The future of biological diversity in a crowded world*

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Scientific advances over the past century have led to improvements in most peoples' lives, in both developed and developing worlds. But increasingly we recognize that many of these benefits have not been produced in a sustainable way, particularly as human populations continue to grow and the diversity and abundance of many other species diminishes. What happens to our world, and to us and the creatures we share the world with, in the future depends on the actions we take now.

HOW well do we know the world of plants, animals and micro-organisms with which we share this planet? The answer, by any one of a variety of objective measures, must be: not very well. First, estimates of the number of species that have been named and recorded (a simple factual question, like how many books in the library catalogue?) range from 1.4 to 1.8 million. Second, estimates of the total number of species present on earth today range over more than an order-of-magnitude, from a low of around 3 million to a high of 30 million or possibly much more. And third, we have even less idea of the rates at which species may currently be going extinct, as a result of habitat destruction and other consequences of human population growth.

In this brief overview, I outline my own best guess of the answers to these three questions. For the number of distinct species named and recorded, I emphasize the uncertainties caused by unresolved synonymies. For the likely total number of living species, I set out my reasons for leaning to the lower end of the range of published estimates. And for present and likely future extinctions, I sketch a relatively precise approach, based on comparative rates of extinction, which avoids some of the imprecisions inherent in dealing with the total number of species. I end by discussing estimates of the costs of effective action, and more generally why we should care.

How many species are there?

The systematic naming and recording of species began relatively recently, with Linneaus' standard work which in 1758 recognized some 9000 species. Today the total number of living species named and recorded has been estimated at around 1.7 to 1.8 million. Amazingly, no centralized catalogue exists. There are synoptic and computerized catalogues for some better-known groups, most notably birds and mammals. But more than half (roughly 56%) of all named species are insects, and the majority of these are still on card catalogues in individual museums and other collections. By one estimate, around 40% of all named beetle species are known from only one site, and many from only one specimen. In short, the amount of taxonomic effort varies very widely from group to group, with roughly one-third of all taxonomists working on vertebrates, another third working on the ten times more numerous plant species, and the remaining third working on invertebrate animals, which outnumber vertebrate species by at least a factor of 100 (see Table 1). It should be emphasized that this maldistribution reflects the vagaries of intellectual fashion, and most certainly does not reflect the relative importance of, say, vertebrates versus invertebrates in maintaining the structure and function of ecosystems. Reorganizing our priorities

Table 1. Taxonomy of taxonomists: A rough estimate of the distribution of the taxonomic workforce among broad taxonomic groups in Australia, USA and UK (after Gaston and May[23])

		Animal			
	Plants	Vertebrates	Invertebrates	Micro-organisms	Fossils
Approximate division of workforce (%)	30	25	35	2–3	5
Estimated total number of living species (thousands)	300	45	3000 +	?	–

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*Based on a lecture delivered at the Indian Institute of Science, Bangalore on 1 February 2002.

rapidly, to learn more about the little things that arguably run a lot of the natural world, will not be easy. Fascination with the furries and featheries goes deep: in the UK, the Royal Society for the Protection of Birds (RSPB) has almost 1 million members; the analogous society for plants (the Botanical Society of the British Isles) has around 10,000; and there is no corresponding society to express affection for nematodes.

In what follows, I will restrict attention to eukaryotic species – essentially animals, plants and fungi (broadly defined). A molecular biologist could justifiably argue that these eukaryotic species represent only a recently diversified tip of an evolutionary tree whose main flowering is among bacteria and archaea. But what is meant by species among bacteria and the like is vastly different from what is meant among plants and animals (see, for example, refs 1 and 2). For instance, different strains of what is currently classified as a single bacterial species, *Legionella pneumophila*, have nucleotide-sequence homologies (as revealed by DNA hybridization) of less than 50%; this is as large as the characteristic genetic distance between mammals and fishes. Relatively easy exchange of genetic material among different 'species' of such microorganisms means, I think, that basic notions about what constitutes a species are necessarily different between animals and bacteria. This holds even more strongly for viral species, many of which are best regarded as 'quasispecies swarms'[3].

Numbers of named species

A recent major assessment, for the International Union for the Conservation of Nature (IUCN)[4], of the total number of distinct species that have been named and recorded emphasizes the uncertainties caused by synonyms. This survey estimates that around 13,000 new species are currently named each year, but current rates of resolving synonymies – the same species inadvertently given different names by different people in different collections – reduce this number to around 10,000 distinct new species added yearly to the known total. In effect, this corresponds to a synonymy rate of around 20% in named species, a figure elsewhere cited as representative on more direct grounds[5]. Of course, any such assessment of known synonymy rates must be a lower limit, with other synonyms yet to be uncovered or accumulating in new work. Solow *et al.*[5] have made a start on this important problem, suggesting the true synonymy rate may be more like 40%.

Allowing for all this, my recent assessment[6] is that the current global total of distinct eukaryotic species (broadly, plants, animals and fungi) that have been named and recorded is around 1.5 million. This is lower than Hammond's[4] 1.74 million, but is consistent with Wilson's[7] estimate of 1.4 million roughly ten years ago (augmented by 0.01 million each year for roughly 10 years; see Table 2).

Total number of species living today

So much for named and recorded species of eukaryotes. However, as Lewis Carroll's Gnat responded to Alice's remark that it is useful to people to give names to insects: 'further on, in the wood down there, they've got no names'. The true total of extant species, as distinct from those we have named and recorded, is hugely uncertain. My recent assessment of the evidence and uncertainties led to a guess of around 7 million in total, with a plausible range of 5 to 15 million[6]. This is lower than Hammond's[4] guess of 12 million eukaryotic species, but higher than other estimates which are as low as 3 million or so species in total. Estimates as low as 3 million, or as high as 100 million or more, can be defended (see Table 3).

All such estimates are dominated by insect totals. And the way such estimates are made provides eloquent testimony to the deep connection between taxonomy and systematics on the one hand, and fundamental questions in ecology and evolution on the other. By way of illustration, I sketch just three examples of such intertwining.

Suppose we really understood how the working of the evolutionary play, in varied ecological theaters, has shaped food webs. We would then, for example, understand some of the observed patterns, such as the ubiquitous rule that the number of links in food chains connecting eater to eaten (plant to herbivore; herbivore to carnivore; carnivore to top predator, etc.) rarely exceeds four, regardless of the productivity of the environment or whether the constituent animals are warm or cold-blooded (with very different efficiencies of energy transfer from

Table 2. Number of named, distinct species of eukaryotes (in thousand).

Group	Hammond[4]	May[6]
Protozoa	40	40
Algae	40	40
Plants	270	270
Fungi	70	70
Animals	1320	1080
Vertebrates	45	45
Nematodes	25	15
Molluscs	70	70
Arthropods	1085	855
Crustaceans	40	40
Arachnids	75	75
Insects	950	720
Others	20	20
Others	95	95
Total	1740	1500

one level to the next). If we had such understanding, we could derive from it a rough, overall average ratio of numbers of animal species (secondary consumers) to plant species (primary producers). And, given that we know the total number of plant species, fairly reliably, to be of the general order of 300,000, we could thus assess the rough total number of animal species. Sadly – some would say incredibly – we do not have this ecological understanding. We have a few scattered studies in large and small food webs (although even here, such empirical knowledge is vastly less than it should be), which broadly suggest ten animal species per plant species on average. So, on this empirical basis, but lacking any fundamental understanding, we might guess at something of the order of 3 million animal species in total.

The line of attack which I favour has been elaborated by Gaston and Hudson[8]. They first ask what fractions of the species, in particular, taxa are found in each of nine biogeographic realms? (These nine representing a slight extension of the conventional Wallace scheme). The reference taxa range from general categories (such as higher plants, amphibians, birds and mammals) to very particular ones (such as dragonflies, tiger beetles and swallowtails). Gaston and Hudson then take a range of estimated total number of insect species in the Nearctic realm (i.e. North America) and in Australia, and scale them up to global totals on these biogeographic bases. For example, given that Nearctic higher plants represent 6.5% of the global total, an estimated total 200,000 Nearctic insect species would imply around 3 million species. For their fairly wide range of estimators, Gaston and Hudson arrive at global insect totals in the range of 1–10 million. And, looking at this range in a bit more detail, my best guess would be 4 million. This estimate also accords with Terry Erwin's (personal commun.) recent estimate that preliminary keying-out of some of his tropical-canopy beetle collection suggests around 80% of the species are new (which, multiplying total number of the insects in Table 2 by 5, also gives around 4 million).

Yet another approach is to look at empirical patterns in the number of species in different categories of physical size, which, for animals of characteristic length above about 0.5 cm, suggest a roughly 100-fold increase in species numbers for each 10-fold decrease in characteristic length. Extending this down to sub-millimeter size categories, where our current taxonomic knowledge is so deficient, would imply a global total of something like 3–10 million species. The problem, yet again, is that we are utterly ignorant of the ecological and evolutionary forces that underpin these interesting but empirical species-size patterns. Such ignorance simultaneously undermines the above estimate, and highlights the interconnection between ecological/evolutionary questions and basic taxonomic facts/ignorance. For a more full discussion, see May[6,9].

Extinction rates

The past

The history of life on earth, written in the fossil record over the past 600 million years (my) since the Cambrian explosion in the diversity of multicellular organisms, is one of broadly increasing diversity, albeit with many fluctuations and punctuated by episodes of mass extinction (see Figure 1). As reviewed in more detail else-

Table 3. Estimated total number of living species (in thousand).

Group	Hammond[4] High – low	Hammond[4] Working figure	May[6]
Protozoa	200 – 60	200	100
Algae	1000 – 150	400	300
Plants	500 – 300	320	320
Fungi	2700 – 200	1500	500
Animals	100,000 – 3000	9800	5570
Vertebrates	55 – 50	50	50
Nematodes	1000 – 100	400	500
Molluscs	200 – 100	200	120
Arthropods	1000,000 – 2400	8900	4650
Crustaceans	200 – 75	150	150
Arachnids	1000 – 300	750	500
Insects	100,000 – 2000	8000	4000
Others	800 – 200	250	250
Total	100,000 – 3500	12,200	6800

Range: 100 – 3 million; Plausible range: 15 – 5 million; Best guess: 7 million.

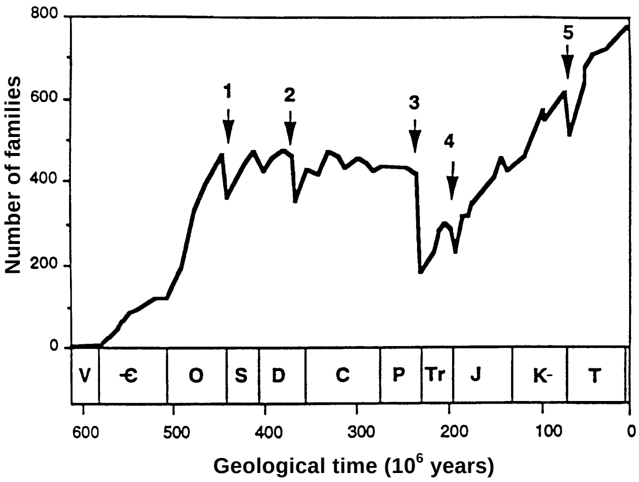

Figure 1. History of the diversity of marine animal families, as shown by the fossil record over time. The curve connects 77 discrete data points, each giving the total number of well-skeletonized families from a particular stratigraphic stage. Arrows indicate the Big Five episodes of mass extinction. Length of the various geological epochs is indicated on the time axis (V, Vendian; Є, Cambrian; O, Ordovician; S, Silurian; D, Devonian; C, Carboniferous; P, Permian; Tr, Triassic; J, Jurassic; K-, Cretaceous; T, Tertiary).

where[6,10], the average lifespan of a species in the fossil record, from origination to extinction, is typically a few million years (that is, of the order 10^6 to 10^7 years); there is, however, much variation both within and among groups, and some groups have lifespans significantly longer or shorter than this (see Table 4). Comparing this few million year average lifespan with the 600 my fossil record span, we might estimate that 1–2% of all species ever to have lived are with us today. But, allowing for the fluctuating but steady – very roughly linear – average growth in species diversity since the Cambrian, a better estimate might be 2–4%. And if we recognize that most of today's species are terrestrial invertebrates (mainly insects), whose patterns of diversification began around 450 my ago and whose average lifespan may be characteristically longer than 10 my, it could be that today's species represent more like 5%, or conceivably even 10%, of those ever to have graced our planet.

Current extinction rates

Our ignorance about total number of insect and other invertebrate species is nothing compared with our ignorance about current extinction rates among them. Over

Table 4. Estimated lifespans, from origination to extinction, of various taxa in the fossil record (measured in millions of years). The first part of the table is after May *et al.*[15], whereas the second part is a new compilation by Robin Cocks (Natural History Museum, London)

Taxon	Date of estimate	Average lifespan (millions of years)
Part I: References in May *et al.*[15]		
All invertebrates	Raup (1978)	11
Marine invertebrates	Valentine (1970)	5–10
Marine animals	Raup (1991)	4
Marine animals	Sepkoski (1992)	5
All fossil groups	Simpson (1952)	0.5–5
Mammals	Martin (1993)	1
Cenzoic mammals	Raup and Stanley (1978)	1–2
Diatoms	Van Valen (1973)	8
Dinoflagellates	Van Valen (1973)	13
Planktinic foraminifers	Van Valen (1973)	7
Cenozoic bivalves	Raup and Stanley (1978)	10
Echinoderms	Durham (1970)	6
Silurian graptolites	Rickards (1977)	2
		6–7
Part II: Information compiled by Robin Cocks		
Silurian graptolites	Koren and Rickards (1996)	0.2
Cambrian trilobites	Davidek *et al.* in press	0.4
Brachiopods	R. Cocks, pers. commun.	0.5
Rodents	R. Cocks, pers. commun.	0.3–1.0
Perrissodactyls	R. Cocks, pers. commun.	0.5
Insectivores	J. J. Hooker, pers. commun.	3.0
Corals (Tertiary-Recent)	Budd *et al.* (1996)	0.2–7 (average 4)
Forams	Buzas and Culver (1984)	14–16
Coccoliths	J. R. Young, pers. commun.	c.10

the past century, rigorously documented extinctions in well-studied groups – primarily birds and mammals – have run around one species each year. Even for these groups, such certified extinctions are surely underestimates. Diamond[11], for instance, found that of 164 recorded bird species in the Solomon Islands, 12 had apparently not been seen since 1953 (nor could he find them), yet only one had a IUCN extinction certificate. This stimulated interesting further work – no fun like scoring off a friend – which found seven of the putatively extinct 12. But five almost certainly are gone, representing a 5-fold IUCN underestimate in this instance. More striking is Mohsin and Ambok's[12] four-year search for the 266 species of exclusively freshwater fishes recorded in the 19th century in lowland peninsular Malaysia, which found only 122; many of these are surely extinct, yet none show in the IUCN catalogue. And the IUCN extinctions for insects tell only of intellectual fashion, and nothing of real extinctions: of 73 recorded extinct, 43 are Hawaiian *Drosophila*; only 8 are mainland insects (7 from USA, 1 from Germany); not one is a tropical insect.

The essential problem is our lack of systematic knowledge. Reviewing Terborgh's *Requiem for Nature*[13], McKibben[14] has written: 'You can follow the changes in the value of the Japanese yen second by second from your desktop; reporters by the dozen struggle valiantly to explain the particulars of Microsoft's antitrust defense. But who can tell whether the tropical forest is disappearing more or less speedily than it was in the late 1980s when every singer worth her faded jeans was cutting a CD in its defense? This question is surely worth attention, since the equatorial jungles contain more examples of creation's fabulous imagination than any other ecosystem, and since its trees are a key part of the earth's system for cleansing excess carbon dioxide from the atmosphere. Perhaps you have a dim sense that some agreements have been signed to protect the rainforests, some programs put in place. But are they working? What strategies make the most sense to preserve what's left? Far more money and attention is devoted to, say, searching for and describing the possible remains of microbial life in the dust of Mars.'

Given that we do not know today's total numbers of species to within a factor ten or so, and that we know even less about number of extinctions, anyone who purports to tell you how many species went extinct last year is a fool. But that does not mean we cannot say some relatively precise things.

Comparing past with present extinction rates

We have just noted that among the relatively well-studied bird and mammal species there has been roughly one extinction per year over the past century, and that this estimate is very conservative. There are a total of around 14,000 such species. So the typical bird or mammal species has, in effect, in recent years been playing a game of Russian Roulette with a single bullet in a gun of 14,000 chambers. This translates into an average expected species lifetime, before extinction, of around 10^4 years at current rates, if birds and mammals are typical (which, of course, they might not be). Ten thousand years may sound a long time, but it is shorter by a factor of order 10^{-2} to 10^{-3} than the background average lifespan of 10^6 to 10^7 years seen in the fossil record. That is, recent extinction rates in well-documented groups have run one hundred to one thousand times faster than the average background rates.

Looking toward the immediate future, four different approaches to estimating impending rates of extinction suggest species' life expectancies of around a few hundred to one thousand years. One of these approaches is based on ecological species – area relations, coupled with assessments of current rates of tropical deforestation or other habitat loss (if tropical forests are being lost at the rate of 1–2% each year, the species–area relation suggests this commits 0.25 – 0.5% of their species to extinction, which inverts to a rough estimate of species' lifetimes of roughly 200–400 years). Two other methods are based in different ways on the IUCN's current catalogue of 'endangered' or 'vulnerable' species. As reviewed elsewhere[15], one of these estimates the average rate at which species in better-studied groups (birds, mammals, palm trees) are climbing the ladder of IUCN categories of endangerment; this suggests expected species' lifetimes in the range 100 to 800 years in these groups. A more precise variant of this approach uses species-by-species assessments of extinction probability distributions as a function of time. Using ten vertebrate groups (3, 4, 3 orders or families of reptiles, birds and mammals respectively), Mace[16] estimates average species' lifetimes in the range 100 to 1000 years, and mainly in the 300 to 400 year range for mammals and birds. The fourth method uses models for branching processes in phylogenetic trees, along with recent data for bird and mammal orders, to project average times to extinction within bird and mammal orders[17]. Under a range of assumptions about branching processes, these models suggest species' lifetimes again of the order of a few hundred years (characteristically shorter for mammals than birds). Thus all four of these methods, each of which is unreliable in its own distinctive way, agree in suggesting a further shortening of expected species' lifetimes, to around 10^2 to 10^3 years.

Such figures correspond to likely extinction rates of a factor of ten thousand, give or take at most an order of magnitude, above background, over the next century or so. This represents a sixth great wave of extinction, fully comparable with the Big Five mass extinctions of the geological past, but different in that it results from the activities of a single other species rather than from external environmental changes.

As we face this future, we must ask: Does it matter more if we lose 25% of all mammal species than if we lose 25% of the vastly more numerous insect species? Or does it matter equally? Or less? There is need not only for more taxonomic information, but also for a 'calculus of biodiversity' based on this information. Such a calculus should, ideally, quantify the taxonomic uniqueness, or amount of independent evolutionary history, inherent in individual species[18,19]. I would like to see such quantification, along with more explicit recognition of constraining political, economic and social realities, replace emotion in assigning conservation priorities and places on the Ark (although emotional elements should, certainly, also be part of such a quantification). For further review and remarks on this topic, see May *et al.*[15].

Costs and concerns

The causes of extinction are many and varied. Immediate causes can be overexploitation, habitat destruction, introduced alien species, and commonly combinations of two or all three of these. The ultimate cause, of course, is still-expanding human populations, currently sequestering to our own use somewhere between one quarter to one half of all terrestrial primary productivity – an event no other species has approached in the history of life on earth. Against this background, currently about 6.3% of the earth's land area is set aside as wildlife refuges or other protected areas of one kind or another, at an estimated annual cost of around £ 6 billion per year[20].

James *et al.*[20] estimate that it would cost around £ 30 billion per year to expand this to 10% of the terrestrial surface, properly protected and with compensation to indigenous peoples. Some of this area is envisioned as wilderness, but much as sustainably used by people with sympathetic regard to their environment. More ambitious and yet more speculative, the authors suggest that the 'greening' of agriculture – a Doubly Green or Evergreen Revolution – would cost around £300 billion per year, creating a world less in tension between 'refuges' and 'agribusiness'. By now, the sums seem vast. Viewed in perspective, however, this ambitious figure is only 1% of global GDP. And this conventionally calculated GDP takes no account of the ecosystem services which built the biosphere and continue to keep it a place where life can flourish (pollinating plants; cleaning waters; absorbing or balancing greenhouse gases; breeding fish in estuaries; and endlessly on). Recent and necessarily rough estimates put the value of such services as comparable with conventional GDP, at around £ 30 trillion per year[21].

It seems to me that investing 1% of global GDP to ensure the continuing delivery of such ecosystem services (themselves of magnitude comparable to such GDP) is wise. But the problem – a deep and intractable one – is that we have no evolutionary experience of asking people to act, at inconvenience to many, on behalf of a seemingly distant future and for the general good.

And anyway, some will say, do we really need today's biodiversity to ensure tomorrow's ecosystem services? More generally, why should we care about preserving biological diversity. I would list the reasons for caring under three broad headings, which might be called narrowly utilitarian, broadly utilitarian, and ethical.

A narrowly utilitarian argument

One argument for the preservation of biological diversity is narrowly utilitarian. It correctly emphasizes the benefits already derived from natural products, as foods, medicines, and so on. Currently, 25% of the drugs on the shelves in the pharmacy derive from a mere 120 species of plants. But, throughout the world, the traditional medicines of native peoples make use of around 25,000 species of plants (about 10% of the total number of plant species); we have much to learn. More generally, as our understanding of the natural world advances, both at the level of new species and at the level of the molecular machinery from which all organisms are self-assembled, the planet's genetic diversity is increasingly the raw stuff from which our future can be constructed. It seems a pity to be burning the books before we can read them, and before we can create wealth from the recipes on their pages.

A broadly utilitarian argument

Another class of arguments is more diffusely utilitarian. The interactions between biological and physical processes created and maintain the earth's biosphere as a place where life can flourish. With impending changes in climate caused by the increasing scale of human activity, we should be worried about reductions in biological diversity, at least until we understand its role in maintaining the planet's life-support systems. The first rule of intelligent tinkering is to keep all the pieces.

An ethical argument

For me, however, a third class of argument is the most compelling. It is clearly set out by the UK Government in *This Common Inheritance*[22]. It is 'the ethical imperative of stewardship . . . we have a moral duty to look after our planet and hand it on in good order to future generations'.

The problem, however, is that no one of these three arguments is necessarily compelling. First, it seems likely to me that tomorrow's Biotechnological Revolution will design its new medicines, new materials, and other new products from the molecules up, based on our increasing understanding of the molecular machinery of life. Second, I fear that we may be clever enough to create a world that is grievously biologically impoverished, but nevertheless sustainable – the hateful world of the cult movie *Blade-runner*. And although I find the third, ethical argument totally compelling, I wonder what force it would have if I were dirt poor, struggling to feed my children. These are uncomfortable admissions.

Conclusion

The previous century has seen more advance in our understanding of the natural world than has all previous human history. We have applied this scientific understanding to improve lives, in both developed and developing countries. We are, however, now beginning to realize some of the unintended adverse consequences of well-intentioned actions: arguably the most significant is the accelerating loss of biological diversity. What happens to our world, and to us and the creatures we share the world with, in the future depends on the actions we take now. As a new century dawns, our greatest challenge remains to ensure that necessary increases in global productivity are achieved in a sustainable and environmentally friendly way.

For most who share the beliefs set out in the previous sentence, the motives come from the heart, from beliefs and values. But the actions, to be effective, need to come from the head, to be coldly analytic. There are tensions here. Too much conservation action is directed to the targets the heart engages – furries and featheries. Table 1 shows taxonomic effort improperly skewed to vertebrates, but the academic conservation literature is worse: one recent count gives 60% papers on vertebrates, 20% on plants, 10% on invertebrates, and 10% not amenable to such classification. And conservation action is worse again, being almost exclusively focused on 'charismatic megafauna', big mammals and attractive birds. We need the motives from the heart, but the analytic actions from the head. Writing of the icy analysis the great Indian author V. S. Naipaul brings to bear on the world's problems, Anita Desai has said he inhabits a space 'beyond regret or hope'. We need something even more difficult: deep regret and powerful hope for heartfelt motivation, but ecological and environmental understanding, beyond regret or hope, to guide effective action. No easy trick.

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Received and accepted 2 May 2002

Balancing the approaches of environmental conservation by considering ecosystem services as well as biodiversity

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In recent years, most plans for conservation have focused on biodiversity, ignoring the importance of the ecosystem services. This paper discusses limitations of the biodiversity-centred approach to conservation and reasons why ecosystem services need to be included to provide a balanced approach to conservation. To achieve this objective, there is need to improve the identification and valuation of ecosystem services. By focusing on biodiversity conservation, we may ignore many areas that are not rich in biodiversity but are important to human welfare and are under the threat of environmental degradation.

RECENT initiatives of environmental conservation, particularly in tropical parts of the world, are unduly oriented towards biodiversity, ignoring ecosystem services, though conserving biodiversity is often justified on the ground that it contributes to ecosystem services[1]. Recent exercises on the prioritization of creatures and places deserving most attention for conservation, and on developing national biodiversity conservation plans in several Asian countries, may further increase this imbalance. These also include India's National Biodiversity Strategy and Action Plan (NBSAP), regarded as one of the greatest exercises on conservation ever taken place in the developing world. Because conservation is tightly connected with funding, attempts are being made to find ways to reduce costs and maximize benefits of biodiversity conservation. For example, Myers *et al.*[2] argue that by protecting 25 top hot spots, comprising only 1.4% of the earth's surface, 44% of all plant species and 35% of vertebrate species worldwide can be saved. It is important to develop strategies to conserve as high a proportion of the species on the planet as possible, but a balanced approach of conservation should also consider other environmental issues such as carbon sequestration, waste dissipation, the hydrological balance, soil formation, health of local ecosystems, and others not intimately connected with biodiversity.

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