Biological Diversity: Differences between Land and Sea [and Discussion]

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Biological diversity: differences between land and sea

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SUMMARY

This paper begins with a brief survey of the numbers of species that have been named and recorded on land and in the sea. It then assesses how many species there may be in total, giving particular attention to recent suggestions for dramatic upward revision of species totals for tropical invertebrates, fungi, benthic macrofauna, and microorganisms in general. Against this background, I comment on patterns of diversity on land and in the sea at higher taxonomic levels – orders through phyla – and on the possible causes and consequences of these patterns. I conclude with some estimates of impending extinction rates.

1. INTRODUCTION

Biological diversity within assemblies of organisms is found at many different levels. At the basic level there is genetic diversity within a species or population. Such genetic diversity is of fundamental importance, providing the natural variation which is the raw stuff of evolution. In current discussions of 'biodiversity', the term is usually taken to refer to number of species, either within a defined region or more globally. But biologically diversity may, in other contexts, refer to other levels in the taxonomic hierarchy ranging upwards from genera, through families and orders, to phyla. And, in conservation contexts, biological diversity is increasingly being interpreted at the level of ecosystems or communities of interacting organisms.

In this chapter, I will confine attention to biological diversity within taxonomic categories (mainly species, but paying attention also to other levels, particularly phyla). Genetic diversity is obviously important, both to evolutionary biologists and to biotechnologists and plant and animal breeders, but to my knowledge there is no systematic difference between average levels of genetic diversity on land and in the sea (although different groups exhibit interesting differences in both environments). At the opposite end of the spectrum, although there is a trend for conservation legislation to be written in terms of ecosystems or habitats rather than individual species, most implementation remains species-oriented (Wilcove 1994).

In what follows, I first survey the numbers of species currently recorded in various groups, on land and in the sea. I then survey recent revisionist speculations about what the true numbers of such species might be. Roughly 15% of recorded species are found in the sea, and my guess is that this fraction is not likely to be greatly changed as knowledge grows. Next I survey phyla, at which level the sea is much more diverse than the land. Some possible reasons for this land–sea disjunction between species diversity and phylum diversity are then summarized. I conclude with a sketch of various estimates of impending extinction rates. Much of the presentation is a bit telegraphic, giving a terse survey of material presented in detail elsewhere.

2. SPECIES DIVERSITY

The total number of species that have so far been recorded on earth is around 1.8 million (Stork 1988). Amazingly, this number is not known precisely, because there is no central catalogue. The uncertainty is compounded by synonymies, which typically have been identified as running around 20% in groups which have been carefully analysed (Gaston & Mound 1993); a recent analysis suggests that the true fraction of species that are synonymous may be more like 40% (Solow *et al.* 1993). Such synonymies could reduce the true number of different species that have been recorded to around 1.4–1.5 million (Wilson 1992), or even lower.

Table 1 summarizes how animal species are distributed among phyla, and between land and sea; animal species represent roughly 76% of all recorded species (Hammond 1992). Although many more animal phyla are found in the sea, the species count is dominated by terrestrial insects, which account for an estimated 56% of all species. Vascular plants (not listed in table 1) come next, with 14% of the grand total, essentially all on land. All recorded species of viruses, bacteria, fungi, protozoans and algae add up to only 10% of the global total.

Of all the species currently named and recorded, fewer than 15% are found in the ocean, most of them on or in ocean-floor sediments (Barnes 1983). This contrasts with any kind of global 'species–area' relation, because the sea covers 71% of the planet's surface, and 40% of it to a depth of 4 km or more. Nevertheless, most biologists have tended to accept the 15% figure as broadly representative of the true

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Table 1. *Distribution of phyla of metazoans by habitat, along with an indication of how speciose the phyla are in particular habitats*

(The number 0 denotes complete absence of the phylum from that habitat, and the numbers 1–5 indicate the number of recorded species, to within a rough order-of-magnitude, in phyla that are present (1 spans two orders-of-magnitude, from 1 to 100 species; 2 means 10^2 to 10^3; 3 means 10^3 to 10^4; 4 means 10^4 to 10^5; and 5 means 10^5 and up). This table is revised from May (1988), as modified by M. Angel (personal communication). Note that most phyla are predominantly marine and benthic, with 32 found in the sea and 21 exclusively marine (ten endemic to benthic environments, and one endemic to pelagic ones), whereas only 12 are found on land, and only one exclusively so. On the other hand, most species are terrestrial insects.)

	marine				
plylum	benthic	pelagic	freshwater	symbiotic	terrestrial
Acanthocephala	0	0	0	2	0
Annelida	4	1	2	2	3
Arthropoda	4	3	3	2	5
Brachipoda	2	0	0	0	0
Bryozoa	3	0	1	0	0
Chaetognatha	1	1	0	0	0
Chordata	3	3	3	1	3
Cnidaria	3	2	1	1	0
Ctenophora	0	1	0	0	0
Dicyemida	0	0	0	1	0
Echinodermata	3	1	0	0	0
Echiura	2	0	0	0	0
Gastrotricha	2	0	2	0	0
Gnathostomulida	2	0	0	0	0
Hemichorodata	1	0	0	0	0
Kamptozoa	1	0	1	1	0
Kinorhyncha	2	0	0	0	0
Loricifera	1	0	0	0	0
Mollusca	4	2	3	2	4
Nematoda	3	0	3	3	3
Nematomorpha	0	0	0	2	0
Nemertea	2	1	1	1	1
Onychophora	0	0	0	0	1
Orthonectida	0	0	0	1	0
Phoronida	1	0	0	0	0
Placozoa	1	0	0	0	0
Platyhelminthes	3	1	3	4	2
Pogonophora	2	0	0	0	0
Porifera	3	0	1	1	0
Priapula	1	0	0	0	0
Rotifera	1	1	2	1	1
Sipuncula	2	0	0	0	1
Tardigrada	1	0	2	0	1
total (33)	27	11	14	15	11
endemic	10	1	0	4	1

total, seeing the oceans as ‘a vast desert desperately short of nutrients and with living things spread most thinly through them’ (Colinvaux 1980).

There are, however, great disparities in the attention received by different groups and different regions. Studies of the ‘taxonomy of taxonomists’ suggest that roughly one third work on plants, while the remaining two thirds are roughly equally divided between vertebrate and invertebrate animals (with only 2–3% working on microorganisms). The estimated total number of vertebrate species is of order 40 000, and of plants 300 000, whereas for invertebrates the recorded total is around 1 million and the reality is surely at least 3 million. Thus for every n taxonomists studying a vertebrate species, there are 0.1 n studying a plant species, and around 0.01 n studying an invertebrate species (and 0.01 n for a species of microorganism). Analyses of publications against numbers of species give similar estimates of gross disparities in the distribution of the workforce among different groups (May 1988). For a more full discussion see Gaston & May (1991).

Given these facts, is it not surprising that new species of birds and mammals turn up rarely (currently at the average rate of 3–5 per year for birds, and slightly more for mammals, not counting reclassifications). Tropical botanists can expect to find roughly one new species per one hundred species collected (G. T. Prance, personal communication), which is broadly consistent with estimates that 80–

90% of plant species have been recorded. But among invertebrates and other groups, uncertainties are so great that some dramatic revisions have recently been proposed.

(*a*) *Insects*

Studies of beetles in the canopies of tropical trees have lead, by an indirect chain of argument, to widely-cited estimates of 30 million tropical insects (Erwin 1982; for downward reappraisal of those estimates, see Stork (1988), May (1990) and Gaston (1991)). Another approach is to 'scale up' from well-known groups and places. Thus butterflies are better known than most insects, with a global total estimated at 20000 species; among Britain's comparatively well-known fauna, 66 of the roughly 22000 insects are butterflies; if this proportion holds globally, we arrive at around 5–6 million insects (Hammond 1992).

I think the most reliable approach, albeit the most labour-intensive, is to make direct estimates of the proportion of species previously unrecorded, within a newly studied region. Thus, among hemiptera in Sulawesi, Hodkinson & Casson (1990) found 63% of their species to be previously unrecorded, which suggests an upward revision to a global total of around 3 million insect species.

(*b*) *Fungi*

Another interesting and dramatic revision is by Hawksworth (1991) for fungi. Currently some 70000 species of fungi, *sensu latu*, are recognized. But Hawksworth notes that in Britain, the ratio of fungal to vascular plant species is around 6:1. If this is applied globally to the quarter million or so plant species, we arrive at 1.5 million species of fungi. But this would imply that, on average, 96% of the fungal species found in a newly studied region should be previously unrecorded (May 1991). In fact, the proportion of new species found in such studies is typically 15–30%, and rarely higher. On the other hand, it can be argued that these studies tend to focus on better-known groups, and in other ways to be unrepresentative. My guess remains at a few hundred thousand species of fungi, in total.

(*c*) *Marine macrofauna*

Particularly relevant to land–sea comparisons of diversity is the suggestion by Grassle & Maciolek (1992) that there may be 10 million, and possibly more, species of marine 'macrofauna' (mostly molluscs, crustaceans and polychaete worms). This estimate is based on 233 'box core' samples (each covering an area 30 cm × 30 cm) at depths of around 2 km along a 176 km transect off the coastlines of New Jersey and Delaware.

Grassle & Maciolek (1992) find a fairly typical 'rarefaction curve' in the numbers of species added as they accumulate miles (or total numbers of individuals) along their transect; in the later stages, they found around 100 new species per 100 km along a contour at constant depth. They argue that rates of adding species across depth contours is likely to be greater than along them. On this basis, they tentatively suggest that the rate of one new species per linear kilometre generalizes to one per square kilometre. With an ocean floor area of 300 million km^2 deeper than 1 km, this yields a global total of several hundred million marine macrofaunal species. But, recognizing that the deepest and most oligotrophic parts of the ocean have densities of living things about an order-of-magnitude lower than found in their continental shelf samples, Grassle & Maciolek scale their estimates of the total number of benthic species back to 10 million or so.

This study, however, found 58% of the species to be new (64% of the polychaete worms, the most abundant group; 37% of the better-known molluscs). So, by the direct method which I favour, we would go from the present recorded total of fewer than 200000 to a total of about half a million marine macrofaunal species (May 1992). The counter-argument could reasonably be made that Grassle & Maciolek's deep-sea fauna off the U.S. coast is better known than most, and therefore that a direct estimate made from their 58% finding is low. Poore & Wilson (1993) survey studies, particularly in southern seas, which suggest figures up to 90% new species in box core collections, and they suggest a total of around 5 million. Conversely, studies in Baltic regions are more consistent with my lower estimate (J. Gray, personal communication), and I continue to guess a number below 1 million.

(*d*) *Microorganisms*

Currently some 40000 species of algae and 40000 species of protozoans are recognized. Although new and interesting species continue to be discovered (see Esteban *et al.* 1993), studies of new systems typically find most of the species are already recorded. Estimates of the global totals of algae and protozoans are 60000 and 100000, respectively (Hawksworth 1992).

The story is different for viruses and bacteria (6–7000 and 3–4000 species currently recorded, respectively). Recent studies, based on molecular biology rather than conventional culturing techniques, have uncovered vastly greater diversity of bacterial species in hot springs, artesian wells, or simply in forest soils and coastal mud (Wilson 1992). The task of classifying bacteria and viruses is, however, complicated by the fact that different strains readily exchange genetic material. This, often coupled with relatively high mutation rates (especially among retroviruses, which lack error-correcting mechanisms), means that ideas about what constitutes a species are rather different for viruses and bacteria than for invertebrate and vertebrate animals or plants.

We need to know more about the diversity of bacteria, not least for the part they play in helping to create and maintain soils. In the sea, the tiny cyanobacteria (0.2–1.0 μm) were only discovered in the late 1970s, and yet they may constitute the greater part of primary production, feeding the protozoa (D. H. Cushing, personal communication). However, for many practical purposes it may be that characterization in terms of 'functional groups' or 'consortia' is sufficient (Finlay & Embley 1992). For viruses, Eigen & Schuster (1977; see also Nowak 1992) argue that the basic unit of classification should be the 'quasispecies', a well-defined set of molecular sequences; natural selection acts on the quasispecies swarm, rather than on individual viral sequences as such. As viruses and bacteria are widespread both on land and in the sea, dismissing them, as I just have, may bias any subsequent view of land–sea contrasts in diversity.

(*e*) *Parasites and pathogens*

One view is that for every vertebrate or invertebrate animal species, and possibly also for every vascular plant species, there is (on average) at least one specialized nematode, one protozoan, one bacterium, and one virus. This would automatically multiply any conventional estimate of species totals by a factor of five or more. Whatever the merits of this argument, it obviously has essentially no effect on land–sea comparisons, which would remain dominated by the contrast between numbers of plant and animal species in the two realms.

In summary, many revisionist views about particular groups are in the air. Especially relevant are the suggestions by Grassle & Maciolek, Poole & Wilson, and other 'marine chauvinists', for upward revisions – by factors of 20 or more – in numbers of marine species. I think, however, that the most reliable estimates are those based simply on the proportions of new species found in newly studied groups or regions. These rarely find more than 50% new species, whether the organisms be invertebrates or microorganisms, on land or in the sea. I therefore believe that the current split of species 85:15 between land and sea is unlikely to change radically as the revisionist dust settles. But I could easily be wrong.

3. DIVERSITY AT HIGHER TAXONOMIC LEVELS

Table 1 lists a total of 33 phyla of animals. Of these, representatives of 32 are found in the sea, and only of 12 on land.

More emphatically, only one phylum occurs only on land, whereas 21 are found only in the sea. Of this 21, ten phyla are purely benthic, and one is purely pelagic (no phyla are found only in freshwater).

We noted earlier that only 15% of all species are found in the sea. At the opposite end of the taxonomic hierarchy, we could score 0.5 each to land and to sea for phyla found in both, to say that 80% of all animal phyla are found in the sea (20% on land); alternatively, 64% of animal phyla are found only in the sea, were as only 3% are found only on land. This is an extraordinary reversal in land–sea patterns of biological diversity, as we ascend from species to phylum. Tentative assessments suggest, not surprisingly, that patterns at the level of genera, families, or orders are appropriately intermediate.

4. POSSIBLE REASONS FOR LAND–SEA CONTRASTS IN DIVERSITY

What follows is a short list of ideas that have been proposed to explain why the sea is poorer in species, or richer in phyla, or both. It is more a list of questions than answers.

1. Life began in the sea. The Post-Cambrian explosion of diversity began with around 50 orders of aquatic animals in the fossil records, rapidly climbing to around 100 orders, which then remained roughly steady. It was over 100 million years before animals invaded the land, and it was a further 100 million years before numbers of orders climbed to around 30 or so (Simpson 1969). It has been argued that many basic 'body plans' and ways of life were 'tried out' early on, with many still leaving descendants in the sea, whereas chance or virtue had sorted out the relatively fewer number of winners by the time the land was colonized. I do not find this a persuasive explanation for the great differences between land–sea patterns of diversity at species versus phylum level.

2. Another suggestion is that continental environments are much more heterogeneous than marine ones. Continental climates show more variability over time, on scales ranging from one year to the 20–100 thousand years of the Milankovitch cycles, than do oceans (Lindzen 1993). They arguably also show more spatial heterogeneity, from local topography to biogeographic changes associated with continental drift. Such patchiness in space and time, on many different scales, is likely to create many opportunities for specialization to local conditions, and for readjustment to changing circumstances, all of which could promote increased species diversity.

Two comments seem relevant here. First, while this argument might apply to plants and animals, it seems less applicable to microorganisms, where many groups are widespread on land and in the sea. But, as explained above, this paper focuses more on animals. Second, Grassle & Maciolek (1992), Rice *et al.* (1990), and others have recently emphasized that the input of nutrients to deep sea sediments is inherently a patchy and ephemeral process. Moreover, sediment dwellers create small scale disturbances, which increase environmental heterogeneity. And the effects on diversity in the sea may be compounded by the lack of barriers (compared with terrestrial environments) to long-distance dispersal, which may allow distant migrants to contribute to reshuffling patterns of local diversity. In summary, insofar as spatial heterogeneity is an important promoter of species diversity (Atkinson & Shorrocks 1981; Ives & May 1985), the ocean bottom may in many places be as patchy as terrestrial environments (although in other places, areas of the deep sea are stable and homogeneous: A. L. Rice, personal communication).

3. The pelagic marine environment, although it represents the greater part of the volume of the biosphere, is relatively species-poor; most marine species are benthic. The ocean-bed environment is, in general, significantly less 'architecturally elaborate' than the forests which until recently covered most of

the land surface, and still cover much of it in the tropics. Such architectural complexity, from the leaves and stems of single shrubs and trees, to the overall structure of forests and woodlands, provides a physical environment much more complex than is typically found in the sea, apart from coral reefs (which are hotspots of marine diversity anyway). It can be argued that the architecture, and even the fractal geometry (Morse *et al.* 1985), of plants and forests is a cause of diversity among the animals who eat or otherwise use plants, and thence among their predators. I have difficulty, however, in accepting that this could explain the 85:15 land–sea difference in species numbers.

(In passing, I mention a puzzle which has received little, if any, systematic attention. Tropical forests and coral reefs are often mentioned in the same breath, as land–sea twins. Although both may be highly species rich, and both engage the romantic imagination, there is one enormous difference: the coral reef teems with conspicuous animal life, at densities similar to those seen in large aquariums; by contrast, in the tropical forest vertebrates are rarely glimpsed, and even invertebrates are not all that conspicuous. Whence this difference?)

4. Patterns of herbivory differ between land and sea. Cyr & Pace (1992) have recently reviewed a lot of data from aquatic systems, finding that the median proportion of net primary productivity grazed by herbivores was 79%. Other studies of phytoplankton in the North Atlantic showed that zooplankton of copepod size (0.2–2 mm) 'only' grazed about 1–5% of the primary production per day, whereas the microzooplankton (larval forms and protozoa) graze 50–100% of the daily production of small (less than 5 μm) phytoplankton (M. Fasham, personal communication). Sarmiento *et al.*'s (1993) seasonal model of nitrogen cycling in the North Atlantic assumes 70% of primary production is grazed. Hay (1991) cites similar figures for grazing on seaweeds, which commonly lose 1–4% of their total mass each day, and 60–100% of total production, to herbivores. This contrasts markedly with terrestrial systems. Among the most intensively grazed ecosystems are African grasslands, where large herds of ungulates remove as much as 66% of above-ground productivity (McNaughton 1985); given the large allocation to below-ground structures, this may correspond to around 30% of total primary productivity. More typical figures for herbivory on terrestrial plants run around 10%, with a range of roughly 5–20% (Crawley 1983), which is 'why the world is green' (Slobodkin *et al.* 1967). This boils down to levels of herbivory in the sea being at least three times, and more typically 10–20 times, those on land. The underlying reason may be partly that terrestrial plants allocate biomass to below-ground structures that are unavailable to many herbivores, and much of the above-ground mass may be woody structural tissue that is of little nutritional value; seaweeds and phytoplankton are essentially all foliage, as it were, completely above ground and available to herbivores.

Hay (1991) has also reviewed the similarities and differences in patterns of coevolution between primary producers and herbivores on land and in the sea. He finds that acquiring 'enemy-free space' is very important in selecting for host plants in both marine mesograzers and terrestrial insects, but this is not sufficient to explain the differing degrees of specialization between these two groups; both generalist insects and marine mesograzers can selectively feed on toxic plants, and reap the associated rewards of decreased predation, without becoming specialized as is common among insects more generally. Hay (1991, p. 365) ends his review with the important conclusion: 'the unresolved question of why insects are so commonly host-plant specialists and why this occurs so rarely among other herbivores, either terrestrial or marine, is one of the most vexing questions to arise from contrasts or marine and terrestrial systems and deserves increased intention.' Whatever the ultimate cause, such specialized plant–insect associations on land have surely been a major force driving toward increased diversity, which may help explain why these two terrestrial groups account for 70% of the world's species. (It could also help explain Cohen's (this symposium) paradox that terrestrial species typically have fewer links to other species than do marine ones, even though there are many more terrestrial species.)

5. A very different approach is to ask about numbers of species in different categories of physical size, on land and in the sea. Hutchinson & MacArthur (1959) suggested that most organisms see the world as a two-dimensional mosaic, with a structure which scales with the typical physical dimension, L, of the organism. On this basis, we might expect the total number of species to scale inversely as L^{-2}; as we go down a factor of ten in characteristic length, we find 100 times more species. Questions of the fractal geometry of nature may alter this expectation somewhat, but not a lot (May 1986). A study of the actual relations between numbers of species and their physical size for terrestrial animals found roughly the L^{-2} power law, down to a characteristic size of around 3–10 mm; below this, as we go to smaller size classes, we find fewer species (May 1978). I interpreted this as arising largely from lack of study of smaller terrestrial animals, at least down to the 0.5–1 mm length classes. But Fenchel (1993) has challenged this interpretation, suggesting there are globally fewer species in smaller size classes because such organisms typically have wider geographical distributions. In support of this view, Fenchel (1993) presents data on species–size relations for each of four different aquatic communities, and for all recorded free-living aquatic species. The latter histogram looks like mine for terrestrial animals, with a peak at a characteristic length of around 1 cm, a roughly L^{-2} falling away at larger dimensions, and a slower decline at smaller dimensions. But for each of the four aquatic communities, there was monotone increase in the numbers of species in smaller size classes. Fenchel suggests that, in both terrestrial and marine environments, there may be roughly the L^{-2} rule, or something like it, in any one community. He further suggests, however, that the smaller organisms typically have larger geographic distributions than do organisms of intermediate

length. Thus when all the species are put together, the resulting species–size distribution shows a peak at an intermediate size.

Fenchel's ideas are of fundamental importance. They also have implications for land–sea diversity patterns. Much primary production, herbivory, and predation in the sea involves smaller organisms than on the land: phytoplankton and zooplankton rather than vascular plants and insects. Such smaller organisms in the sea thus sit lower on the global species–size curve than do most terrestrial ones. And so, if Fenchel is right, the average species in the sea tends to have a wider geographical distribution than those on land. Hence, fewer species in the sea. Support for this notion comes from Rapoport's (this symposium) analysis of average 'cosmopolitan indices' for a range of terrestrial and marine species; these average around $c = 0.03$ and $c = 0.2$, respectively, indicating that indeed the typical marine species has a wider biogeographical distribution. All this is admittedly speculative.

5. IMPENDING EXTINCTION RATES

Most estimates of impending extinction rates are derived from broad species-area relations. These relations (MacArthur & Wilson, 1967), which have some basic theoretical underpinning (May 1975), suggest that, within real or virtual archipelagos of islands, the number of species, S, in a given taxonomic group found on an island of area A will obey the power law $S = cA^z$. Here the exponent z lies in the range 0.2–0.3, and the constant, c, depends on the taxonomic group in question. It follows that a small fractional reduction in area, ΔA, will eventually result in a corresponding reduction in numbers of species, ΔS, given by $\Delta S \approx z\Delta A$. To this empirical relation, one now adds the observation that 1–2% of all tropical forests are being destroyed each year, to arrive at a global species extinction rate of very roughly $\frac{1}{2}$–$\frac{1}{4}$% each year. On this basis, compounded annually, half of the world's species will become extinct within the next 100–300 years. This is the estimate from which widely quoted figures for daily extinction rates are obtained.

It would be nice to have better estimate. As recently summarized by Smith *et al.* (1993), the data compiled by the World Conservation Monitoring Centre (WCMC) tell us more about the different attention given to different groups – the taxonomy of taxonomists discussed above – than about global extinction rates themselves. The strict criteria needed for certified extinction have been satisfied only by some 485 animal (229 vertebrate) and 584 plant species since around the year 1600. Many more vertebrates are surely extinct, but have not yet been so certified (Diamond 1989). For invertebrates, we are simply ignorant. WCMC databases show only 0.07% of insects in the categories 'endangered' (E) or 'vulnerable' (V) (as defined by the International Union for the Conservation of Nature; see Smith *et al.* 1993). But for the better-studied insects and other invertebrate fauna of Britain, 1% have gone extinct this century, and 7% are E or V. Globally, 11% of bird species and 11% of mammal species are in the categories E and V, as are 9% of the world's species of angiosperms and 32% of gymnosperms. Thus the status of threat to well-studied invertebrate groups seems similar to plants and vertebrates, in notable contrast to invertebrates more generally. Most marine species are akin to terrestrial invertebrates; if anything, we know even less about their rates of impending extinction.

Focusing on better-studied groups, namely birds and mammals among animals, and palms among plants, Smith *et al.* (1993) venture a very crude estimate of future extinction rates, based on the average rate at which species in these groups have climbed the ladder of threat category (from unthreatened, to V, to E, to 'probably extinct', to extinct) in recent years. On this extremely rough basis, half of all bird and mammal species will be extinguished within the next 100–300 years, and half the world's palm species within the next 50–100 years. These crude estimates are in surprising agreement with the equally crude species–area ones, although the two kinds of estimate have no elements in common.

The WCMC databases have essentially no information about most marine species. It does seem, however, that the closer one is to the shore – and, on a larger scale, the closer to the continental shelf – the richer the assembly of species. But the coastal margins are characteristically the places where human impacts, in the shape either of direct exploitation or of pollution (broadly interpreted), is greatest. There is thus a rough parallel between coastal regions and tropical forests: these kinds of systems are arguably the most species rich, and also the most under threat, in the sea and on land, respectively.

Although it seems likely that increasing human impacts in the sea, especially in coastal regions, will have effects, as yet there are not even enough data for a species–area kind of estimate of marine extinction rates. Such ignorance may be one of the most significant differences between our understanding of biological diversity on land versus in the sea. Byron summarized one, still prevalent, view: 'Man marks the earth with ruin, his control stops with the shore.' I think this is too optimistic.

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Discussion

J. Godfrey (*41 Lawford Road, London, U.K.*). May I suggest a possible answer to Professor May's puzzle about why tropical rain forests share with coral reefs a large number of species, but whereas individuals seem rare in the forests, they are obviously abundant on the reefs? Only the coral reefs have manna from heaven. The plankton passing through a coral reef is almost infinite. Aerial plankton makes a negligible contribution to the nutrition for inhabitants of tropical rain forests, although it is important to the life of glaciers. The nutrients passing through should help individuals to breed and grow.