

Getting the measure of biodiversity

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The term 'biodiversity' is a simple contraction of 'biological diversity', and at first sight the concept is simple too: biodiversity is the sum total of all biotic variation from the level of genes to ecosystems. The challenge comes in measuring such a broad concept in ways that are useful. We show that, although biodiversity can never be fully captured by a single number, study of particular facets has led to rapid, exciting and sometimes alarming discoveries. Phylogenetic and temporal analyses are shedding light on the ecological and evolutionary processes that have shaped current biodiversity. There is no doubt that humans are now destroying this diversity at an alarming rate. A vital question now being tackled is how badly this loss affects ecosystem functioning. Although current research efforts are impressive, they are tiny in comparison to the amount of unknown diversity and the urgency and importance of the task.

To proceed very far with the study of biodiversity, we need to pin the concept down. We cannot even begin to look at how biodiversity is distributed, or how fast it is disappearing, unless we can put units on it. However, any attempt to measure biodiversity quickly runs into the problem that it is a fundamentally multidimensional concept: it cannot be reduced sensibly to a single number^{1,2}. A simple illustration can show this. Figure 1 shows samples from the insect fauna in each of two habitats. Which sample is more diverse? At first sight it must be sample A, because it contains three species to sample B's two. But sample B is more diverse in that there is less chance in sample B that two randomly chosen individuals will be of the same species. Neither of these measures of diversity is 'wrong' — species richness and evenness are two (among many) of biodiversity's facets,

and no single number can incorporate them both without loss of information. This should not be disappointing; indeed we should probably be relieved that the variety of life cannot be expressed along a single dimension. Rather, different facets of biodiversity can each be quantified (Box 1).

Knowing the diversity (however measured) of one place, group or time is in itself more-or-less useless. But, as we shall discuss later, comparable measurements of diversity from multiple places, groups or times can help us to answer crucial questions about how the diversity arose and how we might best act to maintain it. We shall see also how the usefulness of the answers depends critically on the selection of an appropriate diversity measure. No single measure will always be appropriate (indeed, for some conservation questions, no single measure can probably ever be appropriate). The choice of a good measure is complicated by the frequent

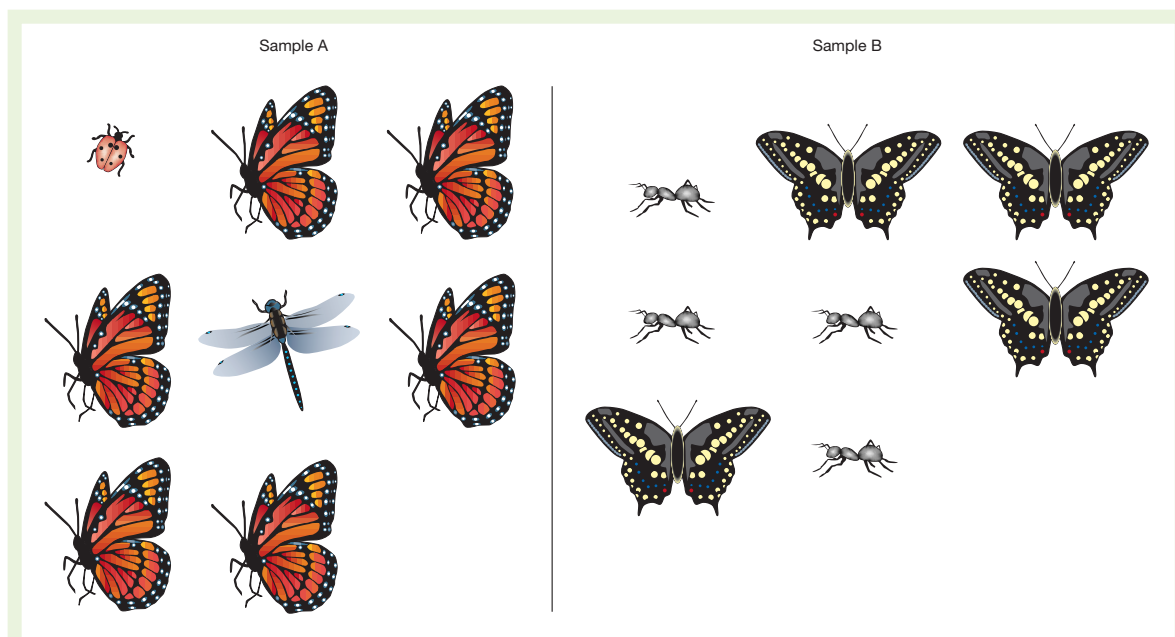


Figure 1 Two samples of insects from different locations, illustrating two of the many different measures of diversity: species richness and species evenness. Sample A could be described as being the more diverse as it contains three species to sample B's two. But there is less chance in sample B than in sample A that two randomly chosen individuals will be of the same species.

Box 1

Parts of the whole: numbers, evenness and difference

Biodiversity has a multitude of facets that can be quantified. Here we classify some commonly used measures into three conceptually different (although not orthogonal) approaches.

Numbers

The most commonly considered facet of biodiversity is species richness — the number of species in a site, habitat or clade. Species are an obvious choice of unit when trying to measure diversity. Most people have an idea what 'species' means and, although their ideas differ considerably (reviewed in ref. 96), there is even less commonality about other levels in the taxonomic hierarchy³⁰ (Fig. 3). Many other measures are less intuitive, and have arisen only through appreciation of limitations of measures of species richness. Species are also sensible units to choose from a biological perspective: they keep their genes more or less to themselves, and to that extent have independent evolutionary trajectories and unique histories. The current 'best guess'¹⁷ is that there are around 14 million species, but this is very much a provisional working figure. Regions with many species, especially endemic species, are sometimes called hotspots⁹⁷.

Species and regions differ in their number of populations. Populations of a given species, if defined on the basis of limited gene flow among them, will evolve to an extent independently. Each population contributes additional diversity. The number of genetic populations in the world has been estimated to lie between 1.1 and 6.6 billion⁶⁶.

Species or populations differ in the numbers of alleles they have at given loci. For instance, Mauritius kestrels (*Falco punctatus*) have lost over half of the alleles present historically at 12 sampled microsatellite loci⁹⁸.

Moving above the species level, higher-taxon richness is often used in studies of biodiversity, usually as a less data-demanding surrogate for species richness⁹⁹.

Evenness

A site containing a thousand species might not seem particularly diverse if 99.9% of individuals that you find belong in the same species. Many diversity indices have been developed to convey the extent to which individuals are distributed evenly among species². Most but not all combine evenness with species richness, losing information by reducing two dimensions to one. There are genetic analogues of these indices¹⁰⁰, such as heterozygosity, that incorporate both allele number and relative frequencies.

Difference

Some pairs of species (or alleles or populations) are very alike, whereas others are very different. Disparity¹⁰¹ and character diversity⁹³ are measures of phenotypic difference among the species in a sample, and can be made independent of species number. Some phenotypic characteristics might be considered more important than others, for instance the ecological diversity among species may be crucial for ecosystem functioning. Genetic variability among populations can also be measured in various ways¹⁰⁰. If populations within species differ enough either genetically or phenotypically, they may be considered to be subspecies, management units or evolutionarily significant units¹⁰²; numbers of these therefore provide estimates of difference. All these kinds of difference are likely to be at least partly reflected by the phylogenetic diversity¹⁰³ among organisms, which is estimated as the sum total of the branch lengths in the phylogeny (evolutionary tree) linking them.

Sample in different places, and you will find different things. This spatial turnover itself has many facets² (for example, beta diversity, gamma diversity and numbers of habitat types), and important consequences for any attempt to conserve overall diversity (see review by Margules and Pressey, pages 243–253, and refs 104, 105). Likewise, temporal turnover¹⁰⁶ is the extent to which what is found changes over time.

need to use surrogates for the aspect in which we are most interested^{3,4}. Surrogacy is a pragmatic response to the frightening ignorance about what is out there. Some recent discoveries highlight just how much we probably still do not know.

The growing biosphere

Technological advances and the sense of urgency imparted by the rate of habitat loss are combining to yield discoveries at an incredible rate. This may seem surprising, given that expedition accounts of natural historians from the 18th and 19th centuries conjure up images of discovery on a grand scale that seemingly cannot be matched today — look in the rocks ... a new fossil mammal; look in the lake ... a new fish genus; look on the dinner plate ... a new species of bird. Finding new large vertebrates nowadays is indeed newsworthy, but a new species of large mammal is still discovered roughly every three years⁵ and a new large vertebrate from the open ocean every five years⁶. And most organisms are much smaller than these are. An average day sees the formal description of around 300 new species across the whole range of life, and there is no slowdown in sight. Based on rates of discovery and geographical scaling-up, it seems that the roughly 1.75 million described species of organism may be only around 10% of the total⁷.

It is not only new species that are discovered. Cycliophora and Loricifera are animal phyla (the level just below kingdom in the taxonomic hierarchy) that are new to science in the past 20 years⁸. Within the Archaea, the discovery of new phylum-level groups proceeds at the rate of more than one a month⁹. The physical limits of the biosphere have been pushed back by the recent discovery of microbial communities in sedimentary and even igneous rocks over 2 km

below the surface; these subsurface lithoautotrophic microbial ecosystems (termed SLiMEs) may have persisted for millions of years without any carbon from the surface¹⁰. Controversy surrounds another proposed discovery: whether or not the 100-nm-diameter nanobacteria found in, among other places, kidney stones are living organisms¹¹. At an even smaller scale, genomes provide fossils that indicate great past retroviral diversity¹². Genomes have also been found to provide habitats for many kinds of genetic entity — transposable elements — that can move around and replicate themselves. Such elements can provide important genetic variation to their hosts, can make up more than half of the host's genome¹³, and have life histories of their own¹⁴.

There are two other ways in which the biosphere can perhaps be said to be growing. The first is that the rate at which taxonomists split one previously recognized species into two or more exceeds the rate at which they lump different species together, especially in taxa that are of particular concern to conservationists (for example, platyrrhine primates¹⁵). Part of the reason is the growing popularity of one way of delimiting species — the phylogenetic species concept (PSC)¹⁶ — under which taxa are separate species if they can be diagnosed as distinct, whether on the basis of phenotype or genotype. If the PSC becomes widely applied — which is a controversial issue¹⁷ — then the numbers of 'species' in many groups are sure to increase greatly¹⁸ (although the amount of disparity will barely increase at all).

A second way in which the catalogue of diversity is growing is that computer databases and the Internet are making the process of information gathering more truly cumulative than perhaps ever before. Some existing sites serve to provide examples of the information already available: not just species lists (<http://www.sp2000.org/>), but

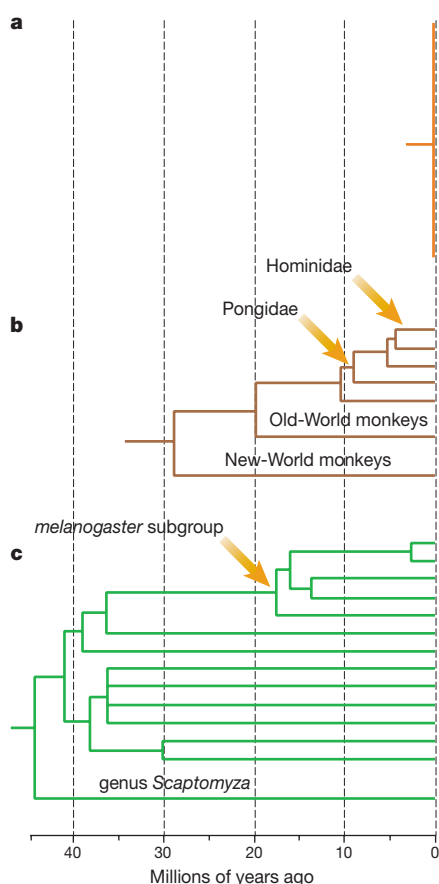


Figure 2 Taxonomic boundaries are not comparable among major groups. **a**, Fourteen species in nine genera representative of cichlid fish in Lake Victoria. **b**, Seven species representative of several families in anthropoid primates. **c**, Thirteen species representative of a single genus, *Drosophila*. Figure reproduced from ref 30, with permission.

also maps of the geographical ranges of species (<http://www.gisbau.uniroma1.it/amd/homepage.html>), information on conservation status of species (<http://www.wcmc.org.uk>), bibliographies (http://etweb.lscf.ucsb.edu/bfv/bfv_form.html), data on molecular sequence (<http://www.ebi.ac.uk/> and <http://www.ncbi.nlm.nih.gov/Genbank/GenbankOverview.html>), data on phylogenetic position (<http://phylogeny.arizona.edu/tree/phylogeny.html> and <http://herbaria.harvard.edu/treebase/>), information on the stratigraphic range of species (<http://ibs.uel.ac.uk/ibs/palaeo/benton/> and <http://www.nceas.ucsb.edu/~alroy/nafmtd.html>) and much more. Although the terabytes of information already stored constitute only a small drop in the ocean, the next two sections show how much can be seen in that droplet about the distribution of biodiversity among evolutionary lineages and through time.

Learning from the tree of life

The ongoing explosion of phylogenetic studies not only provides an ever-clearer snapshot of biodiversity today, but also allows us to make inferences about how the diversity has come about^{19–21}. (For an ecological perspective, see review by Gaston, pages 220–227.) Phylogenies give key information that is not available from species lists or taxonomies. They detail the pattern of nested relationships among species, and increasingly provide at least a rough timescale even without reliance on a molecular clock²². These new phylogenies are pushing back the origins of many groups to long before their earliest

known fossils. The palaeontological record indicates a Cambrian explosion of phyla around 540 million years (Myr) ago, but sequences suggest a more gradual series of splits around twice as old²³. Likewise, many orders of mammals and birds are now thought to have originated long before the end-Cretaceous extinction^{24,25}, which occurred 65 Myr ago and which was thought previously to have been the signal for their radiation. If the new timescale can be trusted²⁶, these findings present a puzzle and a warning. The puzzle is the absence of fossils. Why have we not found traces of these lineages in their first tens or even hundreds of millions of years? It seems likely that the animals were too small or too rare, with the sudden appearance in the rocks corresponding to an increase in size and rise to ecological dominance²⁷. The warning is that current biodiversity is in a sense greater than we had realized. Major lineages alive today represent more unique evolutionary history than previously suspected — history that would be lost with their extinction.

Analysis of the shape of phylogenies has shown that lineages have differed in their potential for diversification. Darwin²⁸ had noted that species in species-rich genera had more subspecific varieties, and subtaxa within taxa are often distributed very unevenly²⁹, as Fig. 2 illustrates for eutherian species. But these taxonomic patterns can be taken at face value only if taxa are comparable, which they may not be. For example, species-rich groups may simply be older, and it is clear that workers on different groups currently place taxonomic boundaries in very different places³⁰ (Fig. 3). Phylogenies allow comparison of sister clades — each other's closest relatives — which by definition are the same age. Time and again, species are distributed too unevenly for simple null models to be tested in which all species have the same chances of diversifying^{31,32}.

What are the species-rich groups 'doing right'? Many explanations fall broadly into two types. Key innovation hypotheses³³ posit the evolution of some trait that permits its bearers to gain access to more resources or be more competitive than non-bearers. Examples include phytophagy in insects³⁴ and high reproductive rate in mammals³⁵. Other hypotheses focus on traits that facilitate the evolution of reproductive isolation — speciation — without necessarily increasing the fitness of bearers. Sexual selection³⁶ and range fragmentation³⁷ are examples of this kind. These two types can be contrasted as 'bigger cake' and 'thinner slices' explanations, although some traits may act in both ways (for example, body size^{38,39}); another way to split them is to view diversity as 'demand-driven' (niches are waiting to be filled, and differentiation leads to speciation) or 'supply-driven' (speciation occurs unbidden, with differentiation arising through character displacement). Statistical testing of many key innovation hypotheses is hampered by a lack of replication — often, the trait in question is unique, and all that can be done is to model the trait's evolution to assess how well it fits the scenario⁴⁰. When characters have evolved multiple times in independent lineages, sister clades provide automatic matched pairs for hypothesis testing (although other phylogenetic approaches are also available^{41,42}). Comparing sister clades (the procedure used in most of the examples above) avoids two problems that otherwise cloud the issue. First, taxa may not be comparable (Fig. 3), and second, they are not statistically independent — related clades inherit their traits from common ancestors, so are pseudoreplicates⁴³. Nonetheless, there is ongoing debate about the role and limitations of phylogenetic tests for correlates of species richness^{44,45}.

Temporal patterns in biodiversity

Is biodiversity typically at some equilibrium level, with competition setting an upper limit, or do mass extinctions occur so regularly that equilibrium is never reached? And, with one eye on the future prospects for biodiversity, how quickly does diversity recover from mass extinctions? Palaeontologists have addressed these questions at many scales, from local to global. For the global view, the data come from huge compendia of stratigraphic ranges of

taxonomic families (see, for example, refs 46, 47), led by Sepkoski's ground-breaking efforts, and made possible by the development of computer databases. There are more families now than ever before, and a model of exponential growth provides a good overall fit to the numbers of families through time, suggesting expansion without limit and no major role for competition in limiting diversity⁴⁸. But a significantly better fit is provided by a set of three logistic curves, each with a different carrying capacity, punctuated by mass extinction events⁴⁹. Leaving aside the thorny issue of multiplicity of tests and the big question of why the three carrying capacities are different, there may be a perceptual problem at play here. Families do not arise overnight: they are the result of speciation and a lot of time. Consequently, exponential growth at the species level might appear like logistic growth at higher levels⁵⁰. This problem of perception is a recurrent one in palaeontology. For instance, good evidence that biodiversity is often near equilibrium comes from the fact that extinction events are commonly followed by higher than normal rates of diversification⁴. However, the peak of origination rates of genera and families is not straight after the extinction peak. Instead, there is a 10-Myr time-lag throughout the fossil record, implying a lag phase before diversification occurs⁵¹. But could the same pattern arise if speciation rates rose immediately in response to the extinction, but the new lineages are given generic or familial rank only after being around for some time? This scenario would predict (incorrectly) that family diversification rates would take longer to respond than generic rates, so cannot be the whole story, but it

highlights the difficulties of taking taxonomic patterns at face value. Neontologists may face much the same problem with species: taxonomists tend to recognize bird lineages as species if they are older than 2.8 Myr but not if they are younger than 1.1 Myr (ref. 52), so apparent logistic growth in species numbers through time within bird genera⁵³ might be expected even without a slow-down of cladogenesis.

The patchy nature of the known fossil record means that some taxa in some places at some times can be studied in much greater detail than is possible for the biota as a whole. Studies at these smaller scales can analyse the record at the species level, within a region or biome, and can better control for problems such as incomplete and uneven sampling^{54,55}. Such studies find a range of answers: communities may show an equilibrium diversity^{55,56}, an increasing geographical turnover⁵⁷, or radiation punctuated by mass extinction⁵⁸. This may be a more appropriate spatial scale at which to look for equilibrium, as the units have a greater chance of interacting⁵⁹.

The temporal pattern of disparity is also of great interest. Does difference accumulate gradually and evenly as lineages evolve their separate ways, or is evolutionary change more rapid early in a group's history, as it stakes its claim to a new niche? Information from living and fossil species and phylogenies can be combined with statistical models^{41,60,61} to answer this question, although so far relatively little work has combined palaeontological and neontological data. Rates of morphological and taxic diversification are often incongruent, or even uncoupled⁶¹, again highlighting that there is

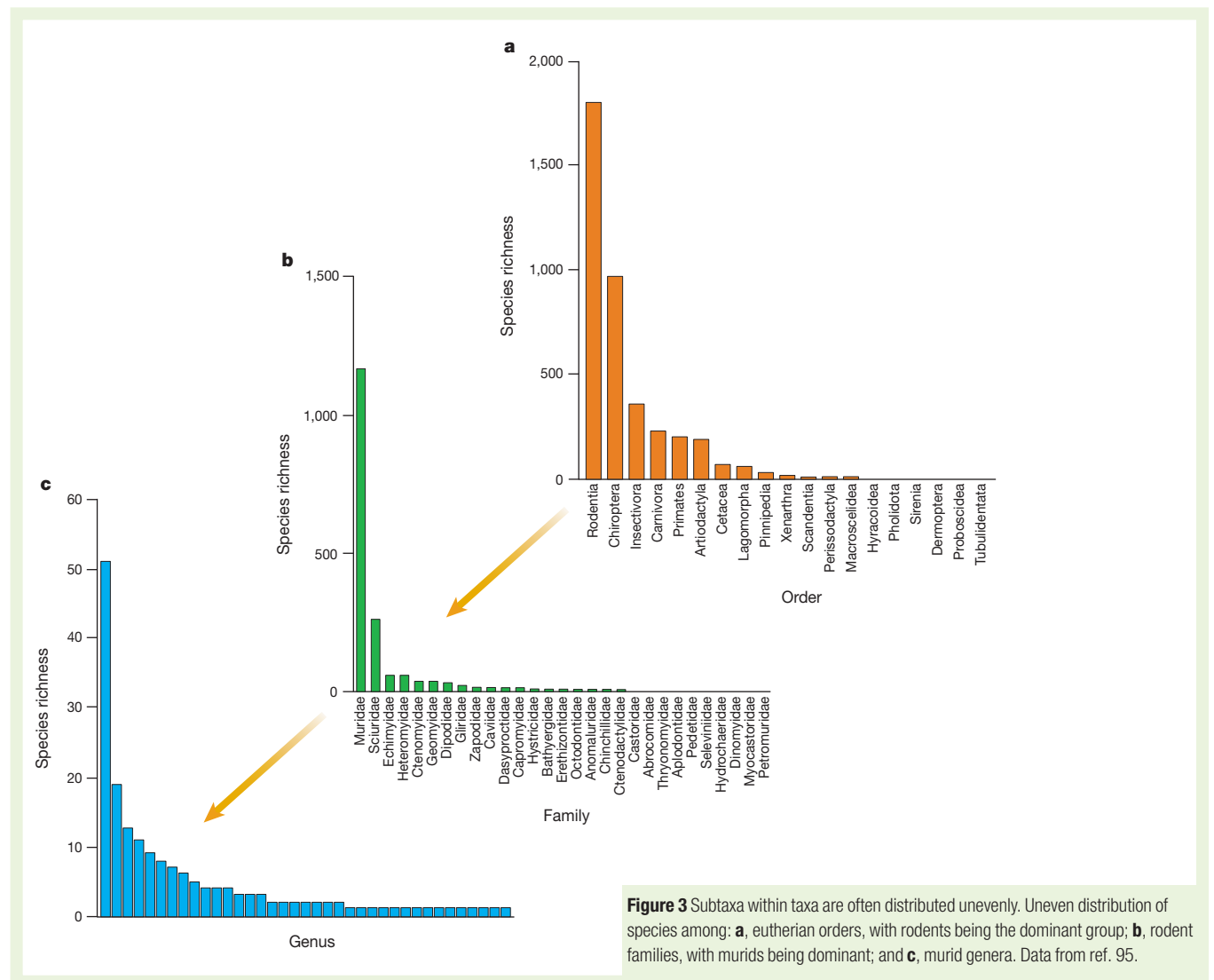


Figure 3 Subtaxa within taxa are often distributed unevenly. Uneven distribution of species among: **a**, eutherian orders, with rodents being the dominant group; **b**, rodent families, with murids being dominant; and **c**, murid genera. Data from ref. 95.

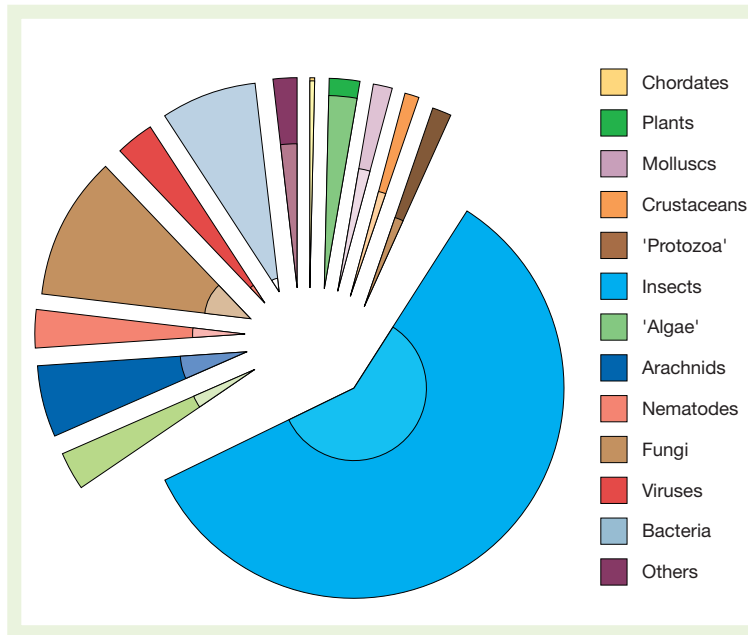


Figure 4 Species richness in major groups of organisms. The main 'pie' shows the species estimated to exist in each group; the hatched area within each slice shows the proportion that have been formally described. Data from ref. 7.

more to biodiversity than numbers of taxa. At present, it is hard to tell under what circumstances disparity precedes, or perhaps drives, species richness, and when the reverse applies. Different models can give very similar patterns of diversity and disparity over time⁶⁰, and detailed studies at smaller scale^{62,63} may provide the greatest chance of an answer.

The shrinking biosphere

What about human impacts on biodiversity? A simple calculation shows that recent rates of species losses are unsustainable. If there are 14 million species at present⁷, then each year the tree of life grows by an extra 14 Myr of branch length. The average age of extant species is nearly 5 Myr (in primates and carnivores anyway, and species in most other groups probably tend to be older rather than younger). So the tree can 'afford' at most about three species extinctions per year without shrinking overall. There have been roughly this many documented species extinctions per year since 1600⁶⁴, and most extinctions must have passed us by. The rate has been increasing too: the last century saw the end of 20 mammalian species alone, a pruning of the mammalian tree that would take at least 200 centuries to redress.

Estimates of current and future rates of loss make even more sobering reading. The rate at which tropical forest — probably the habitat for most species — is lost is about 0.8% to 2% per year⁶⁵ (call it 1% for the purpose of this example). We must expect about 1% of the tropical forest populations to be lost with it, a figure that may be as high as 16 million populations per year, or one every two seconds⁶⁶. Most species have multiple populations, so rates of species loss will obviously be much lower. They are most commonly estimated through species–area relationships⁶⁵, although other approaches are used too⁶⁷. Wilson⁶⁸ famously used the species–area relationship to estimate an annual extinction rate of 27,000 species — one species every twenty minutes. This and similar estimates have attracted criticism but recent work^{67,69,70} has shown that levels of species endangerment are rising in line with species–area predictions, provided the analysis is conducted at the appropriate scale. What are the implications of such rapid pruning for the tree of life? Simulations in which species are wiped out at random⁷¹ indicate that most of the phylogenetic diversity would survive even a major extinction: up to 80% of the branch length could survive even if 95% of the species were lost. This result assumes extinction to befall species at random; scenarios of non-random extinction can have very different outcomes⁷². The current crisis, like previous mass

extinctions, is highly non-random^{73–76}, with related twigs on the tree tending to share the same fate. This selectivity greatly reduces the ability of the phylogenetic hierarchy to retain structure in the face of a given severity of species extinction^{77,78}.

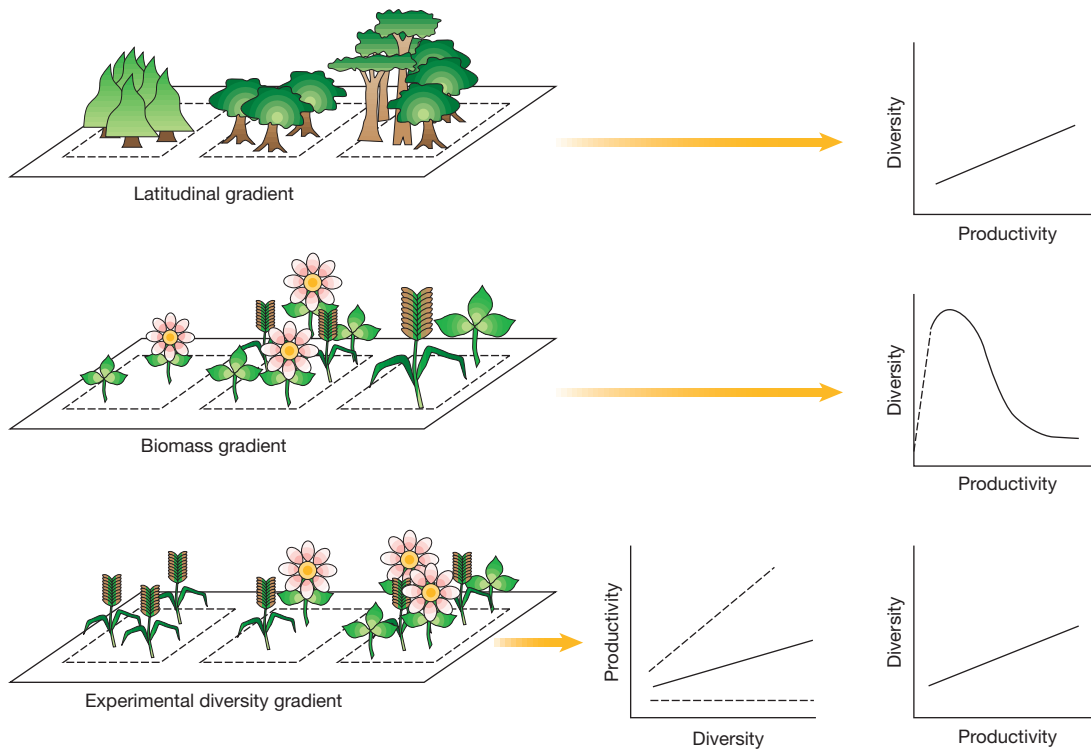
But how much structure is needed? Imagine if the only function of this article was the transfer of information. Many of the words could be deleted and you would still get the message. It would (we hope) be less pleasant to read. Similarly, for many people we need biodiversity because we like it; it should be conserved just as we conserve Mozart concertos and Van Gogh paintings⁷⁹. But how many words could you delete before the meaning starts to get lost? Recently, ecologists have begun asking similar questions about our environment.

Biodiversity and the stability and functioning of ecosystems

How many species can we lose before we start to affect the way ecosystems function? Principal environmental factors such as climate, soil type and disturbance^{80,81} strongly influence ecosystem functioning, but likewise organisms can affect their environment⁸². Some of the first ideas on how biodiversity could affect the way ecosystems function are attributable to Darwin and Wallace^{28,83}, who stated that a diverse mixture of plants should be more productive than a monoculture. They also suggested the underlying biological mechanism: because coexisting species differ ecologically, loss of a species could result in vacant niche-space and potential impacts on ecosystem processes. Defining ecological niches is not straightforward, but Darwin and Wallace's hypothesis, if correct, provides a general biological principle which predicts that intact, diverse communities are generally more stable and function better than versions that have lost species. Recent experimental evidence (reviewed by Chapin *et al.*, pages 234–242, and McCann, pages 228–233), although pointing out important exceptions, generally supports this idea. Compared with systems that have lost species, diverse plant communities often have a greater variety of positive and complementary interactions and so outperform any single species^{84,85}, and have more chance of having the right species in the right place at the right time. This last 'sampling effect' mechanism has prompted much debate on the design, analysis and interpretation of experiments that aim to manipulate biodiversity⁸⁶. Although the sampling effect is biological in part — it requires both differences between species and an ecological mechanism making some species more abundant than others — the probabilistic component (more diverse communities have a greater chance of containing a species with particular properties) has made it controversial. Nevertheless, loss of species with key

Box 2

Plant diversity and productivity at different scales



For plants, the relationship between diversity and productivity changes with scale^{107,108}. At global scales (panel **a** in the figure above), from high latitudes to the tropics, plant diversity in large areas may be positively related to increasing productivity. At regional scales (**b**), plant diversity in small plots is frequently negatively related to increasing productivity, often as part of a larger unimodal 'hump-shaped' distribution of diversities. Numbers of species correlate with several factors including the size and hence number of individual plants sampled, spatial heterogeneity, and competitive exclusion as

productivity increases. Experimental manipulations of plant diversity within habitats (**c**) reveal that, although relationships vary, productivity tends to increase with diversity owing to increasing complementary or positive interactions between species and the greater likelihood of diverse communities containing a highly productive species. In manipulation experiments, biodiversity is the explanatory variable and productivity the response, whereas in observational studies the relationship is usually viewed the other way round as illustrated here for all three cases.

traits, as in the sampling effect, is not restricted to ecological experiments: logging, fishing, trapping and other harvesting of natural resources frequently remove particular organisms, often including dominant species.

Although 95% of experimental studies support a positive relationship between diversity and ecosystem functioning, many have found that only 20–50% of species are needed to maintain most biogeochemical ecosystem processes⁸⁷. Do the other, apparently redundant, species have a role to play over longer timescales, providing insurance against environmental change? We need to know. Biodiversity can also impact ecological processes such as the incidence of herbivory and disease, and the resistance of communities to invasion. Once again, although exceptions exist, in experiments which manipulate diversity directly, communities with more species are often more resistant to invasion^{88,89}, probably for the same reason that they are more productive. Diversity of one group of organisms can also promote diversity of associated groups, for example between mycorrhizas and plants⁹⁰ or plants and insects⁸⁸.

The study of the relationship between biodiversity and ecosystem processes has made rapid progress in the past decade, and is proving an effective catalyst for linking the ecology of individuals, communities and ecosystems. Some general, although not universal, patterns are emerging as theory and experiment progress together⁹¹. We have a good understanding of the underlying causes, where we see both

agreement and differences in experimental results. Nevertheless, this work represents only a first general approach to the subject; many issues remain outstanding and other areas are as yet uninvestigated. First, do these short-term and small-scale experiments in field plots reveal the full effects of diversity, and how do we scale up in time and space⁹²? Second, although we know that local extinction is often not random, many recent experiments compare the performance of communities differing in the presence or absence of a random set of species. How adequate is this model? Third, how will species loss interact with other components of global change such as rising CO₂? Darwin and Wallace observed that niche differentiation could cause changing diversity to have consequences for ecosystem processes, but the magnitude of these effects could depend crucially on the exact mechanism of coexistence. Finally, how do we integrate these new within-habitat relationships between diversity and ecosystem processes with large-scale patterns in biodiversity and environmental parameters, as reviewed by Gaston on pages 220–227 of this issue? Box 2 suggests one way in which the relationship between plant diversity and productivity could vary with scale.

Challenges and prospects

Recent years have seen exciting advances in our knowledge of biodiversity, our identification of factors that have shaped its evolution and distribution, and our understanding of its importance. But we

can see only a small, probably atypical, part of the picture (Fig. 4). A detailed view is emerging of birds, mammals, angiosperms, and shallow-sea, hard-bodied invertebrates, but much less is known about most of the rest of life. How far are we justified in generalizing from the groups we know well to biodiversity as a whole? This is a crucial question, for instance in the choice of protected areas (see review by Margules and Pressey, pp. 243–253). There is no short cut — we need more basic information about more groups; and not just species lists, but who does what and with whom.

A related point is that biodiversity cannot be reduced to a single number, such as species richness. This is a real problem for biologists, because a single number is often what policy-makers want. Perhaps it will be possible to go part way if the many indices (Box 1) are intercorrelated, as some certainly are^{93,94}. The stronger the correlations, the more reasonable it will be to reduce multiple measures to a few principal components, to create dimensions of diversity. We must of course recognize — and explain to policy-makers — that combining these dimensions into a single number would be arbitrary. We must not make the mistake of thinking or claiming that maintaining, say, species richness of a particular taxon is the same as conserving overall biodiversity. To revisit an earlier metaphor, conserving one population of every species is rather like having one of each note in the Mozart concerto.

Two themes running through this review pertain to scale. The first is that the study of biodiversity is becoming an ever-bigger research enterprise. The database is (more than ever) cumulative, the analyses more ambitious and involving more people. We see this trend continuing. The second issue is whether we can study all processes at all scales. Perhaps large-scale patterns are a blunt instrument for studying the underlying processes, which may operate on much smaller scales. That said, we nonetheless would often like to scale our answers up: if a small experimental plot ‘needs’ *n* angiosperm species, or functional groups, for good ecosystem functioning, how many does 200 km² — or the planet — ‘need’?⁹². Given the speed at which we are pruning the tree of life, we need good answers quickly. □

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