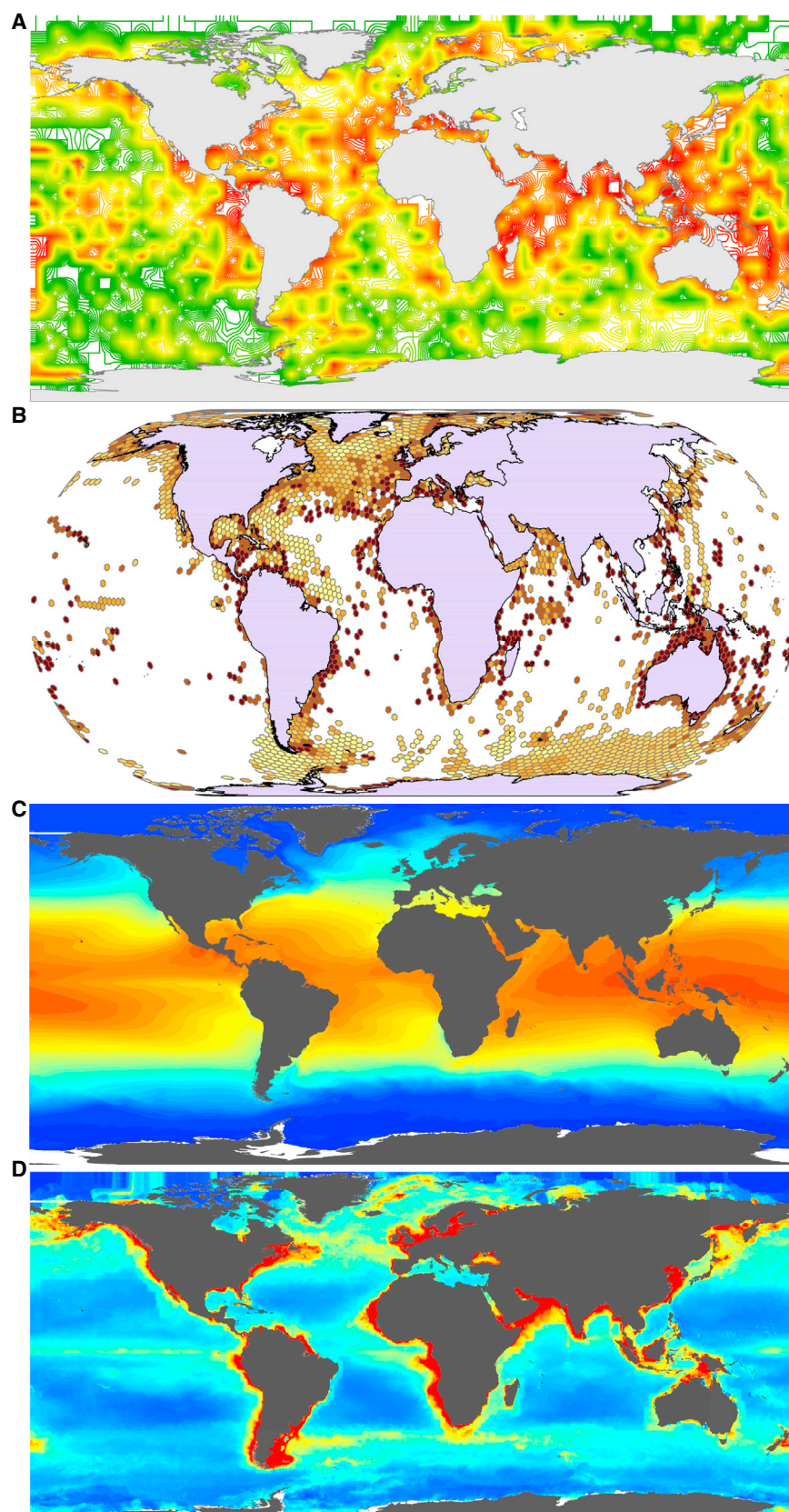
Figure 2. Marine species richness, temperature and productivity.

Maps of the relative richness of species in the oceans (A,B), and average annual sea temperature (C) and productivity (D). To minimise sampling effort bias, Estimated Species richness (ES_{50}) was calculated, as the number of species in 50 random samples in (A) each 5° latitude-longitude cell derived from a dataset of 65,000 species distributions from OBIS in 2009 where species names were validated against WoRMS, and (B) equal area hexagons from 51,670 species from OBIS in 2015 [13]. Map colours: (A) red=more, green=less, with values interpolated as contours; (B) dark= more, yellow=less, with actual values per hexagon (A,B) white=insufficient data; (C) sea surface temperature and (D) chlorophyll production in the oceans [267];dark red=more and dark blue=less.
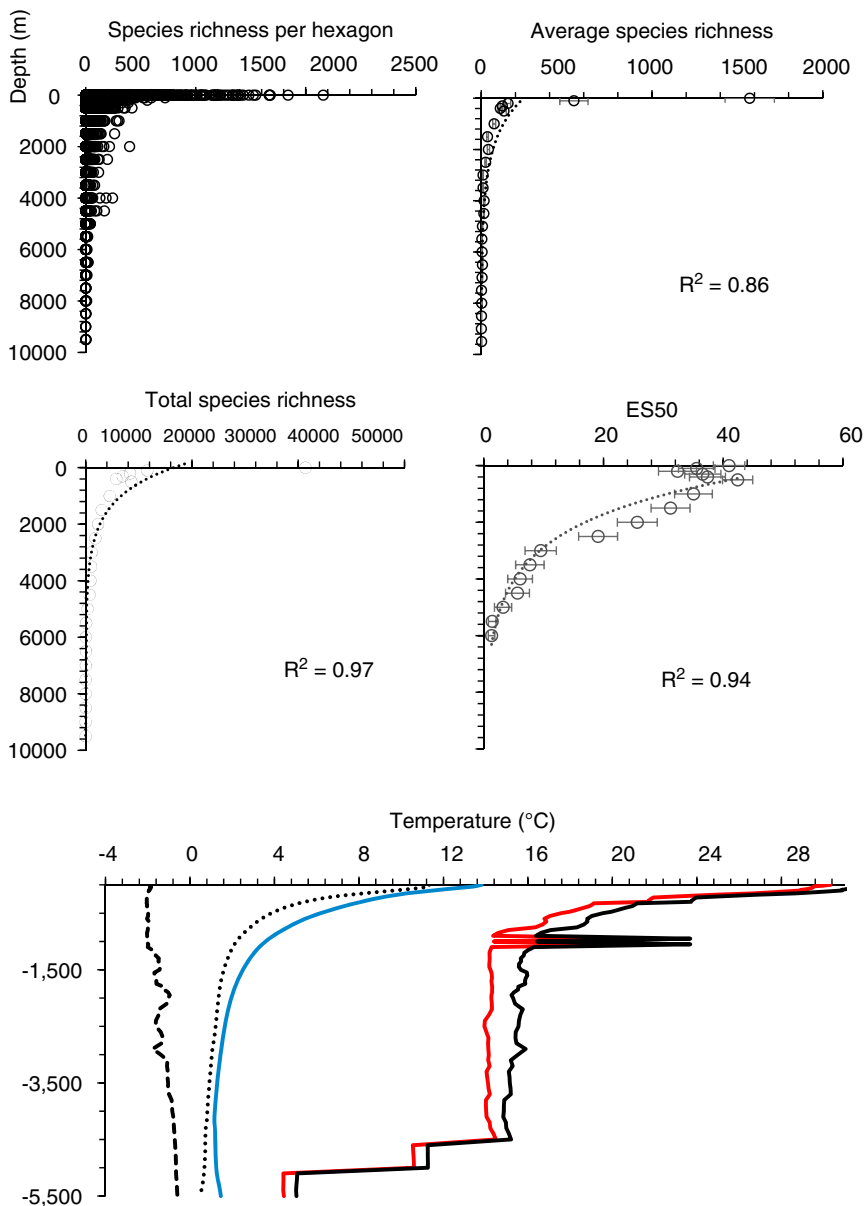
Figure 3. Depth gradients of species diversity and sea temperature.
Species richness calculated for each 50,000 km^2 hexagrid in the depth range 0–500 m (intervals of 100) and 500–9,000 m (intervals of 500), for the (top left) number of species recorded, (top right) average (±95% CI) number of species (alpha diversity), (bottom left) total number of species (gamma diversity), and (bottom right) ES50 (±95% CI) which accounts for sampling effort. The lower graph shows the temperature gradient, with depth as minimum (dashed line), standard deviation (dotted line), mean (blue line), maximum (red line) and range (solid line).

richness (comprised of both growing organisms and resting stages), but relatively low global richness.

Parasitic Species

If every species has one or more host-specific parasites, then over half of all species should be parasites [6]. Yet less than 5% of species are parasites of animals, and with the exception of endoparasitic helminths, marine and terrestrial parasite taxa appear to have most of their species described [160]. Well-known parasites, such as those of humans and domestic animals, have multiple hosts. Thus, under-sampling has exaggerated the apparent host specificity of the less-studied species. The use of host species to differentiate between parasite species has also inflated the apparent host specificity [161]. Contrary to the idea of high speciation due to host specificity, parasites actually have lower rates of diversification than their hosts [30].

Parasites, and other species with highly specific habitats, need especially effective dispersal mechanisms to ensure they find a suitable host to complete their life cycle, and need to be able to adapt to alternative hosts to survive varying host abundance. Similarly, despite their specialist habitat, sponge-specific bacteria are widespread [162,163]. The host specificity of herbivorous insects on trees was found to be lower than initial estimates, and resulted in greatly reduced estimates of global species richness based on insect–tree specificity [164–166]. Parasites and other commensal organisms can also use their hosts to aid dispersal, in addition to having free-living life-stages. Long life spans, and asexual reproduction that increases the production of propagules, may be more common in parasites than in non-parasitic species. This widespread dispersal would increase gene flow and reduce the likelihood of new species arising. Thus, parasites, like some other microscopic species, may be locally rare and geographically widespread due to high dispersal. Further studies on the relative geographic ranges of parasites and their hosts are necessary to confirm this hypothesis.

found to be better explained by the salinity [151], pH [152,153], and moisture [154] of their immediate environment than their geographic location or other environmental variables such as temperature. Thus, it appears that many protists, bacteria, fungi, and meiofauna are so resilient to adverse conditions, and so abundant in suitable conditions, that they have low probabilities of extinction [155–157]. They also have high genetic diversity due to large population sizes, short generation times, and low extinction rates, as predicted by genetic theory [42,158,159]. This diversity may enable rapid adaptation to local environmental conditions, and distinct genotypes dominating, but not necessarily new species forming due to high gene flow [158].

In conclusion, it appears that microscopic organisms exhibit far less biogeography in terms of endemism than larger organisms due to their wide dispersal. This results in high local species
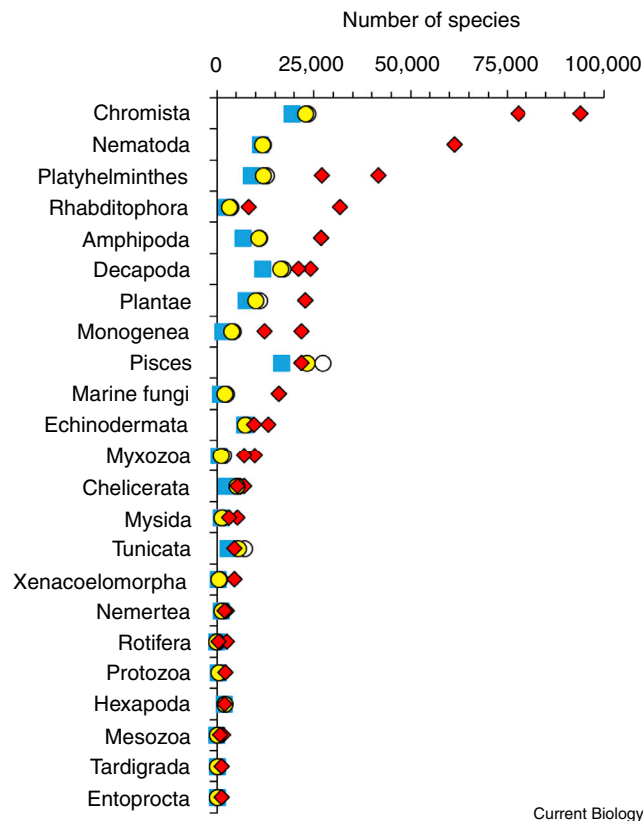
Figure 4. Comparison between estimates of global marine species richness.
Comparison between estimates of how many marine species may exist between number of accepted species (blue squares), statistical extrapolation of rates of description (circles show upper and lower confidence limits), and expert estimates (red diamonds for upper and lower estimates where available) (data from [15]).

How Many Species May Exist?

Most estimates of how many species may exist were made in the absence of knowing how many had already been named. WoRMS provides a solid foundation for estimates of how many new-to-science species may be named in the future. Using WoRMS, three methods were used to estimate the proportion of species yet-to-be discovered [15]. The first method counted the number of undescribed species reported in field sampling. The second modelled the rate of species descriptions to predict how many more species would be discovered. Both methods concluded that two-thirds of species had been described. Similarly, several detailed taxonomic reviews of particular taxa indicated that half to three-quarters of their species were known — 45–64% of soil ciliates [167]; 61–64% of micro- and macro-algae [168,169]; 65% of freshwater catfish [170]; 67% of amphibians [171]; 70% of sea anemones [172] and scale insects [173]; 75% of world flowering plants [174]; 77% of marine fish [101]; 81% of water bugs [175]; and 97% of land mammals [171]. These studies supported statistical modelling, of over 140,00 marine and 370,000 terrestrial species, that predicted 69–71% and 71–79% of species had been described, respectively [9].

The third method used to estimate the proportion of undescribed species was to poll experts for their best estimates

(supplementary material in [15]). Most expert estimates were reasonably close to the statistical model, and some less (fish, tunicates and chelicerates; Figure 4). Expert estimates where much higher for algae (Chromista), nematodes and fungi. The estimate for Chromista was subsequently revised downwards [169]. A more objective estimate of 15,000 free-living marine nematodes based on biogeographic analysis [176] would suggest 46% of species have been described. The estimate for fungi applied the proportion that marine species were of all species on Earth (15%) to global estimates of fungi. At present, only 2% of fungi are considered marine [177]. The global estimates for fungi do not consider that high local richness does not imply high global diversity, and that fungi are relatively cosmopolitan (see above for microbes). Indeed, the fact that many fungi exist in both marine and terrestrial environments [178,179] suggests lower endemicity than is seen in other eukaryotes. A major effort to resolve synonymies is also needed [177]. For other taxa, the expert and model estimates were similar, with the exceptions of flatworms (Monogenea, Rhabditophora and other Platyhelminthes), amphipods, and plantae (Figure 4). However, experts did not provide estimates for all taxa and the statistical model could not be applied with confidence for all taxa. Thus, fuller assessments for the species-rich peracarid (amphipods, isopods, tanaids, cumaceans) and copepod crustaceans, gastropods, platyhelminthes, and oligochaetes will most improve estimates of marine species richness. Nevertheless, there seems convergence of empirical (field data), statistical, and expert opinion that about two-thirds of species are now described. In other words, the total number of species is more likely to be about 0.3 million in the ocean, and 1.7 million on land and in fresh waters.

Biogeography

We have described how the biogeography of marine and terrestrial species has some similar characteristics, including the relative species richness across broad body sizes. In both environments, about one-third of species are yet to be discovered, synonyms will reduce apparent species richness, and discoveries of cryptic, deep-sea, microscopic, and parasitic diversity will not alter the overall pattern of species richness. Because microscopic species, and perhaps other taxa, have high local but low global species richness compared with larger taxa, estimates of global species richness that do not account for biogeography in terms of the varying geographic distribution of species amongst taxa and body sizes are questionable. Across all environments, the proportions of species being described each year matches the proportion already named [76]. Thus, there is sufficient knowledge of biodiversity overall to understand the factors that have led to species richness and endemicity, two of the fundamental measures of biogeography. We suggest the three key factors are temperature, productivity and habitat complexity.

Temperature

Part of the explanation for greater marine and terrestrial species richness in the tropics [97,180] is that warmer temperatures cause higher metabolism and mutation rates and shorter generation times — all of which provide opportunities for speciation [181–186]. The increased demand for food at warmer temperatures leads to increased competition and predator–prey interactions. Thus, diversification is primed by warmer temperatures,

but is a consequence of spatial isolation (allopatric speciation) and ecological interactions (sympatric speciation) [7,187]. This is supported by higher rates of speciation (but also extinction) with temperature in the fossil record [188]. Such conditions, combined with a high density of species and productive coastal areas, will drive speciation through ecological competition, herbivory and predation. Temperature may thus influence speciation in all global environments, including by species adapting to temperature variation at the edges of the tropics [189]. Tropical sea temperatures have been stable for 15 million years [190], in contrast to repeated glaciations affecting higher latitudes [191]. Thus, the shallow tropics have been the 'Goldilocks zone' for marine life, and are where it is most species rich (Figure 2). As most higher taxa appear to have evolved in the tropics, this will be where their growth and fecundity will be optimal when nutrients are adequate. However, the latitudinal gradient in marine species richness (at least), dips at the equator for both pelagic and benthic, invertebrate and vertebrate, species [13,97]. This dip may be due to speciation being higher at the edges of the tropics [189], and/or the equator being too hot for some species [192].

Productivity

Photosynthesis-fuelled primary productivity will produce more abundant populations, and this abundance will mitigate against extinction. Coastal seas will be oxygenated by physical air–water mixing and by photosynthesis, also mitigating the effects of mass extinctions that would have had catastrophic effects in the deep sea [193]. However, while past mass extinctions reduced biodiversity, they were followed by diversification of new taxa [194]. Thus, high species richness in coastal seas may have had direct and indirect benefits from photosynthesis over the millennia. However, ocean phytoplankton productivity does not show a geographical (and temperature) gradient like species richness does — it is greatest in coastal waters, and more so near large landmasses in the tropics (Figure 3). The mechanism by which productivity would influence speciation is less evident because greater species abundance does not imply greater speciation (even if it reduces the likelihood of extinction) depending on gene flow [195]. However, although the net primary productivities of the ocean and land are similar, productivity per unit area is over three times higher on land [196,197]. By contrast with coastal seas, the dark deep sea has far lower primary productivity. Thus, primary production decreases from land to coastal seas to the open ocean and deep sea; as is the case for species richness.

Habitat Complexity

Species diversity and habitat diversity are intrinsically linked [198]. In an area of low habitat diversity, the entire area may represent one habitat and thus the population range. Where habitat diversity (or beta diversity) is high, each habitat patch is separated by unsuitable habitat across which individuals must travel. These vagrants risk high mortality due to environmental stress, lack of food, or predation, while outside their preferential habitat. They can lower this risk in three ways — being very small and using passive dispersal to save energy, being so large and fast as to minimise predation, or if 'bite size' by migrating at night to avoid visual predators. Benthic macroinvertebrates are thus most abundant in the marine and aerial plankton, and freshwater drift, at night. Thus, greater habitat heterogeneity will increase

spatial separation of sub-populations, as well as opportunities for sub-populations to adapt to different microhabitats, and consequently the opportunity for speciation.

With the exception of deep-sea corals and sponges, three-dimensional biological habitats are largely limited to the ocean fringe, which is less than 4% of the planet surface if defined as to 100 m depth [5]. Forests (trees over 5 m tall) cover twice this area (30% of land [199]), represent 80% of earth's plant biomass [200], and are supplemented with additional vegetation. Previous reviews that compared diversity on land and in the sea emphasised the role of greater physical complexity on land. That is, higher species richness in the terrestrial environment was related to greater spatial variation in climate, topography, and habitat distribution [6–8,201]. The greater variety of environmental niches on land provides the opportunity for species to specialise. This specialization leads to greater occupation of space, and in turn, to more biological niches. This has led to an extraordinary diversity of relationships between flowering plants and arthropods (insects, spiders, mites), including herbivory, pollination, plant chemical defences and semiochemicals to attract parasitoids [187]. These plant–animal and predator–prey arms races drive speciation. Thus, sympatric speciation is common in both marine and terrestrial environments [202]. That arthropods existed for nearly 200 million years in the ocean, and it took another 275 million years for their terrestrial descendants (insects) to overtake their diversity [203], further suggests that it was flowering plants that provided the new niches for their diversification on land. Across latitudes, insect species richness is highly correlated with plant diversity [204].

Species richness on land appears to have overtaken that in the oceans about 125 million years ago [3,205,206]. This coincided with the diversification of flowering plants, which now represent 79% of all photosynthetic eukaryote species [207]. Flowering plants increased terrestrial productivity, leading to rates of herbivory three times higher than in the ocean [6,7,187]. Following the increase in terrestrial biodiversity, marine diversity again increased, possibly due to nutrient inputs from the now greater terrestrial productivity [208]. The importance of terrestrial nutrients is evident in that marine primary production is highest near land (Figure 2). Furthermore, terrestrial pollen may be a significant food source in deep-sea sediments [209]. This greater productivity was followed by greater animal diversity, and predators increased in richness from 10% to 25% of all marine species [210].

Some studies emphasise the importance of the contrasting air–water medium. Air provides ease of movement to mobile animals and forty times more oxygen than in aquatic habitats [211]. High oxygen may be significant in enabling efficient flight in insects so they can find rare host plants and animals [187] — thus, greater spatial rarity is possible. Indeed, more mobile taxa are the most species-rich on land (arthropods) and comprise 68% of species in the ocean (notably crustaceans, gastropods, vertebrates). Their proportion of all marine fauna has increased over geological time, and a more active fauna correlates with greater productivity and energy [210]. More mobile individuals have greater control over where they can feed, reproduce, and to modify (e.g. burrow) and avoid unsuitable environments — thereby favouring survival and speciation. In addition, because plants may compete most with similar organisms,

they can grow better when they live next to different species [212] and such spatial patchiness may reduce grazing and predation. Similarly, inter-species facilitation in aquatic invertebrates increased individual animal food capture [213]. Thus, spatial heterogeneity of physical and biological habitats can increase productivity and further fuel diversification.

It appears that body size, temperature, oxygen, productivity and habitat complexity affect the biogeography and species richness of taxa similarly on land and in the sea. However, it was the diversification of flowering plants that led to greater species richness on land than in the sea due to its effects on primary production, habitat hetergeneity, and consequent ecological interactions. Warmth, food and physical habitat lead to high abundance and intra- and inter-specific competition that promotes diversification.

Implications for Conservation

Human fishing practices have removed about 90% of fish biomass worldwide [214], over two-thirds of fish abundance has been removed from reefs worldwide [215], and globally, fisheries continue to decline due to over-fishing [216]. Fishing removes the top and mid-trophic level predators from ecosystems, in contrast to hunting on land, which largely targets herbivores. In addition to fisheries, more marine mammal species have been killed in recent decades by people than ever before [217]. Thus, food webs in marine ecosystems have been altered globally through the removal of marine mammals and turtles in past centuries, and large fish in the past century. This shift in the food webs leads to 'trophic cascades', which have indirect effects. The most widespread and best known indirect effect has been the release of sea urchins from predation, allowing them to graze down seaweeds and change the nature of marine habitats [218], but impacts in pelagic ecosystems at regional scales also occur [219].

Our knowledge of marine biodiversity and biogeography allows us to predict that the species most sensitive to extinction will be large with low abundance, and will have small geographic ranges (i.e. endemic). Unfortunately, the first group is also highly hunted, fished, and killed accidentally in bycatch and lost fishing nets, and ship strikes [220,221]. They also tend to be long-lived species and accumulate contaminants that affect reproductive success. These megafauna represent 78% of the 18 marine species that are known to have gone extinct [222]. In contrast, hunting caused the extinction of less than half of terrestrial species, while introduced animals caused extinction of more than half of terrestrial species; particularly of birds and other species on islands that were naïve to mammalian predators [223–225]. To date, introduced species and habitat loss have not had such significant impacts in marine ecosystems as they have in terrestrial and freshwater [226].

Unknown extinctions of invertebrates may also have occurred, particularly on land and in fresh water due to introduced predators and habitat loss [227,228]. Benthic invertebrates are especially sensitive to seabed trawling and dredging, which destroys and fragments habitats (including those created by long-lived, slow-growing corals and sponges) with consequent loss of productivity and biodiversity [229]. Such trawling needs to be replaced by more ecologically sustainable methods.

The only refuges for the currently threatened and yet-to-be threatened marine species will be large, permanent, fully protected marine reserves [215,230,231]. Apart from the ethical need to protect biodiversity, conservation has economic and educational benefits [230]. In addition to fisheries benefiting from the recovery of fish broodstock and spillover of fish from reserves into fished areas, their management will benefit by having unfished 'control' areas as baselines to judge the sustainability of fisheries [232]. Combined with more sustainable practices including reserves, fisheries can become more productive [233,234]. Furthermore, tourism is the largest and most valuable maritime activity in Europe, and depends on a healthy environment — including nature reserves [235]. While fished species recover in abundance within a few years in reserves, it takes decades for full ecosystem recovery, because the top predators tend to be older animals [215,218]. Reserves also need to be located to protect endemic species because they have a high risk of extinction due to their limited geographic range [236]. Species that are in both groups, such as localised coastal populations of marine mammals, are the most highly threatened and merit the most active conservation measures.

Identifying areas of high species' endemicity is critical because these indicate geographic isolation and high risk due to climate change [237]. Species distribution models have proven invaluable for mapping the ranges of marine species (e.g., [238]). They can be applied to identify climate refugia for endemic species, such as where Antarctic shrimp species would have had refugia during the last ice age, and will have refugia in a warmer ocean [239]. Analyses of the fossil record indicate that species with restricted ranges (high endemicity), as occur in the tropics and Antarctica, are at greatest risk to climate change [240–242]. Maps identifying regions of marine species, endemicity and richness based on empirical data analysis, from a global to regional scale, are necessary to prioritise locations for conservation [236,243,244].

Due to climate change, the ocean has been warming [245] and losing oxygen [246], and its pH has been decreasing [247,248]. Many marine species have already been adjusting their geographic and depth ranges with changes in sea temperature [249–254]. Marine species have shifted their range on average 72 km per decade [255]. Global warming models predicted the dip in marine species richness recently found at the equator across all taxa [13,97,256,257]. However, not all species may be able to move to avoid thermal stress, and global warming has already been correlated with mass mortalities in the Mediterranean [258]. Marine species move more rapidly than on land in response to temperature [256,259,260], and this is their only way to avoid thermal stress. The high thermal (heat) capacity of water buffers changes in temperature but also means that aquatic species cannot find microhabitat shelter (e.g. shade, burrows) from ambient temperatures like terrestrial species can [261]. The fossil record indicates that the species that survived previous mass extinctions were those with wide geographic ranges [262,263]. Thus, we may expect microscopic species to be less threatened than larger organisms. However, although wide-ranging megafauna may rapidly adjust their distribution to ocean warming, their populations have already been greatly reduced by hunting, fishing and bycatch.

The higher biological connectivity in the ocean as a whole compared with land enables species to recolonise areas where they may have been lost, for example due to over-fishing.

Thus, the far lower number of marine extinctions means that, in theory, marine biodiversity could recover with little need for active restoration efforts. However, without global scale networks of large marine reserves, this cannot happen because fishing occurs in almost all of the ocean and moves onto alternative species in over-fished locations. Even if not targeted, threatened species may be killed as bycatch. Furthermore, the ocean is only highly connected for a small proportion of the largest and smallest species. Areas of higher endemicity do occur, but need to be better mapped to prioritise conservation actions. Overall, a double whammy of deteriorating environmental conditions due to climate change and pollution, and disruption of ecological interactions, particularly by removal of top predators, is unravelling millions of years of evolution in the ocean.

Conclusions

At least two-thirds of marine and terrestrial species have been described. Thus, the present proportions of species across taxa and environments are representative of biodiversity overall. After accounting for sampling effort, there are fewer species in the deep sea than continental shelves due to the lower temperature, productivity, and habitat heterogeneity in the deep sea. The fact that there are six times more species on land than in the ocean is due to the diversification of flowering plants and their associated arthropods and fungi on land.

Dispersal is greatest in microscopic organisms and large animals, so the macro-invertebrates (such as arthropods and molluscs) are the most species-rich marine taxa. Future discoveries are highly unlikely to alter the fact that there are fewer species known from the oceans than on land, nor radically alter the relative richness of species across taxa and body sizes. However, terrestrial species have evolved from marine species, and the most unique taxa are in the oceans, reflected by there being 39% of phyla unique (endemic) to the oceans and none to land and freshwaters. While species may have greater dispersal and larger distribution ranges in the ocean than land, in the deep than shallow seas, and in the pelagic than benthic environments, rare species dominate both environments. Species are but one measure of biodiversity. In contrast to the species pattern, phylogenetic diversity is higher in the oceans than on land. How genetic diversity relates to species and phylogenetic diversity merits further research. Cryptic (genetic) diversity should not be conflated with 'species' diversity, as they are not necessarily correlated. The term 'species' should be restricted to formally described and named organisms with robust phenotypic differences to avoid confusion between these different components of biodiversity.

The species most sensitive to extinction from human activities and climate change are large megafauna and species with restricted geographic ranges. Marine reserves are a simple, practical way to protect both groups of threatened species, as well as co-occurring species. Taxonomic and conservation efforts should focus on areas of high endemicity, on land and sea, because the species there represent the rarest genetic, physiological and ecological traits and they cannot be protected elsewhere. In addition, reserves will benefit fisheries, tourism, and public education, and act as the scientific controls for understanding human impacts on ecosystems. Disappointingly, only one-quarter of coastal countries have designated even one marine reserve, <1% of the ocean area is in fully protected reserves, over 90% of so-called Marine Protected Areas allow fishing, and most reserves are too small to fully protect fished populations (average <3 km^2) [37].

Areas with higher habitat heterogeneity, whether geological (e.g., seamounts, canyons) or biological (e.g., coral reefs) in origin, should be prioritized for conservation, as they are likely to harbour more habitats and species. Protection of ecosystems in areas of high endemicity will generally include populations of the more widespread species [72,264]. Thus, for conservation prioritization, endemicity may be a better metric of biodiversity than species richness. However, it requires more taxonomic effort to distinguish species, especially rare species, and more geographically complete species' distribution data, and one-third of species may not yet even be named (the first step in knowing their ecological role). Fortunately, the Ocean Biogeographic Information System and Global Biodiversity Information Facility provide open-access services for the standardisation, integration and publication of species distribution data, and models that predict species distributions using environmental correlates are well-established [265,266]. However, because most species are rare and lack sufficient data for distribution modelling, recognising marine areas of endemicity is still at an early stage.

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