

highly-organized terrestrial gait for one in which only one or a few legs give appropriately-directed shoves to propel the animal in the desired direction, with the animal gliding through the water between shoves, a prediction borne out experimentally [7].

The work of Levy *et al.* [2] is thus a compelling example of how body form and environmental circumstances affect neural system structure and control strategies [8,9]. The radial distribution of octopus arms means that shoving with at most two arms can propel the body in any direction. The very low weight of the octopus body in water means that there is no great requirement to support the body off of the substrate. There are thus no fundamental pressures against evolving the most simple of control

strategies — activate a set of arms that will push in the right direction, and always do so to approximately the same degree — which is indeed the strategy evolution discovered.

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Biodiversity: The Known, Unknown, and Rates of Extinction

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How many species are there and how many have we lost? New estimates shed light on this question in the marine realm.

Two of the greatest unknowns in science are how many species exist on Earth and at what rate they are going extinct. Taxonomy has been making good progress in publishing new species descriptions (Figure 1) [1]. About 1.5 million species have been described, and although at least one-third of all species remain to be discovered in both marine and terrestrial environments, it appears that most will be named before they go extinct [2–4]. Quantifying current and predicting future rates of extinction are proving more difficult because the causes of extinction change over time and biodiversity monitoring is insufficient. Up to date taxonomy is essential to know if species no longer reported are now being called a different name [5]. There are narrower estimates of how many species exist

(2–8 million) than of current extinction rates (0.01 to 1.0 % of species per decade) [3,6]. Knowing what species exist is a prerequisite for knowing how many are threatened with extinction. Two recent papers in *Current Biology* use data on how many species have been formally described, that is, named, and thus their existence is known to science. Webb and Mindel [7] compared the proportions of extinct and threatened species between marine and terrestrial environments, and Fisher *et al.* [8] estimated how many species may exist in coral reef ecosystems.

Estimating Species Richness

Fisher *et al.* [8] estimated the proportion and number of species in ‘shallow-water coral reef ecosystems’ which included

associated rocky, sediment and plant dominated habitats. They estimated that these regions contained 32% of all marine species. This seems reasonable, because a similar proportion of marine fish species (27%, ~4,500) are reef-associated [9], and 34% of marine species were predicted to occur on coral reefs based on area-diversity relationships [10]. This proportion could be validated further by comparison of species richness in tropical coastal versus deep-sea, temperate and polar regions.

The estimated proportion of marine species occurring in coral reef ecosystems finds independent support. However, the estimate (derived from solicitation of taxonomic experts) by Fisher *et al.* [8] of 830,000 species living in this region and that only 9% of

species have been described contrasts with a global study where almost twice as many marine taxonomic experts estimated 0.7–1 million marine species on Earth of which about 25% have been named [11]. The latter experts estimated that over 50% of species were known for 88, and over 25% known for 111, of the 138 higher taxa studied [11]. A further indication that over half of all species have been named is that the annual number of new species described correlates linearly with the number of existing species [4]. If the estimates for taxa where experts considered less than 10% named were adjusted to one-third or half, then more than half of all marine species would have been named [11]. In both studies [8,11] the high overall estimates were driven by a minority of taxa, including nematode worms, isopod crustaceans, and flatworms; plus mites [8] and fungi and diatoms [11]. Most of these species are microscopic (<1 mm), a size class not rich in species (~11% of all [4]), probably because they are abundant, widely dispersed, and with long-lived resting life-stages. They may have high local species richness, but that does not imply high global richness [2]. Indeed, sample data suggest that on average 28% of free-living marine nematodes are undescribed [11]. Further data on all of these taxa are necessary to confirm these biogeographic patterns and better estimate their global species richness.

Fisher *et al.* [8] used carefully planned, formal and standardised procedures. They elicited some experts repeatedly, assessed several taxa by different experts, and produced the first statistical confidence limits for estimates of species richness using expert opinion. They employed methods to account for any varying ability of experts to apply and remember relevant information, and to quantify estimates. Although this is the best attempt yet at using expert opinion, there are limitations to opinion-based methods [12]. For example, experts may have unconscious 'anchoring' bias towards numbers presented by others in the literature, conferences and personal communications; their passion for their specialist taxon may extend to chauvinism for or against various taxa;



Figure 1. Marine biodiversity.

Examples of marine species discoveries and habitat diversity: marine snails (top left), deep-sea crustaceans (hydro-thermal vent copepod; shrimps and lobster) (centre), cave dwelling coral (top right), the disc antenna bryozoan (below coral) and a sea spider (bottom right) discovered recently (images with permission from E. Rolán and S. Gori; M. Caballer; V.N. Ivanenko and P.H.C. Corgosinho; T.-Y. Chan; M. Türkay; B.W. Hoeksema; D. Gordon, C. Taylor and C. Arango). The main image is a deep-sea coral skeleton with species from at least eight phyla: anemones, starfish, basketstars, brittlestars, squat lobster, barnacles, hydroids, eel, worm tubes, sponge and other corals (image by S. Johnsen *et al.*).

and they may be concerned that to suggest most of the species in their taxon have been discovered will result in less research funding. In addition, experts will have different experiences in sampling methods and places, and of specimen collections and donations from collectors. These experiences do not necessarily prepare experts for predicting the number of species that may live in places and habitats of which they have no experience. It is not possible to standardise for these biases because they vary by person, taxon, environment and over time. This may explain why 12 of 16 estimates of species richness of the

same taxon by different experts were significantly different. Fisher *et al.* [8] may have avoided some social bias by polling each expert independently. However, group debate also has advantages (and disadvantages) [12], and it may be fruitful future research where a sufficient range of taxonomic, biogeographic and statistical expertise is available. Although expert opinion can never be a substitute for objective and holistic analysis of data, the outcome nevertheless reflects the current thinking of the experts and their views will be better informed than those of non-experts.

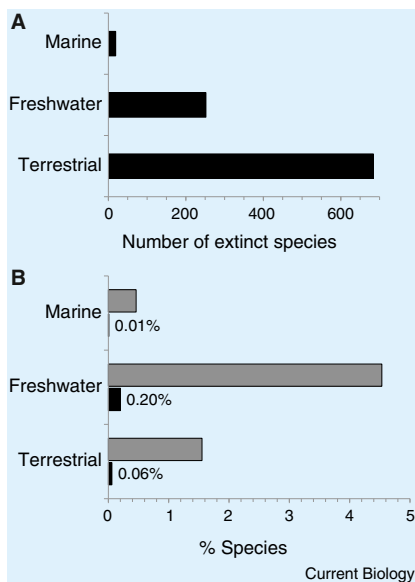


Figure 2. Extinctions.

(A) The number of extinct species amongst the 226,000 marine, 126,000 freshwater and 1,150,000 terrestrial named species. (B) The percentage of species in these environments that are extinct (black bars) and threatened (hollow bars). Data from IUCN Red List of Threatened Species (version 2014.2 accessed www.iucnredlist.org, 17 December 2014).

A commonly overlooked problem in estimates of species richness is that a significant proportion, perhaps 20–40%, of present species names will be found to be synonyms [3,13]. Indeed, as yet unknown synonyms are likely to reduce the number of e.g. flowering plant species by as much as new species will add to it [14,15]. While the experts in Fisher *et al.* [8] will have accounted for known synonyms, the numbers of known species and those yet to be discovered will have been inflated by unknown synonyms.

Extrapolating to the world from small samples, be they geographically local, or of few taxa or habitats, is problematic in estimating global species richness and extinction rates. Appeltans *et al.* [11] reviewed estimates of global marine species richness. They noted that extrapolation from deep-sea samples at sites in the Atlantic and off Australia, and rates of naming higher taxa, produced high estimates of over 10, 5 and 2.2 million marine species, respectively. Another method used to estimate global species richness is to assume that the

proportions of species amongst higher taxa are the same in different geographic regions, and use the number of species in a well-known taxon to estimate the number of less well studied taxa. However, the ratio of fish in Europe estimated 0.36 million species globally and that of crabs suggested there were 1.5 million marine species globally. These estimates require species richness and the relative proportions of species across higher taxa to be evenly distributed geographically. However, species richness varies greatly with latitude and depth [1], and evolutionary history and environmental adaption mean that higher taxa are not equally distributed geographically (e.g. 13 phyla only occur in the ocean). Higher classifications can change radically, such as new Kingdoms being created, without concomitant changes in species discovery. The problems in using such methods to estimate global species richness may also apply to estimates of extinction rates across taxa. While all methods have their limitations, it is notable that those based on data from 0.2 million species, all higher taxa, and locations worldwide have indicated that there are 0.3–0.7 million marine species [2,12].

Extinction Rates

Taxa that are the best known to science may have their conservation status assessed first, such as mammals and birds. These taxa are generally larger in body size than, and contribute only 1% of, all species on Earth. Other species may not be threatened by the same factors, may or may not be threatened by other factors, and/or may respond differently to different threats [16]. In addition, the future threats may differ from those that have caused extinctions [16]. Thus, it seems unjustified to extrapolate recent rates of extinction based on a few taxa to the future because both the cause and response variables are likely to be different. Problems also arise in comparing recent extinctions over centuries to those over millions of years in the fossil record because fossils are an unknown proportion of the then living species, are mostly marine and only identified to genus, the

relative richness across taxa is unknown but appears different from what it is today, and fossils and extant species are sampled differently [16]. However, assessing how threatened existing species are immediately identifies priorities for conservation. At present, fewer species have been reported to have gone extinct in marine than freshwater and terrestrial environments (Figure 2A), but the greatest proportion of named species that are extinct and threatened live in freshwater (Figure 2B).

In recent centuries, most extinctions were caused by hunting and predators introduced by humans [17]. Because the species most sensitive to such predation have gone extinct and those remaining are a focus of conservation efforts, such predation may be less of a threat than it once was. Current IUCN Red List assessments indicate that habitat loss may be the greatest threat to species in freshwater and on land. However, in the ocean, hunting continues to threaten many species of mammals, birds and fish through fishing, by-catch and ecosystem-altering trophic cascades. Recent decades have also seen more marine mammals and mammal species being hunted for human consumption [18]. Thus, the factors that drove most species to extinction in recent times continue in the ocean. It is thus timely to compare threats to marine and terrestrial species.

Webb and Mindel [7] found that although 20 marine and 831 non-marine species were listed as extinct in the IUCN Red List in 2012, similar proportions of assessed marine and non-marine taxa, 23% and 26%, respectively, had been classified as threatened with extinction. In addition, they found that assessments categorised proportionally more marine species as threatened than for non-marine; and that more marine species were categorised as ‘Data Deficient’, reflecting the difficulties in sampling in the ocean compared to land. Extinction is an unequivocal measure but ‘threatened’ spans three categories of concern, namely ‘vulnerable’, ‘endangered’ and ‘critically endangered’. Thus, it is easier for a species to qualify as threatened than

extinct, and scope for experts to be more or less inclusive between taxa. If more marine than non-marine species were assessed, then it may appear that the former are more threatened. However, over seven times more non-marine species had been assessed by IUCN. These findings support previous suggestions that extinctions and threats to marine species may have been underestimated [5].

Webb and Mindel [7] argue that there is little evidence to show that marine species are any less sensitive to extinction than terrestrial ones. Population size and geographic distribution are used as indicators of a species sensitivity to extinction. As even species with once millions of individuals have gone extinct, it cannot be assumed that species now numbering in the hundreds of thousands of individuals cannot be hunted or fished to extinction. As they note, despite the high number of eggs produced by some marine fish species, their populations have not recovered from over-fishing. The main threat to marine species is the direct and indirect effects of fishing which targets many predatory species, whereas hunting on land has been replaced by agriculture and forestry and where it continues, targets relatively few species of herbivores. Thus, fishing not only threatens species but may alter food webs and ecosystems more than present hunting on land.

Species with smaller geographic ranges, such as those limited to islands compared to continental mainlands, have suffered higher extinction rates [17]. Webb and Mindel [7] state that there is little evidence that marine species have generally larger geographic ranges than terrestrial species. This seems unlikely because the ocean covers 71% of the planet and is continuous, whereas land and freshwater environments have more barriers to species dispersal. Rates of endemism are thus higher for terrestrial than marine species per unit area. For example, while 80% of New Zealand's terrestrial species are endemic, less than half of its marine species are [19]. However, differences in endemism

between environments may not be important if human impacts are global in scale. The ocean's continental shelves have been trawled for decades and fishing is going deeper. This trawling destroys slow-growing habitats such as deep-sea coral, bryozoans and sponge reefs that provide rich 3-D habitat for many other species. Such widespread destruction may have comparable consequences for biodiversity to habitat loss due to deforestation and spread of agriculture. These findings add to calls for more effort to pro-actively protect marine biodiversity through no-take marine reserves [20].

Both Webb and Mindel [7] and Fisher *et al.* [8] illustrate that ecology and conservation require specialists in taxonomy, biogeography and ecology of species. A synergy of effort, building on their respective databases, could accelerate both the discovery of new species and the assessment of the conservation status of all species. The availability of comprehensive and standardised data on species' distributions over time will enable more accurate expert assessments of how many species do and may exist, and population trends.

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