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Biodiversity

Biodiversity may be a buzzword, but as a concept it sits at the heart of ecological research. Some ecological communities, such as pristine coral reef systems, are astonishingly rich in the number and types of species that they support, whereas others are relatively species poor. Natural communities also differ greatly in the proportion of species performing different ecological functions. What determines such differences and how these differences are related to ecosystem functioning are questions that have occupied the minds of ecologists for decades.

But these questions are so much more pressing now. We live at a time of rapid environmental change, resulting largely from our own activities, and a concomitant, accelerating rate of habitat loss and species extinctions. Like children playing with fire, we do not fully understand, and therefore cannot predict, the ultimate consequences of tampering with global biodiversity. This collection of reviews — the second in our new section called 'Nature Insight' — focuses on the science of biodiversity.

We are pleased to acknowledge the financial support of the Center for Applied Biodiversity Science (CABS), a division of Conservation International, in producing this Insight. The content is in accord with the philosophy that biodiversity conservation is a human-centred pursuit that must be underpinned by solid science. Of course, *Nature* carries sole responsibility for all editorial content and rigorous peer-review.

This Insight is deliberately broad in scope, covering underlying concepts, pure and applied research, and biodiversity loss from the human perspective. We hope that scientists, policy-makers and general readers alike will find the reviews both informative and thought provoking. Given that environmental change and biodiversity loss is a global concern, and understanding that not everyone will have easy access to the print version, this Insight is freely available to all readers, regardless of subscriber status, on our website at www.nature.com.

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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

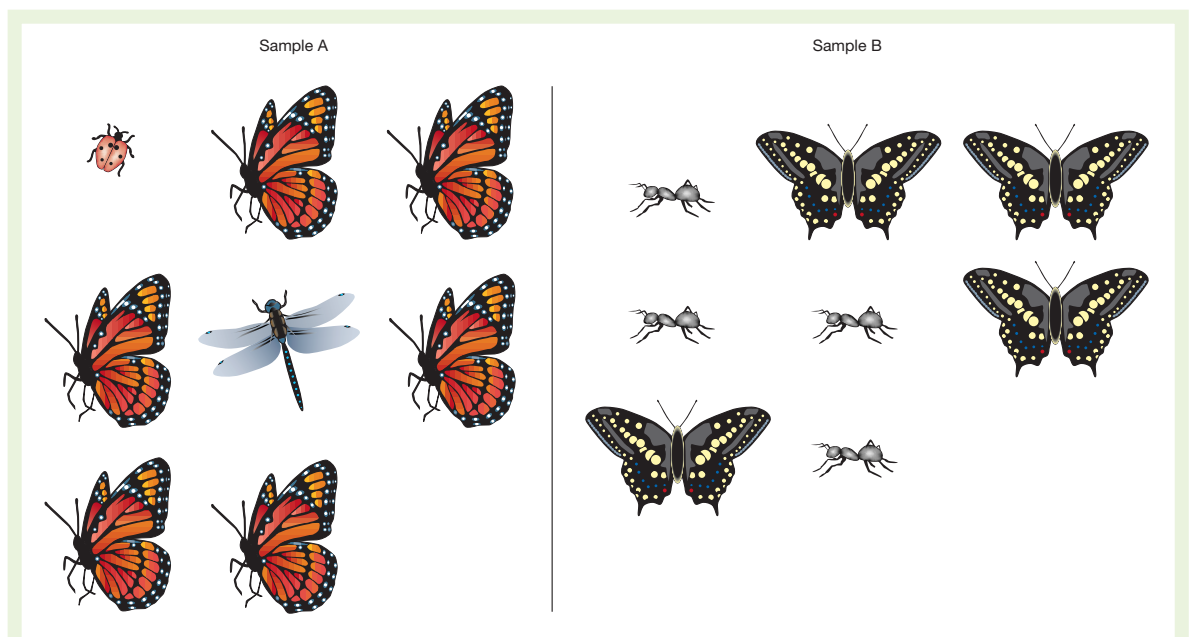


Figure 1 Two samples of insects from different locations, illustrating two of the many different measures of diversity: species richness and species evenness. Sample A could be described as being the more diverse as it contains three species to sample B's two. But there is less chance in sample B than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

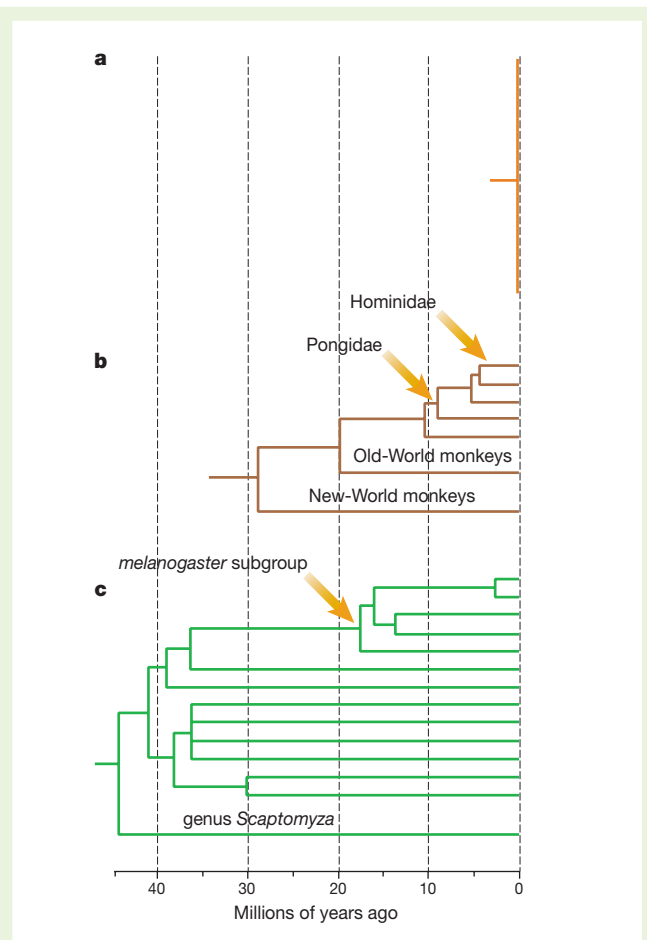


Figure 2 Taxonomic boundaries are not comparable among major groups. **a**, Fourteen species in nine genera representative of cichlid fish in Lake Victoria. **b**, Seven species representative of several families in anthropoid primates. **c**, Thirteen species representative of a single genus, *Drosophila*.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

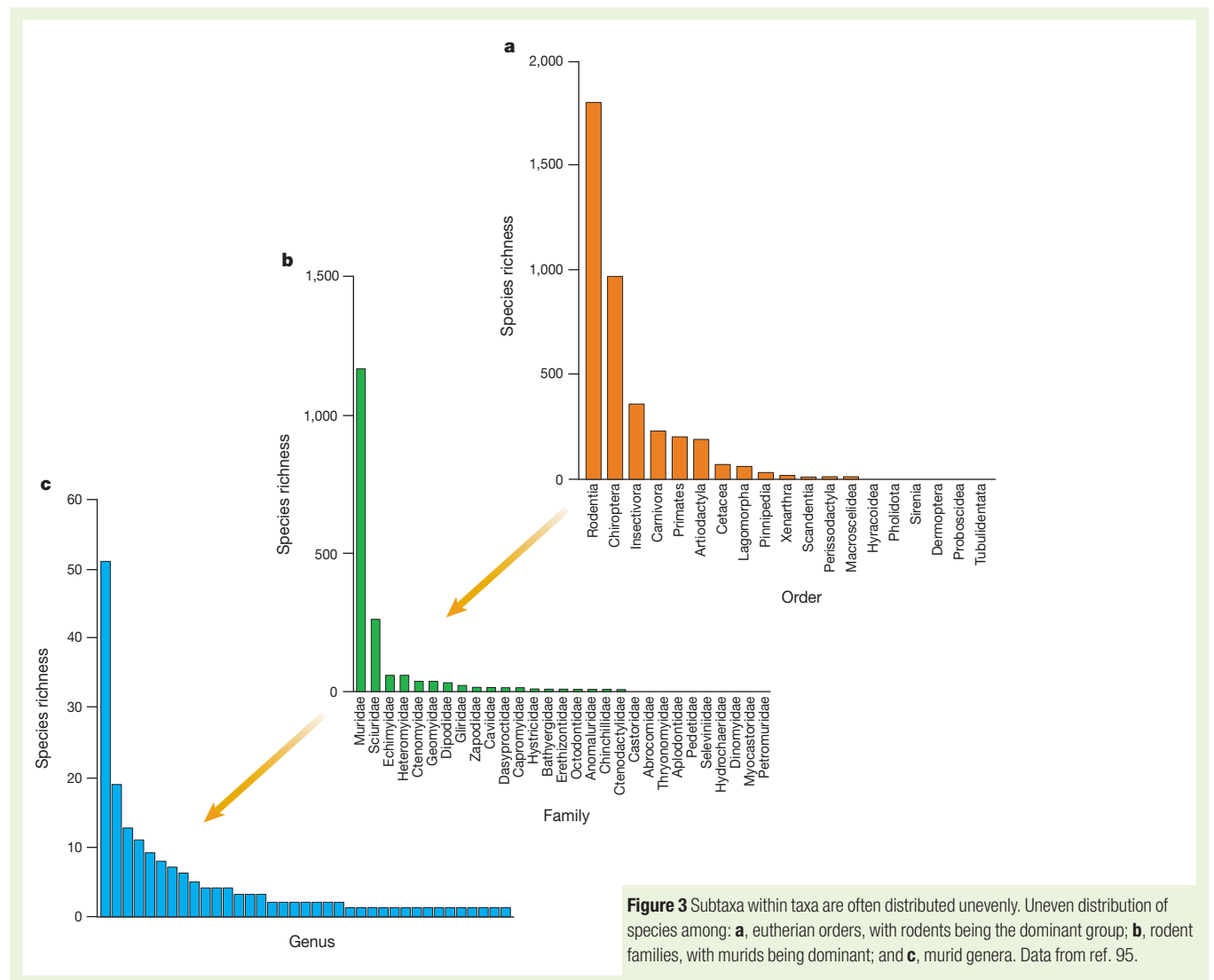


Figure 3 Subtaxa within taxa are often distributed unevenly. Uneven distribution of species among: **a**, eutherian orders, with rodents being the dominant group; **b**, rodent families, with murids being dominant; and **c**, murid genera. Data from ref. 95.

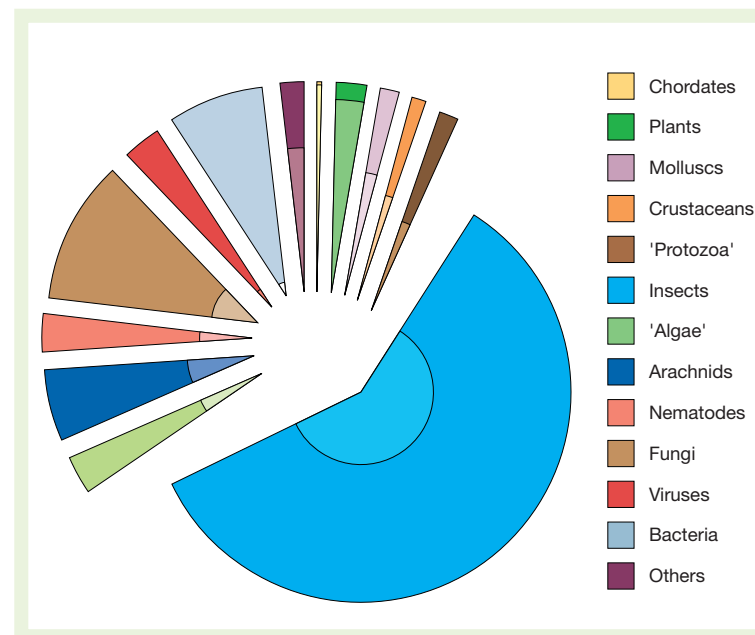


Figure 4 Species richness in major groups of organisms. The main 'pie' shows the species estimated to exist in each group; the hatched area within each slice shows the proportion that have been formally described. Data from ref. 7.

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}.

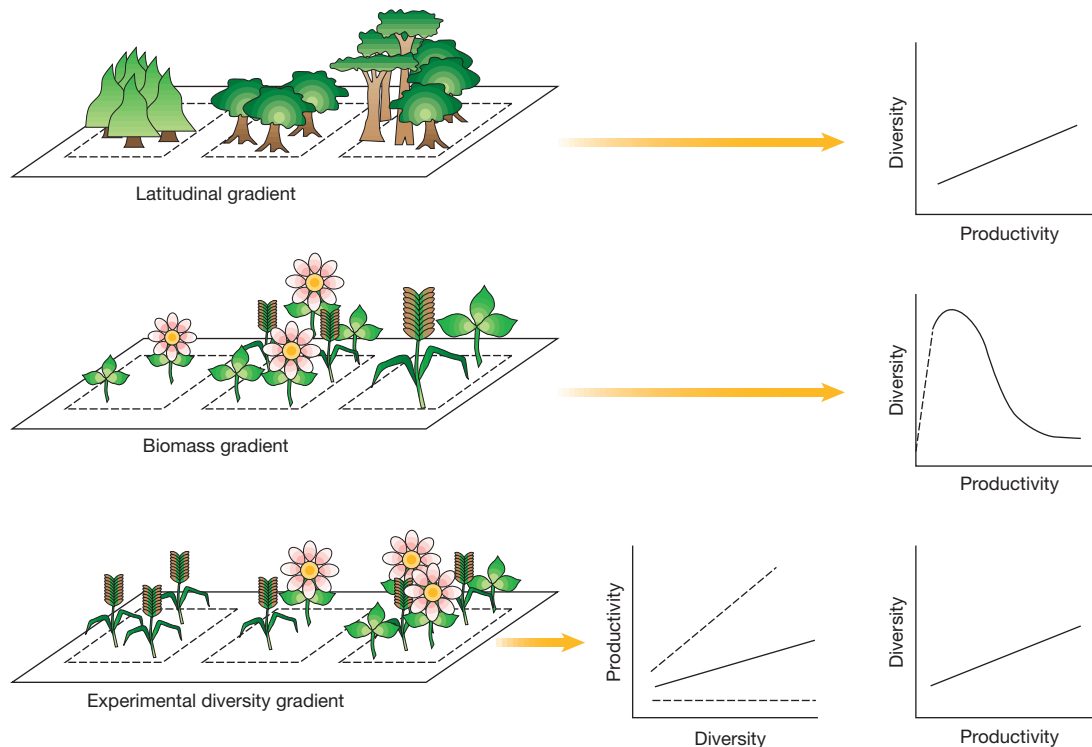
But how much structure is needed? Imagine if the only function of this article was the transfer of information. Many of the words could be deleted and you would still get the message. It would (we hope) be less pleasant to read. Similarly, for many people we need biodiversity because we like it; it should 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. □

1. Whittaker, R. H. Evolution and measurement of species diversity. *Taxon* **21**, 213–251 (1972).
2. Magurran, A. E. *Ecological Diversity and its Measurement* (Croom Helm, London, 1988).
3. Balmford, A., Green, M. J. B. & Murray, M. G. Using higher-taxon richness as a surrogate for species-richness: I. Regional tests. *Proc. R. Soc. Lond. B* **263**, 1267–1274 (1996).
4. Sepkoski, J. J. Jr Rates of speciation in the fossil record. *Proc. R. Soc. Lond. B* **353**, 315–326 (1998).
5. Pine, R. H. New mammals not so seldom. *Nature* **368** (1994).
6. Paxton, C. G. M. A cumulative species description curve for large open water marine animals. *J. Mar. Biol. Assoc.* **78**, 1389–1391 (1998).
7. Hawksworth, D. L. & Kalin-Arroyo, M. T. in *Global Biodiversity Assessment* (ed. Heywood, V. H.) 107–191 (Cambridge Univ. Press, Cambridge, 1995).
8. Funch, P. & Kristensen, R. M. Cyclophora is a new phylum with affinities to Entoprocta and Ectoprocta. *Nature* **378**, 711–714 (1995).
9. Fuhrman, J. A. & Campbell, L. Marine ecology: microbial microdiversity. *Nature* **393**, 410–411 (1998).
10. Goss, M. *Life on the Edge* (Plenum, New York, 1998).
11. Abbott, A. Battle lines drawn between ‘nanobacteria’ researchers. *Nature* **401**, 105 (1999).
12. Tristem, M. Identification and characterization of novel human endogenous retrovirus families by phylogenetic screening of the human genome mapping project database. *J. Virol.* **74**, 3715–3730 (2000).
13. Kidwell, M. G. & Lisch, D. Transposable elements as sources of variation in animals and plants. *Proc. Natl Acad. Sci. USA* **94**, 7704–7711 (1997).
14. Goddard, M. R. & Burt, A. Recurrent invasion and extinction of a selfish gene. *Proc. Natl Acad. Sci. USA* **96**, 13880–13885 (1999).
15. Rylands, A. B., Mittermeier, R. A. & Luna, E. R. A species list for the New World Primates (Platyrrhini): distribution by country, endemism, and conservation status according to the Macle-Lande system. *Neotrop. Primates* **35**, 113–160 (1995).
16. Cracraft, J. Species concepts and speciation analysis. *Curr. Ornithol.* **1**, 159–187 (1983).
17. Avise, J. C. & Wollenberg, K. Phylogenetics and the origin of species. *Proc. Natl Acad. Sci. USA* **94**, 7748–7755 (1997).
18. Hanken, J. Why are there so many new amphibian species when amphibians are declining? *Trends Ecol. Evol.* **14**, 7–8 (1999).
19. Harvey, P. H., Leigh Brown, A. J., Maynard Smith, J. & Nee, S. *New Uses for New Phylogenies* (Oxford Univ. Press, Oxford, 1996).
20. Nee, S., Barraclough, T. G. & Harvey, P. H. in *Biodiversity: A Biology of Numbers and Difference* (ed. Gaston, K. J.) 230–252 (Blackwell Science, Oxford, 1996).
21. Pagel, M. Inferring the historical patterns of biological evolution. *Nature* **401**, 877–884 (1999).
22. Sanderson, M. J. A nonparametric approach to estimating divergence times in the absence of rate constancy. *Mol. Biol. Evol.* **14**, 1218–1231 (1997).
23. Wang, D. Y.-C., Kumar, S. & Hedges, S. B. Divergence time estimates for the early history of animal phyla and the origin of plants, animals and fungi. *Proc. R. Soc. Lond. B* **266**, 163–171 (1999).

24. Bromham, L., Phillips, M. J. & Penny, D. Growing up with dinosaurs: molecular dates and the mammalian radiation. *Trends Ecol. Evol.* **14**, 113–118 (1999).
25. Cooper, A. & Penny, D. Mass survival of birds across the Cretaceous-Tertiary boundary: molecular evidence. *Science* **275**, 1109–1113 (1997).
26. Foote, M., Hunter, J. P., Janis, C. M. & Sepkoski, J. J. Evolutionary and preservational constraints on the origins of biological groups: divergence times of eutherian mammals. *Science* **283**, 1310–1314 (1999).
27. Cooper, A. & Fortey, R. Evolutionary explosions and the phylogenetic fuse. *Trends Ecol. Evol.* **13**, 151–156 (1998).
28. Darwin, C. *On the Origin of Species by Means of Natural Selection* (Murray, London, 1859).
29. Dial, K. P. & Marzluff, J. M. Nonrandom diversification within taxonomic assemblages. *Syst. Zool.* **38**, 26–37 (1989).
30. Avise, J. C. & Johns, G. C. Proposal for a standardized temporal scheme of biological classification for extant species. *Proc. Natl Acad. Sci. USA* **96**, 7358–7363 (1999).
31. Purvis, A. in *New Uses for New Phylogenies* (eds Harvey, P. H., Leigh Brown, A. J., Maynard Smith, J. & Nee, S.) 153–168 (Oxford Univ. Press, Oxford, 1996).
32. Mooers, A. Ø. & Heard, S. B. Evolutionary process from phylogenetic tree shape. *Q. Rev. Biol.* **72**, 31–54 (1997).
33. Heard, S. B. & Hauser, D. L. Key evolutionary innovations and their ecological mechanisms. *Hist. Biol.* **10**, 151–173 (1995).
34. Mitter, C., Farrell, B. & Wiegmann, B. The phylogenetic study of adaptive zones: has phytophagy promoted insect diversification? *Am. Nat.* **132**, 107–128 (1988).
35. Marzluff, J. M. & Dial, K. P. Life history correlates of taxonomic diversity. *Ecology* **72**, 428–439 (1991).
36. Barraclough, T. G., Harvey, P. H. & Nee, S. Sexual selection and taxonomic diversity in passerine birds. *Proc. R. Soc. Lond. B* **259**, 211–215 (1995).
37. Owens, I. P. F., Bennett, P. M. & Harvey, P. H. Species richness among birds: body size, life history, sexual selection or ecology? *Proc. R. Soc. Lond. B* **266**, 933–939 (1999).
38. Gardezi, T. F. & da Silva, J. Diversity in relation to body size in mammals: a comparative study. *Am. Nat.* **153**, 110–123 (1999).
39. Gittleman, J. L. & Purvis, A. Body size and species richness in primates and carnivores. *Proc. R. Soc. Lond. B* **265**, 113–119 (1998).
40. Sanderson, M. J. & Donoghue, M. J. Shifts in diversification rate with the origin of angiosperms. *Science* **264**, 1590–1593 (1994).
41. Pagel, M. Inferring evolutionary processes from phylogenies. *Zool. Scripta* **26**, 331–348 (1997).
42. Kelley, S. T. & Farrell, B. D. Is specialization a dead end? The phylogeny of host use in *Dendroctonus* bark beetles (Scolytidae). *Evolution* **52**, 1731–1743 (1998).
43. Harvey, P. H. & Pagel, M. D. *The Comparative Method in Evolutionary Biology* (Oxford Univ. Press, Oxford, 1991).
44. Rosenzweig, M. L. Colonial birds probably do speciate faster. *Evol. Ecol.* **10**, 681–683 (1996).
45. Barraclough, T. G., Nee, S. & Harvey, P. H. Sister-group analysis in identifying correlates of diversification. *Evol. Ecol.* **12**, 751–754 (1998).
46. Benton, M. J. *The Fossil Record 2* (Chapman & Hall, London, 1993).
47. Sepkoski, J. J. A compendium of fossil marine families. *Milwaukee Publ. Mus. Contrib. Biol. Geol.* **51**, 1–125 (1982).
48. Benton, M. J. Diversification and extinction in the history of life. *Science* **268**, 52–58 (1995).
49. Courtillot, V. & Gaudemer, Y. Effects of mass extinctions on biodiversity. *Nature* **381**, 146–148 (1996).
50. Benton, M. J. Models for the diversification of life. *Trends Ecol. Evol.* **12**, 490–495 (1997).
51. Kirchner, J. W. & Weil, A. Delayed biological recovery from extinctions throughout the fossil record. *Nature* **404**, 177–180 (2000).
52. Avise, J. C., Walker, D. & Johns, G. C. Speciation durations and Pleistocene effects on vertebrate phylogeography. *Proc. R. Soc. Lond. B* **265**, 1707–1712 (1998).
53. Zink, R. M. & Slowinski, J. B. Evidence from molecular systematics for decreased avian diversification in the Pleistocene epoch. *Proc. Natl Acad. Sci. USA* **92**, 5832–5835 (1995).
54. Marshall, C. R. in *The Adequacy of the Fossil Record* (ed. Paul, C. R. C.) 23–53 (Wiley, Chichester, 1998).
55. Alroy, J. in *Biodiversity Dynamics* (eds McKinney, M. L. & Drake, J. A.) 232–287 (Columbia Univ. Press, New York, 1999).
56. Alroy, J. Constant extinction, constrained diversification, and uncoordinated stasis in North American mammals. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **127**, 285–311 (1996).
57. Van Valkenburgh, B. & Janis, C. in *Species Diversity in Ecological Communities* (eds Ricklefs, R. E. & Schluter, D.) 330–340 (Chicago Univ. Press, Chicago, 1993).
58. Kauffman, E. G. & Fagerstrom, J. A. in *Species Diversity in Ecological Communities* (eds Ricklefs, R. E. & Schluter, D.) 315–329 (Chicago Univ. Press, Chicago, 1993).
59. McKinney, M. L. in *Biodiversity Dynamics* (eds McKinney, M. L. & Drake, J. A.) 1–16 (Columbia Univ. Press, New York, 1999).
60. Foote, M. in *Evolutionary Paleobiology* (eds Jablonski, D., Erwin, D. H. & Lipps, J. H.) 62–86 (Chicago Univ. Press, Chicago, 1996).
61. Roy, K. & Foote, M. Morphological approaches to measuring biodiversity. *Trends Ecol. Evol.* **12**, 277–281 (1997).
62. Schluter, D. Ecological causes of adaptive radiation. *Am. Nat.* **148**(Suppl.), S40–S64 (1996).
63. Barraclough, T. G., Vogler, A. P. & Harvey, P. H. Revealing the factors that promote speciation. *Phil. Trans. R. Soc. Lond. B* **353**, 241–249 (1998).
64. Barbault, R. & Sastrapradja, S. D. in *Global Biodiversity Assessment* (ed. Heywood, V. H.) 193–274 (Chicago Univ. Press, Cambridge, 1995).
65. May, R. M., Lawton, J. H. & Stork, N. E. in *Extinction Rates* (eds Lawton, J. H. & May, R. M.) 1–24 (Oxford Univ. Press, Oxford, 1995).
66. Hughes, J. B., Daily, G. C. & Ehrlich, P. R. Population diversity: its extent and extinction. *Science* **278**, 689–692 (1997).
67. Pimm, S. L. in *Conservation Science and Action* (ed. Sutherland, W. J.) 20–38 (Blackwell Science, Oxford, 1998).
68. Wilson, E. O. *The Diversity of Life* (Norton, New York, 1992).
69. Grelle, C. E. d. V., Fonseca, G. A. B., Fonseca, M. T. & Costa, L. P. The question of scale in threat analysis: a case study with Brazilian mammals. *Anim. Conserv.* **2**, 149–152 (1999).
70. Cowlshaw, G. Predicting the pattern of decline of African primate diversity: an extinction debt from historical deforestation. *Conserv. Biol.* **13**, 1183–1193 (1999).
71. Nee, S. & May, R. M. Extinction and the loss of evolutionary history. *Science* **278**, 692–694 (1997).

72. Heard, S. B. & Mooers, A. Ø. Phylogenetically patterned speciation rates and extinction risks change the loss of evolutionary history during extinctions. *Proc. R. Soc. Lond. B* **267**, 613–620 (2000).
73. Mace, G. M. & Balmford, A. in *Future Priorities for the Conservation of Mammalian Diversity* (eds Entwistle, A. & Dunstone, N.) (Cambridge Univ. Press, Cambridge, 1999).
74. Bennett, P. M. & Owens, I. P. F. Variation in extinction risk among birds: chance or evolutionary predisposition? *Proc. R. Soc. Lond. B* **264**, 401–408 (1997).
75. McKinney, M. L. Extinction vulnerability and selectivity: combining ecological and paleontological views. *Annu. Rev. Ecol. Syst.* **28**, 495–516 (1997).
76. Russell, G. J., Brooks, T. M., McKinney, M. M. & Anderson, C. G. Present and future taxonomic selectivity in bird and mammal extinctions. *Conserv. Biol.* **12**, 1365–1376 (1998).
77. McKinney, M. L. Branching models predict loss of many bird and mammal orders within centuries. *Anim. Conserv.* **1**, 159–164 (1998).
78. Purvis, A., Agapow, P.-M., Gittleman, J. L. & Mace, G. M. Nonrandom extinction risk and the loss of evolutionary history. *Science* **288**, 328–330 (2000).
79. Kunin, W. E. & Lawton, J. H. in *Biodiversity: a Biology of Numbers and Difference* (ed. Gaston, K. J.) 283–308 (Blackwell Science, Oxford, 1996).
80. MacGillivray, C. W. *et al.* Testing predictions of the resistance and resilience of vegetation subjected to extreme events. *Funct. Ecol.* **9**, 640–649 (1995).
81. Wardle, D. A., Zackrisson, O., Hörnberg, G. & Gallet, C. The influence of island area on ecosystem properties. *Science* **277**, 1296–1299 (1997).
82. Jones, C. J., Lawton, J. H. & Shachak, M. Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* **78**, 1946–1957 (1997).
83. Darwin, C. & Wallace, A. On the tendency of species to form varieties; and on the perpetuation of varieties and species by natural means of selection. *J. Proc. Linn. Soc. Lond., Zool.* **3**, 45–62 (1858).
84. Tilman, D. Ecological consequences of biodiversity: a search for general principles. *Ecology* **80**, 1455–1474 (1999).
85. Spehn, E. M., Joshi, J., Schmid, B., Diemer, M. & Körner, C. Aboveground resource use increases with plant species richness in experimental grassland ecosystems. *Funct. Ecol.* **14** (in the press).
86. Allison, G. W. The implications of experimental design for biodiversity manipulations. *Am. Nat.* **153**, 26–45 (1999).
87. Schwartz, M. W. *et al.* Linking biodiversity to ecosystem functioning: implications for conservation ecology. *Oecologia* **122**, 297–305 (2000).
88. Knops, J. M. H. *et al.* Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundance and diversity. *Ecol. Lett.* **2**, 286–294 (1999).
89. Stachowicz, J. J., Whitlatch, R. B. & Osman, R. W. Species diversity and invasion resistance in a marine ecosystem. *Science* **286**, 1577–1579 (1999).
90. Van der Heijden, M. G. A. *et al.* Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. *Nature* **396**, 69–72 (1998).
91. Loreau, M. Biodiversity and ecosystem functioning: a mechanistic model. *Proc. Natl Acad. Sci. USA* **95**, 5632–5636 (1998).
92. Tilman, D. Diversity and production in European Grasslands. *Science* **286**, 1099–1100 (1999).
93. Williams, P. H. & Humphries, C. J. in *Biodiversity: A Biology of Numbers and Difference* (ed. Gaston, K. J.) 54–76 (Blackwell Scientific, Oxford, 1996).
94. May, R. M. in *Ecology and Evolution of Communities* (eds Cody, M. L. & Diamond, J. M.) 81–120 (Belknap, Cambridge, MA, 1975).
95. Corbet, G. B. & Hill, J. E. *A World List of Mammalian Species* (Natural History Museum, London, 1991).
96. Bisby, F. A. in *Global Biodiversity Assessment* (ed. Heywood, V. H.) 21–106 (Cambridge Univ. Press, Cambridge, 1995).
97. Myers, N., Mittermeier, R. A., Mittermeier, C. G., de Fonseca, G. A. B. & Kent, J. Biodiversity hotspots for conservation priorities. *Nature* **403**, 853–858 (2000).
98. Groombridge, J. J., Jones, C. G., Bruford, M. W. & Nichols, R. A. 'Ghost' alleles of the Mauritius kestrel. *Nature* **403**, 616 (2000).
99. Williams, P. H., Humphries, C. J. & Vane-Wright, R. I. Centres of seed-plant diversity: the family way. *Proc. R. Soc. Lond. B* **256**, 67–70 (1994).
100. Mallet, J. in *Biodiversity: A Biology of Numbers and Difference* (ed. Gaston, K. J.) 13–53 (Blackwell Science, Oxford, 1996).
101. Gould, S. J. *Wonderful Life: The Burgess Shale and the Nature of History* (Norton, New York, 1989).
102. Moritz, C. Defining 'evolutionarily significant units' for conservation. *Trends Ecol. Evol.* **9**, 373–375 (1994).
103. Faith, D. P. in *Systematics and Conservation Evaluation* (eds Forey, P. L., Humphries, C. J. & Vane-Wright, R. I.) 251–268 (Clarendon, Oxford, 1994).
104. Vane-Wright, R. I., Humphries, C. J. & Williams, P. H. What to protect? Systematics and the agony of choice. *Biol. Conserv.* **55**, 235–254 (1991).
105. Pressey, R. L., Johnson, I. R. & Wilson, P. D. Shades of irreplaceability: towards a measure of the contribution of sites to a reservation goal. *Biodiv. Conserv.* **3**, 242–262 (1994).
106. Russell, G. J. in *Biodiversity Dynamics* (eds McKinney, M. L. & Drake, J. A.) 377–404 (Columbia Univ. Press, New York, 1999).
107. Grace, J. B. The factors controlling species density in herbaceous plant communities: an assessment. *Persp. Plant Ecol. Evol. Syst.* **2**, 1–28 (1999).
108. Waide, R. B. *et al.* The relationship between productivity and species richness. *Annu. Rev. Ecol. Syst.* **30**, 257–300 (1999).

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Causes, consequences and ethics of biodiversity

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The existence of so great a diversity of species on Earth remains a mystery, the solution to which may also explain why and how biodiversity influences the functioning of ecosystems. The answer may lie in quantifying the trade-offs that organisms face in dealing with the constraints of their environment. Societal responses to the loss of biodiversity also involve trade-offs, and the elaboration of these will be essential in developing wiser environmental ethics and policy.

The most striking feature of Earth is the existence of life, and the most striking feature of life is its diversity. This biological diversity, or biodiversity, has long been a source of wonderment and scientific curiosity, but is increasingly a source of concern. Human domination of Earth's ecosystems¹ is markedly reducing the diversity of species within many habitats worldwide, and is accelerating extinction. One of the more pragmatic questions raised by these threats to biodiversity is the extent to which this loss of biodiversity matters; that is, are stability, productivity and other aspects of the functioning of both managed and natural ecosystems dependent on biodiversity?

There are strong reasons to hypothesize, as did Darwin² and Elton³, that biodiversity might impact ecosystem processes. But ecology is no longer a discipline in which natural history observations and simple verbal logic hold sway. The rekindled interest in the potential effects of biodiversity on ecosystem processes, which followed the publication in 1993 of a book edited by Schulze and Mooney⁴, is occurring in a discipline for which hypotheses are now tested against the results of field experiments, mechanistic theory and quantitative field observations. Anything less than the concordance of all three lines of evidence leads to the modification or rejection of hypotheses. Given that this topic became a principal focus of scientific inquiry only about seven years ago, it is not surprising that it remains contentious. Indeed, the greatest surprise may be the rapidity, breadth and depth of work that already has occurred, and the generalities that are emerging from it.

Five papers in this issue summarize this work. Purvis and Hector (pages 212–219), McCann (pages 228–233), and Chapin and collaborators (pages 234–242) review and synthesize recent experimental, theoretical and observational studies that have demonstrated links between biodiversity and the stability, productivity and nutrient dynamics of ecosystems. Gaston (pages 220–227) summarizes global patterns of biodiversity and some possible explanations for these patterns. Margules and

Pressey (pages 243–253) discuss strategies for the preservation of biodiversity.

The effects of biodiversity on ecosystems

In broad summary, these reviews show that, on average, greater diversity leads to greater productivity in plant communities, greater nutrient retention in ecosystems and greater ecosystem stability. For instance, grassland field experiments both in North America (Fig. 1)^{5,6} and across eight different European sites, ranging from Greece in the south and east to Portugal and Ireland in the west and Sweden in the north⁷, have shown that each halving of the number of plant species within a plot leads to a 10–20% loss of productivity. An average plot containing one plant species is less than half as productive as an average plot containing 24–32 species^{5–7}. Lower plant diversity also leads to greater rates of loss of limiting soil nutrients through leaching, which ultimately should decrease soil fertility, further lowering plant productivity.

Both laboratory and field studies have shown that ecosystem processes are more variable (less stable or reliable) at lower diversity (see review by McCann, pages 228–233, and refs 8–10). The greater stability of more diverse ecosystems seems to result from three processes^{11–14}. The first is comparable to the economic process that causes a more diverse investment portfolio to be less volatile. Because species, like corporations, differ from each other, they tend to respond somewhat independently to environmental variability. The more species that such variability is averaged across, the less variable is their total¹¹. Second, species within a given trophic level often compete with each other, which causes their abundances to negatively covary. When one species declines, another is freed from competition and increases. This negative covariance reduces the variability of the community as a whole^{13,14}. Finally, measures of temporal stability compute variability relative to mean abundance, such as by using the ratio of community abundance to its temporal standard deviation. The tendency for community

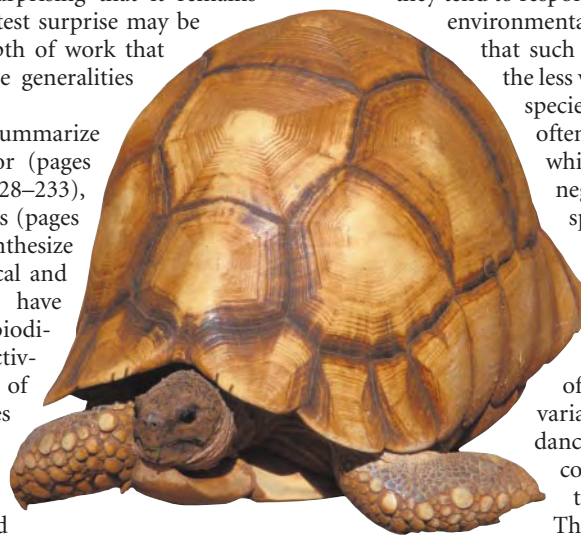




Figure 1 Biodiversity experiments, such as this one in Minnesota⁶ or the other experiments reviewed by Chapin *et al.* (pages 234–242) and by Purvis and Hector (pages 212–219), have shown that a greater number of plant species leads to greater community productivity. In the experiment shown, 245 plots, each 9 m × 9 m, were assigned randomly to have from 1 to 16 prairie plant species, with the species composition of each plot being separately chosen at random⁶. Species composition and plant diversity were both strong determinants of ecosystem functioning.

abundance to increase as diversity increases thus causes this ratio, which is a measure of stability, to increase as diversity increases¹⁴.

In total, biodiversity, which ten years ago was considered unimportant by most ecosystem ecologists, has now been shown to impact significantly upon many aspects of ecosystem functioning. Diversity must now be added to the list of factors — including species composition, disturbance regime, soil type and climate — that influence ecosystem functioning. The recent rediscovery of the importance of biodiversity highlights an under-appreciated truth — although society is dependent on natural and managed ecosystems for goods and services that are essential for human survival, we know all too little about how ecosystems work.

Two sets of unanswered scientific questions come to the forefront. First, why is the world so diverse; that is, what forces and processes led to the evolution and persistence of so many species? This is not merely an academic question. The processes that allow interacting species to coexist in an ecosystem simultaneously influence the productivity, nutrient dynamics and stability of that ecosystem. Second, what are the mechanisms by which the loss of diversity impacts the functioning of ecosystems, how general are these mechanisms, and how important is biodiversity relative to other factors that influence ecosystem functioning? In addition, the realization that human actions are harming, perhaps irreversibly, the ecosystems upon which humans depend raises a third, philosophical question: what should be the role of scientists and science in the development of ethics and policy?

Coexistence and ecosystem functioning

Both our understanding of the effects of biodiversity on ecosystem processes, and the effectiveness of alternative strategies for the preservation of biodiversity, are limited by our knowledge of the mechanisms that maintain diversity. The mechanisms most relevant to ecosystem functioning are those that maintain diversity on the

local scales within which individuals of one species interact with individuals of other species. It is from such interactions among individuals of different species that diversity is expected to impact ecosystem processes.

What are these mechanisms of coexistence? At present there are an abundance of alternative hypotheses but no clear demonstrations of the actual processes that maintain the diversity of species-rich ecosystems. In a general sense, coexistence requires the existence of evolutionarily persistent interspecific trade-offs in the abilities of species to deal with the factors that constrain their fitness and abundance. However, there are many potential constraints and trade-offs. Species may coexist because of interspecific trade-offs (1) between their competitive abilities and their dispersal abilities; (2) between their competitive abilities and their susceptibility to disease, herbivory or predation; (3) between their abilities to live off average conditions and their abilities to exploit resource pulses; or (4) between their abilities to compete for alternative resources in a heterogeneous landscape^{15–18}.

The effects on ecosystem functioning of many such mechanisms of coexistence have yet to be determined theoretically. However, it is already clear that the underlying mechanisms of coexistence can greatly influence how diversity affects ecosystem processes^{19,20}. Consider, for instance, plant species that coexist in a spatially heterogeneous habitat because of differences in both the soil pH and the temperature (which varies seasonally) at which each grows optimally (Fig. 2a). Such niche differentiation²⁰ causes the predicted productivity of plant communities to be an increasing function of plant diversity (Fig. 2b). Moreover, the pattern of this increase is such that there are some species combinations at a given level of diversity that are more productive than any possible combination of fewer species (Fig. 2b). The greater productivity of higher diversity communities occurs because, in such heterogeneous habitats, each species is a superior performer in only a portion of sites. Clearly, the magnitude

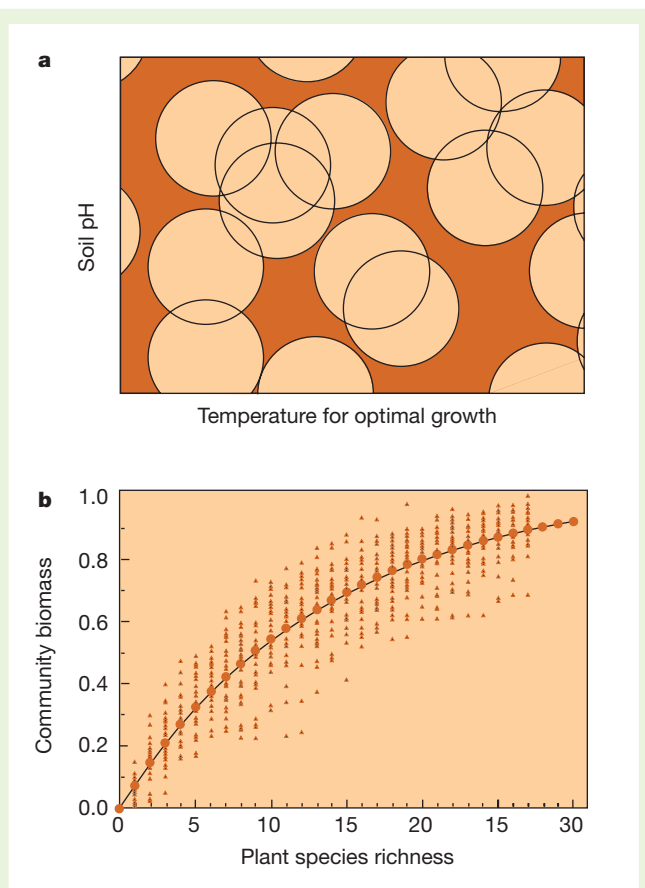


Figure 2 Niche differentiation and productivity. **a**, A simple model — the ‘snowballs on the barn’ model — of niche differentiation and coexistence²⁰. The range of conditions in which each species can exist is shown with a circle, the position of which is defined by its centre. By randomly choosing locations for various numbers of circles (species), it is possible to calculate the effect of diversity on the ‘coverage’ of the heterogeneous habitat. The amount of such coverage is proportional to community biomass. **b**, Results of simulations (triangles) and of an analytical solution (solid curve) to the effects of diversity on community productivity for the snowballs on the barn model²⁰.

of this effect increases as heterogeneity or diversity increase. Increased diversity leads, on average, to increased ‘coverage’ of the habitat conditions, that is, to increased efficiency of resource capture and use, because diversity increases the chance that the species that are better able to handle particular conditions are present. Assuming that species are chosen at random, diversity is a simple way to measure the range and coverage of species traits in a community.

In contrast, consider a case in which interspecific interactions are based on direct antagonism and not on efficiency of resource use. For a simple formulation, let there be an interspecific trade-off between competitive ability and productivity. Species that achieve greater productivity in monoculture would be poorer competitors, attaining lower abundances when competing. Because greater diversity increases the chance that a competitively superior but lower-yielding species would be present, productivity would, on average, be a decreasing function of diversity. This is a simple variant on the sampling-effect model^{20–22}, here modified to have better competitors be less, rather than more, productive.

What, then, is implied by available experimental results, which have shown that productivity is an increasing function of plant species diversity? They indicate that coexistence through niche differentiation and related processes may be more prevalent in nature than coexistence through antagonism and related processes, at least

for the types of communities studied so far. Expressed another way, much of nature may have a free-market economy, structured by the efficiencies of open competition among species, rather than an economy structured by pre-emption and other monopolistic practices. Such speculations may be premature, especially because complex systems containing many trophic levels (for example, plants, decomposers, herbivores and predators) are, as yet, poorly studied. However, they highlight the conceptual links between economics and ecology — disciplinary links that must be strengthened if ecological knowledge is to be used to help create a sustainable human economy.

Societal trade-offs and ethics

The progress made during the past seven years in understanding these issues underscores the potential implications of habitat simplification and loss of diversity for the ecosystem goods and services²³ upon which humans depend. The species presently inhabiting Earth are the result of over 3 billion years of natural selection that likely favoured efficiency, productivity and specialization. These organisms are the catalysts that capture and transform energy and materials, producing, among other things, food, fuel, fibre and medicines. These species recycle wastes, create pure drinking water, drive global biogeochemical cycles that created and maintain an aerobic atmosphere, regulate global climate through effects on greenhouse gases and local climate through effects on evapotranspiration, generate soil fertility, and provide other ecosystem goods and services²³. In addition, the Earth’s biodiversity is the source of all crops and all pollinators of crops, of all livestock, and of many pharmaceuticals and pesticides. Just three crops — corn, rice and wheat — provide about 60% of the human food supply. The viability of these crops depends on the maintenance of high genetic diversity²⁴, which can allow, among other things, development of strains that are resistant to emerging and evolving diseases and pests²⁵. In the long term, food stability will require development of new crops from what are now wild plants, because disease or pesticide-resistant pests will cause the loss of current crops, just as disease caused the loss of chestnut, elm and other tree species from North American forests.

Humans, like all other organisms, experience trade-offs. The loss of biodiversity will diminish the capacity of ecosystems to provide society with a stable and sustainable supply of essential goods and services, but many of the very actions that harm biodiversity simultaneously provide valuable societal benefits. There exists a trade-off defining the net benefits that society receives from the various ways that humans could use and impact nature, but, as yet, this is poorly defined. This trade-off itself is likely to shift through time in response to the remaining amounts and states of various resources, including biodiversity. The amounts and states of biotic resources have changed rapidly during the past century, as global population increased 3.7-fold and per capita gross domestic product, a reasonable proxy for consumption, increased 4.6-fold²⁶. It seems likely that environmental policy that is optimal from a societal perspective would be markedly different now from that of 250 years ago. However, we still use environmental and land-use ethics, codified in law, that were articulated during the era when the human population, at one-tenth its present size, tamed wilderness with axe and ox.

Science has much to contribute to dialogues on policy and ethics. Although academic institutions seem to value such contributions less than contributions to peer-reviewed journals, this is short-sighted. Ultimately, society invests in science because advances in scientific knowledge benefit society. The ethics of science cannot eschew involvement in public discourse. Science must contribute, in an open, unbiased manner, to relevant issues.

Because of the emergence of human domination of global ecosystems, society faces new, tough trade-offs. These include trade-offs between the current benefits and the future costs of environmental damage, and between benefits to a few and costs to many. Research is needed to quantify these trade-offs, and the work done so far on

biodiversity provides a good start. Additional work, at the interface between ecology and economics, is needed to quantify the immediate and long-term costs and benefits of alternative actions.

The world that will exist in 100 and 1,000 years will, unavoidably, be of human design, whether deliberate or haphazard. The principles that should guide this design must be based on science, much of it done only sketchily to date, and on ethics. Ethics should, among other things, apportion costs and benefits between individuals and society as a whole, and between current generations and all future generations. A sustainable world will require an ethic that is ultimately as incorporated into culture and as long lasting as a constitutional bill of rights or as religious commandments. The Earth will retain its most striking feature, its biodiversity, only if humans have the prescience to do so. This will occur, it seems, only if we realize the extent to which we use biodiversity. □

1. Vitousek, P. M., Mooney, H. A., Lubchenco, J. & Melillo, J. M. Human domination of earth's ecosystems. *Science* **277**, 494–499 (1997).
2. Darwin, C. *The Origin of Species by Means of Natural Selection* (reprinted by The Modern Library, Random House, New York, 1859).
3. Elton, C. S. *The Ecology of Invasions by Animals and Plants* (Methuen, London, 1958).
4. Schulze, E. D. & Mooney, H. A. *Biodiversity and Ecosystem Function* (Springer, Berlin, 1993).
5. Tilman, D., Wedin, D. & Knops, J. Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature* **379**, 718–720 (1996).
6. Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M. & Siemann, E. The influence of functional diversity and composition on ecosystem processes. *Science* **277**, 1300–1302 (1997).
7. Hector, A. *et al.* Plant diversity and productivity experiments in European grasslands. *Science* **286**, 1123–1127 (1999).
8. Tilman, D. & Downing, J.A. Biodiversity and stability in grasslands. *Nature* **367**, 363–365 (1994).
9. McGrady-Steed, J., Harris, P. M. & Morin, P. J. Biodiversity regulates ecosystem predictability. *Nature* **390**, 162–165 (1997).
10. Naeem, S. & Li, S. Biodiversity enhances ecosystem reliability. *Nature* **390**, 507–509 (1997).
11. Doak, D. F. *et al.* The statistical inevitability of stability-diversity relationships in community ecology. *Am. Nat.* **151**, 264–276 (1998).
12. Tilman, D., Lehman, C. L. & Bristow, C. E. Diversity-stability relationships: statistical inevitability or ecological consequence? *Am. Nat.* **151**, 277–282 (1998).
13. Tilman, D. Biodiversity: population versus ecosystem stability. *Ecology* **77**, 350–363 (1996).
14. Tilman, D. The ecological consequences of changes in biodiversity: a search for general principles. *Ecology* **80**, 1455–1474 (1999).
15. Hastings, A. Disturbance, coexistence, history, and competition for space. *Theor. Popul. Biol.* **18**, 363–373 (1980).
16. Armstrong, R. A. & McGehee, R. Competitive exclusion. *Am. Nat.* **115**, 151–170 (1980).
17. Huisman, J. & Weissing, F. J. Biodiversity of phytoplankton by species oscillations and chaos. *Nature* **402**, 407–410 (1999).
18. Tilman, D. *Resource Competition and Community Structure* (Monographs in Population Biology, Princeton Univ. Press, 1982).
19. Loreau, M. Biodiversity and ecosystem functioning: a mechanistic model. *Proc. Natl Acad. Sci. USA* **95**, 5632–5636 (1998).
20. Tilman, D., Lehman, C. L. & Thomson, K. T. Plant diversity and ecosystem productivity: theoretical considerations. *Proc. Natl Acad. Sci. USA* **94**, 1857–1861 (1997).
21. Huston, M. A. Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia* **110**, 449–460 (1997).
22. Aarssen, L. W. High productivity in grassland ecosystems: effected by species diversity or productive species? *Oikos* **80**, 183–184 (1997).
23. Daily, G. C. *Nature's Services: Societal Dependence on Natural Ecosystems* (Island, Washington DC, 1997).
24. Fehr, W. H. *Genetic Contributions to Yield Gains of Five Major Crop Plants* (Crop Science Society of America, Madison, WI, 1984).
25. Roelfs, A. P. Genetic control of phenotypes in wheat stem rust. *Annu. Rev. Phytopathol.* **26**, 351–367 (1988).
26. Maddison, A. *Monitoring the World Economy 1820–1992* (Development Centre of the Organization for Economic Co-operation and Development, Paris, 1995).



Consequences of changing biodiversity

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Human alteration of the global environment has triggered the sixth major extinction event in the history of life and caused widespread changes in the global distribution of organisms. These changes in biodiversity alter ecosystem processes and change the resilience of ecosystems to environmental change. This has profound consequences for services that humans derive from ecosystems. The large ecological and societal consequences of changing biodiversity should be minimized to preserve options for future solutions to global environmental problems.

Humans have extensively altered the global environment, changing global biogeochemical cycles, transforming land and enhancing the mobility of biota. Fossil-fuel combustion and deforestation have increased the concentration of atmospheric carbon dioxide (CO₂) by 30% in the past three centuries (with more than half of this increase occurring in the past 40 years). We have more than doubled the concentration of methane and increased concentrations of other gases that contribute to climate warming. In the next century these greenhouse gases are likely to cause the most rapid climate change that the Earth has experienced since the end of the last glaciation 18,000 years ago and perhaps a much longer time. Industrial fixation of nitrogen for fertilizer and other human activities has more than doubled the rates of terrestrial fixation of gaseous nitrogen into biologically available forms. Run off of nutrients from agricultural and urban systems has increased several-fold in the developed river basins of the Earth, causing major ecological changes in estuaries and coastal zones. Humans have transformed 40–50% of the ice-free land surface, changing prairies, forests and wetlands into agricultural and urban systems. We dominate (directly or indirectly) about one-third of the net primary productivity on land and harvest fish that use 8% of ocean productivity. We use 54% of the available fresh water, with use projected to increase to 70% by 2050¹. Finally, the mobility of people has transported organisms across geographical barriers that long kept the biotic regions of the Earth separated, so that many of the ecologically important plant and animal species of many areas have been introduced in historic time^{2,3}.

Together these changes have altered the biological diversity of the Earth (Fig. 1). Many species have been eliminated from areas dominated by human influences. Even in

preserves, native species are often out-competed or consumed by organisms introduced from elsewhere. Extinction is a natural process, but it is occurring at an unnaturally rapid rate as a consequence of human activities. Already we have caused the extinction of 5–20% of the species in many groups of organisms (Fig. 2), and current rates of extinction are estimated to be 100–1,000 times greater than pre-human rates^{4,5}.

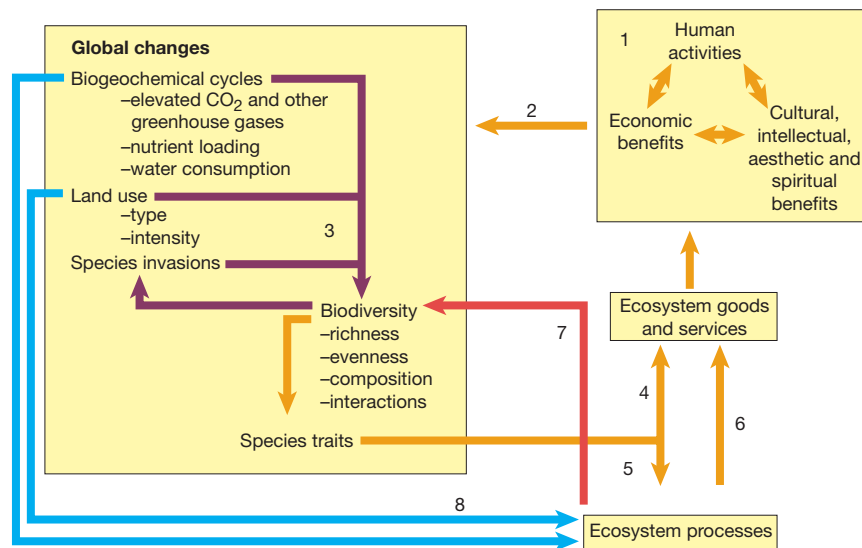
In the absence of major changes in policy and human behaviour, our effects on the environment will continue to alter biodiversity. Land-use change is projected to have the largest global impact on biodiversity by the year 2100, followed by climate change, nitrogen deposition, species introductions and changing concentrations of atmospheric CO₂ (ref. 6). Land-use change is expected to be of particular importance in the tropics, climatic change is likely to be important at high latitudes, and a multitude of interacting causes will affect other biomes (Fig. 3)⁶. What are the ecological and societal consequences of current and projected effects of human activity on biological diversity?

Ecosystem consequences of altered diversity

Diversity at all organizational levels, ranging from genetic diversity within populations to the diversity of ecosystems in landscapes, contributes to global biodiversity. Here we focus on species diversity, because the causes, patterns and consequences of changes in diversity at this level are relatively well documented. Species diversity has functional consequences because the number and kinds of species present determine the organismal traits that influence ecosystem processes. Species traits may mediate energy and material fluxes directly or may alter abiotic conditions (for example, limiting resources, disturbance and climate) that regulate process rates. The components of species diversity that determine this expression of traits include the number of species present (species richness), their relative abundances (species

Figure 1 The role of biodiversity in global change.

Human activities that are motivated by economic, cultural, intellectual, aesthetic and spiritual goals (1) are now causing environmental and ecological changes of global significance (2). By a variety of mechanisms, these global changes contribute to changing biodiversity, and changing biodiversity feeds back on susceptibility to species invasions (3, purple arrows; see text). Changes in biodiversity, through changes in species traits, can have direct consequences for ecosystem services and, as a result, human economic and social activities (4). In addition, changes in biodiversity can influence ecosystem



processes (5). Altered ecosystem processes can thereby influence ecosystem services that benefit humanity (6) and feedback to further alter biodiversity (7, red arrow). Global changes may also directly affect ecosystem processes (8, blue arrows). Depending on the circumstances, the direct effects of global change may be either stronger or weaker than effects mediated by changes in diversity. We argue that the costs of loss of biotic diversity, although traditionally considered to be 'outside the box' of human welfare, must be recognized in our accounting of the costs and benefits of human activities.

evenness), the particular species present (species composition), the interactions among species (non-additive effects), and the temporal and spatial variation in these properties. In addition to its effects on current functioning of ecosystems, species diversity influences the resilience and resistance of ecosystems to environmental change.

Species richness and evenness

Most theoretical and empirical work on the functional consequences of changing biodiversity has focused on the relationship between species richness and ecosystem functioning. Theoretical possibilities include positive linear and asymptotic relationships between richness and rates of ecosystem processes, or the lack of a simple statistical relationship⁷ (Box 1). In experiments, species richness correlates with rates of ecosystem processes most clearly at low numbers of species. We know much less about the impact of species richness in species-rich, natural ecosystems. Several studies using experimental species assemblages have shown that annual rates of primary productivity and nutrient retention increase with increasing plant species richness, but saturate at a rather low number of species^{8,9}. Arbuscular

mycorrhizal species richness also seems to enhance plant production in an asymptotic fashion, although phosphorus uptake was enhanced in a linear fashion from 1 to 14 species of fungi¹⁰. Microbial richness can lead to increased decomposition of organic matter¹¹. In contrast, no consistent statistical relationship has been observed between plant species richness of litter inputs and decomposition rate¹². Thus, in experimental communities (which typically focus on only one or two trophic levels), there seems to be no universal relationship between species richness and ecosystem functioning, perhaps because processes differ in their sensitivity to species richness compared with other components of diversity (such as evenness, composition or interactions). The absence of a simple relationship between species richness and ecosystem processes is likely when one or a few species have strong ecosystem effects.

Although the relationship of species richness to ecosystem functioning has attracted considerable theoretical and experimental attention because of the irreversibility of species extinction, human activities influence the relative abundances of species more frequently than the presence or absence of species. Changes in species evenness warrant increased attention, because they usually respond more rapidly to human activities than do changes in species richness and because they have important consequences to ecosystems long before a species is threatened by extinction.

Species composition

Particular species can have strong effects on ecosystem processes by directly mediating energy and material fluxes or by altering abiotic conditions that regulate the rates of these processes (Fig. 4)^{13,14}. Species' alteration of the availability of limiting resources, the disturbance regime, and the climate can have particularly strong effects on ecosystem processes. Such effects are most visible when introduced species alter previous patterns of ecosystem processes. For example, the introduction of the nitrogen-fixing tree *Myrica faya* to nitrogen-limited ecosystems in Hawaii led to a fivefold increase in nitrogen inputs to the ecosystem, which in turn changed most of the functional and structural properties of native forests¹⁵. Introduction of the deep-rooted salt cedar (*Tamarix* sp.) to the Mojave and Sonoran Deserts of North America increased the water and soil solutes

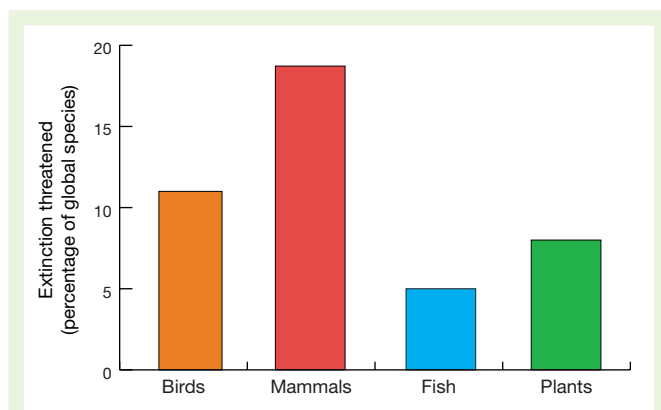


Figure 2 Proportion of the global number of species of birds, mammals, fish and plants that are currently threatened with extinction⁴.

Box 1

Species richness and ecosystem functioning

There has been substantial debate over both the form of the relationship between species richness and ecosystem processes and the mechanisms underlying these relationships⁶⁵. Theoretically, rates of ecosystem processes might increase linearly with species richness if all species contribute substantially and in unique ways to a given process — that is, have complementary niches. This relationship is likely to saturate as niche overlap, or ‘redundancy’, increases at higher levels of diversity⁶⁶. Several experiments indicate such an asymptotic relationship of ecosystem process rates with species richness. An asymptotic relationship between richness and process rates could, however, arise from a ‘sampling effect’ of increased probability of including a species with strong ecosystem effects, as species richness increases¹³. The sampling effect has at least two interpretations. It might be an important biological property of communities that influences process rates in natural ecosystems¹⁹, or it might be an artefact of species-richness experiments in which species are randomly assigned to treatments, rather than following community assembly rules that might occur in nature⁶⁷. Finally, ecosystem process rates may show no simple correlation with species richness. However, the lack of a simple statistical relationship between species richness and an ecosystem process may mask important functional relationships. This could occur, for example, if process rates depend strongly on the traits of certain species or if species interactions determine the species traits that are expressed (the ‘idiosyncratic hypothesis’)⁷. This mechanistic debate is important scientifically for understanding the functioning of ecosystems and effective management of their biotic resources. Regardless of the outcome of the debate, conserving biodiversity is essential because we rarely know *a priori* which species are critical to current functioning or provide resilience and resistance to environmental changes.

accessed by vegetation, enhanced productivity, and increased surface litter and salts. This inhibited the regeneration of many native species, leading to a general reduction in biodiversity¹⁶. The perennial tussock grass, *Agropyron cristatum*, which was widely introduced to the northern Great Plains of North America after the 1930s ‘dustbowl’, has substantially lower allocation to roots compared with native prairie grasses. Soil under *A. cristatum* has lower levels of available nitrogen and ~25% less total carbon than native prairie soil, so the introduction of this species resulted in an equivalent reduction of 480×10^{12} g carbon stored in soils¹⁷. Soil invertebrates, such as earthworms and termites, also alter turnover of organic matter and nutrient supply, thereby influencing the species composition of the aboveground flora and fauna¹⁸.

Species can also influence disturbance regime. For example, several species of nutritious but flammable grasses were introduced to the Hawaiian Islands to support cattle grazing. Some of these grasses spread into protected woodlands, where they caused a 300-fold increase in the extent of fire. Most of the woody plants, including some endangered species, are eliminated by fire, whereas grasses

rebound quickly¹⁹. Similar increases in the ecological role of fire resulting from grass invasions have been widely observed in the Americas, Australia and elsewhere in Oceania. The invasion of cheatgrass (*Bromus tectorum*) into western North America is one of the most extensive of these invasions. Cheatgrass has increased fire frequency by a factor of more than ten in the >40 million hectares (1 ha = 10^4 m²) that it now dominates²⁰.

Species-induced changes in microclimate can be just as important as the direct impacts of environmental change. For example, in late-successional boreal forests, where soil temperatures have a strong influence on nutrient supply and productivity, the presence of moss, which reduces heat flux into the soil, contributes to the stability of permafrost (frozen soils) and the characteristically low rates of nutrient cycling²¹. As fire frequency increases in response to high-latitude warming, moss biomass declines, permafrost becomes less stable, the nutrient supply increases, and the species composition of forests is altered. Plant traits can also influence climate at larger scales. Simulations with general circulation models indicate that widespread replacement of deep-rooted tropical trees by shallow-

Figure 3 Scenarios of change in species diversity in selected biomes by the year 2100. The values are the projected change in diversity for each biome relative to the biome with greatest projected diversity change⁶. Biomes are: tropical forests (T), grasslands (G), Mediterranean (M), desert (D), north temperate forests (N), boreal forests (B) and arctic (A). Projected change in species diversity is calculated assuming three alternative scenarios of interactions among the causes of diversity change. Scenario 1 assumes no interaction among causes of diversity change, so that the total change in diversity is the sum of the changes caused by each driver of diversity change. Scenario 2 assumes that only the factor with the greatest impact on diversity influences diversity change. Scenario 3 assumes that factors causing change in biodiversity interact multiplicatively to determine diversity change. For scenarios 1 and 2, we show the relative importance of the major causes of projected change in diversity. These causes are climatic change, change in land use, introduction of exotic species, and changes in atmospheric CO₂ and/or nitrogen deposition (labelled ‘other’). The graph shows that all biomes are projected to experience substantial change in species diversity by 2100, that the most important causes of diversity change differ among biomes, and that the patterns of diversity change depend on assumptions about the nature of interactions among the causes of diversity change. Projected biodiversity change is most similar among biomes if causes of diversity change do not interact (scenario 1) and differ most strongly among biomes if the causes of biodiversity change interact multiplicatively (scenario 3).

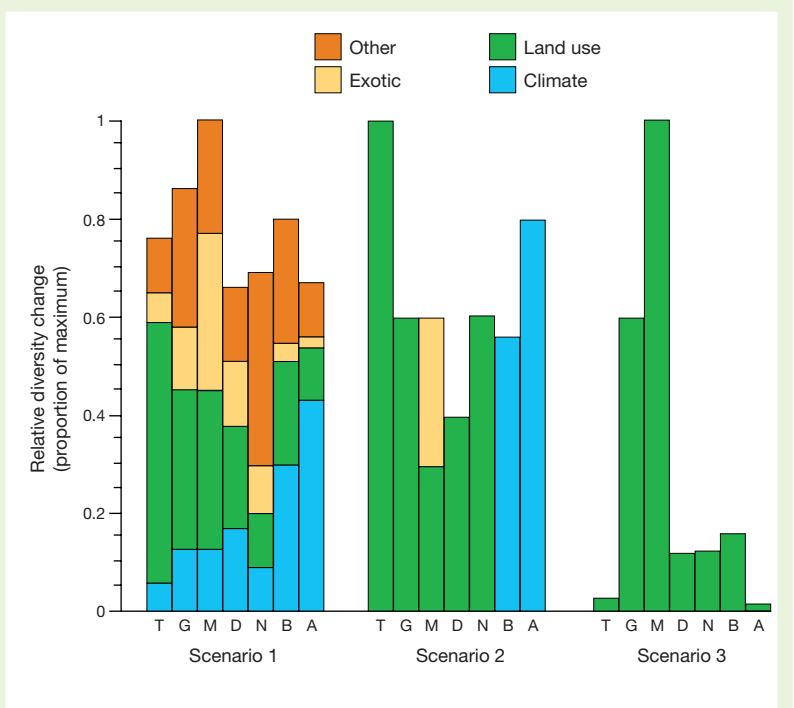
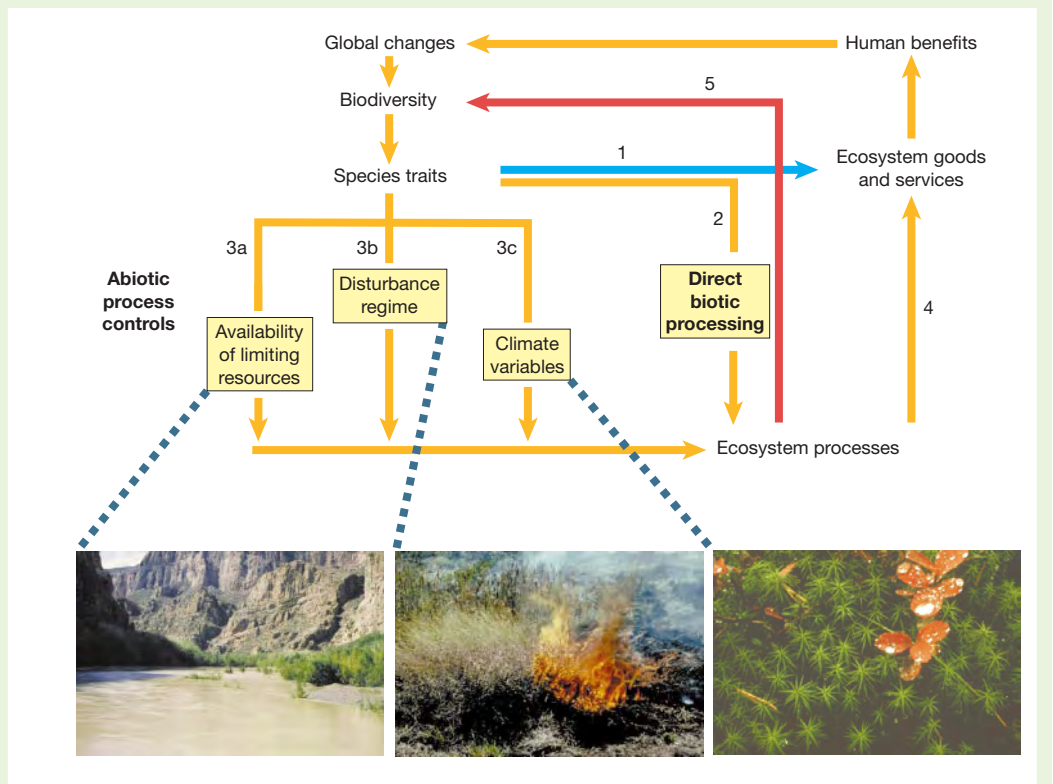


Figure 4 Mechanisms by which species traits affect ecosystem processes. Changes in biodiversity alter the functional traits of species in an ecosystem in ways that directly influence ecosystem goods and services (1) either positively (for example, increased agricultural or forestry production) or negatively (for example, loss of harvestable species or species with strong aesthetic/cultural value). Changes in species traits affect ecosystem processes directly through changes in biotic controls (2) and indirectly through changes in abiotic controls, such as availability of limiting resources (3a), disturbance regime (3b), or micro- or macroclimate variables (3c). Illustrations of these effects include: reduction in river flow due to invasion of deep-rooted desert trees (3a; photo by E. Zavaleta); increased fire frequency resulting from grass invasion that destroys native trees and shrubs in Hawaii (3b, photo by C. D'Antonio); and insulation of soils by mosses in arctic tundra, contributing to conditions that allow for permafrost (3c; photo by D. Hooper). Altered processes can then influence the availability of ecosystem goods and services directly (4) or indirectly by further altering biodiversity (5), resulting in loss of useful species or increases in noxious species.



rooted pasture grasses would reduce evapotranspiration and lead to a warmer, drier climate²². At high latitudes, the replacement of snow-covered tundra by a dark conifer canopy will probably increase energy absorption sufficiently to act as a powerful positive feedback to regional warming²³.

Species interactions

Most ecosystem processes are non-additive functions of the traits of two or more species, because interactions among species, rather than simple presence or absence of species, determine ecosystem characteristics (Fig. 5). Species interactions, including mutualism, trophic interactions (predation, parasitism and herbivory), and competition may affect ecosystem processes directly by modifying pathways of energy and material flow²⁴ or indirectly by modifying the abundances or traits of species with strong ecosystem effects²⁵.

Mutualistic species interactions contribute directly to many essential ecosystem processes. For example, nitrogen inputs to terrestrial ecosystems are mediated primarily by mutualistic associations between plants and nitrogen-fixing microorganisms. Mycorrhizal associations between plant roots and fungi greatly aid plant nutrient uptake from soil, increase primary production and speed succession²⁶. Highly integrated communities (consortia) of soil microorganisms, in which each species contributes a distinct set of enzymes, speeds the decomposition of organic matter²⁷. Many of these interactions have a high degree of specificity, which increases the probability that loss of a given species will have cascading effects on the rest of the system.

Trophic interactions can have large effects on ecosystem processes either by directly modifying fluxes of energy and materials, or by influencing the abundances of species that control those fluxes. When top predators are removed, prey populations sometimes explode and deplete their food resources, leading to a cascade of ecological effects. For example, removal of sea otters by Russian fur traders allowed a population explosion of sea urchins that

overgrazed kelp²⁸ (Fig. 6a). Recent over-fishing in the North Pacific may have triggered similar outbreaks of sea urchin, as killer whales moved closer to shore and switched to sea otters as an alternate prey²⁹. In the absence of dense populations of sea urchins, kelp provides the physical structure for diverse subtidal communities and attenuates waves that otherwise augment coastal erosion and storm damage³⁰. Removing bass from lakes that were fertilized with phosphorus caused an increase in minnows, which depleted the biomass of phytoplankton grazers and caused algal blooms³¹ (Fig. 6b). The algal blooms turned the lake from a net source to a net sink of CO₂. Thus, biotic change and altered nutrient cycles can interact to influence whole-system carbon balance. The zebra mussel (*Dreissena polymorpha*) is a bottom-dwelling invasive species that, through its filter feeding, markedly reduces phytoplankton while increasing water clarity and phosphorus availability³². Introduction of this species shifts the controlling interactions of the food web from the water column to the sediments. Trophic interactions are also important in terrestrial ecosystems. At the micro scale, predation on bacteria by protozoan grazers speeds nitrogen cycling near plant roots, enhancing nitrogen availability to plants³³. At the regional scale, an improvement in hunting technology at the end of the Pleistocene may have contributed to the loss of the Pleistocene megafauna and the widespread change from steppe grassland to tundra that occurred in Siberia 10,000–18,000 years ago³⁴. The resulting increase in mosses insulated the soil and led to cooler soils, less decomposition and greater sequestration of carbon in peat. Today, human harvest of animals continues to have a pronounced effect of the functioning of ecosystems.

Competition, mutualisms and trophic interactions frequently lead to secondary interactions among other species, often with strong ecosystem effects (Fig. 5). For example, soil microbial composition can modify the outcome of competition among plant species³⁵, and plants modify the microbial community of their

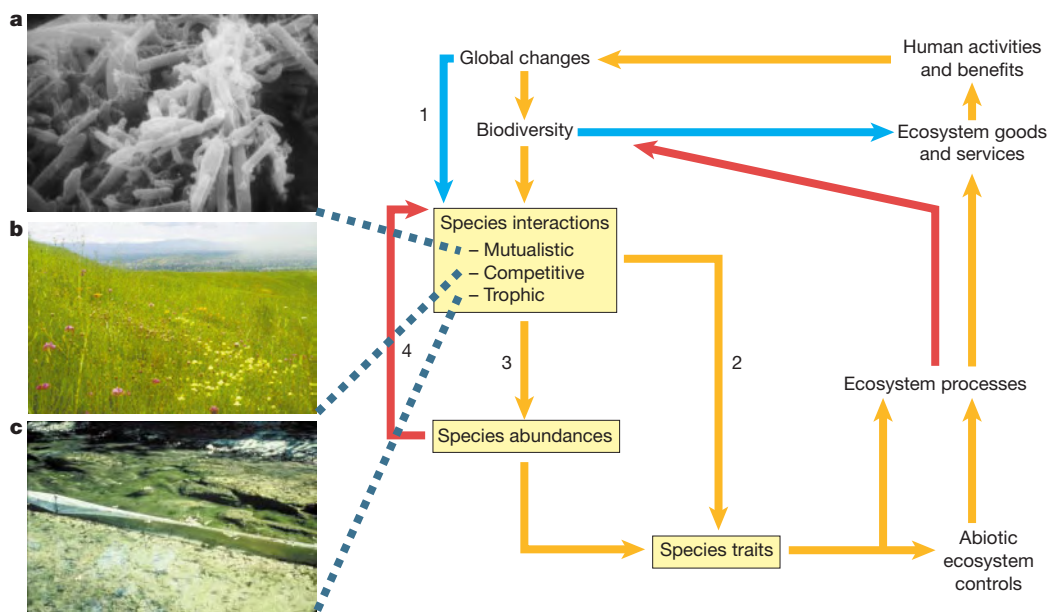


Figure 5 Mechanisms by which species interactions affect ecosystem processes. Global environmental change affects species interactions (mutualism, competition and trophic interactions) both directly (1) and through its effects on altered biodiversity. Species interactions may directly affect key traits (for example, the inhibition of microbial nitrogen fixation by plant secondary metabolites) in ecosystem processes (2) or may alter the abundances of species with key traits (3). Examples of these species interactions include (a) mutualistic consortia of microorganisms, each of which produces only some of the enzymes required to break down organic matter (photo by M. Klug), (b) altered abundances of native California forbs due to competition from introduced European grasses (photo by H. Reynolds), and (c) alteration of algal biomass due to presence or absence of grazing minnows⁸⁴ (photo by M. Power). Changes in species interactions and the resulting changes in community composition (3) may feedback to cause a cascade of further effects on species interactions (4).

neighbours, which, in turn, affects nitrogen supply and plant growth³⁶. Stream predatory invertebrates alter the behaviour of their prey, making them more vulnerable to fish predation, which leads to an increase in the weight gain of fish³⁷. In the terrestrial realm, grazers can reduce grass cover to the point that avian predators keep vole populations at low densities, allowing the persistence of *Erodium botrys*, a preferred food of voles³⁸. The presence of *E. botrys* increases leaching³⁹ and increases soil moisture⁴⁰, which often limits production and nutrient cycling in dry grasslands. These examples clearly indicate that all types of organisms — plants, animals and microorganisms — must be considered in understanding the effects of biodiversity on ecosystem functioning. Although each of these examples is unique to a particular ecosystem, the ubiquitous nature of species interactions with strong ecosystem effects makes these interactions a general feature of ecosystem functioning. In many cases, changes in these interactions alter the traits that are expressed by species and therefore the effects of species on ecosystem processes. Consequently, simply knowing that a species is present or absent is insufficient to predict its impact on ecosystems.

Many global changes alter the nature or timing of species interactions⁴¹. For example, the timing of plant flowering and the emergence of pollinating insects differ in their responses to warming, with potentially large effects on ecosystems and communities⁴². Plant–herbivore interactions in diverse communities are less likely to be disrupted by elevated CO₂ (ref. 43) than in simple systems involving one specialist herbivore and its host plant⁴⁴.

Resistance and resilience to change

The diversity–stability hypothesis suggests that diversity provides a general insurance policy that minimizes the chance of large ecosystem changes in response to global environmental change⁴⁵. Microbial microcosm experiments show less variability in ecosystem processes in communities with greater species richness⁴⁶, perhaps because every species has a slightly different response to its physical and biotic environment. The larger the number of functionally similar species

in a community, the greater is the probability that at least some of these species will survive stochastic or directional changes in environment and maintain the current properties of the ecosystem⁴⁷. This stability of processes has societal relevance. Many traditional farmers plant diverse crops, not to maximize productivity in a given year, but to decrease the chances of crop failure in a bad year⁴⁸. Even the loss of rare species may jeopardize the resilience of ecosystems. For example, in rangeland ecosystems, rare species that are functionally similar to abundant ones become more common when grazing reduces their abundant counterparts. This compensation in response to release from competition minimizes the changes in ecosystem properties⁴⁹.

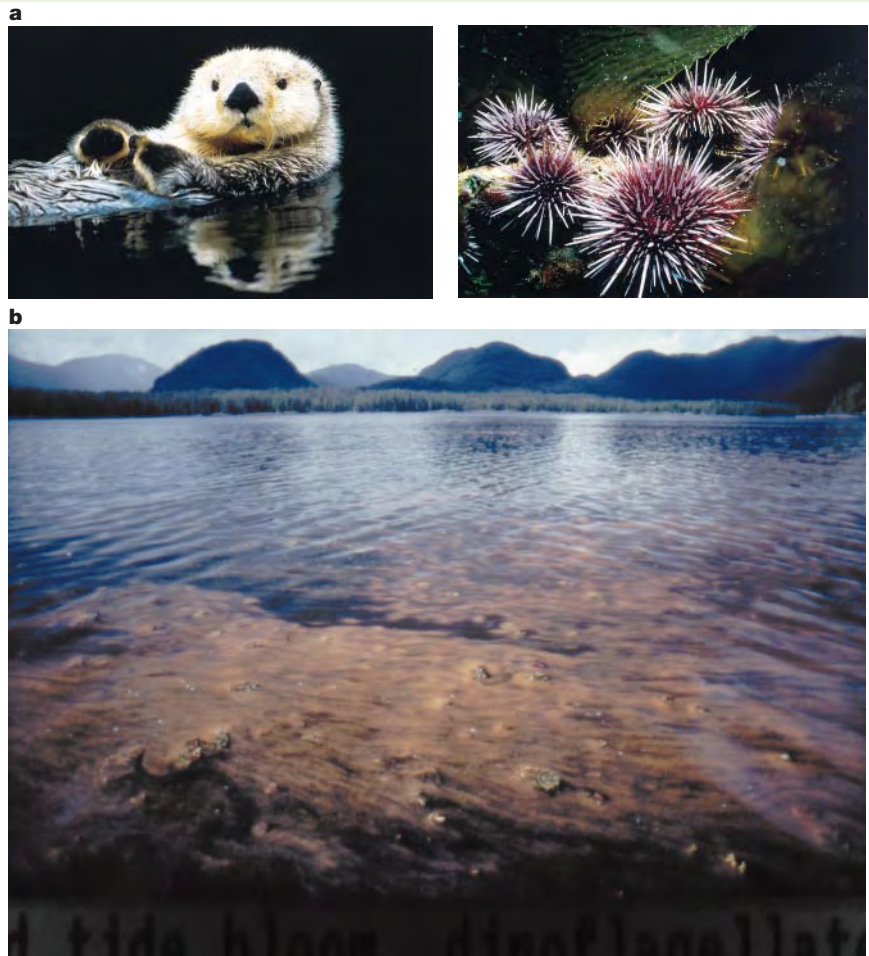
Species diversity also reduces the probability of outbreaks by ‘pest’ species by diluting the availability of their hosts. This decreases host-specific diseases⁵⁰, plant-feeding nematodes⁵¹ and consumption of preferred plant species⁵². In soils, microbial diversity decreases fungal diseases owing to competition and interference among microbes⁵³.

Resistance to invasions

Biodiversity can influence the ability of exotic species to invade communities through either the influence of traits of resident species or some cumulative effect of species richness. Early theoretical models and observations of invasions on islands indicated that species-poor communities would be more vulnerable to invasions because they offered more empty niches⁵⁴. However, studies of intact ecosystems find both negative⁵⁵ and positive⁵⁶ correlations between species richness and invasions. This occurs in part because the underlying factors that generate differences in diversity (for example, propagule supply, disturbance regime and soil fertility) cannot be controlled and may themselves be responsible for differences in invasibility⁵⁶. The diversity effects on invasibility are scale-dependent in some cases. For example, at the plot scale, where competitive interactions might exert their effect, increased plant diversity correlated with lower vulnerability to invasion in Central Plains grasslands of the United States. Across landscape scales, however, ecological factors that promote

Figure 6 Trophic interactions can affect ecosystem processes by influencing species' abundances.

a. Removal of sea otters by Russian fur traders caused an explosion in the population of sea urchins that overgrazed kelp. (Photographs courtesy of M. Sewell/Still Pictures and J. Rotman/BBC Natural History Unit.) **b.** Similarly, changes in the species balance and the abundance of fish can deplete phytoplankton grazers and cause algal blooms. (Photograph courtesy of J. Foott/BBC Natural History Unit.)



native plant diversity (for example, soil type and disturbance regime) also promote species invasions⁵⁷.

Experimental studies with plants⁵⁸ or soil microorganisms⁵⁹ often show that vulnerability to invasion is governed more strongly by the traits of resident and invading species than by species richness *per se*. Both competition and trophic interactions contribute to these effects of community composition on invasibility. For example, in its native range, the Argentine ant (*Linepithaema humile*) is attacked by species-specific parasitoids that modify its behaviour and reduce its ability to dominate food resources and competitively exclude other ant species⁶⁰. These parasitoids are absent from the introduced range of Argentine ants, which may explain their success at eliminating native ant communities in North America⁶¹. Observational and experimental studies together indicate that the effect of species diversity on vulnerability to invasion depends on the components of diversity involved (richness, evenness, composition and species interactions) and their interactions with other ecological factors such as disturbance regime, resource supply and rate of propagule arrival. Humans significantly affect all of these factors (Figs 1, 4), thereby dramatically increasing the incidence of invasions worldwide.

Societal consequences of altered diversity

Biodiversity and its links to ecosystem properties have cultural, intellectual, aesthetic and spiritual values that are important to society. In addition, changes in biodiversity that alter ecosystem functioning have economic impacts through the provision of ecosystem goods and services to society (Fig. 1 and Box 2). Changes in diversity can directly reduce sources of food, fuel, structural materials, medicinals or genetic resources. These changes can also alter the abundance of other species that control ecosystem processes, leading to further

changes in community composition and vulnerability to invasion. Introduction of exotic species or changes in community composition can affect ecosystem goods or services either by directly reducing abundances of useful species (by predation or competition), or by altering controls on critical ecosystem processes (Fig. 4).

These impacts can be wide-ranging and costly. For example, the introduction of deep-rooted species in arid regions reduces supplies and increases costs of water for human use. Marginal water losses to the invasive star thistle, *Centaurea solstitialis*, in the Sacramento River valley, California, have been valued at US\$16–56 million per year (J. D. Gerlach, unpublished results) (Fig. 7). In South Africa's Cape region, the presence of rapidly transpiring exotic pines raises the unit cost of water procurement by nearly 30% (ref. 62). Increased evapotranspiration due to the invasion of *Tamarix* in the United States costs an estimated \$65–180 million per year in reduced municipal and agricultural water supplies⁶³. In addition to raising water costs, the presence of sediment-trapping *Tamarix* stands has narrowed river channels and obstructed over-bank flows throughout the western United States, increasing flood damages by as much as \$50 million annually⁶³.

Those species changes that have greatest ecological impact frequently incur high societal costs. Changes in traits maintaining regional climate²² constitute an ecosystem service whose value in tropical forests has been estimated at \$220 ha⁻¹ yr⁻¹ (ref. 64). The loss or addition of species that alter disturbance regimes can also be costly. The increased fire frequency resulting from the cheatgrass invasion in the western United States has reduced rangeland values and air quality and led to increased expenditures on fire suppression⁶⁵. The disruption of key species interactions can also have large societal and ecological consequences. Large populations of passenger pigeons (*Ectopistes migratorius*) in the northeastern United States

may once have controlled Lyme tick-bearing mice by out-competing them for food⁶⁶. The loss of the passenger pigeon to nineteenth-century over-hunting may, therefore, have contributed to the rise of Lyme disease in humans in the twentieth century. The economic impacts of invasions of novel species are particularly well documented. The introduction and spread of single pests such as the golden apple snail (*Pomacea canaliculata*) and the European corn borer (*Ostrinia nubilalis*) have had major impacts on food production and farm incomes^{67,68}. Estimates of the overall cost of invasions by exotic species in the United States range widely from \$1.1 to \$137 billion annually^{69,70}. In Australia, plant invasions alone entail an annual cost of US\$2.1 billion⁷¹.

The provision of tangible ecosystem goods and services by natural systems depends not only on species' presence or absence but also on their abundance. Large populations of the white-footed mouse (*Peromyscus leucopus*) in the northeastern United States control outbreaks of gypsy moth (*Lymantria dispar*) but spread Lyme disease, whereas small populations of the mouse decrease the incidence of Lyme disease but allow gypsy moth defoliation⁷². An analysis of the costs of changes in biodiversity thus involves more than just analysis of extinctions and invasions. The loss of a species to extinction is of special societal concern, however, because it is irreversible. Future opportunities to learn and derive newly recognized benefits from an extinct species are lost forever. Preventing such a loss preserves an 'option value' for society — the value of attaining more knowledge about species and their contribution to human well being in order to make informed decisions in the future^{73,74}. For example, significant value (\$230–330 million) has been attributed to genetic information gained from preventing land conversion in Jalisco, Mexico, in an area containing a wild grass, teosinte (*Euchlaena mexicana*), that can be used to develop viral-resistant strains of perennial corn⁷³. If this land had been converted to agriculture or human settlements, the societal benefits of development would have come at the expense of an irreversible loss in genetic material that could be used for breeding viral resistance in one of the most widely consumed cereal crops in the world. The perceived costs of diversity loss in this situation might have been small — especially relative to the development benefits — whereas the actual (unrecognized) costs of losing genetic diversity would have been significant (Fig. 8). Decisions to preserve land to gain further information about the societal value of species diversity or ecosystem function typically involve a large degree of uncertainty, which often leads to myopic decisions regarding land use.

Figure 7 Water losses to the invasive, deep-rooted star thistle, *C. solstitialis*, provides an example of the financial impacts of introducing exotic species on ecosystem composition. (Photograph courtesy of P. Collins/A-Z Botanical Collection.)



Box 2

Ecosystem services

Ecosystem services are defined as the processes and conditions of natural ecosystems that support human activity and sustain human life. Such services include the maintenance of soil fertility, climate regulation and natural pest control, and provide flows of ecosystem goods such as food, timber and fresh water. They also provide intangible benefits such as aesthetic and cultural values⁸⁸. Ecosystem services are generated by the biodiversity present in natural ecosystems. Ecologists and economists have begun to quantify the impacts of changes in biodiversity on the delivery of ecosystem services and to attach monetary value to these changes. Techniques used to attach value to biodiversity change range from direct valuation based on market prices to estimates of what individuals are willing to pay to protect endangered wildlife⁸⁹. Although there are estimates of the global values of ecosystem services⁶⁴, valuation of the marginal losses that accompany specific biodiversity changes are most relevant to policy decisions. Predicting the value of such losses involves uncertainty, because ecological and societal systems interact in nonlinear ways and because human preferences change through time. Assumptions today about future values may underestimate the values placed on natural systems by future generations⁸⁹. Therefore, minimizing loss of biodiversity offers a conservative strategy for maintaining this value.

Global environmental changes have the potential to exacerbate the ecological and societal impacts of changes in biodiversity⁶. In many regions, land conversion forces declining populations towards the edges of their species range, where they become increasingly vulnerable to collapse if exposed to further human impact⁷⁵. Warming allows the poleward spread of exotics and pathogens, such as dengue- and malaria-transmitting mosquitoes (*Aedes* and *Anopheles* sp.)⁷⁶ and pests of key food crops, such as corn-boring insects⁶⁸. Warming can also exacerbate the impacts of water-consuming invasive plant species in water-scarce areas by increasing regional water losses. The *Tamarix*-invaded Colorado River in the United States currently has a mean annual flow that is 10% less than regional water allocations for human use⁷⁷. Warming by 4°C would reduce the flow of the Colorado River by more than 20%, further increasing the marginal costs of water losses to *Tamarix*⁷⁸. Similar impacts of global change in regions such as Sahelian Africa, which have less water and less well developed distribution mechanisms, might directly affect human survival. In many cases, accelerated biodiversity loss is already jeopardizing the livelihoods of traditional peoples⁷⁹.

The combination of irreversible species losses and positive feedbacks between biodiversity changes and ecosystem processes are likely to cause nonlinear cost increases to society in the future, particularly when thresholds of ecosystem resilience are exceeded⁸⁰. For example, *Imperata cylindrica*, an aggressive indigenous grass, colonizes forest lands of Asia that are cleared for slash-and-burn agriculture, forming a monoculture grassland with no vascular plant diversity and many fewer mammalian species than the native forest. The total area of *Imperata* in Asia is currently about 35 million ha (4% of land area)⁸¹. Once in place, *Imperata* is difficult and costly to remove and enhances fire, which promotes the spread of the grass. The annual cost of reversing this conversion in Indonesia, where 4% of the nation's area (8.6 million ha) is now in *Imperata* grasslands, would be over \$400 million if herbicides are used, and \$1.2 billion if labour is used to remove the grass manually. Farmers typically burn the fields because herbicides and labour are too expensive. Burning these grasslands, however, increases losses of soil nitrogen and carbon, which erode agricultural productivity, and enhances regeneration of *Imperata*. This positive feedback with nonlinear changes in land cover will probably continue in the future as lands are deforested

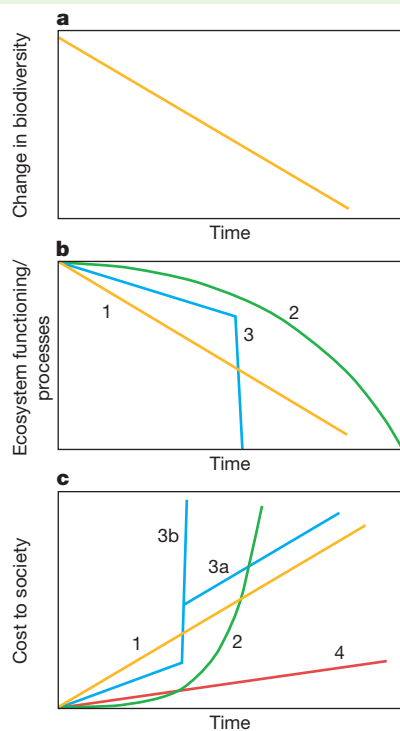


Figure 8 Ecosystem and societal consequences of changes in biodiversity. **a**, A linear change in biodiversity through time. **b**, This change might (1) induce a linear response in ecosystem processes, (2) have increasingly large impacts on ecosystem functioning, yielding exponential ecosystem change through time, or (3) exhibit abrupt thresholds owing to the loss of a keystone species, the loss of the last member of a key functional group, or the addition of a new species trait. **c**, Even if ecosystem response to diversity changes is linear, associated societal costs through time may respond nonlinearly. Departures from a linear increase (1) in societal costs over time might include larger cost increases (2) associated with each additional unit of change in ecosystem processes, yielding an exponential cost curve through time. Reductions of resource supply below threshold levels may induce step increases in societal costs (3a), such as reductions in water supply below the point where all consumers have access to enough for desired uses. If changes in resource supply or ecosystem processes exceed thresholds for supporting large segments of society, stepwise cost increases may be unmeasurable or essentially infinite (3b). The perceived ecological changes and societal costs of diversity change may be small (4). Actual, unrecognized costs may be far higher (lines 1, 2 and 3) and discovered only later as lost option values. Conservation of biodiversity can help avoid such negative ecological and economic ‘surprises’.

for timber and agricultural purposes, causing further declines in regional biodiversity.

Uncertainty related to positive feedbacks and nonlinear changes in land cover and biodiversity make social adaptation to change more difficult and costly (Fig. 8). It may be more important from an economic perspective to understand the nature and timing of rapid or nonlinear changes in societal costs caused by loss of biodiversity and associated ecosystem services than it is to predict average consequences of current trends of species decline. By analogy, economic models of ecological ‘surprises’ in response to climatic change show that the information about the nonlinearities in damage from warming is worth up to six times more than information about current trends in damage levels⁸². In the *Imperata* example, the costs of replacing the original ecosystem goods and services from the forest — including timber products, fire stability and soil nutrients — rise sharply as *Imperata* spreads. If these nonlinearities in the ecological and economic effects of this conversion had been anticipated, policies could have been implemented to encourage agroforestry instead of rice production or to reduce migration and settlement in

the most vulnerable areas⁸³.

In sum, these examples indicate a tight coupling between altered species diversity, ecosystem function and societal costs. A pressing task for ecologists, land managers and environmental policy makers is to determine where and when such tight couplings exist. Policies to safeguard ecosystem services must be able to respond dynamically to new knowledge, the rapidly changing global environment, and evolving societal needs. Nonlinearity, uncertainty and irreversibility call for a more aggressive approach to mitigating changes in biodiversity than is now being pursued so that future options are not foreclosed.

Conclusion

We are in the midst of one of the largest experiments in the history of the Earth. Human effects on climate, biogeochemical cycles, land use and mobility of organisms have changed the local and global diversity of the planet, with important ecosystem and societal consequences (Fig. 1). The most important causes of altered biodiversity are factors that can be regulated by changes in policy: emissions of greenhouse gases, land-use change and species introductions. In the past, the international community has moved to reduce detrimental human impacts with unambiguous societal consequences. For example, the Montreal Protocol prohibited release of chlorofluorocarbons in response to evidence that these chemicals caused loss of ozone and increased levels of cancer-producing UV-B radiation. Strong evidence for changes in biodiversity and its ecosystem and societal consequences calls for similar international actions. We urge the following blueprint for action.

- The scientific community should intensify its efforts to identify the causes of nonlinearities and thresholds in the response of ecosystem and social processes to changes in biodiversity.
- The scientific community and informed citizens should become engaged in conveying to the public, policy-makers and land managers the enormity and irreversibility of current rapid changes in biodiversity. Despite convincing scientific evidence, there is a general lack of public awareness that change in biodiversity is a global change with important ecological and societal impacts and that these changes are not amenable to mitigation after they have occurred.
- Managers should consider the ecological and social consequences of biodiversity change at all stages in land-use planning. For example, environmental impact assessments should consider both the current costs of ecosystem services that will be lost and the risk of nonlinear future change. Managed landscapes can support a large proportion of regional biodiversity with proper planning, management and adaptive responses.
- Scientists and other citizens should collaborate with governmental organizations, from local to national levels, in developing and implementing policies and regulations that reduce environmental deterioration and changes in biodiversity. For example, more stringent restrictions on the import of biotic materials could curb the rate of biotic invasions, and improved land and watershed management could reduce their rates of spread.
- A new international body that would be comparable to the Intergovernmental Panel on Climate Change (IPCC) should assess changes in biodiversity and their consequences as an integral component of the assessment of the societal impacts of global change.
- International bodies should establish and implement agreements such as the Convention on Biological Diversity that institute mechanisms for reducing activities that drive the changes in biodiversity. These activities include fossil-fuel emissions, land-use change and biotic introductions. □

1. Postel, S. L., Daily, G. C. & Ehrlich, P. R. Human appropriation of renewable fresh water. *Science* **271**, 785–788 (1996).
2. Vitousek, P. M., Mooney, H. A., Lubchenco, J. & Melillo, J. M. Human domination of Earth’s ecosystems. *Science* **277**, 494–499 (1997).
3. Kattenberg, A. et al. in *Climate Change 1995. The Science of Climate Change* (ed. Houghton, J. T.) 285–357 (Cambridge Univ. Press, Cambridge, 1996).

4. Pimm, S. L., Russell, G. J., Gittleman, J. L. & Brooks, T. M. The future of biodiversity. *Science* **269**, 347–350 (1995).
5. Lawton, J. H. & May, R. M. *Extinction Rates* (Oxford Univ. Press, Oxford, 1995).
6. Sala, O. E. *et al.* Global biodiversity scenarios for the year 2100. *Science* **287**, 1770–1776 (2000).
7. Lawton, J. H. What do species do in ecosystems? *Oikos* **71**, 367–374 (1994).
8. Tilman, D., Wedin, D. & Knops, J. Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature* **379**, 718–720 (1996).
9. Hector, A. *et al.* Plant diversity and productivity experiments in European grasslands. *Science* **286**, 1123–1127 (1999).
10. van der Heijden, M. G. A. *et al.* Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. *Nature* **396**, 69–72 (1998).
11. Saloniemi, P. O. Metabolic capabilities of forest soil microbial populations with reduced species diversity. *Soil Biol. Biochem.* **13**, 1–10 (1981).
12. Wardle, D. A., Bonner, K. I. & Nicholson, K. S. Biodiversity and plant litter: experimental evidence which does not support the view that enhanced species richness improves ecosystem function. *Oikos* **79**, 247–258 (1997).
13. Hooper, D. U. & Vitousek, P. M. The effects of plant composition and diversity on ecosystem processes. *Science* **277**, 1302–1305 (1997).
14. Tilman, D. *et al.* The influence of functional diversity and composition on ecosystem processes. *Science* **277**, 1300–1302 (1997).
15. Vitousek, P. M., Walker, L. R., Whiteaker, L. D., Mueller-Dombois, D. & Matson, P. A. Biological invasion by *Myrica faya* alters ecosystem development in Hawaii. *Science* **238**, 802–804 (1987).
16. Berry, W. L. Characteristics of salts secreted by *Tamarix aphylla*. *Am. J. Bot.* **57**, 1226–1230 (1970).
17. Christian, J. M. & Wilson, S. D. Long-term impacts of an introduced grass in the northern Great Plains. *Ecology* **80**, 2397–2407 (1999).
18. Lavelle, P., Bignell, D. & Lepage, M. Soil function in a changing world: the role of invertebrate ecosystem engineers. *Eur. J. Soil Biol.* **33**, 159–193 (1997).
19. D'Antonio, C. M. & Vitousek, P. M. Biological invasions by exotic grasses, the grass-fire cycle, and global change. *Annu. Rev. Ecol. Syst.* **23**, 63–87 (1992).
20. Whisenant, S. *Changing Fire Frequencies on Idaho's Snake River Plains: Ecological Management Implications 4–10* (US Forest Service General Technical Report INT-276, Washington, 1990).
21. Van Cleve, K., Chapin, F. S. III, Dryness, C. T. & Viereck, L. A. Element cycling in taiga forest: state-factor control. *BioScience* **41**, 78–88 (1991).
22. Shukla, J., Nobre, C. & Sellers, P. Amazon deforestation and climate change. *Science* **247**, 1322–1325 (1990).
23. Foley, J. A., Kutzbach, J. E., Coe, M. T. & Levis, S. Feedbacks between climate and boreal forests during the Holocene epoch. *Nature* **371**, 52–54 (1994).
24. de Ruiter, P. C., Neutel, A. & Moore, J. C. Energetics, patterns of interaction strengths, and stability in real ecosystems. *Science* **269**, 1257–1260 (1995).
25. Power, M. E. *et al.* Challenges in the quest for keystones. *BioScience* **46**, 609 (1996).
26. Read, D. J. Mycorrhizas in ecosystems. *Experientia* **47**, 376–391 (1991).
27. Paerl, H. W. & Pinckney, J. L. A mini-review of microbial consortia: their roles in aquatic production and biogeochemical cycling. *Microbial Ecol.* **31**, 225–247 (1996).
28. Estes, J. A. & Palmisano, J. F. Sea otters: their role in structuring nearshore communities. *Science* **185**, 1058–1060 (1974).
29. Estes, J. A., Tinker, M. T., Williams, T. M. & Doak, D. F. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science* **282**, 473–476 (1998).
30. Mork, M. The effect of kelp in wave damping. *Sarsia* **80**, 323–327 (1996).
31. Schindler, D. E., Carpenter, S. R., Cole, J. J., Kitchell, J. F. & Pace, M. L. Influence of food web structure on carbon exchange between lakes and the atmosphere. *Science* **277**, 248–251 (1997).
32. Caraco, N. F. *et al.* Zebra mussel invasion in a large, turbid river: phytoplankton response to increased grazing. *Ecology* **78**, 588–602 (1997).
33. Clarholm, M. Interactions of bacteria, protozoa and plants leading to mineralization of soil nitrogen. *Soil Biol. Biochem.* **17**, 181–187 (1985).
34. Zimov, S. A. *et al.* Steppe-tundra transition: an herbivore-driven biome shift at the end of the Pleistocene. *Am. Nat.* **146**, 765–794 (1995).
35. Chanway, C. P., Turkington, R. & Holl, F. B. Ecological implications of specificity between plants and rhizosphere micro-organisms. *Adv. Ecol. Res.* **21**, 121–169 (1991).
36. Lawley, R. A., Newman, E. I. & Campbell, R. Abundance of endomycorrhizas and root-surface microorganisms on three grasses grown separately and in mixtures. *Soil Biol. Biochem.* **14**, 237–240 (1982).
37. Soluck, D. A. & Richardson, J. S. The role of stoneflies in enhancing growth of trout: a test of the importance of predator–predator facilitation within a stream community. *Oikos* **80**, 214–219 (1997).
38. Rice, K. J. Interaction of disturbance patch size and herbivory in *Erodium* colonization. *Ecology* **68**, 1113–1115 (1987).
39. Shock, C. C., Jones, M. B., Williams, W. A. & Center, D. M. Competition of S and N by associations of three annual range species in lysimeters. *Plant Soil* **81**, 311–321 (1984).
40. Gordon, D. R. & Rice, K. J. Partitioning of space and water between two California annual grassland species. *Am. J. Bot.* **79**, 967–976 (1992).
41. Jifon, J. L., Friend, A. L. & Berrang, P. C. Species mixture and soil-resource availability affect the root growth response of tree seedlings to elevated atmospheric CO₂. *Can. J. For. Res.* **25**, 824–832 (1995).
42. Harrington, R., Woiwod, I. & Sparks, T. Climate change and trophic interactions. *Trends Ecol. Evol.* **14**, 146–150 (1999).
43. Diaz, S., Fraser, L. H., Grime, J. P. & Falczuk, V. The impact of elevated CO₂ on plant–herbivore interactions: experimental evidence of moderating effects at the community level. *Oecologia* **117**, 177–186 (1998).
44. Lindroth, R. L. In *Carbon Dioxide and Terrestrial Ecosystems* (eds Koch, G. W. & Mooney, H. A.) 105–120 (Academic Press, San Diego, 1996).
45. McNaughton, S. J. Diversity and stability of ecological communities: a comment on the role of empiricism in ecology. *Am. Nat.* **111**, 515–525 (1977).
46. Naem, S. & Li, S. Biodiversity enhances ecosystem reliability. *Nature* **390**, 507–509 (1997).
47. Chapin, F. S. III & Shaver, G. R. Individualistic growth response of tundra plant species to environmental manipulations in the field. *Ecology* **66**, 564–576 (1985).
48. Altieri, M. A. In *Agroecology* (eds Carrol, C. R., Vandermeer, J. H. & Rosset, P. M.) 551–564 (McGraw Hill, New York, 1990).
49. Walker, B., Kinzig, A. & Langridge, J. Plant attribute diversity, resilience, and ecosystem function: the nature and significance of dominant and minor species. *Ecosystems* **2**, 95–113 (1999).
50. Burdon, J. J. The structure of pathogen populations in natural plant communities. *Annu. Rev. Phytopathol.* **31**, 305–323 (1993).
51. Wasilewska, L. Differences in development of soil nematode communities in single- and multi-species grass experimental treatments. *Appl. Soil Ecol.* **2**, 53–64 (1995).
52. Bertness, M. D. & Leonard, G. H. The role of positive interactions in communities: lessons from intertidal habitats. *Ecology* **78**, 1976–1989 (1997).
53. Nitta, T. Diversity of root fungal floras: its implications for soil-borne diseases and crop growth. *Jap. Agric. Res. Quart.* **25**, 6–11 (1991).
54. Elton, C. S. *The Ecology of Invasions by Animals and Plants* (Methuen, London, 1958).
55. Tilman, D. Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology* **78**, 81–92 (1997).
56. Levine, J. M. & D'Antonio, C. M. Elton revisited: a review of evidence linking diversity and invasibility. *Oikos* **87**, 15–26 (1999).
57. Stohlgren, T. J. *et al.* Exotic plant species invade hot spots of native plant diversity. *Ecol. Monogr.* **69**, 25–46 (1999).
58. Lavorel, S., Prieur-Richard, A.-H. & Grigulis, K. Invasibility and diversity of plant communities: from patterns to processes. *Diversity Distrib.* **5**, 41–49 (1999).
59. McGrady-Steed, J., Harris, P. M. & Morin, P. J. Biodiversity regulates ecosystem predictability. *Nature* **390**, 162–165 (1997).
60. Orr, M. R. & Seike, S. H. Parasitoids deter foraging by Argentine ants (*Linepithema humile*) in their native habitat in Brazil. *Oecologia* **117**, 420–425 (1998).
61. Holway, D. A. Competitive mechanisms underlying the displacement of native ants by the invasive Argentine ant. *Ecology* **80**, 238–251 (1999).
62. Van Wilgen, B. W., Cowling, R. M. & Burgers, C. J. Valuation of ecosystem services: a case study from South African fynbos ecosystems. *BioScience* **46**, 184–189 (1996).
63. Zavaleta, E. S. In *Invasive Species in a Changing World* (eds Hobbs, R. J. & Mooney, H. A.) (Island, Washington DC, in the press).
64. Costanza, R. *et al.* The value of the world's ecosystem services and natural capital. *Nature* **387**, 253–260 (1997).
65. Stewart, G. & Hull, A. C. Cheatgrass (*Bromus tectorum* L.) — an ecological intruder in southern Idaho. *Ecology* **30**, 58–74 (1949).
66. Blockstein, D. E. Letter to the editor. *Science* **279**, 1831 (1998).
67. Naylor, R. L. Invasions in agriculture: assessing the cost of the golden apple snail in Asia. *Ambio* **25**, 443–448 (1996).
68. Porter, J. H., Parry, M. L. & Carter, T. R. The potential effects of climatic change on agricultural insect pests. *Agric. For. Meteorol.* **57**, 221–240 (1991).
69. Pimentel, D., Lach, L., Zuniga, R. & Morrison, D. Environmental and economic costs of nonindigenous species in the United States. *BioScience* **50**, 53–65 (2000).
70. USOT Assessment. *Harmful Non-indigenous Species in the United States* (US Government Printing Office, Washington, 1993).
71. Thorp, J. *The National Weeds Strategy: A Strategic Approach to Weed Problems of National Significance* (Agriculture and Resource Management Council of Australia and New Zealand, Canberra, 1997).
72. Jones, C. G., Ostfeld, R. S., Richard, M. P., Schaubert, E. M. & Wolff, J. O. Chain reactions linking acorns to gypsy moth outbreaks and Lyme disease risk. *Science* **279**, 1023–1026 (1998).
73. Fisher, A. C. & Hanemann, W. M. Option value and the extinction of species. *Adv. Appl. Micro-Econ.* **4**, 169–190 (1986).
74. Naylor, R. L. In *Invasive Species in a Changing World* (eds Hobbs, R. & Mooney, H. A.) (Island, Washington DC, in the press).
75. Channell, R. & Lomolino, M. V. Dynamic biogeography and conservation of endangered species. *Nature* **403**, 84–86 (2000).
76. Bryan, J. H., Foley, D. H. & Sutherst, R. W. Malaria transmission and climate change in Australia. *Med. J. Aust.* **164**, 345–347 (1996).
77. Morrison, J. I. *The Sustainable Use of Water in the Lower Colorado River Basin* (Pacific Institute and the Global Water Policy Project, Oakland, 1996).
78. Zavaleta, E. S. The emergence of waterfowl conservation among Yup'ik hunters in the Yukon-Kuskokwim Delta, Alaska. *Hum. Ecol.* **27**, 231–266 (2000).
79. Warren, D. M. & Pinkston, J. In *Linking Social and Ecological Systems* (eds Berkes, F. & Folke, C.) 158–189 (Cambridge Univ. Press, Cambridge, 1998).
80. Schlesinger, W. H. *et al.* Biological feedbacks in global desertification. *Science* **247**, 1043–1048 (1990).
81. Garrity, D. P. *et al.* The *Imperata* grasslands of tropical Asia: area, distribution, and typology. *Agrofor. Syst.* **36**, 1–29 (1997).
82. Peck, S. C. & Teisberg, T. J. In *Assessing Surprises and Nonlinearities in Greenhouse Warming* (eds Darmstadter, J. & Toman, M. A.) 80–83 (Resources for the Future, Washington, 1993).
83. Tomich, T. P., Kuusipalo, J., Menz, K. & Byron, N. *Imperata* economics and policy. *Agrofor. Syst.* **36**, 233–261 (1997).
84. Power, M. E., Matthews, W. J. & Steward, A. J. Grazing minnows, piscivorous bass, and stream algae: dynamics of a strong interaction. *Ecology* **66**, 1448–1456 (1985).
85. Johnson, K. G., Vogt, K. A., Clark, H. J., Schmitz, O. J. & Vogt, D. J. Biodiversity and the productivity and stability of ecosystems. *Trends Ecol. Evol.* **11**, 372–377 (1996).
86. Vitousek, P. M. & Hooper, D. U. In *Biodiversity and Ecosystem Function* (eds Schulze, E.-D. & Mooney, H. A.) 3–14 (Springer, Berlin, 1993).
87. Huston, M. A. Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia* **110**, 449–460 (1997).
88. Daily, G. C. *Nature's Services: Societal Dependence on Natural Ecosystems* (Island, Washington DC, 1997).
89. Goulder, L. H. & Kennedy, D. In *Nature's Services: Societal Dependence on Natural Ecosystems* (ed. Daily, G. C.) 23–48 (Island, Washington DC, 1997).

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Global patterns in biodiversity

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To a first approximation, the distribution of biodiversity across the Earth can be described in terms of a relatively small number of broad-scale spatial patterns. Although these patterns are increasingly well documented, understanding why they exist constitutes one of the most significant intellectual challenges to ecologists and biogeographers. Theory is, however, developing rapidly, improving in its internal consistency, and more readily subjected to empirical challenge.

Biodiversity, the variety of life, is distributed heterogeneously across the Earth. Some areas teem with biological variation (for example, some moist tropical forests and coral reefs), others are virtually devoid of life (for example, some deserts and polar regions), and most fall somewhere in between. Determining why these differences occur has long been a core objective for ecologists and biogeographers. It constitutes a continuing, an important, and to many an enthralling, challenge. Indeed, the past decade has seen a veritable explosion of studies documenting broad-scale (geographical) spatial patterns in biodiversity, seeking to explain them, and exploring their implications. The reasons for this interest are twofold. First, it reflects increased opportunity provided by improvements in available data and analytical tools, the former resulting mostly from extensive collation of existing specimen and species occurrence records, the establishment of dedicated distribution-mapping schemes, and the use of remote-sensing technology (to measure vegetation and other environmental variables). Second, it reflects concern over the future of biodiversity, and the resultant need to determine its current status, to predict its likely response to global environmental change, and to identify the most effective schemes for *in situ* conservation and sustainable use. Many of these issues can be addressed satisfactorily only by resolving the historical mismatch between the fine resolution of study plots in ecological field work (typically a few square metres) and, by comparison, the poor resolution of land-use planning and models of environmental change.

A host of global patterns of spatial variation in biodiversity has been explored (Fig. 1). This includes patterns in hotspots and coldspots (highs and lows) of diversity (including comparisons between biological realms and between biogeographical regions), variation with spatial scale (for example, species–area relationships and relationships between local and regional richness) and along gradients across space or environmental conditions (for example, latitude, longitude, altitude, depth, peninsulas, bays, isolation, productivity/energy and aridity^{1,2}). Although several different levels of organization (genes to

ecosystems) of biological variation can be distinguished, most analyses of spatial variation concern biodiversity as measured by the number of species observed or estimated to occur in an area (species richness). This results from widespread recognition of the significance of the species as a biological unit, and from the practical issues of the ease and magnitude of data acquisition. Consideration of spatial variation in other measures of biodiversity, particularly those concerning the difference between entities rather than simply their numbers, has been remarkably sparse (with the possible exception of patterns in body size and morphology). Thus, although much attention has been paid to latitudinal variation in species richness, little is known about variation in the diversity of genes, individuals or populations along latitudinal gradients.

The growth of interest in broad-scale spatial variation in biodiversity has been particularly striking with regard to four areas of enquiry: latitudinal gradients in species richness, species–energy relationships, relationships between local and regional richness, and taxonomic covariance in species richness. In this review, the progress being made in each of these areas will be used to substantiate four broader cross-cutting observations about global patterns of biodiversity: respectively, that no single mechanism adequately explains all examples of a given pattern, that the patterns observed may vary with spatial scale, that processes operating at regional scales influence patterns observed at local ones, and that the relative balance of causal mechanisms means that there will invariably be variations in and exceptions to any given pattern.

Latitudinal gradients in species richness

High proportions of terrestrial and freshwater species occur in the tropics. Moving from high to low latitudes the average species richness within a sampling area of a given size increases, as has been documented for a wide spectrum of taxonomic groups (including groups as different as protists, trees, ants, woodpeckers and primates) for data across a range of spatial resolutions^{3,4}. Such gradients in species richness may be steep (for a given area, tropical assemblages are often several times more speciose than temperate ones), and have been a persistent feature of the



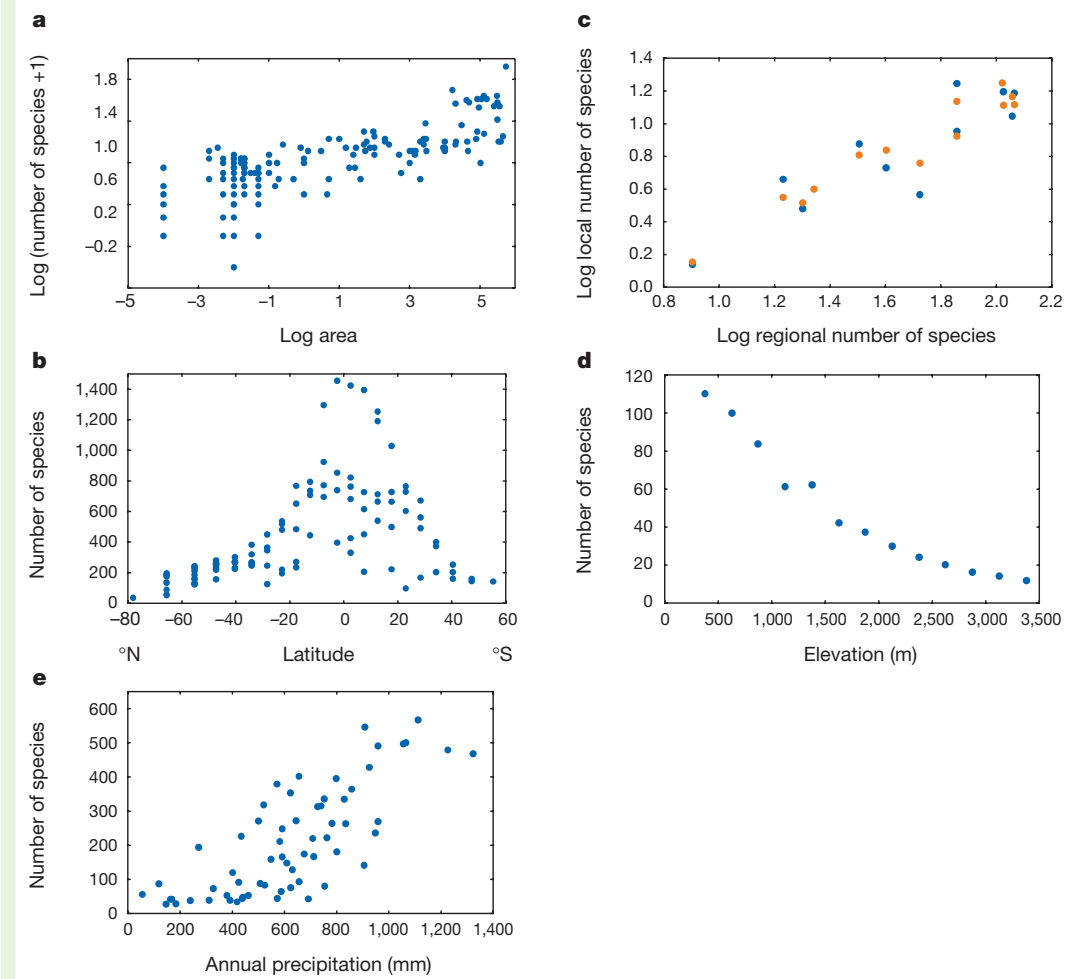


Figure 1 Spatial patterns in species richness. **a**, Species–area relationship: earthworms in areas ranging from 100 m² to >500,000 km² across Europe⁷⁶. **b**, Species–latitude relationship: birds in grid cells (~ 611,000 km²) across the New World⁴⁴. **c**, Relationship between local and regional richness: lacustrine fish in North America (orange circles, large lakes; blue circles, small lakes)⁶¹. **d**, Species–elevation relationship: bats in Manu National Park & Biosphere Reserve, Peru⁷⁷. **e**, Species–precipitation relationship: woody plants in grid cells (20,000 km²) in southern Africa⁷⁸.

history of biodiversity^{5,6}. In the marine environment, open-ocean pelagic and deep-sea taxa also show broad latitudinal gradients in species richness, but some debate continues to surround evidence for shallow-water systems, particularly for non-calcareous taxa⁷.

The growing number of increasingly refined analyses of latitudinal gradients in species richness has begun to suggest some important nuances to this pattern, although the extent of their generality remains uncertain. Thus, it seems that declines in richness with latitude may be faster in the Northern than in the Southern Hemisphere^{8,9}, and that peaks in richness may not lie actually at the Equator itself but some distance away^{10,11}. Although poorly documented, such latitudinal asymmetries would be unsurprising given that these exist also in contemporary climate, in historical climatic events, and in the latitudinal complexities of the geometry and area of land and ocean.

Indeed, the latitudinal gradient in species richness is a gross abstraction. Any underlying pattern is disrupted, sometimes markedly, by variation in species richness with other positional variables (for example, longitude, elevation and depth), and environmental ones (for example, topography and aridity). Thus, the detailed pattern of change with latitude depends on where one looks, reflecting the generally complex patterns of spatial variation in species richness. This indicates that consideration of latitudinal gradients in richness in isolation from other gradients might not be the most profitable way forward. In as much as latitude *per se* (and likewise other positional variables) cannot be a determinant of species richness, but only a correlate of numbers of potentially causal environmental factors, this is doubtless correct. Nonetheless, more than any other pattern the latitudinal gradient in species richness has

held an enduring fascination for biologists, particularly because of the obviously striking diversity of many tropical floras and faunas when contrasted with their counterparts at high latitudes.

The latitudinal gradient in species richness, however complex it might be, is a consequence of systematic spatial variation in the balance of speciation and the immigration of species, which add species to an area, and of the extinction and emigration of species, which take them away. For very large areas, the effects of speciation and regional or global extinction will predominate, and immigration and emigration will be less important. More than 25 different mechanisms have been suggested for generating systematic latitudinal variation in these processes², commonly emphasizing reasons as to why the tropics are highly speciose (although there is no *a priori* expectation that either tropical or temperate zones in any sense represent an ‘unusual’ condition¹²). These include explanations based on chance, historical perturbation, environmental stability, habitat heterogeneity, productivity and interspecific interactions.

Many of these mechanisms are not mutually exclusive, and others merely offer different levels of explanation. Nonetheless, to some, *en masse* they have been perceived to constitute a gordian knot. Two recent attempts to cut it concern the importance of the physical structure of the Earth. First, null models that assume no environmental gradients, but merely a random latitudinal association between the size and placement (midpoint) of the geographical ranges of species, predict a peak of species richness at tropical latitudes¹⁵. This occurs because when the latitudinal extents of species in a given taxonomic group are bounded to north and south — perhaps by a physical constraint such as a continental edge or perhaps by a climatic constraint such as a critical temperature or precipitation threshold — then the

number of ways in which ranges can be distributed changes systematically between the bounds. Thus, whereas species with latitudinal midpoints midway between the bounds can extend a little or a long way before those bounds are encountered, those with midpoints close to the bounds can extend only a little way before this occurs. A null model has been wanting from discussions of latitudinal gradients in species richness. The 'mid-domain' model is thus likely to stimulate much interest. It is also likely to be most applicable for groups whose distributions are genuinely limited by a physical boundary (for example, those of large islands such as Madagascar), although its extension to two spatial dimensions is problematic, given the longitudinal variation in land and ocean area. The application of the model to other kinds of constraints is more questionable, as the position of those constraints that are recognized will be dependent on the inclusiveness of the set of species considered.

The second attempt to explain latitudinal gradients in species richness based on the physical structure of the Earth concerns the role of area (its importance has long been entertained^{14,15} and recently brought to prominence^{16,17}). The tropics have a larger climatically similar total surface area than any other ecoclimatic zone. This is because: (1) the surface area of latitudinal bands decreases towards the poles; (2) the temperature gradient between the Equator and the poles is nonlinear (the mean being relatively constant between approximately 20° N and 20° S); and (3) the regions of similar climate immediately north and south of the Equator abut. It has been contended that, for a given species richness, larger mean geographical-range sizes of species in the tropics result from the large area (which is not to be confused with any observed pattern in mean range sizes at different levels of richness), and that these translate into higher speciation rates (presuming larger ranges have higher probabilities of speciation) and lower extinction probabilities (presuming larger ranges have lower probabilities of extinction)^{16,17}. As a consequence, tropical regions have greater numbers of species than extratropical ones.

Area is almost certainly an important contributor to latitudinal gradients in species richness (indeed, area effects have a pervasive influence on patterns of biodiversity). However, tests of the 'area model' have been limited (and often tangential), and have seldom sought the signal of the influence of area on latitudinal gradients when other factors have been controlled for. Moreover, as a sole explanation the area model is insufficient. To account fully for a latitudinal gradient in species richness (rather than simply for the greater richness of the tropics) the model requires that ecoclimatic zones decline systematically in area moving from the Equator towards the poles. However, they do not do so (ecoclimatic zones at high latitudes tend to be large^{10,17}). Three possible explanations have been advanced for why a latitudinal gradient in species richness might nonetheless be expressed: (1) low productivity/energy availability at high latitudes reduces the species richness they would gain as a result of area alone^{10,17}; (2) zonal bleeding of tropical species into extratropical regions smooths out species-richness gradients^{18,19}; and (3) high

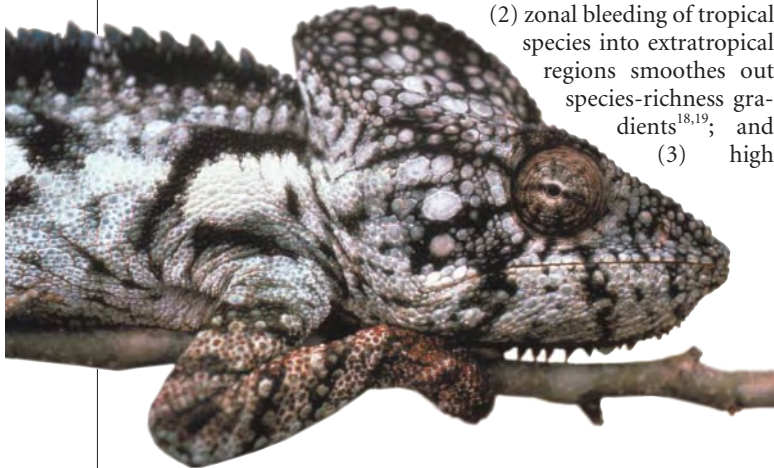
local climatic variability at high latitudes effectively increases the area of ecoclimatic zones that species can actually occupy, because it requires that individuals have broad environmental tolerances³.

The observation that area alone is insufficient as a determinant of latitudinal gradients in species richness could equally be made about almost any other factor that has been proposed as being important (although critical tests are typically lacking). This highlights an issue that has been central to much of the debate about the cause of this and other global patterns in biodiversity, namely the assumption that where a pattern is common to many taxa it must result from the same single mechanism — "wherever there is a widespread pattern, there is likely to be a general explanation which applies to the whole pattern"²⁰. To argue for a single primary cause may be to expect from ecological interactions a simplicity for which there is little evidence. There is no necessary reason why latitudinal gradients exhibited by taxa as distinct as protozoa and mammals, and in environments as structurally different as the deep sea and tropical forests, need be generated in the same way, whatever the attractions of Occam's razor. Increasingly it seems that patterns in biodiversity are likely to be generated by several contributory mechanisms^{12,21}. The strongest and most general may be those where all the different mechanisms pull in the same direction²². It is instructive that although numerous mechanisms for latitudinal gradients in species richness have been identified, and rather few processes that would oppose such a trend, no single mechanism has of itself proven sufficient.

Species–energy relationships

One factor thought to be important in modulating any effect of the physical structure of the Earth in determining latitudinal gradients in species richness is the relationship between the number of species in an area and ambient available ('usable') environmental energy. (This energy is usually estimated from models or indirectly from other variables, and often used interchangeably with 'net primary productivity'.) The form and cause of this relationship are some of the most hotly debated topics in the study of global patterns in biodiversity, with many fundamental issues as yet unresolved. Much of the discussion centres on the influence of spatial scale on observed relationships.

At a relatively local scale (spatial resolution and extent), there is a marked tendency for a general hump-shaped relationship between species richness and available energy, with species richness increasing from low to moderate levels of energy and then declining again towards high levels of energy when a sufficient range of energy values is sampled^{16,17,23}. At least across temperate to polar areas, at geographical scales there is substantial evidence for a broadly positive monotonic relationship between species richness and energy availability to be common^{10,24–33} (Fig. 2). The best correlates for plants tend to be measures of both heat and water (such as actual evapotranspiration and net primary productivity), whereas for terrestrial, and perhaps marine, animals the best correlates are measures of heat (such as mean annual temperature and potential evapotranspiration)^{28,29,34}. For example, whereas the species richness of trees in temperate Europe, eastern North America and East Asia increases with primary productivity²⁷, the richness of butterflies and birds in areas of Britain increases with the temperature during the appropriate season^{25,26}, and the species richness of amphibians, reptiles, birds and mammals in areas of North America increases with annual potential evapotranspiration (estimated as a measure of the net atmospheric energy balance, independent of water availability²⁸). The form taken by species–energy relationships at geographical scales, when extended to include subtropical and tropical areas, or at least to include the fullest range of variation in available energy (which may not be the same thing), remains unclear. There is evidence to suggest that they remain broadly positive and monotonic, that they become mildly or strongly hump-shaped, and that they begin to break down altogether^{10,32,35–37}; the answer may depend critically on the measure of energy used and the taxon concerned.



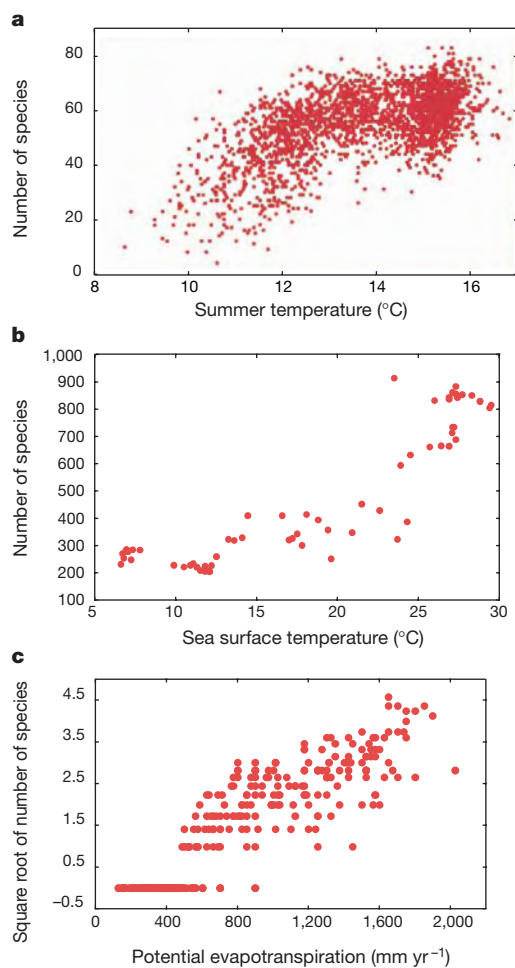


Figure 2 Species–energy relationships. **a**, Mean monthly summer temperature (°C) and richness of breeding birds in Britain (grid cells of 10 km × 10 km)³³. **b**, Mean annual sea surface temperature and richness of eastern Pacific marine gastropods (bands of 1° latitude)¹⁰. **c**, Potential evapotranspiration (mm yr⁻¹) and richness of *Epicauta* beetles (Meloidae) in North America (grid cells of 2.5° × 2.5° south of 50° N, 2.5° × 5° north of 50° N)³¹.

Any contingency of the gross or more detailed form of patterns in biodiversity on the spatial extent and dispersion of sampling units is not restricted to species–energy relationships. Indeed, the almost ubiquitous positive relationship between the numbers of species in an area and the size of that area (the species–area relationship) may itself vary in form with the absolute sizes of areas, their spatial relationships (for example, isolation), and their latitudinal position^{38,39}; this is often forgotten when attempting to control for differences in area in analyses of global patterns of biodiversity. Reconciliation of the patterns in biodiversity that are observed at different scales may provide significant insights into their determinants. If this is to be achieved, it is important to ensure that the scale of sampling and the scale of processes that are postulated to explain patterns in species richness are closely matched. One criticism of some discussion of species–energy relationships at broad scales has been that this has not been done; curiously, this has been interpreted, by different parties, as yielding species–energy relationships that may be misleadingly strong or misleadingly weak^{40–42}. Matching scales of sampling and processes is more readily achievable at local scales, and constitutes one of the most significant obstacles to testing mechanisms over broader areas.

Although other explanations have been offered, the processes

resulting in a broadly positive relationship between species richness and energy availability at geographical scales (and at low-to-moderate energy levels at more local scales) are believed to be reasonably straightforward. Greater energy availability is assumed to enable a greater biomass to be supported in an area. In turn, this enables more individual organisms to coexist, and thus more species at abundances that enable them to maintain viable populations. The result is an increase in species richness with energy availability. This assumes a basic equivalence between species in their energetic requirements at different levels of energy availability⁴³. Although there is some evidence in animal systems that average densities and body sizes of species in an area decrease as energy availability increases (that is, energy is divided more finely⁴⁴), this will tend to enhance the species–energy relationship provided these trends are sufficiently marked compared with the scaling of metabolic rate to body mass.

There are important similarities between this ‘more-individuals model’⁴⁵ and the area model as explanations of variation in species richness⁴⁴. First, both to some degree concern variation in solar energy (and water availability), with the level and availability of this energy source being important in the former case, and the spatial extent of a given level (as reflected in an ecoclimatic zone) in the latter. If ecoclimatic zones vary in available energy, then observed species–energy relationships (and those between richness and latitude) may reflect the joint effects of their area and this availability³⁷. Second, the area model assumes that area influences richness through its effect on geographical-range size, and the more-individuals hypothesis that energy influences richness through its effect on population size. There is a general, positive, interspecific relationship between total population size (or local density) and size of geographical range⁴⁶. Any factor that increases one of these variables will also be likely to increase the other. Both mechanisms therefore depend, in effect, on some factor that is posited to influence the biomass available to be worked on by the processes of speciation and extinction, which will be a product of both area and available energy per unit area^{29,47}. Presumably, it is for this reason that small areas tend to be species poor however high their energy input, whereas large areas tend to be species poor if there is low energy input.

Assuming that species–energy relations are causal and that a more-individuals model is operating, then it is unlikely that the path of causality is simple. Levels of available energy may constrain the amount of biomass that is achieved in an area, but characteristics of the biosphere, and particularly those of vegetation, are themselves known to be key influences on climate, including temperature and precipitation⁴⁸. For example, the coupling of an atmospheric model and a simple land-surface scheme has indicated that coastal deforestation in West Africa has been a significant contributor to the observed drought in the region⁴⁹; this deforestation has resulted in a number of species being threatened with extinction⁵⁰. Complex patterns of causality suggest an important connection between species–energy theory and debates over the ecosystem function of biodiversity^{51,52}.

Even accepting that paths of causality may be complex, there are some potentially significant difficulties with a more-individuals model.

1. The assumption that the number of individual organisms increases with available energy and total biomass may not apply to plants, for which there is evidence that as standing crop increases the numbers of adult individuals per unit area actually declines (and their size increases), which should tend to reduce species richness rather than increase it³⁵. However, this argument is based in large part on findings from monospecific stands of species differing substantially in their architecture, and it is unclear to what extent it generalizes to multispecies stands and systems that are structurally more similar (for example, temperate compared with tropical forests). Evidence as to how overall biomass and numbers of individuals change with species richness in animal systems is scant, even for well-known groups such as birds, and is plagued by a paucity

of strictly comparable studies from areas differing markedly in species richness.

2. Many taxa use such a small proportion of the total energy available in an area, or at least of the energy that is being measured, that it seems unlikely that detectable relationships with species richness would arise (especially given the likely magnitude of measurement errors). Thus, although species richness of birds tends to increase with available energy, avian assemblages may, directly and indirectly, commonly exploit only a small proportion of the primary production in a locality. (The avian community of the forested watersheds of the Hubbard Brook Experimental Forest has an average ingestion rate which represents 0.17% of ecosystem net annual productivity⁵³.)

3. In its simplest form, the more-individuals model ignores the likely effects of temporal variance in energy levels on species richness. High average levels of energy may not result in large numbers of species if they are accompanied by high temporal variability in those levels. The relationship between levels of available energy and their variance may be broadly different between some terrestrial and marine systems (negative in the former, positive in the latter), perhaps explaining why even at very broad spatial scales high richness may not be associated with high productivity in marine systems³⁷.

4. At regional scales, levels of species richness have not been produced directly by present environmental conditions, as processes of speciation and extinction do not operate on these timescales. If the more-individuals model is to apply this must mean that present environmental conditions are a good proxy for past ones, or at least of relative differences in the conditions in different areas.

Alternatives to the more-individuals model have been advanced to explain positive species–energy relationships. These have been based particularly on variation with energy in levels of constraints on geographical ranges, specialization, population growth rates and number of trophic levels⁴⁵. Foremost is the idea that the relationships may reflect physiological constraints on the distribution of species, with energy availability capturing factors that limit distributions as a result of metabolic considerations³⁰.

In the absence of strong support for any of these alternative explanations, difficulties with the more-individuals model fuel growing speculation that at least some species–energy relationships may not be causal, and that energy availability may often be only a covariate of some other factor that is actually driving species richness. Bird richness may, for example, be responding to a second-order effect of greater vegetational complexity with increased available environmental energy. Likewise, recent work has shown that whereas sea surface temperature explained nearly 90% of geographical variation in planktonic foraminiferal diversity throughout the Atlantic Ocean, this temperature was also correlated with temperatures at different depths. This indicates that the diversity may be controlled by the physical structure of the near-surface ocean and not directly by available energy³².

Continuing with this theme, there has been debate as to the respective roles of contemporary levels of energy and of historical factors in generating global patterns of tree species richness in moist forests. The debate has centred on the extent to which differences in richness between continents and between latitudes result from variation in annual actual evapotranspiration (a good, but not universal, predictor of primary productivity) or from long-term evolutionary and geographical processes^{40–42}. The practical constraints on conducting experiments at relevant scales mean that differentiating between hypotheses necessarily requires that they make divergent testable predictions, and even then may not enable the relative roles of different factors to be quantified. Historical factors have doubtless had a substantial role in shaping contemporary spatial patterns of biodiversity, but deriving such *a priori* predictions and quantifying the part played by history can often prove difficult. Molecular phylogenies, with estimated dates of diversification events, provide

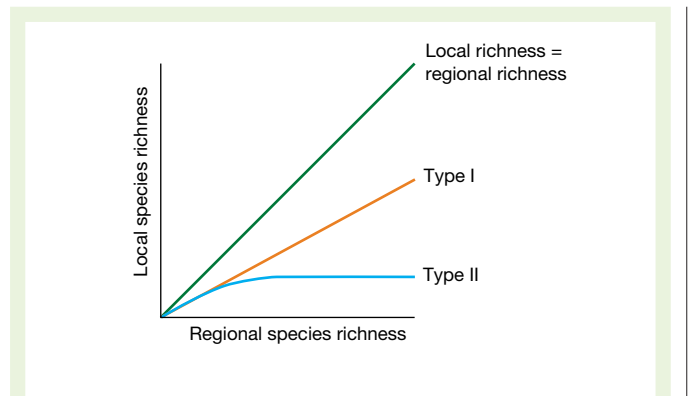


Figure 3 Relations between local and regional species richness, illustrating the form of type I and type II relationships and the limiting condition where local richness equals regional richness.

one rich source of data for testing hypotheses about the significance of history.

Relationships between local and regional richness

In exploring global variation in biodiversity, we need to understand not only the importance of differences in spatial scale for the patterns that are observed (for example, hump-shaped species–energy relationships at local scales and positive relationships at regional ones), but also how diversity at one scale might relate to that at another. Indeed, it is increasingly apparent that knowledge of the roles of pattern and process at different scales is at the very heart of an understanding of global variation in biodiversity.

Two theoretical types of relationship have been contrasted between the local richness an assemblage might attain and the species richness of the region in which that assemblage resides⁵⁴ (Fig. 3). Local richness may be directly proportional to, but less than, regional richness, following a proportional-sampling model (type I). Alternatively, as regional richness increases, local richness might attain a ceiling above which it does not rise despite continued increases in regional richness (type II).

Acknowledging a number of technical concerns^{55–57}, most real systems seem to exhibit an underlying type I relationship^{54,56,58}, not uncommonly, regional richness explains a large proportion (>75%) of variance in local richness, and local richness constitutes a marked proportion (>50%) of regional richness. For example, type I relationships have been documented for fig wasps and their parasitoids in southern and central Africa⁵⁹, tiger beetles in North America and in India⁶⁰, lacustrine fish in North America⁶¹ (Fig. 1c), and primates in Africa and in South America⁶². The predominance of type I relationships is supported by the observation that some spatial gradients in species richness are documented both for localities and regions across those gradients (with obvious implications for the interpretation of regional collations of fossil records).

A recurrent problem in studies of spatial patterns in biodiversity has been the conflation of pattern with mechanism. Nonetheless, the preponderance of examples of type I relationships, particularly where habitat type has been kept constant, backed up with other evidence (for example, the limited support for community convergence, density compensation and invasion resistance), indicates that there are not hard limits to levels of local richness⁶³. That is, local assemblages do not seem to be saturated, in the way one might have expected if ecological interactions (for example, competition, predation and parasitism) limited local richness. Three potential anomalies arise if this conclusion is correct. First, it suggests that although ecological interactions are known to be strong in some circumstances, they may typically not be sufficient to have a marked effect on species richness. Second, it may be at odds with the more-individuals

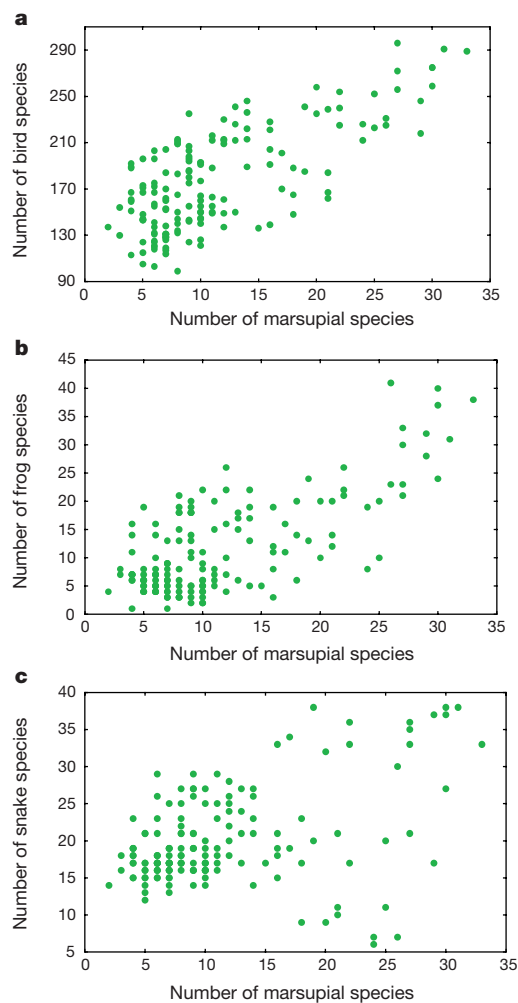


Figure 4 Relationships between species richness of different vertebrate groups (in grid cells of 240 km × 240 km) across Australia. **a**, Birds; **b**, frogs; and **c**, snakes, with marsupials (from data in ref. 79).

hypothesis as an explanation for positive species–energy relationships based on local site data, because this requires that energy levels limit the number of species that can co-occur (through limitation on the number of individuals). And third, it seems at odds with the existence of marked regional (for example, latitudinal) variation in beta diversity, although this variation may be confounded by differences in habitat composition. (Defining beta diversity as $(S/\alpha) - 1$ (where S is regional and α is local richness⁶⁴), regions having the same ratio of local-to-regional richness should have the same beta diversity³⁷.) The marked growth in studies of global patterns in biodiversity is steadily resolving such apparent anomalies by examining multiple patterns for the same assemblage, and thus generating a more coherent picture of the inter-relationships between them. But high-quality data sets documenting at high resolution the occurrence of large numbers of species over extensive areas are desperately required.

If most systems exhibit type I relationships between local and regional richness, then a prime driver of local richness seems to be regional richness. The importance of regional-scale phenomena for local-scale assemblage structure is a general one⁶⁵. A local community is assembled from a regional pool of species (this has variously been defined as the total pool of species in a region, or the pool of species in the region that is actually capable of colonizing a given site). The size and structure of this pool are influenced by regional processes, including the effects of the geophysical properties and history of

the region (its age, geology, size and climate), and broad-scale ecological or evolutionary processes, such as species migrations, invasions, speciation and regional extinction³⁵. They set the species composition and the abundance, body size and trophic structure of the pool from which local communities draw. Indeed, a core issue in ecology is the extent to which local assemblages can be modelled accurately as random draws from regional species pools, or conversely the extent to which local factors modify the similarity of real assemblages to randomly simulated ones⁶⁶. Almost invariably such models can explain some, often much, and occasionally most of the basic structure of local assemblages^{44,66}. Local assemblage structure and the regional context are inseparable.

Recognition of the importance of regional-scale processes and the structure of the regional species pool to local community structure has led to the emergence of macroecology, which is concerned with understanding the abundance and distribution of species at large spatial and temporal scales^{44,67}. However, although regional pools doubtless are important in structuring local assemblages, they are perhaps best seen as contributing to, rather than determining, local assemblage structure—local processes remain important. Resolving the relative contributions of local and regional processes may provide a key to understanding global patterns of biodiversity⁵⁵, but this issue once again emphasizes that patterns in biodiversity are unlikely to have a single primary cause.

Taxonomic covariance in species richness

Most major terrestrial and freshwater groups are more speciose in tropical than temperate regions, at low elevations than at high, and in forests than in deserts. One might therefore expect that the regional richness of different groups of organisms would covary positively and, because of the positive relationship between local and regional richness, local richness would do likewise. This would be important because it would simplify the development of an understanding of global patterns in biodiversity.

In practice, mismatches between the spatial occurrence of peaks in the richness of different groups have often been observed. For example, among trees, tiger beetles, amphibians, reptiles, birds and mammals, the 5% of land area across the United States and southern Canada in which the highest levels of species richness are attained overlap between some pairs of taxa, but this pattern is not a general one⁶⁸. Likewise, although the numbers of species in different, large and similar-sized areas for two groups are often significantly correlated, and may enable a very general impression of the patterns in richness of one group to be obtained from those of another, these correlations are frequently weak, of rather limited predictive value, and in some cases explained by latitudinal gradients in diversity⁶⁸ (Fig. 4). These conclusions seem to hold at finer resolutions over more constrained areas. Thus, at a scale of 10 km × 10 km squares, species-rich areas for different taxa in Britain frequently do not coincide⁶⁹. These areas are not distributed randomly, overlapping more often than expected by chance, but still at a rather low level. Likewise, different taxa are species poor or species rich in different areas of the northern region of South Africa⁷⁰.

Where positive relationships are found between the species richness of two or more groups, this may reflect patterns of sampling effort (a complication plaguing many biodiversity studies), rather than any underlying covariance. If real, then this does not necessarily imply any direct linkage between the richness of those groups. Covariance can occur because of trophic or other relations, but might also result from random effects, because groups share common determinants of richness, or even because groups differ in determinants of richness but these determinants themselves exhibit spatial covariance⁷¹.

The lack of strong positive covariance in the species richness of higher taxa is significant in that it constrains the extent to which observed patterns in biodiversity can be extrapolated from one group to another, and from exemplar groups to biodiversity at large (with implications for the planning and likely success of networks of

protected areas). The latter is particularly important given that only ~15% of the total number of species estimated to be extant has been formally described taxonomically, that the distributions of most of these remain largely unknown (a high proportion are known from only a single locality^{72,73}), and that species whose distributions are well documented are strongly biased with respect to their higher taxonomic affinities. But such outcomes are inevitable, because of the multiple forces at work in structuring global patterns of biodiversity, and because the particular outcomes observed rest fundamentally on the balance of those forces. Indeed, even where two groups exhibit similar spatial gradients in biodiversity there is substantial variation around those trends, and the details are seldom similar. In the extreme, some groups exhibit patterns of biodiversity that are entirely contrary to the norm. For example, several major taxonomic groups exhibit peaks of species richness at high or mid-latitudes (for example, aphids, sawflies, ichneumonids, braconids, bees, various groups of freshwater invertebrates, marine amphipods, and procellariiforms^{1,74}); exceptions to patterns of biodiversity tend to be observed more frequently at lower taxonomic levels than at higher levels. Which particular patterns are and are not expressed by a given taxon rest on contingencies (for example, physiology, dispersal ability, resource requirements and evolutionary history⁵⁶).

In conclusion

Development of a markedly improved understanding of the global distribution of biodiversity is one of the most significant objectives for ecologists and biogeographers. Spatial heterogeneity in species richness, in particular, is an obvious feature of the natural world. An understanding of its determinants will impinge on applied issues of major concern to humankind, including the role of biodiversity in ecosystem processes, the spread of alien invasive species, the control of diseases and their vectors, and the likely effects of global environmental change on the maintenance of biodiversity.

A substantial proportion of regional variation in species richness can be explained statistically in terms of a few environmental variables¹. This is, however, far from a predictive theory of species richness. It is the need to identify the contingencies involved in the expression of patterns in biodiversity, and to weigh their significance, that constitutes the real challenge to developing such a theory. The number of species is determined by the birth, death, immigration and emigration rates of species in an area. These rates in turn are determined by the effects of abiotic and biotic factors (the latter may be intrinsic or extrinsic to the organisms of concern) acting at local and regional scales. Although multiple factors doubtless contribute, if a factor influences biodiversity on one spatial axis (for example, latitude) then it seems reasonable to presume that all else being equal it will do so along others where the factor also varies (for example, elevation). Thus, relationships between species richness and environmental energy have been found to be associated with latitudinal, elevational and depth gradients⁷⁵. If this were the whole story, patterns in richness would seem reasonably straightforward, if not easy, to predict. However, it is not simply the current states of these factors that are important but also their historical dynamics. These have shaped variations in the distribution of different groups of organisms, in their diversification, and hence the availability of species with different attributes to exploit opportunities provided by prevailing conditions. As such, the study of global patterns in biodiversity demands insights from geneticists through to ecosystem ecologists. All concerned will need to remember that no single mechanism need adequately explain a given pattern, that observed patterns may vary with spatial scale, that processes at regional scales influence patterns observed at local ones, and that no pattern is without variations and exceptions. □

- Gaston, K. J. & Williams, P. H. in *Biodiversity: A Biology of Numbers and Difference* (ed. Gaston, K. J.) 202–229 (Blackwell Science, Oxford, 1996).
- Brown, J. H. & Lomolino, M. V. *Biogeography* 2nd edn (Sinauer, Sunderland, MA, 1998).
- Stevens, G. C. The latitudinal gradient in geographical range: how so many species co-exist in the

- tropics. *Am. Nat.* **133**, 240–256 (1989).
- Gaston, K. J. Biodiversity — latitudinal gradients. *Prog. Phys. Geogr.* **20**, 466–476 (1996).
- Stehli, F. G., Douglas, D. G. & Newell, N. D. Generation and maintenance of gradients in taxonomic diversity. *Science* **164**, 947–949 (1969).
- Crane, P. R. & Lidgard, S. Angiosperm diversification and paleolatitudinal gradients in Cretaceous floristic diversity. *Science* **246**, 675–678 (1989).
- Clarke, A. & Crame, J. A. in *Marine Biodiversity: Patterns and Processes* (eds Ormond, R. F. G., Gage, J. D. & Angel, M. V.) 122–147 (Cambridge Univ. Press, Cambridge, 1997).
- Platnick, N. I. Patterns of biodiversity: tropical vs temperate. *J. Nat. Hist.* **25**, 1083–1088 (1991).
- Blackburn, T. M. & Gaston, K. J. Spatial patterns in the species richness of birds in the New World. *Ecography* **19**, 369–376 (1996).
- Roy, K., Jablonski, D., Valentine, J. W. & Rosenberg, G. Marine latitudinal diversity gradients: tests of causal hypotheses. *Proc. Natl Acad. Sci. USA* **95**, 3699–3702 (1998).
- Lyons, S. K. & Willig, M. R. A hemispheric assessment of scale dependence in latitudinal gradients of species richness. *Ecology* **80**, 2483–2491 (1999).
- Blackburn, T. M. & Gaston, K. J. A sideways look at patterns in species richness, or why there are so few species outside the tropics. *Biodiv. Lett.* **3**, 44–53 (1996).
- Colwell, R. K. & Hurr, G. C. Nonbiological gradients in species richness and a spurious Rapoport effect. *Am. Nat.* **144**, 570–595 (1994).
- Terborgh, J. On the notion of favorableness in plant ecology. *Am. Nat.* **107**, 481–501 (1973).
- Osman, R. W. & Whitlatch, R. B. Patterns of species diversity: fact or artifact? *Paleobiology* **4**, 41–54 (1978).
- Rosenzweig, M. L. Species diversity gradients: we know more and less than we thought. *J. Mamm.* **73**, 715–730 (1992).
- Rosenzweig, M. L. *Species Diversity in Space and Time* (Cambridge Univ. Press, Cambridge, 1995).
- Blackburn, T. M. & Gaston, K. J. The relationship between geographic area and the latitudinal gradient in species richness in New World birds. *Evol. Ecol.* **11**, 195–204 (1997).
- Rosenzweig, M. L. & Sandlin, E. A. Species diversity and latitudes: listening to area's signal. *Oikos* **80**, 172–176 (1997).
- MacArthur, R. H. & Connell, J. H. *The Biology of Populations* (Wiley, New York, 1966).
- Gaston, K. J. & Blackburn, T. M. A critique for macroecology. *Oikos* **84**, 353–368 (1999).
- Lawton, J. H. Patterns in ecology. *Oikos* **75**, 145–147 (1996).
- Rosenzweig, M. L. & Abramsky, Z. in *Species Diversity in Ecological Communities* (eds Ricklefs, R. E. & Schlüter, D.) 52–65 (Univ. Chicago Press, Chicago, 1993).
- Currie, D. J. & Paquin, V. Large-scale biogeographical patterns of species richness of trees. *Nature* **329**, 326–327 (1987).
- Turner, J. R. G., Gatehouse, C. M. & Corey, C. A. Does solar energy control organic diversity? Butterflies, moths and the British climate. *Oikos* **48**, 195–205 (1987).
- Turner, J. R. G., Lennon, J. J. & Lawrenson, J. A. British bird species distributions and energy theory. *Nature* **335**, 539–541 (1988).
- Adams, J. M. & Woodward, F. I. Patterns in tree species richness as a test of the glacial extinction hypothesis. *Nature* **339**, 699–701 (1989).
- Currie, D. J. Energy and large-scale patterns of animal- and plant-species richness. *Am. Nat.* **137**, 27–49 (1991).
- Wright, D. H., Currie, D. J. & Maurer, B. A. in *Species Diversity in Ecological Communities* (eds Ricklefs, R. E. & Schlüter, D.) 66–74 (Univ. Chicago Press, Chicago, 1993).
- Kerr, J. T., Vincent, R. & Currie, D. J. Lepidopteran richness patterns in North America. *Ecoscience* **5**, 448–453 (1998).
- Kerr, J. T. & Packer, L. The environmental basis of North American species richness patterns among *Epicauta* (Coleoptera: Meloidae). *Biodiv. Conserv.* **8**, 617–628 (1999).
- Rutherford, S., D'Hondt, S. & Prell, W. Environmental controls on the geographic distribution of zooplankton diversity. *Nature* **400**, 749–753 (1999).
- Lennon, J. J., Greenwood, J. J. D. & Turner, J. R. G. Bird diversity and environmental gradients in Britain: a test of the species-energy hypothesis. *J. Anim. Ecol.* (in the press).
- Kerr, J. T. & Currie, D. J. The relative importance of evolutionary and environmental controls on broad-scale patterns of species richness in North America. *Ecoscience* **6**, 329–337 (1999).
- Tilman, D. & Pacala, S. in *Species Diversity in Ecological Communities* (eds Ricklefs, R. E. & Schlüter, D.) 13–25 (Univ. Chicago Press, Chicago, 1993).
- Gaston, K. J. & Blackburn, T. M. Mapping biodiversity using surrogates for species richness: macro-scales and New World birds. *Proc. R. Soc. Lond. B* **262**, 335–341 (1995).
- Chown, S. L. & Gaston, K. J. Patterns in procellariiform diversity as a test of species-energy theory in marine systems. *Evol. Ecol. Res.* **1**, 365–373 (1999).
- Martin, T. E. Species-area slopes and coefficients: a caution on their interpretation. *Am. Nat.* **118**, 823–837 (1981).
- Palmer, M. W. & White, P. S. Scale dependence and the species-area relationship. *Am. Nat.* **144**, 717–740 (1994).
- Latham, R. E. & Ricklefs, R. E. Global patterns of tree species richness in moist forests: energy-diversity theory does not account for variation in species richness. *Oikos* **67**, 325–333 (1993).
- Francis, A. P. & Currie, D. J. Global patterns of tree species richness in moist forests: another look. *Oikos* **81**, 598–602 (1998).
- Ricklefs, R. E., Latham, R. E. & Qian, H. Global patterns of tree species richness in moist forests: distinguishing ecological influences and historical contingency. *Oikos* **86**, 369–373 (1999).
- Cousins, S. H. Species richness and the energy theory. *Nature* **340**, 350–351 (1989).
- Gaston, K. J. & Blackburn, T. M. *Pattern and Process in Macroecology* (Blackwell Science, Oxford, in the press).
- Srivastava, D. S. & Lawton, J. H. Why more productive sites have more species: an experimental test of theory using tree-hole communities. *Am. Nat.* **152**, 510–529 (1998).
- Gaston, K. J., Blackburn, T. M. & Lawton, J. H. Interspecific abundance-range size relationships: an appraisal of mechanisms. *J. Anim. Ecol.* **66**, 579–601 (1997).
- Wright, D. H. Species-energy theory: an extension of species area-theory. *Oikos* **41**, 496–506 (1983).
- Hayden, B. P. Ecosystem feedbacks on climate at the landscape scale. *Phil. Trans. R. Soc. Lond. B* **353**, 5–18 (1998).
- Zheng, X. Y. & Eltahir, E. A. B. The role of vegetation in the dynamics of West African monsoons. *J. Clim.* **11**, 2078–2096 (1998).
- Collar, N. J., Crosby, M. J. & Stattersfield, A. J. *Birds to Watch 2: The World List of Threatened Birds* (BirdLife International, Cambridge, 1994).
- Schläpfer, F. & Schmid, B. Ecosystem effects of biodiversity: a classification of hypotheses and

- exploration of empirical results. *Ecol. Appl.* **9**, 893–912 (1999).
52. Tilman, D. The ecological consequences of changes in biodiversity: a search for general principles. *Ecology* **80**, 1455–1474 (1999).
53. Holmes, R. T. & Sturges, F. W. Avian community dynamics and energetics in a northern hardwoods ecosystem. *J. Anim. Ecol.* **44**, 175–200 (1975).
54. Cornell, H. V. & Lawton, J. H. Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. *J. Anim. Ecol.* **61**, 1–12 (1992).
55. Huston, M. A. Local processes and regional patterns: appropriate scales for understanding variation in the diversity of plants and animals. *Oikos* **86**, 393–401 (1999).
56. Lawton, J. H. Are there general laws in ecology? *Oikos* **84**, 177–192 (1999).
57. Srivastava, D. S. Using local-regional richness plots to test for species saturation: pitfalls and potentials. *J. Anim. Ecol.* **68**, 1–16 (1999).
58. Caley, M. J. & Schluter, D. The relationship between local and regional diversity. *Ecology* **78**, 70–80 (1997).
59. Hawkins, B. A. & Compton, S. G. African fig wasp communities: undersaturation and latitudinal gradients in species richness. *J. Anim. Ecol.* **61**, 361–372 (1992).
60. Pearson, D. L. & Juliano, S. A. in *Species Diversity in Ecological Communities* (eds Ricklefs, R. E. & Schluter, D.) 194–202 (Univ. Chicago Press, Chicago, 1993).
61. Griffiths, D. Local and regional species richness in North American lacustrine fish. *J. Anim. Ecol.* **66**, 49–56 (1997).
62. Eeley, H. A. C. & Lawes, M. J. in *Primate Communities* (eds Feagle, J. G., Janson, C. & Reed, K. E.) 191–219 (Cambridge Univ. Press, Cambridge, 1999).
63. Cornell, H. V. Unsaturation and regional influences on species richness in ecological communities: a review of the evidence. *Ecoscience* **6**, 303–315 (1999).
64. Whittaker, R. H. Vegetation of the Siskiyou mountains, Oregon and California. *Ecol. Monogr.* **30**, 279–338 (1960).
65. Ricklefs, R. E. & Schluter, D. (eds) *Species Diversity in Ecological Communities* (Univ. Chicago Press, Chicago, 1993).
66. Gotelli, N. J. & Graves, G. R. *Null Models in Ecology* (Smithsonian Institution Press, Washington DC, 1996).
67. Brown, J. H. *Macroecology* (Univ. Chicago Press, Chicago, 1995).
68. Flather, C. H., Wilson, K. R., Dean, D. J. & McComb, W. C. Identifying gaps in conservation networks: of indicators and uncertainty in geographic-based analyses. *Ecol. Appl.* **7**, 531–542 (1997).
69. Prendergast, J. R., Quinn, R. M., Lawton, J. H., Eversham, B. C. & Gibbons, D. W. Rare species, the coincidence of diversity hotspots and conservation strategies. *Nature* **365**, 335–337 (1993).
70. van Jaarsveld, A. S. *et al.* Biodiversity assessment and conservation strategies. *Science* **279**, 2106–2108 (1998).
71. Gaston, K. J. Biodiversity — congruence. *Prog. Phys. Geogr.* **20**, 105–112 (1996).
72. Stork, N. E. in *Biodiversity II: Understanding and Protecting our Biological Resources* (eds Reaka-Kudla, M. L., Wilson, D. E. & Wilson, E. O.) 41–68 (Henry, Washington DC, 1997).
73. Andersen, M., Thornhill, A. & Koopowitz, H. in *Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities* (eds Laurance, W. F. & Bierregaard, R. O. Jr) 281–291 (Univ. Chicago Press, Chicago, 1997).
74. Chown, S. L., Gaston, K. J. & Williams, P. H. Global patterns in species richness of pelagic seabirds: the Procellariiformes. *Ecography* **21**, 342–350 (1998).
75. Rohde, K. Latitudinal gradients in species diversity: the search for the primary cause. *Oikos* **65**, 514–527 (1992).
76. Judas, M. The species-area relationship of European Lumbricidae (Annelida, Oligochaeta). *Oecologia* **76**, 579–587 (1988).
77. Patterson, B. D., Stotz, D. F., Solari, S., Fitzpatrick, J. W. & Pacheco, V. Contrasting patterns of elevational zonation for birds and mammals in the Andes of southeastern Peru. *J. Biogeogr.* **25**, 593–607 (1998).
78. O'Brien, E. M. Climatic gradients in woody plant species richness: towards an explanation based on an analysis of southern Africa's woody flora. *J. Biogeogr.* **20**, 181–198 (1993).
79. Pianka, E. R. & Schall, J. J. in *Ecological Biogeography of Australia* Vol. 3 (ed. Keast, A.) 1677–1694 (Junk, The Hague, 1981).

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The diversity–stability debate

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There exists little doubt that the Earth's biodiversity is declining. The Nature Conservancy, for example, has documented that one-third of the plant and animal species in the United States are now at risk of extinction. The problem is a monumental one, and forces us to consider in depth how we expect ecosystems, which ultimately are our life-support systems, to respond to reductions in diversity. This issue — commonly referred to as the diversity–stability debate — is the subject of this review, which synthesizes historical ideas with recent advances. Both theory and empirical evidence agree that we should expect declines in diversity to accelerate the simplification of ecological communities.

We now realize that the world's flora and fauna are disappearing at rates greater than the mass extinction events whose collapses punctuate the fossil record^{1–3}. It is also true that species invasions have been elevated to unprecedented rates accompanying the increased globalization of our world^{4,5}. These high rates of extinction and invasion put ecosystems under enormous stress, making it critical that we understand how the loss, or addition, of a species influences the stability and function of the ecosystems we rely on. We are, in a very real sense, deconstructing the Earth under the implicit assumption that ecosystems have evolved the ability to withstand such assault without collapse.

Several advances in the diversity–stability debate form a conceptual thread that suggests that diversity can be expected, on average, to give rise to ecosystem stability. This does not infer that diversity is the driver of this relationship. Instead, diversity can be regarded as the passive recipient of important ecological mechanisms that are inherent in ecosystems. One promising mechanism that has been proposed recently is that weakly interacting species stabilize community dynamics by dampening strong, potentially destabilizing consumer–resource interactions⁶. Empirical descriptions of the distribution of interaction strengths in real communities are consistent with this theory. If this is true then, all else being equal, decreasing biodiversity will be accompanied by increases in average interaction strengths within ecosystems, and a concomitant decrease in ecosystem stability.

Historical perspectives of the diversity–stability debate

The relationship between diversity and stability has fascinated ecologists. Before the 1970s, ecologists believed that more diverse communities enhanced ecosystem stability^{7–9}. A strong proponent of this view was Charles Elton⁸, who argued that “simple communities were more easily upset than that of richer ones; that is, more subject to destructive oscillations in populations, and more vulnerable to invasions”. In fact, both Odum⁷ and Elton⁸ arrived at similar conclusions based on the repeated observation that greatly simplified terrestrial communities are characterized by more violent fluctuations in population density than diverse terrestrial communities. For example, invasions most frequently occur on cultivated land where human influence had produced greatly simplified ecological communities, and outbreaks of phytophagous insects occur readily in boreal forests but are unheard of in diverse tropical forests. These observations led Elton⁸ to believe that

complex communities, constructed from many predators and parasites, prevented populations from undergoing explosive growth. His ideas were closely akin to MacArthur⁹, who reasoned that multiplicity in the number of prey and predator species associated with a population freed that population from dramatic changes in abundance when one of the prey or predator species declined in density.

These early intuitive ideas were challenged by the work of Robert May¹⁰ in 1973. May turned to mathematics to rigorously explore the diversity–stability relationship. By using linear stability analysis on models constructed from a statistical universe (that is, randomly constructed communities with randomly assigned interaction strengths), May found that diversity tends to destabilize community dynamics. Other ecologists, using similar approaches, found results that were consistent with this hypothesis^{11,12}. The results were puzzling, as real ecosystems were undoubtedly complex and diverse. The results also seemed to counter the ideas of Elton⁷, Odum⁸ and MacArthur⁹. Yodzis¹³ heightened this paradox by showing that models structured from compiled food-web relationships, with plausible interaction strengths, were generally more stable than randomly constructed food webs. Although the early food-web data that Yodzis structured his models around were incomplete, these data reflected real feeding relationships. Yodzis' result indicated that interaction strength was probably crucial to stability; but the exact reason for this remained elusive. If diversity and stability were positively correlated, as early empirical evidence had indicated, then more had to be happening than simply increasing the number of species and the number of pathways. Something fundamental was missing from the early arguments.

In the remainder of this paper I review recent investigations of the diversity–stability debate. I first discuss a change in perspective that is beginning to allow us to unravel this long-standing problem and then review two different lines of investigation. One approach has searched for a general diversity–stability relationship, and a second, more mechanistic approach has sought a relationship between food-web structure and stability.

Changing perspectives

Much of ecological theory is based on the underlying assumption of equilibrium population dynamics. Although this assumption is aesthetically pleasing, in that it suggests the balance of nature is infinitely precise, an alternative and viable ecological perspective exists. As real populations are variable, it is possible that the persistence of complex communities depends to some degree on population fluxes (that is, the



Figure 1 The Ecotron experiment creates model multitrophic community assemblages containing plants, herbivores, parasitoids and decomposers in 16 different chambers. The Ecotron is an ambitious attempt to bridge the scale between field communities and laboratory experiments. (Photographs show the inside of an Ecotron chamber and a technical service corridor between two banks of chambers; courtesy of the Centre for Population Biology, Imperial College at Silwood Park.)

fairly regular waxing and waning of a population's density). Such background population variability, whether driven by biotic or abiotic processes, can provide species with the opportunity to respond differentially to their environment. In turn, these differential species responses weaken the destructive potential of competitive exclusion.

Because such variability can significantly change our understanding of ecological interactions^{6,14–19}, ecologists have begun to relax equilibrium-based measures of stability. A recent theoretical analysis¹⁷ has shown that population fluctuations, driven by competition, can actually promote the persistence of large numbers of competing phytoplankton communities on a minimal number of limiting resources (but greater than two resources). Coexistence was found to rely on the fluctuation in population densities, while community-level densities (the summation of the competing plankton densities) varied little. We will see that a similar relationship appears in diversity–stability experiments. Here, too, the evidence points to variable population densities that sum to produce a relatively constant biomass at the community level.

Definitions of stability

Definitions of stability in ecology can be classified generally into two categories (Table 1) — stability definitions that are based on a system's dynamic stability, and stability definitions that are based on a system's ability to defy change (resilience and resistance in Table 1). Despite the breadth of definitions, ecological theory has tended traditionally to rely on the assumption that a system is stable if, and only if, it is governed by stable equilibrium dynamics (that is, equilibrium stability and equilibrium resilience). As discussed in the previous section, these are strong assumptions with no *a priori* justification. In fact, the variable nature of population dynamics found both in field and in laboratory experiments has led experimentalists to use measures of variability as indices of a system's stability. This discontinuity between stability experiments and equilibrium-based theory has made it difficult to unite theory and experiment in the diversity–stability debate.

More general definitions of stability exist. In Table 1, general stability is defined such that stability increases as population

densities move further away from extremely low or high densities. This is a broad definition, including equilibrium and non-equilibrium dynamics as well as subsuming the definition of permanence¹⁸ (a population is considered permanent if the lower limit to its density is greater than zero). Because the definition of general stability implies decreased variability (owing to greater limits on density), it is closely related to field measurements of stability, which tend to rely on variability in population or community densities as a measure of stability. One can also extend equilibrium resilience to a less biologically restrictive form by defining resilience as the return time after a perturbation to an equilibrium or a non-equilibrium attractor (Table 1). In a nonlinear system there is no reason to believe that an equilibrium that attracts weakly in a local setting (near the equilibrium) also attracts weakly far away from the equilibrium, where the issue of a species' permanence is resolved¹⁸. For the remainder of the paper, unless stated otherwise, the definitions of general stability and variability will be used to consider empirical and theoretical results on the relationship between diversity and stability under a common framework.

The search for a general diversity–stability relationship

In 1982, David Tilman began a long-term study to delineate experimentally the relationship between diversity and stability in plant communities. The undertaking involved four grassland fields at Cedar Creek Natural History Area, Minnesota, divided into over 200 experimental plots, and gathered information on species richness, community biomass and population biomass through time. The results of this and other extensive studies converge on the finding that diversity within an ecosystem tends to be correlated positively with plant community stability (that is, decreased coefficient of variability in community biomass)^{20–23}. At the same time, diversity seems to show little influence on population variability²². The basic arguments for a positive relationship between diversity and stability for primary producers at the community level have been classified into two, not mutually exclusive, hypotheses called the averaging effect²⁴ and the negative covariance effect²⁵ (see Table 2 for the underlying logic behind these ideas). In essence, these hypotheses argue that diversity

(species richness) increases stability at the community level because diverse plant communities respond differentially to variable background processes. The differential responses of populations sum, through time, to give stable community dynamics.

If diversity and stability are positively correlated, then both the averaging and negative covariance effect predict that population variance has to scale as a function of mean population densities in a precise way (see Table 2). Tilman²⁰ has used these predictions to show that his field experiments are consistent with the interpretation that increasing diversity increases community stability. Although this is a clever combination of theory and experiment, it cannot be used to infer that diversity is responsible directly for stability^{26,27}. As a counter example, no correlation was found between diversity and stability at the cross-ecosystem scale²⁶. Other experiments have found that the positive diversity–stability correlation is not a pure species effect (that is, a diversity effect), and have indicated that ecosystem function and stability are more directly related to functional diversity (for example, graminoids or grasses, nitrogen-fixing legumes and other herbs)^{27–30}.

In a similar manner, plant community stability and productivity in European grasslands were shown to be tightly coupled to the functional diversity of mutualistic arbuscular mycorrhizal fungi (AMF)³¹. In this system, large fluctuations in plant biomass were associated with low diversities of AMF, whereas more constant biomass and greater productivity accompanied high AMF diversities. This study highlights that higher-level interactions, which are inherent in food webs (for example, microbial interactions, herbivory and predation), are of great importance in understanding the relationship between the diversity and stability of whole ecological communities. The complexity of whole ecological communities — the basis from which Odum, Elton and MacArthur formed their diversity–stability hypotheses — cannot manifest itself in experiments that focus on single trophic levels.

Field tests at the scale of the food web are few in number. But one thorough examination³² tested seven different stability–diversity criteria in the grazing ecosystem of the Serengeti under naturally variable conditions (that is, strong seasonal changes). Of these seven stability measures, five were positively related to diversity whereas two were unrelated to diversity. The study found that greater diversity reduced the relative magnitudes of fluctuations in productivity induced by seasonal change. Although a relationship between stability and diversity exists within the Serengeti, the evidence again points to the importance of functional species in understanding this relationship. For example, the grazing-tolerant plant species have a disproportionately large role in the Serengeti community dynamics by preventing herbivores from dramatically reducing plant biomass.

The paucity of field tests at the scale of the food web reflects the fact that such experiments require an enormous undertaking. As an alternative, ecologists have approached this problem by investigating how diversity influences stability and function within a multitrophic setting in controlled microcosm experiments (often referred to as bottle experiments as they are attempts to create realistic ecological

Table 1 Definitions of stability

Term	Definition
Definitions of dynamic stability	
Equilibrium stability	A discrete measure that considers a system stable if it returns to its equilibrium after a small perturbation away from the equilibrium. A stable system, therefore, has no variability in the absence of perturbations.
General stability	A measure which assumes that stability increases as the lower limit of population density moves further away from zero. Under non-equilibrium dynamics, such limits to population dynamics generally imply a decrease in population variance (see variability definition below).
Variability	The variance in population densities over time, usually measured as the coefficient in variation. Common in experimental tests of stability.
Definitions of resilience and resistance stability	
Equilibrium resilience	A measure of stability that assumes system stability increases as time required to return to equilibrium decreases after a perturbation. A rapid response means that a system recoils rapidly back to its equilibrium state.
General resilience	A measure of stability that assumes system stability increases as return time to the equilibrium/non-equilibrium solution decreases after a perturbation. A rapid response means that a system recoils rapidly back to its equilibrium/non-equilibrium state.
Resistance	A measure of the degree to which a variable changes after a perturbation. Frequently used as a discrete measure that assesses a community's ability to resist invasion (that is, if an invader fails, the community resists invasion).

communities within a controlled setting). The main advantage of microcosms is that the experiments can easily be manipulated and replicated³³. Nonetheless, the issue of how scale influences outcome looms over microcosm experiments — can we extrapolate results to the whole ecosystem? Ambitious experimental set ups such as that currently underway in the Ecotron (Fig. 1) are attempting to bridge the gap between the complexity of real field communities and the simplicity of laboratory or greenhouse experiments.

The evidence that has emerged from microcosm experiments, regardless of scale and system type (that is, terrestrial or aquatic), has tended to agree that diversity is positively related to ecosystem stability^{34–39}. In addition, and consistent with field experiments on plant communities, experiments using aquatic microcosms have shown that population-level variation is relatively uninfluenced by diversity, whereas community-level variance tends to decrease with increased diversity³⁵. Two ideas have been advanced in explanation of these findings. One explanation is that increasing diversity increases the odds that at least some species will respond differentially to variable conditions and perturbations^{37–39}. The second is that greater diversity increases the odds that an ecosystem has functional redundancy by containing species that are capable of functionally replacing important species^{37–39}. Taken together, these two notions have been called the insurance hypothesis (Table 2). This idea has been extended to suggest that the greater the variance in species' responses contained in a community then the lower the species richness required to insure the ecosystem⁴⁰. As with the averaging and negative covariance effect,

Table 2 General diversity–stability theory

Theory	Underlying logic
Averaging effect ^{24,25}	Assume covariances between species are zero and variance (s_i^2) in abundance of individual species i in a plant community is equal to cm_i^2 , where c and z are constants and m_i is the mean density of species i . Given that all k species of a community are equal in abundance and sum to m (that is, $m_i = m/k$), then the coefficient of variation (CV) of community abundance can be determined as: $CV = 100s/m = 100(c/k)^{1/2}$ For the case $z > 1$, increasing k (species number) decreases the variation in biomass for the plant community.
Negative-covariance effect ²⁵	If covariances between species (say, species a and b) are negative (that is, $cov(a,b) < 0$), then the variance in the abundance of two species $s_{(a+b)}^2 = s_a^2 + s_b^2 + 2cov(a,b)$ will be less than the sum of the individual variances (that is, $s_a^2 + s_b^2$), and so will decrease overall biomass variance in the plant community.
Insurance effect ^{37–40}	An ecosystem's ability to buffer perturbations, loss in species and species invasions is dependent on the redundancy of the species having important stabilizing roles, as well as on the ability of the species in the community to respond differentially to perturbations. Increasing diversity increases the odds that such species exist in an ecosystem. This idea has been extended ⁴⁰ to suggest that the greater the variance of species' responses in a community then the lower the species richness required to buffer an ecosystem.

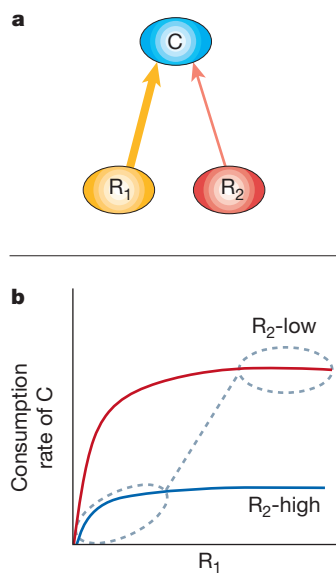


Figure 2 Consumer–resource interactions. **a**, A simple food-web diagram depicting a strong consumer–resource interaction ($C-R_1$) coupled to a weak consumer–resource interaction ($C-R_2$). **b**, Consumption rates by consumer C of R_1 for two different densities of R_2 . Because the resources negatively covary, the actual consumption response is qualitatively similar to a combination of these two curves (dashed circles and line). In the presence of R_2 , resource R_1 is less influenced by consumption when at low densities.

which are intimately related, the insurance hypothesis does not infer that diversity actively promotes stability.

In summary, the results indicate that within an ecosystem, diversity tends to be correlated positively with ecosystem stability. This correlation does not necessarily extend to population-level stability. Much work is still required to determine the driver of the positive diversity–stability relationship; however, it seems that community-level stability is dependent on the differential response of species or functional groups to variable conditions, as well as the functional redundancy of species that have important stabilizing roles. I now turn to a separate approach that has not focused on diversity, but has concentrated instead on understanding the implications of common food-web structures on stability.

Food-web structure and stability

In an important theoretical contribution, Chesson and Huntley⁴¹ showed that diversity cannot be maintained by variation alone. Rather, maintenance of diversity requires the two following components: the existence of flux or variability in ecosystems; and populations capable of differentially exploiting this flux or variability. Regardless of the source of the variability (for example, whether spatially or temporally generated), their results indicate that coexistence requires that populations must be released, either directly or indirectly, from the limiting influences of species interactions such as predation and competition. Species interactions, therefore, must be important in maintaining and promoting persistence in diverse communities in spite of, and perhaps because of, the variability that underlies ecosystems. Several more specific models can be included under this general framework, and all reveal that flux interacting with specific biotic, nonlinear responses can promote persistence^{6,14,17}. We now turn to a set of food-web models that have shown how persistent, complex ecosystems can be an outcome of this combination of flux and density-dependent food-web interactions (that is, competitive and predatory influences that vary with density).

The weak-interaction effect

Over the past decade, ecologists have begun to replace the conceptu-

alization of the ecosystem as a linear food chain with the view that food webs are highly interconnected assemblages^{42–45} characterized by recurrent food-web structures (for example, omnivory and apparent competition). Because combinations of competition and predation can represent these common food-web structures, the use of simple food-web modules has been advocated⁴⁶ to explore the repercussions of these ubiquitous species interactions.

Several model investigations have grown out of this approach to show that natural food-web structures can, indeed, enhance ecosystem stability^{6,47–49}. These food-web models are extensions of a bioenergetic consumer–resource model⁵⁰ that constrains parameters to empirically determined relationships of body size. The approach is akin to the dynamic modelling of a population’s energy budgets through time, and has the important consequence of placing food-web models within a biological universe with reasonable constraints operating on energy flow between any consumer–resource interaction—a feature that is considerably different from a statistical universe. The result is that increasing diversity can increase food-web stability under one condition: the distribution of consumer–resource interaction strengths must be skewed towards weak interaction strengths. I will refer to this as the weak-interaction effect (Table 3), and to connect this to general diversity–stability theory I briefly discuss the stabilizing mechanisms behind this effect.

Two general stabilizing mechanisms underlie the weak-interaction effect. First, the weak-interaction effect generates negative covariances and promotes community-level stability. Second, these negative covariances ensure that the weak interactors dampen the destabilizing potential of strong consumer–resource interactions. These mechanisms can be best understood with a simple example.

Figure 2a depicts a simple food-web interaction in which a strong consumer–resource interaction ($C-R_1$) is coupled to a weak consumer–resource interaction ($C-R_2$). Being a weakly interacting species, R_2 is an inferior competitor whose ability to persist is mediated by the top predator. This food-web relationship ensures that the resources negatively covary. For example, R_2 is released from competitive limitation to flourish whenever R_1 is suppressed by high densities of consumer C . This occurs because R_2 is weakly coupled to C and so is not strongly influenced by high densities of C . In this manner, the weak interaction drives the differential responses of species.

We can use the knowledge of this negative covariance to determine qualitatively the consumption rate of C on its preferred resource, R_1 . Figure 2b depicts C ’s consumption rate on R_1 under two different densities of R_2 , assuming an optimally foraging, type II multispecies functional response (for full details, see refs 49, 51). High densities of R_2 reduce the overall consumption rates on R_1 . Because the resources negatively covary, then for low densities of R_1 we expect C ’s consumption rates to fall on the R_2 -high curve in Fig. 2 (the lower dashed circle). Similarly, for high densities of R_1 we expect consumption rates to be on the R_2 -low curve in Fig. 2 (the upper dashed circle). Piecing these functions together we see that the asynchrony in resource densities drives a sigmoid-shaped response that is qualitatively similar to what ecologists refer to as a type III functional response. This has the non-equilibrium effect of releasing the prey (R_1) from strong consumptive pressures when it is at low densities, and thereby the weak interaction dampens the oscillatory potential of the strong $C-R_1$ interaction. Consistent with the above discussion is the fact that investigators have found that donor control (in which a consumer responds numerically to a resource but has no influence on resource dynamics) also promotes community stability^{45,48}. Donor control can generate differential responses of species by allowing species using these resources to disconnect themselves from fluxes that are inherent to the community.

I have discussed the weak-interaction effect within the context of relatively simple food-web modules. Does the effect operate for real, complex communities with enormous numbers of direct and indirect interactions? It is still too early to tell, but Kokkoris *et al.*⁵² followed the distribution of interaction strengths as competitive

model communities were assembled. They found that as the assembly process progressed, larger permanent communities (that is, with a lower limit above zero) attained lower mean interaction strengths. They also found that communities with lower mean interaction strength were more resistant to invasion. These results are encouraging and indicate that the weak-interaction effect might scale to the whole ecosystem. If the weak-interaction mechanism is operating in real communities then the distributions of interaction strengths will be skewed towards weak interactions in order that a few potentially excitable consumer–resource interactions are muted. I now turn to empirical investigations of food-web structure and stability, first reviewing experiments concerned with the distribution of interaction strengths in natural communities before examining experiments that have investigated directly the influence of food-web structure on stability.

Interaction strength and species invasions

Although quantitative field estimates of interaction strength are still in the process of development, work by a few ecologists has enabled a preliminary glimpse into the nature of the distributions of interaction strength within real food webs^{53–57}. The early data indicate unequivocally that distributions of interaction strength are strongly skewed towards weak interactions^{53–57}. Nonetheless, these experiments also highlight that the removal or addition of a single key species can have pronounced impacts on the dynamics and persistence of the species in the enclosure or enclosure. For example, experimental removal of the predatory starfish, *Pisaster ochraceus*, resulted in greatly simplified lower-intertidal communities because the mussel, *Mytilus californianus*, competitively dominates all other sessile benthic organisms when freed from predation⁵⁸.

A recent experiment⁵⁹ has confirmed the abundance of weak interactions in ecosystems, but showed that weak average interaction strength in a rocky intertidal community tends to be correlated with high variability in interaction strength. In this study, variation in the magnitude of the weak interactions seemed to excite spatial variation in community structure. The variation in interaction strength may be important in generating landscape-scale variation that promotes the maintenance of diversity, an area that demands further investigation.

It is important to know if these phenomena can be extended beyond the scale of the enclosure/exclosure experiment. Species invasions may be seen as the uncontrolled version of species addition experiments. Similar to the experiments described above, the current evidence indicates that, although most species invasions have a weak impact on ecosystems⁶⁰, the occasional invasive species alters an ecosystem profoundly^{61–63}. For example, a recent study⁶¹ used stable isotopes to document energy flow through food webs. Lakes that were uninvaded by bass were compared with lakes that had just been invaded, and the recently invaded lakes showed marked differences in energy flow patterns (implying a severely altered food-web structure) as well as rapid declines in forage fish diversity⁶¹. These results indicate that the addition of a single species can precipitate a form of ecosystem collapse that sends a wave of extinction through the ecosystem. Another noteworthy case concerns the introduction of the large predatory fish, the Nile perch (*Lates niloticus*), in Lake Victoria in the 1950s. The addition of the Nile perch was followed by a sequence of amazing ecological and genetic changes that culminated in a cascade of cichlid extinctions⁶³. Overall, however, the invasion literature is harmonious with enclosure/exclosure experiments⁶⁰ — most invasions have a weak impact with infrequent occurrences of an invasive species capable of precipitating monumental changes to an ecosystem.

Food-web structure and stability experiments

Some direct experimental tests of stability and food-web structure exist. In a clever experimental manipulation, Fagan⁶⁴ tested community response to a perturbation (aphicide application) as a function of the degree of omnivory. Fagan accomplished this by controlling

Table 3 Food-web structure and stability theory

Theory	Underlying logic
Weak-interaction effect ^{65,46–48}	Weak interactions serve to limit energy flow in a potentially strong consumer–resource interaction and, therefore, to inhibit runaway consumption that destabilizes the dynamics of food webs. In addition, the weak interactions serve to generate negative covariances between resources that enable a stabilizing effect at the population and community level. The negative covariances ensure that consumers have weak consumptive influences on a resource when the resource is at low densities. See text and Fig. 2 for further clarification.
	Berlow ⁵⁷ suggested an additional influence of weak interactions. Weak interactions in intertidal communities seem to be extremely variable in strength, and as a result may drive spatial variability in community structure. This community variability in space can provide a canvas for species to respond differentially, and so may further promote the maintenance of diversity.

the relative proportion of nonomnivorous damselbugs versus omnivorous wolf spiders in arthropod assemblages of the Mount Saint Helen ‘blowdown zone’. The results showed that increasing the degree of community omnivory (that is, increasing the proportion of wolf spiders) decreased variation in the population responses after an aphicide application.

In an earlier investigation, de Ruiter *et al.*⁶⁵ investigated model communities constructed from empirical estimates based on some well-studied food webs from native and agricultural soils. Their results are consistent with the experiments on interaction strength and the weak-interaction effect discussed above, as most interactions had only a negligible impact on community dynamics. Although their results indicate that energetics are important in constraining interaction strength, they found no positive correlation between feeding rates and community impact. This, too, is consistent with the weak-interaction effect. Similarly, experiments on both terrestrial and aquatic microcosms have tended to find that increasing the number of prey items enhances stability^{66–68}, although one microcosm experiment⁶⁹ found that the addition of an alternate prey destabilized community dynamics. This last case can be reconciled with other experiments as the alternate prey introduced was efficient fare for the predator. In essence, the alternative prey energetically fuelled the predator, and so the experiment may be viewed as evidence that a strong consumer–resource interaction is potentially destabilizing.

Conclusion

Taken together, recent advances indicate that diversity can be expected, on average, to give rise to ecosystem stability. The evidence also indicates that diversity is not the driver of this relationship; rather, ecosystem stability depends on the ability for communities to contain species, or functional groups, that are capable of differential response. All of these views are consistent with the ideas put forth by the influential figures of Odum⁷, Elton⁸, MacArthur⁹ and May¹⁰. May’s result reflects the fact that random distributions (that is, a null universe where dynamics are influenced by diversity alone), on average, do not create the necessary tension between community members that forces differential response and community stability. In a randomly constructed community, for example, strong interactions are not necessarily coupled to weak interactions that mute their destabilizing potential. In fact, one can expect that random communities will generally not create such couplings, and so tend to produce diverse communities with complex, wildly oscillatory dynamics. Furthermore, Odum, Elton and MacArthur recognized that real food webs contain a complex array of energetic pathways that can act as buffers against dramatic population explosions. Specifically, MacArthur’s hypothesis — that greater connectance drives community and ecosystem stability — seems a strong possibility provided most pathways are constructed from weak interactions that mute the potentially destabilizing roles of a few strong consumer–resource interactions.

The current empirical evidence indicates that communities may be dominated by such weak trophic interactions. If this is true, then it is also true that the removal, or addition, of any species (weak or strong) can lead to pronounced changes in community composition and structure. It follows that decreasing biodiversity will tend to increase the overall mean interaction strength, on average, and thus increase the probability that ecosystems undergo destabilizing dynamics and collapses. Just how much ecosystem deterioration is sufficient to precipitate a collapse is difficult to assess, but current experiments and theory agree that drastic community changes can accompany the removal or addition of even a single species. Furthermore, if Elton's observation is correct — that simplified communities are more vulnerable to invasion — than we should also expect an increase in frequency of successful invaders as well as an increase in their impact as our ecosystems become simplified. The lessons for conservation are obvious: (1) if we wish to preserve an ecosystem and its component species then we are best to proceed as if each species is sacred; and (2) species removals (that is, extinction) or species additions (that is, invasions) can, and eventually will, invoke major shifts in community structure and dynamics.

It is important to point out that the mechanistic ideas outlined here omit higher-scale ecosystem influences that are likely to be linked intricately to ecosystem stability and function^{70–73}. Some promising work is now beginning to show us how we can link models of nutrient and energy flow^{70–72} as well as uncover the potential influence of diversity and stability on large-scale biogeochemical processes⁷³. Investigations of this sort will be necessary to bridge important stabilizing processes that act across ecological scales. □

- Ricciardi, A. & Rasmussen, J. B. Extinction rates of North American freshwater fauna. *Conserv. Biol.* **13**, 1220–1222 (2000).
- Reid, W. V. Strategies for conserving biodiversity. *Environment* **39**, 16–43 (1997).
- Levin, S. *Fragile Dominion: Complexity and the Commons* (Helix books, Reading, MA, 1999).
- Lodge, D. Biological invasions: lessons for ecology. *Trends Ecol. Evol.* **8**, 133–137 (1993).
- Cohen, A. & Carlton, J. T. Accelerating invasion rate in a highly invaded estuary. *Science* **279**, 555–558 (1998).
- Odum, E. P. *Fundamentals of ecology* (Saunders, Philadelphia, 1953).
- Elton, C. S. *Ecology of Invasions by Animals and Plants* (Chapman & Hall, London, 1958).
- MacArthur, R. H. Fluctuations of animal populations and a measure of community stability. *Ecology* **36**, 533–536 (1955).
- May, R. M. *Stability and complexity in model ecosystems* (Princeton Univ. Press, 1973).
- Gardner, M. R. & Ashby, W. R. Connectance of large dynamic (cybernetic) systems: critical values for stability. *Nature* **228**, 784 (1970).
- Pimm, S. L. & Lawton, J. H. On feeding on more than one trophic level. *Nature* **275**, 542–544 (1978).
- Yodzis, P. The stability of real ecosystems. *Nature* **289**, 674–676 (1981).
- Armstrong, R. A. & McGehee, R. Competitive exclusion. *Am. Nat.* **115**, 151–170 (1980).
- DeAngelis, D. & Waterhouse, J. C. Equilibrium and nonequilibrium concepts in ecological models. *Ecol. Monogr.* **57**, 1–21 (1987).
- Michalski, J. & Arditi, R. in *Advances in Environmental and Ecological Modelling* (ed. Weill, A.), 1–20 (Elsevier, Paris, 1999).
- Huisman, J. & Weissing, F. J. Biodiversity of plankton by species oscillations and chaos. *Nature* **402**, 407–410 (1999).
- McCann, K., Hastings, A. & Huxel, G. R. Weak trophic interactions and the balance of nature. *Nature* **395**, 794–798 (1998).
- Law, R. & Morton, D. Permanence and the assembly of ecological communities. *Ecology* **77**, 762–775 (1996).
- Hastings, A. & Higgins, K. Persistence of transients in spatially structured ecological models. *Science* **263**, 1133–1136 (1994).
- Tilman, D. & Downing, J. A. Biodiversity and stability in grasslands. *Nature* **367**, 363–365 (1994).
- Tilman, D., Wedin, D. & Knops, J. Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature* **379**, 718–720 (1996).
- Tilman, D. Biodiversity: population versus ecosystem stability. *Ecology* **77**, 350–363 (1996).
- Schapfer, F. & Schmid, B. Ecosystem effects of biodiversity: a classification of hypotheses and exploration of empirical results. *Ecol. Applic.* **9**, 893–912 (1999).
- Doak, D. F. *et al.* The statistical inevitability of stability-diversity relationships in community ecology. *Am. Nat.* **151**, 264–276 (1998).
- Tilman, D., Lehman, C. L. & Bristow, C. E. Diversity-stability relationships: statistical inevitability or ecological consequence. *Am. Nat.* **151**, 277–282 (1998).
- Sankaran, M. & McNaughton, S. J. Determinants of biodiversity regulate compositional stability of communities. *Nature* **401**, 691–693 (1999).
- Huston, M. A. Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia* **110**, 449–460 (1997).
- Tilman, D. *et al.* The influence of functional diversity and composition on ecosystem processes. *Science* **277**, 1300–1302 (1997).
- Hooper, D. U. & Vitousek, P. M. The effects of plant composition and diversity on ecosystem processes. *Science* **277**, 1302–1305 (1997).
- Wardle, D. A. *et al.* Plant removals in perennial grassland: vegetation dynamics, decomposers, soil biodiversity, and ecosystem properties. *Ecol. Monogr.* **69**, 535–568 (1999).
- van der Heijden, M. *et al.* Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. *Nature* **396**, 69–72 (1998).
- McNaughton, S. J. Ecology of a grazing ecosystem: the Serengeti. *Ecol. Monogr.* **55**, 259–294 (1985).
- Lawton, J. H. Ecological experiments with model systems. *Science* **269**, 328–331 (1995).
- McGrady-Steed, J., Harris, P. & Morin, P. J. Biodiversity regulates ecosystem predictability. *Nature* **390**, 162–165 (1997).
- McGrady-Steed, J. & Morin, P. J. Biodiversity, density compensation, and the dynamics of populations and functional groups. *Ecology* **81**, 361–373 (2000).
- Morin, P. J. & Lawler, S. P. Food web architecture and population dynamics: theory and empirical evidence. *Annu. Rev. Ecol. System.* **26**, 505–529 (1995).
- Naeem, S. & Li, S. Biodiversity enhances ecosystem reliability. *Nature* **390**, 507–509 (1997).
- Naeem, S. Species redundancy and ecosystem reliability. *Conserv. Biol.* **12**, 39–45 (1998).
- Lawton, J. H. & Brown, V. K. in *Biodiversity and Ecosystem Function* (eds Schulze, E. D. & Mooney, H. A.), 255–270 (Springer, New York, 1993).
- Yachi, S. & Loreau, M. Biodiversity and ecosystem functioning in a fluctuating environment: the insurance hypothesis. *Proc. Natl Acad. Sci. USA* **96**, 1463–1468 (1999).
- Chesson, P. & Huntley, N. The roles of harsh and fluctuating conditions in the dynamics of ecological communities. *Am. Nat.* **150**, 519–553 (1997).
- Winemiller, K. O. Spatial and temporal variation in tropical fish trophic networks. *Ecol. Monogr.* **60**, 331–367 (1990).
- Polis, G. A. Complex trophic interactions in deserts: an empirical critique of food web theory. *Am. Nat.* **138**, 123–155 (1991).
- Polis, G. A. & Strong, D. Food web complexity and community dynamics. *Am. Nat.* **147**, 813–846 (1996).
- Strong, D. Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. *Ecology* **73**, 747–754 (1992).
- Holt, R. D. in *Multitrophic interactions* (eds Begon, M., Gange, A. & Brown, V.) 333–350 (Chapman & Hall, London, 1996).
- McCann, K. & Hastings, A. Re-evaluating the omnivory-stability relationship in food webs. *Proc. R. Soc. Lond. B* **264**, 1249–1254 (1997).
- Huxel, G. R. & McCann, K. Food web stability: the influence of trophic flows across habitats. *Am. Nat.* **152**, 460–469 (1998).
- Post, D. M., Connors, E. & Goldberg, D. S. Prey preference by a top predator and the stability of linked food chains. *Ecology* **81**, 8–14 (2000).
- Yodzis, P. & Innes, S. Body-size and consumer-resource dynamics. *Am. Nat.* **139**, 1151–1175 (1992).
- Chesson, J. The estimation and analysis of preference and its relationship to foraging models. *Ecology* **64**, 1297–1304 (1983).
- Kokkoris, G. D., Troumbis, A. Y. & Lawton, J. H. Patterns of species interaction strength in assembled theoretical competition communities. *Ecol. Lett.* **2**, 70–74 (1999).
- Paine, R. T. Food-web analysis through field measurements of per capita interaction strengths. *Nature* **355**, 73–75 (1992).
- Fagan, W. F. & Hurd, L. E. Hatch density variation of a generalist arthropod predator: population consequences and community impact. *Ecology* **75**, 2022–2032 (1994).
- Goldwasser, L. & Roughgarden, J. Construction and analysis of a large Caribbean food web. *Ecology* **74**, 1216–1223 (1993).
- Raffaelli, D. G. & Hall, S. J. in *Food Webs: Integration of Patterns & Dynamics* (eds Polis, G. A. & Winemiller, K. O.) 185–191 (Chapman & Hall, New York, 1996).
- Wootton, J. T. Estimates and tests of per capita interaction strength: diet abundance and impact of intertidally foraging birds. *Ecol. Monogr.* **67**, 45–64 (1997).
- Paine, R. T. Ecological determinism in the competition for space. *Ecology* **65**, 1339–1348 (1984).
- Berlow, E. Strong effects of weak interactions in ecological communities. *Nature* **398**, 330–334 (1999).
- Williamson, M. & Fitter, A. The varying success of invaders. *Ecology* **77**, 1661–1666 (1996).
- Vander Zanden, M. J., Casselman, J. M. & Rasmussen, J. B. Stable isotope evidence for the food web consequences of species invasions in lakes. *Nature* **401**, 464–467 (1999).
- Fritts, T. H. & Rodda, G. H. The role of introduced species in the degradation of island ecosystems: a case history of Guam. *Annu. Rev. Ecol. System.* **29**, 113–140 (1998).
- Reinthal, P. N. & Kling, G. W. in *Theory and Application in Fish Feeding Ecology* (eds Stouder, D. J., Fresh, K. L. & Feller, R.) 296–313 (Univ. South Carolina Press, 1994).
- Fagan, W. F. Omnivory as a stabilizing feature of natural communities. *Am. Nat.* **150**, 554–567 (1997).
- de Ruiter, P. C., Neutel, A. & Moore, J. C. Energetics, patterns of interaction strengths, and stability in real ecosystems. *Science* **269**, 1257–1260 (1995).
- Holyoak, M. & Sachdev, S. Omnivory and the stability of simple food webs. *Oecologia* **117**, 413–419 (1999).
- Flaherty, D. Ecosystem trophic complexity and densities of the Williamette mite, *Eotetranychus willamettei ewing* (Acarina: Tetranychidae). *Ecology* **50**, 911–916 (1969).
- Morin, P. Productivity, intraguild predation, and population dynamics in experimental food webs. *Ecology* **80**, 752–760 (1999).
- Luckinbill, L. S. Regulation, stability, and diversity in a model experimental microcosm. *Ecology* **60**, 1098–1102 (1979).
- DeAngelis, D. *Dynamics of Nutrient Recycling and Food Webs* (Chapman & Hall, New York, 1992).
- Andersen, T. *Pelagic Nutrient Cycles: Herbivores as Sources and Sinks* (Springer, New York, 1997).
- Elser, J. J. & Urabe, J. The stoichiometry of consumer-driven nutrient recycling: theory, observations and consequences. *Ecology* **80**, 735–751 (1999).
- Harding, S. P. Food web complexity enhances community stability and climate regulation in a geophysiological model. *Tellus* **51B**, 815–829 (1999).

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Systematic conservation planning

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The realization of conservation goals requires strategies for managing whole landscapes including areas allocated to both production and protection. Reserves alone are not adequate for nature conservation but they are the cornerstone on which regional strategies are built. Reserves have two main roles. They should sample or represent the biodiversity of each region and they should separate this biodiversity from processes that threaten its persistence. Existing reserve systems throughout the world contain a biased sample of biodiversity, usually that of remote places and other areas that are unsuitable for commercial activities. A more systematic approach to locating and designing reserves has been evolving and this approach will need to be implemented if a large proportion of today's biodiversity is to exist in a future of increasing numbers of people and their demands on natural resources.

It is an ancient and widespread human practice to set aside areas for the preservation of natural values. The sacred groves of Asia and Africa and royal hunting forests are historical examples^{1,2}. Other areas protect ecosystem services such as the delivery of clean water or the supply of timber, or mitigate the expected adverse effects of over-clearing³. Others protect recreational and scenic values and some have been planned to foster international cooperation⁴. Many of these areas meet the World Conservation Union's definition of a strictly protected area (IUCN categories I–IV)⁵, and hereafter we refer to such protected areas as 'reserves'. These areas are increasingly being complemented by reserves established principally for the protection of biodiversity, including ecosystems, biological assemblages, species and populations⁶. The basic role of reserves is to separate elements of biodiversity from processes that threaten their existence in the wild. They must do this within the constraints imposed by large and rapidly increasing numbers of humans in many parts of the world and their attendant requirements for space, materials and waste disposal⁷.

The extent to which reserves fulfil this role depends on how well they meet two objectives. The first is representativeness, a long-established goal referring to the need for reserves to represent, or sample, the full variety of biodiversity⁸, ideally at all levels of organization. The second is persistence. Reserves, once established, should promote the long-term survival of the species and other elements of biodiversity they contain by maintaining natural processes and viable populations and by excluding threats⁹. To meet these objectives, conservation planning must deal not only with the location of reserves in relation to natural physical and biological patterns but also with reserve design, which includes variables such as size, connectivity, replication, and alignment of boundaries, for example, with watersheds^{10,11}. A structured systematic approach to conservation planning provides the foundation needed to meet these objectives.

Systematic conservation planning has several distinctive characteristics. First, it requires clear choices about the features to be used as surrogates for overall biodiversity in the planning process. Second, it is based on explicit goals, preferably translated into quantitative, operational targets. Third, it recognizes the extent to which conservation goals

have been met in existing reserves. Fourth, it uses simple, explicit methods for locating and designing new reserves to complement existing ones in achieving goals. Fifth, it applies explicit criteria for implementing conservation action on the ground, especially with respect to the scheduling of protective management when not all candidate areas can be secured at once (usually). Sixth and finally, it adopts explicit objectives and mechanisms for maintaining the conditions within reserves that are required to foster the persistence of key natural features, together with monitoring of those features and adaptive management¹² as required. The effectiveness of systematic conservation planning comes from its efficiency in using limited resources to achieve conservation goals, its defensibility and flexibility in the face of competing land uses, and its accountability in allowing decisions to be critically reviewed. This is an idealized description of a process that is difficult to achieve in practice. Nevertheless, substantial parts have now been implemented around the world^{13–17} and some are used as illustrations below.

The practice of conservation planning has generally not been systematic and new reserves have often been located in places that do not contribute to the representation of biodiversity. The main reason is that reservation usually stops or slows the extraction of natural resources. In some regions, housing and commercial development compete with reserves for land¹⁸. The economic and political implications can be serious and reserves can be degraded or even lose their protected status when they prove to be economically valuable¹⁹. As a result, reserves tend to be concentrated on land that, at least at the time of establishment, was too remote or unproductive to be important economically²⁰. This means that many species occurring in productive landscapes or landscapes with development potential are not protected, even though disturbance, transformation to intensive uses, and fragmentation continue²¹. Another reason for the inappropriate location of reserves is the very diversity of reasons for which reserves are established. A diversity of goals means that different proponents see different places as important. Because highly valued areas arising from alternative conservation goals often fail to overlap²², there is competition among proponents for limited funds and the limited attention spans of decision-makers. Moreover, goals such as the protection of grand scenery and wilderness often focus on areas that are remote, rugged and

Figure 1 Social, economic and political factors often compete with reserves for land. **a**, Kings Canyon, Watarrka National Park, Northern Territory, Australia. This is a spectacular landscape, worthy of protection both for its outstanding natural beauty and for its biodiversity. But it is a remote and rugged area, valuable for tourism but not for extractive uses so it was easier to protect than more productive and economically valuable landscapes. **b**, An agricultural landscape in the Adelaide Hills, South Australia, with remnant woodland in the background. Remnants such as these contain species that are not represented in more remote and inaccessible areas, so their contribution to the overall goal of maintaining biodiversity is just as great. Despite their natural values it is always a difficult social and political decision to protect them because they have economic value as well as biodiversity value. Photographs by Liz Poon.



residual from intensive uses, giving them a political advantage over goals such as representativeness, which focus also on disturbed, economically productive landscapes (Fig. 1).

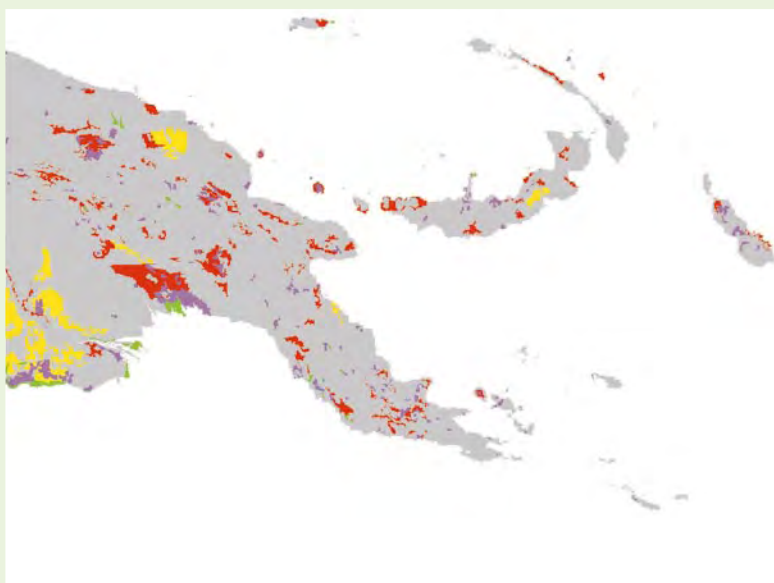
Conservation planning is therefore an activity in which social, economic and political imperatives modify, sometimes drastically, scientific prescriptions. This interaction need not be all one way. Science has at least three means of influencing the practice of nature conservation. First, an available body of scientific theory and application can provide some of the raw material for constructing policies²³. Second, science can offer solutions when called upon to assist in the implementation of policies and conventions, while also clarifying the social and economic implications of alternative methods or scenarios (this role is best filled when science is integral to the process, not simply called in for peer review²⁴ or when technical or political problems emerge). Third, science can and should be used to review the effectiveness of political processes for achieving stated biodiversity goals. A structured framework for conservation

planning will enhance the effectiveness with which science can do these three things.

A framework for systematic conservation planning

Systematic conservation planning can be seen as a process in six stages²⁵ (Box 1), each of which is discussed below with examples of the tasks and decisions required. The process is not unidirectional — there will be many feedbacks and reasons for revised decisions about priority areas. For example, it will be necessary to re-examine conservation goals as knowledge accumulates, and replacement candidate reserves will have to be identified when unforeseen difficulties arise in implementation. Although our discussion focuses on reserves, the framework applies equally well to many problems in 'off-reserve' conservation, including habitat restoration^{25,26}. Decisions about both on- and off-reserve conservation, if they are not to be *ad hoc* and uncoordinated, should be guided by explicit goals, identification of priorities in regional or broader contexts, and clear choices between

Figure 2 A map of biodiversity priority areas in Papua New Guinea¹⁶. The targets that are met by this set of areas are the representation of 608 environmental domains³⁷, 564 vegetation types, 10 species assemblages and 12 rare and threatened species. For the derivation of these targets, see refs 16, 92. In meeting targets, the set of areas also minimizes foregone opportunities for timber extraction, represents all existing reserves, minimizes the number of areas currently used for intensive agriculture, gives preference to areas with low human population density and gives preference to areas identified previously by experts as biodiversity priority areas⁹². The selected areas occupy 16.8% of the country and are inhabited by 210,000 people out of a population of approximately 4 million. A total of 398 areas were selected from 4,470 candidate areas or planning units. These units were aerial photograph patterns that were previously mapped for a database on agricultural and forestry suitability. The trade-off between biodiversity gain and opportunity costs, and the application of the other spatial constraints, was achieved with the TARGET software^{94,109}. The colours represent different index classes of timber volume. Yellow is highest, red next highest, purple next and green lowest.



potential conservation areas and alternative forms of management.

Stage 1. Measure and map biodiversity

Because of the complexity of biodiversity, surrogates such as sub-sets of species, species assemblages and habitat types have to be used as measures of biodiversity, and the locations of these surrogates within areas have to be plotted so that similarities or differences among areas can be estimated.

Biological systems are organized hierarchically from the molecular to the ecosystem level. Logical classes such as individuals, populations, species, communities and ecosystems are heterogeneous. Each member of each class can be distinguished from every other member. It is not even possible to enumerate all of the species of any one area, let alone the members of logical classes at lower levels such as populations and individuals. Yet this is biodiversity, and maintaining that complexity is the goal of conservation planning. For the foreseeable future it will be necessary to accept this incomplete knowledge and adopt methods for making the most of what we do know or can discover from new surveys. Thus, surrogate or partial measures of biodiversity must be used to estimate similarity or difference among areas within planning regions.

The choice of surrogate measures is not trivial. The strong temptation is to use a group of species: for example, vascular plants,

vertebrates or butterflies. We may know that the presence of a butterfly indicates the presence of its food plant somewhere nearby. The real question, however, is whether the presence of that butterfly, or any other taxon, indicates the presence of other taxa to the extent that it can be considered a suitable surrogate for overall biodiversity. Tests of taxonomic surrogacy in Britain²⁷ and South Africa²⁸ are not encouraging, but more promising results have been obtained in Uganda²⁹. Divergent results are attributable to differences in analytical methods, geographical scales and biogeographical histories of the study areas. Reliable generalizations and an understanding of how such factors affect taxonomic surrogacy are still developing. Higher levels in the biological hierarchy, such as species assemblages, habitat types and ecosystems lose biological precision, but have other advantages. They can integrate more of the ecological processes that contribute to the maintenance of ecosystem function³⁰ (although there is active debate on this issue³¹) and the relevant data are more widely and consistently available. In addition, there are sound theoretical reasons why environmental variables should be good estimators of the spatial distribution patterns of species^{32–34} and there are now some empirical studies that add support^{35–37}. New statistical techniques are also being developed to compare how well different environmental surrogates reflect the distribution patterns of species³⁸.

Box 1

Stages in systematic conservation planning

Systematic conservation planning can be separated into six stages, and some examples of tasks and decisions in each are presented below²⁵. Note that the process is not unidirectional; there will be many feedbacks and reasons for altering decisions (see text for examples).

1. Compile data on the biodiversity of the planning region

- Review existing data and decide on which data sets are sufficiently consistent to serve as surrogates for biodiversity across the planning region.
- If time allows, collect new data to augment or replace some existing data sets.
- Collect information on the localities of species considered to be rare and/or threatened in the region (these are likely to be missed or under-represented in conservation areas selected only on the basis of land classes such as vegetation types).

2. Identify conservation goals for the planning region

- Set quantitative conservation targets for species, vegetation types or other features (for example, at least three occurrences of each species, 1,500 ha of each vegetation type, or specific targets tailored to the conservation needs of individual features). Despite inevitable subjectivity in their formulation, the value of such goals is their explicitness.
- Set quantitative targets for minimum size, connectivity or other design criteria.
- Identify qualitative targets or preferences (for example, as far as possible, new conservation areas should have minimal previous disturbance from grazing or logging).

3. Review existing conservation areas

- Measure the extent to which quantitative targets for representation and design have been achieved by existing conservation areas.
- Identify the imminence of threat to under-represented features such as species or vegetation types, and the threats posed to areas that will be important in securing satisfactory design targets.

4. Select additional conservation areas

- Regard established conservation areas as 'constraints' or focal points for the design of an expanded system.
- Identify preliminary sets of new conservation areas for consideration as additions to established areas. Options for doing this include reserve selection algorithms or decision-support software to allow stakeholders to design expanded systems that achieve regional conservation goals subject to constraints such as existing reserves, acquisition budgets, or limits on feasible opportunity costs for other land uses.

5. Implement conservation actions

- Decide on the most appropriate or feasible form of management to be applied to individual areas (some management approaches will be fallbacks from the preferred option).
- If one or more selected areas prove to be unexpectedly degraded or difficult to protect, return to stage 4 and look for alternatives.
- Decide on the relative timing of conservation management when resources are insufficient to implement the whole system in the short term (usually).

6. Maintain the required values of conservation areas

- Set conservation goals at the level of individual conservation areas (for example, maintain seral habitats for one or more species for which the area is important). Ideally, these goals will acknowledge the particular values of the area in the context of the whole system.
- Implement management actions and zonings in and around each area to achieve the goals.
- Monitor key indicators that will reflect the success of management actions or zonings in achieving goals. Modify management as required.



Figure 3 White Rhinos currently persist in relatively small intensively managed populations in game reserves. Off-reserve management in suitable habitat would probably be necessary if populations were to return to self-sustaining levels, although conflict with human populations makes it extremely unlikely that this would ever happen. Photograph by Liz Poon.

Planning is essentially a matter of comparison so it is preferable to compare two or more areas with the same kind of information at the same level of detail. A map of vegetation types (communities or habitat types) and/or environmental classes provides spatial consistency across wide areas. On the other hand, museum and herbarium data on the locations of taxa are notoriously biased, having been collected for a different purpose (systematics), and often in an opportunistic manner, from the places that collectors expected to find what they were looking for or that were conveniently accessible^{39,40}. Plots of the field records from many collections therefore map road networks. Various methods — empirical, statistical and computational — are now available for modelling wider spatial distribution patterns from the point records that field samples represent^{41–43}, but their reliability is also at least partly a function of the degree of spatial bias. New systematic field surveys to fill gaps are the best solution but they can be expensive and time consuming.

There is no best surrogate. The decision on which to use will depend on many factors including what data are available and what resources there are for data analysis (for example, spatial modelling) and the collection of new data. In most parts of the world, the only spatially consistent information available is on higher-order surrogates such as vegetation types and environmental classes. Collections of taxa might form an accurate representation of some biological distributions in some countries where well designed and well resourced surveys have been used to collect the data. Taxa collections may also be used with some reliability at coarse scales (for example, grid cells of 50 km × 50 km), but usually become less reliable at the scale of individual reserves⁴⁴. If taxa sub-sets are used without spatial modelling, it is usually with the understanding that the disadvantage of spatial bias is offset by the advantage of having at least some direct biological information to complement higher-order surrogates. Combinations of surrogates will be most practicable in most situations. In a recent study in Papua New Guinea, environmental domains classified from climate, landform and geology³⁷, vegetation types mapped from aerial photographs, and the known locations of rare and threatened species were all used as biodiversity surrogates (Fig. 2)¹⁶.

A decision is also needed at this stage on how to define planning units, the building blocks of the reserve system. Planning units can be regular (for example, grids or hexagons) or irregular (for example, tenure parcels, watersheds or habitat remnants). A mix of planning units might be appropriate in regions that contain both fragmented landscapes and extensive tracts of uncleared vegetation. The choice has implications for the efficiency with which representation goals can be achieved as well as for the design and management of reserves⁴⁵. For the reserve selection process described in stage 4, it is

necessary to compile data on biodiversity surrogates for each of the planning units in the region. Data on tenure (for stages 3, 4 and 5, below) and other contextual data that might influence selection and implementation (for example, roads, rivers, terrain, timber resources and threats) should also be compiled at this stage.

Stage 2. Identify conservation goals for the planning region

The overall goals of systematic conservation planning — representativeness and persistence — have to be translated into more specific, preferably quantitative, targets for operational use. Targets allow clear identification of the contributions of existing reserves to regional goals and provide the means for measuring the conservation value of different areas during the area selection process in stage 4 below. Targets such as 10 or 12% of the areas of countries or vegetation types have been criticized because they are too small to prevent the extinction of many species, can be subverted by reserving the least productive and least threatened landscapes, and can mislead the public into believing that limited conservation action is adequate⁴⁶. A focus on targets for reserves may also remove incentives to implement other conservation actions such as off-reserve management¹. These criticisms are valid, but are aimed at how targets are set rather than exposing reasons for not setting targets at all. Planners need to know what they are aiming for. ‘More equals better’ is good in principle, but does little to resolve choices between areas with different biotas when other demands narrow the geographical scope for reservation. Accordingly, planners need targets that do several things: focus on scales that are much finer than whole countries or regions; deal with natural processes as well as biodiversity pattern; reflect the relative needs of species and landscapes for protection; recognize that reserves must be complemented by off-reserve management, preferably also with targets; and leave options open for revision as social and economic conditions change. Ideally, reservation targets will be an integral part of policies and government processes⁴⁷. Failure to achieve targets for economically valuable landscapes is likely, so periodic reviews (stage 3, below) are necessary.

Most exercises in systematic conservation planning have chosen areas on the basis of the occurrences of species. Some have used predicted probabilities of occurrence⁴⁸. Recent applications have set targets for the spatial extent of communities, habitat types or environmental classes, sometimes with explicit formulae for adjusting targets according to factors such as natural rarity and vulnerability to threats¹³. These are all targets for representing a biodiversity pattern. Targets for ecological processes can be more problematic. Because conservation planning is a spatial exercise, protection of natural processes must be based on their spatial surrogates rather than the processes themselves (for example, size, lack of roads, watershed

boundaries, and migration routes). Setting process targets can be difficult in practice because the environment is heterogeneous in space and time and different species function at different spatial and temporal scales⁴⁹. Nevertheless, seven aspects of theory on ecological and evolutionary processes, now supported by some empirical evidence, can provide guidelines.

Biogeographical theory

Traditionally, the equilibrium theory of island biogeography⁵⁰ and associated biogeographical theory has been used to help set targets for size, shape and distance between reserves (although usually such targets were not quantitative). This body of theory tells us that bigger reserves are better, the closer they are the better, the more circular the better, and that reserves should be linked by habitat corridors^{51,52}. In the real world of conservation planning, the opportunity to apply such guidelines is constrained by costs and patterns of land-use history. These design principles also introduced an important trade-off into planning that is seldom acknowledged. If the area available for reservation is limited, a choice might have to be made between a few large reserves that favour the persistence of some species or more smaller reserves that together are more representative of the region's biodiversity but individually are less effective for the persistence of some species, for example, large, wide-ranging species^{17,53}. An early and widely ignored criticism of the equilibrium theory was that it treated islands as featureless plains with no internal habitat diversity and species as characterless features with no genetic or geographical variation⁵⁴. There is now some experimental support for the prediction that increased isolation reduces the likelihood of persistence of certain species⁵⁵, supporting targets for connectivity. However, attention has rightly shifted to the roles of environmental heterogeneity, species interactions, local- and regional-scale population dynamics, and the effects of habitat modification in reserve planning.

Metapopulation dynamics

In general, a metapopulation⁵⁶ is a network of local populations linked by dispersal. More narrowly, the term is used to describe systems in which local populations periodically go extinct with recolonization occurring by migration from other local populations⁵⁷. Metapopulations go extinct when the rate of extinction of local populations exceeds the rate of migration and recolonization. Confining a species to a reserve may disrupt metapopulation dynamics, increasing the risk of local extinction due, for example, to a catastrophic event such as wildfire, and decreasing the chances of recolonization. Metapopulation theory calls for targets that consider reservation across species' natural ranges so that some populations might escape the impact of unpredictable events, thereby spreading the risk of extinction⁵⁸. It also calls for the retention of landscape linkages to promote dispersal and the exchange of individuals between geographically separate sub-populations⁵⁹ and for

the retention of patches of suitable, but currently unoccupied, habitat⁶⁰.

Source-pool effects and successional pathways

The species composition of an area changes over time in a process usually called ecological succession. Some of these changes will be due to dispersal but others will be the products of initial conditions. There is a mix of starting propagules available in an area and subsequent changes reflect a sorting of this mix according to life-history traits and interspecific interactions⁶¹. Because of periodic, patchy disturbances, most regions contain areas at various stages along these pathways and many species exploit the temporal and spatial variation of natural disturbance regimes⁶². The implications for target setting are that all successional stages might need to be represented, replication of reserves to sample different successional stages might be desirable, and large reserves are better because they can better accommodate natural patch dynamics without succession being reset throughout by a single event such as a wildfire⁶³.

Spatial autecological requirements

Different species require different amounts of space to complete their life cycles⁵⁷ (Fig. 3). Most reserves contain one or more species that would not persist as residents even for one generation if they became isolated. Many other reserves, without supplementation by unreserved habitat, would be likely to lose species in the long term through a variety of chance events. Thus, the long-term persistence of some taxa requires sustainable populations across entire landscapes or regions as predicted, for example, for the northern spotted owl (*Strix occidentalis caurina*) in the Pacific northwest United States⁶⁴. There is a vast literature on population viability analysis^{65,66}. Reservation targets should include viable population sizes and structures (for example, age classes and sex ratios) when these are known. Many species exploit temporal variation by moving between different habitats, requiring targets to recognize key habitat combinations where these can be identified. The focal species approach⁶⁷ attempts to integrate patterns and processes by identifying those species in a landscape that are most demanding of resources and then targeting them for management. The kinds of resources needed by focal species may be, for example, large areas, connectivity between habitat patches and complex heterogeneous habitats¹⁷. The argument is that if management can maintain these species in a landscape, then most other species will be maintained as well.

Source-sink population structures

If, in some high-quality habitats (sources) a species' reproduction rate exceeds mortality, but in low-quality habitats (sinks) its reproduction rate is lower than mortality, then a net dispersal away from sources may sustain populations in sinks^{57,68}. In southeastern Australia, 63% of the arboreal marsupial population is found in only 9% of the forest with high foliar nutrients⁶⁹. Dispersal throughout the remainder of the forest occurs from these areas of high population



Figure 4 Isolated habitat remnants in the wheat belt of Western Australia. Isolation causes physical changes to habitat remnants, which in turn can lead to changes in species composition and population sizes. Photograph courtesy of CSIRO, Wildlife & Ecology.

density. If population sources for some species are outside reserves or are not targeted for reservation, then the presence of those species within reserves is at risk.

Effects of habitat modification

If reserves become remnants of natural habitat surrounded by alien habitat such as cropland or pasture, changes brought about by isolation and exposure have implications for the persistence of species within them (Fig. 4). Changes in fluxes of wind, water and solar radiation⁷⁰ can lead, in turn, to changes in vegetation structure, microclimate, ground cover and nutrient status⁷¹. These changes may favour some species, but they also lead to reduced population sizes and local extinction of others^{72,73}. Once isolated and exposed, habitat remnants may be placed on a trajectory of continued change. Deleterious effects can feed back on themselves to increase their magnitude⁷⁴, they can simply accumulate with time⁷⁵, or they can cascade, with a change in a species' abundance or productivity leading to unforeseen changes in the populations of other species. In

fragmented landscapes, where reserves are likely to be small and isolated, targets for off-reserve conservation are particularly important and they should include buffers around remnants, sympathetic management of poorly protected vegetation types or environments, and habitat restoration

Species as evolutionary units

It has long been argued that species should be treated as dynamic evolutionary units rather than as types^{76,77}. There are at least two related planning implications. First, areas occupied by taxa that appear from phylogenies to be actively radiating, or are most phylogenetically distinct, might be targeted for protection^{78,79}. Second, with an understanding of the physical and biological processes leading to active diversification of taxa, it is possible to identify and set targets for evolutionary templates. The most distinctive evolutionary feature of the Cape Floristic Region of South Africa has been the recent and massive diversification of many plant lineages. This process has been related to landscape features, such as interfaces between different soil types, which are now targeted for conservation action¹⁴.

These seven aspects of ecological and evolutionary processes have been explored largely as independent lines of research, separate also from the extensive work on the derivation and application of targets for biological patterns. An integration of all these research areas is needed for planning applications if the goals of representation and persistence are to be achieved⁴⁹. The best way forward is not yet clear but some attempts in different regions by different planning groups will allow comparisons to be made and, hopefully, some promising directions to be identified.

Stage 3. Review existing reserves

The extent to which targets for representation and persistence have already been achieved in existing reserves has to be determined. This defines the scope of the task in stage 4. Systematic reviews of existing reserve systems have a long history and are the conceptual basis for the Gap Analysis Program in the United States, now incorporating research and development projects and their applications in the 48 contiguous states⁴⁴. This programme was designed originally to identify gaps in the coverage of reserve networks but its increasing activity in identifying candidate conservation areas⁸⁰ (stage 4, below) is grounded in the systematic planning methods described here, which from the earliest applications have recognized the contribution of existing reserves to explicit targets⁸¹.

Analyses of gaps in networks of reserves have concentrated on which features are represented or not represented and to what extent. Two other aspects of gap analysis have received little attention. The first is the relative imminence or likelihood of species or habitats becoming extinct without conservation action. Because features that are under-reserved according to representation targets vary in their exposure and vulnerability to threatening processes, some gaps are more important than others⁸². Decisions about the scheduling of conservation action relative to threat are crucial for effective implementation (stage 5, below). Gap analyses that incorporate threats can reveal spatial biases in action by agencies and governments that inhibit effective implementation.

The second neglected aspect of gap analysis relates to natural dynamics and the persistence of biodiversity in the long term. Measures of gaps in process and persistence are few^{11,83} and a comprehensive, generic set of criteria for measuring gaps in the coverage of processes is lacking. Although most planners would agree that large size, connectivity and integrity are generally desirable, many species and vegetation types now exist only in remnants of habitat that are altered and surrounded by intensive land uses. The criteria for assessing gaps in coverage will be different in fragmented landscapes than in landscapes in which large contiguous tracts of habitat remain. The relative priority of reserve design criteria when they produce contrasting results (for example, compactness versus replication) has not been adequately addressed, nor has the role of partial contributions to biodiversity protection from areas under different

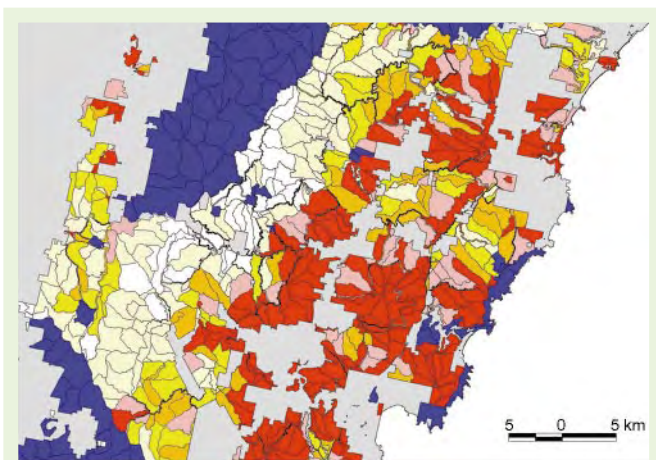


Figure 5 Pattern of complementarity on part of the south coast of New South Wales. The map is based on the same data used in the C-Plan decision-support system¹³ in late 1999 to guide negotiations between interest groups over new forest reserves in the region. The eastern boundary is the coastline. Blue areas are reserves established before the negotiations. Grey areas are tenures not considered in the planning process. Other polygons are logging compartments (average area about 200 ha or 2×10^6 m²) used as the building blocks of the expanded reserve system. Colours of these indicate five intervals of 'percentage contribution', the measure used in this exercise to indicate complementarity with existing reserves. Highest values are red (81–100%) and grade through pink, orange, dark yellow, pale yellow (>0–20%) and white (0%). Values of percentage contribution are based on reservation targets (in hectares) for each of 107 forest ecosystems in the region. Percentage contribution is calculated in two stages. In the first stage, a contribution value (in hectares) for each forest ecosystem in each compartment is calculated using two rules — if $A_i \leq T_i$ then $C_i = A_i$; if $A_i > T_i$ then $C_i = T_i$, where A_i is the extent of forest ecosystem i in the compartment, T_i is the remaining regional reservation target for the forest ecosystem, taking into account the contributions of existing reserves and any compartments previously given notional reserve status, and C_i is the current contribution of the compartment's sample of the forest ecosystem to the target. In the second stage, percentage contribution of the compartment is calculated as the sum of C values across all the forest ecosystems it contains, expressed as a percentage of the compartment's area. Compartments with highest values are largely or fully occupied by forest ecosystems well below target. Compartments with zero values contain only forest ecosystems with targets already achieved. Complementarity values show a marked association with distance eastwards from the large reserves in the westerly escarpment and more rugged foothills. In contrast, the small coastal reserves have no apparent influence on the complementarity of the adjacent compartments because they contain little forest. In the far northwest, higher values reflect the occurrence of forest ecosystems of the tableland, which are poorly reserved in the nearby escarpment reserves. Because complementarity is dynamic, percentage contribution was recalculated and redisplayed during the negotiations whenever one or more compartments were notationally reserved.

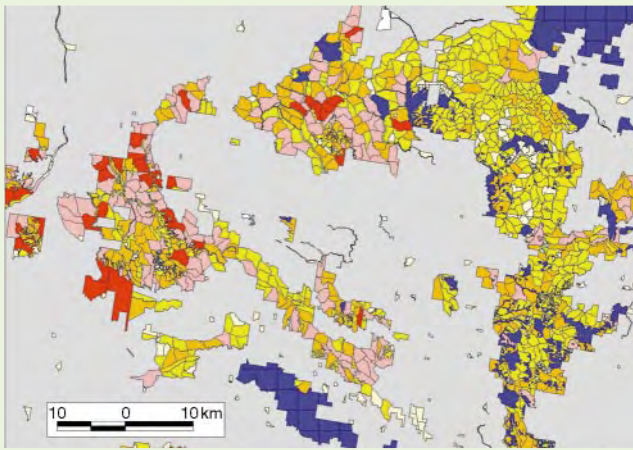


Figure 6 Pattern of irreplaceability in part of the northeast forests of New South Wales. The map is based on the same data and calculations of irreplaceability used in the C-Plan decision-support system¹³ in 1998 to guide negotiations between interest groups over new reserves in the region. Blue areas, grey areas and other polygons as in Fig. 5. The gradient from red to white indicates irreplaceability values of logging compartments based on the mix of forest ecosystems within each compartment, the distributions of 198 forest ecosystems across the region, their individual reservation targets in hectares, and the extent to which each target is already met in the existing reserves. Red areas are totally irreplaceable; if they are not reserved, one or more targets will not be met. Progressively lower values (pink, orange, dark yellow, pale yellow and white) indicate logging compartments with progressively more replacements. With lower values, the options for achieving targets are less constrained if compartments are unavailable or prove unsuitable for reservation. Like complementarity, irreplaceability is a dynamic measure. In the 1998 negotiations, values were recalculated each time one or more compartments were notionally reserved.

management regimes outside strict reserves.

In most planning exercises, implementation (stage 5, below) is likely to be gradual or, if rapid, will often fail to achieve all targets, particularly those for landscapes with economic potential. In these cases, the planning process should loop back periodically from stage 5 to stage 3 so that progress can be updated, new areas selected as appropriate (stage 4), and implementation reconsidered.

Stage 4. Select additional reserves

After the review of existing reserves, the need for additional areas to achieve the outstanding targets will become clear. At least some of the area selections at this stage are only preliminary because implementation (stage 5) invariably reveals practical impediments that require a degree of revision of the initial choices. The existing reserves are recognized not only for their contributions to targets but also because they can become the focal points or spatial constraints around which enlarged reserves or new, separate ones are located. The most convenient tools for the task of selection are algorithms, which apply explicit rules to identify notional sets of areas⁸⁴. These algorithms can be used to investigate various policy options, for example, to include or exclude wilderness areas, old-growth forest or regenerating areas, and to compare outcomes in terms of the number or total extent of new reserves needed. They can also indicate to planners whether the full set of targets is achievable within the expected limits of land area, acquisition cost or opportunity costs for other uses and, if not all are possible, the extent to which trade-offs are necessary (for example, between efficiency and design, or between representation of all forest types and the requirements of industry for timber). They provide a basis for negotiation or refinement of the conservation plan by regional or local experts. A recent development is the incorporation of algorithms into decision-support systems to guide structured negotiations between interest groups¹³. Used in this way, algorithms are able to guide decisions not only about how reserves sample biodiversity, but also about the design of reserve systems.

Complementarity

All selection algorithms use complementarity, a measure of the extent to which an area, or set of areas, contributes unrepresented features to an existing area or set of areas^{78,85}. The precise measure depends on the targets that have been identified and on the type of data. Most simply, it can be thought of as the number of unrepresented species (or other biodiversity features) that a new area adds. It has also been interpreted as a similarity index based on the number of species shared and not shared between two areas^{29,86}, as the contribution a new area makes to sampling a complete multivariate pattern generated by a classification or ordination of all areas⁸⁷, and as the distance in multivariate space that a new area is from existing areas^{88,89}. For targets set in terms of the extent of features such as forest types, complementarity can be measured as the contribution an area makes to outstanding targets according to the proportions of different types within that area (Fig. 5). An area with high complementarity will not necessarily be the richest⁹⁰. If, for example, an area contributes few species or habitat types and those features are not widely represented in the landscape, then its complementarity value could be extremely high. Another important property of complementarity is that it is recalculated for all unselected areas each time a new area is added to the notional reserved set. This recognizes that the potential contribution of an area to a set of targets is dynamic — some or all of the features in an unselected area might have had their targets partly or fully met by the selection of other areas. In contrast, more traditional measures of conservation value such as species richness or the number of rare species are unresponsive to changing targets and decisions to reserve other areas.

Spatial constraints on the selection of reserves

Constraints on the area selection process can be grouped into five kinds. The first, irreplaceability⁹¹, is inherent in any data set. When selection algorithms or regional experts decide on areas for reservation they choose between alternative areas for meeting conservation targets. For some planning exercises, it can be useful to display these alternatives explicitly as a map of irreplaceability (Fig. 6), indicating for each of the areas in a region the options for replacing it while still achieving conservation targets. Some areas have no replacements, whereas others have many. This information can be used to indicate the scope for altering selections by algorithms or experts (for example in trade-offs between targets and extractive land uses), to guide negotiations over new conservation areas, or to set priorities for implementation (stage 5, below). Four other spatial constraints are described below with examples from a recent application in Papua New Guinea (PNG) (Fig. 2)^{16,92}.

Costs. The use of an area for the protection of biodiversity generally means that it should not be available for commercial uses. Thus, biodiversity protection incurs opportunity costs. Trade-offs between opportunity costs and biodiversity gain can be achieved during the area selection process⁹³ or as a separate exercise after an initial selection¹³. It is important for the credibility of conservation planning that conservation goals are seen to be achieved in a way that minimizes, as far as possible, forgone opportunities for production. It is now possible to measure the opportunity costs of achieving a biodiversity goal and, conversely, the biodiversity costs of meeting a production goal, where that goal requires land allocation^{94,95}. Examples of opportunity costs are timber volume and agricultural production. Figure 2 shows the relative timber volumes on selected biodiversity priority areas in PNG. Other kinds of costs such as acquisition costs and the ongoing costs associated with management and maintenance could also be incorporated as constraints in the area selection process.

Commitments. Commitments are areas that must be selected regardless of their contribution to targets. The most common examples are existing reserves (Fig. 5). Other examples might be areas containing rare and threatened species and areas of endemism. Both existing reserves and areas containing rare and threatened species were used in the PNG study. Existing reserves can also require additional commitments of areas, for example when they need to be linked or have

their boundaries rationalized.

Masks. These are areas to be excluded from selection. For the PNG plan, areas smaller than 10 km² and areas used intensively for agriculture were masked initially. It was found, however, that some areas heavily used for agriculture were required if the biodiversity goal was to be achieved because they represented environments that were unavailable for selection elsewhere¹⁶.

Preferences. Sometimes certain characteristics of areas for conservation are to be preferred, if possible, over others. For the PNG plan, areas with low human population density and areas previously identified by expert taxonomists and ecologists as biodiversity priorities were given preference for selection, where there was a choice. Combining expert assessments with explicit analyses of spatially consistent data has advantages. Experts are inevitably biased geographically and taxonomically. On the other hand, data matrices inevitably lack the full store of knowledge in experts' heads.

Stage 5. Implement conservation actions on the ground

There is a world of difference between the selection process described above, and making things happen on the ground. Implementation is usually complicated by the variety of people, agencies and commercial interests with a stake in the region and by the time needed to apply conservation management to particular areas. The eventual system of reserves can be very different from the one designed in stage 4.

An example of a relatively straightforward case of implementation is the 1996 expansion of forest conservation areas in eastern New South Wales, Australia¹³ (Fig. 7). Planning was restricted to public land and the application of conservation action was rapid once the new areas had been negotiated to meet (most) targets and boundaries had been fine-tuned on the ground. Only a few forms of protection were at issue with little uncertainty about where they should most appropriately be applied. The implemented configuration was little different from that produced in the selection stage. A more complex and probably more widespread situation involves a mix of land tenures, ongoing loss and alteration of indigenous vegetation during a protracted process of applying conservation action on the ground, and the need to decide on an appropriate mix of protection measures. Three types of decisions are particularly important⁹⁶. First, the most appropriate or feasible form of management should be identified for each area. This might be complicated by the need to apply particular forms of management in particular designated places, for example in biosphere reserves, which have core and buffer zones. In some cases, the preferred form of management might be infeasible and will need to be changed. Second, if one or more selected areas prove to be unexpectedly degraded or difficult to protect, it will be necessary to return to stage 4 and identify replacements, where they exist (Fig. 6). Third, decisions are needed on the relative timing of conservation action when resources are insufficient to implement the whole network quickly. With ongoing loss and alteration of habitat, a strategy is needed to minimize the extent to which conservation targets are compromised before being achieved.

One strategy for scheduling conservation action within regions is to plot selected areas on two axes⁹⁶. The first is irreplaceability or the extent to which the loss of the area will compromise regional conservation targets⁹¹. The second is vulnerability or the risk of the area being transformed by extractive uses. Areas with high values for both should receive priority for conservation action (Fig. 8). They are most likely to be lost and, because of the absence or small numbers of replacements, their loss will have the most serious impact on the achievement of targets. This approach is similar conceptually to the original definition of global hotspots⁹⁷⁻⁹⁹ and to other assessments of priorities at global or continental scales¹⁰⁰⁻¹⁰³. Plotting selected areas on two axes also has an advantage over combining values for both to produce a single priority score. Different areas of the graph can indicate the need for alternative management prescriptions, subject to regular review (Fig. 8). Three important qualifications are necessary. One is that an exercise in triage¹⁰⁴ might be necessary to decide if strict

Figure 7 Spotted gum, *Eucalyptus maculata*, with an understorey of the cycad, *Macrozamia communis* in southeastern New South Wales, Australia. These forests are now the subject of a regional forest agreement, which allocates some areas to protection based on the contribution they make to agreed biodiversity targets, and allocates other areas to production based on agreed timber harvesting targets¹³.



Most public forests in eastern New South Wales and in other Australian states now have regional forest agreements in place. Photograph by Liz Poon.

reservation is infeasible for some very high priority areas, necessitating other forms of protection such as management agreements with landholders, or outright abandonment. A second is the unresolved question of whether and how vulnerability to different threatening processes (for example, clearing, logging and grazing) should be combined for prioritization. A third is that the idea has been used mainly to prioritize areas for achieving biodiversity pattern targets and has yet to be developed fully for process targets. For some process targets it will be necessary to combine individual candidate areas into larger units before identifying priorities. Conservation planners are then likely to confront some difficult choices. They will often have to decide whether a limited annual budget should be used, for example, to keep intact a movement corridor for ungulates, a block of habitat considered minimal for the viability of a carnivore species, or the only known location of an endemic plant¹⁴. Planning for both the representation of patterns and persistence of species and natural processes requires planners to compare apples and oranges. There are no guidelines for optimizing the outcome and no guarantees that the anticipated outcome will be realized.

Stage 6. Management and monitoring of reserves

Establishing a reserve heralds the beginning of another process that is at least as demanding as the preceding planning process and spans a much longer period of time. Management of reserves should ensure that their natural values are retained in the face of internal natural dynamics, disturbances from outside, and a variety of valid human uses. In practice, the management of many reserves is inadequately resourced, unplanned and often threatened by illegal use for basic human subsistence or commercial activities^{105,106}. Some exist only on paper, never having been implemented⁷.

Sound management effectively involves another cycle of the previous five stages applied to individual reserves. It requires information on the biodiversity of each reserve, knowledge of the processes that underpin ecological functions, and an understanding of the responses of key elements of biodiversity to natural processes and anthropogenic disturbances (stage 1). Management should be based on explicit goals or targets¹⁰⁷ (as in stage 2), preferably acknowledging the contribution of each reserve's particular natural values to the regional system. Based on the extent to which management goals are already being achieved (stage 3), it might be necessary to review prescriptions or zonings and to prepare a new management plan indicating which parts of reserves are appropriate for different uses, require regulation of natural processes or need to be rehabilitated (stage 4). Problems with implementation of the management plan (stage 5) will usually be minimized or avoided if key interest groups are consulted during its development. As with the selection and implementation of new reserves, this process is not fixed and

unidirectional. New data on patterns and processes within a reserve might call for revised goals. More generally, ongoing management should be complemented by periodic monitoring (back to stage 3) to assess the effectiveness of management actions in achieving nominated goals, with subsequent adjustment of goals and activities as appropriate. Adaptive management¹², coupled with a genuine commitment to monitoring, is increasingly recognized as crucial, not only to follow the status of selected elements of biodiversity, but also to assess the adequacy of resources for management, the capability of the responsible institutions, and the accountability with which funds are being used¹⁰⁸.

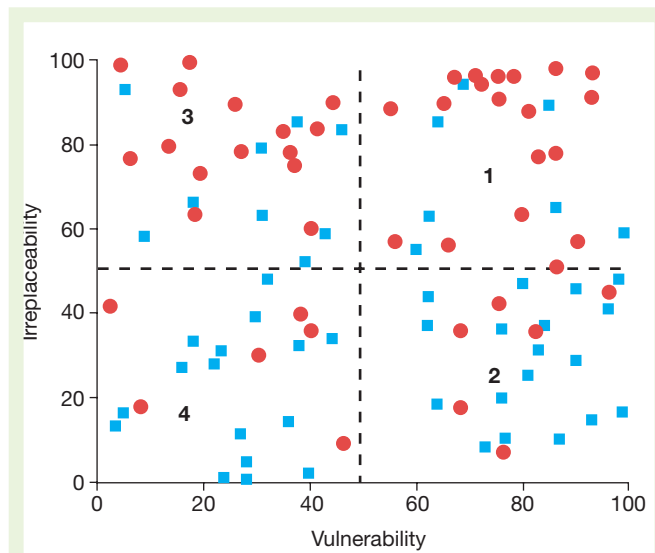


Figure 8 A framework for identifying priority conservation areas in time and space, applicable within regions to environments or other land types²⁰ or to potential conservation areas^{14,96}. The graph shows hypothetical data for 100 potential conservation areas, each with values for irreplaceability and vulnerability (for example, agricultural potential). Red points are a subset of areas that are notionally selected to achieve targets but not yet given reservation status. Blue points are possible replacements. Selected areas occur in all parts of the graph, although the selected proportion increases with higher irreplaceability. If not all selected areas can be protected immediately (a common situation), the positions of areas in the graph will change over time. Some of the more vulnerable areas are likely to be converted to agriculture. As this happens, the irreplaceability of some of the remaining areas will increase as they become more important for achieving targets for features that are now less extensive and/or less frequent elsewhere. Conversely, as areas are progressively reserved, the irreplaceability of others will decrease as the features they contain approach or reach their conservation targets. The vulnerability of areas will also change, most likely upwards as land-use pressures intensify. Appropriate responses by conservation planners can be related to the different quadrants, as in previous studies at broader scales^{100–102}. Quadrant 1: areas most likely to be lost and with fewest replacements. Protection is urgent if targets are not to be compromised. Some will probably be fragments of previously extensive vegetation types where strict reservation is difficult to apply (private tenure) or impractical (management liabilities) and must be supplemented with off-reserve management. Quadrant 2: areas vulnerable to loss but with more replacements, either because features are relatively common and extensive relative to targets or because targets have been partly met in existing reserves. Holding measures are necessary to avoid loss of some areas causing others to move upwards into quadrant 1. Options for protection include reservation where appropriate (and without pre-empting reserves in quadrant 1) complemented with off-reserve management. Quadrant 3: areas with lower present risk of agricultural conversion but high irreplaceability (for example, rocky ranges in a matrix of agricultural land or rare land types outside the climatic limits of agriculture). Protection is less urgent and acquisition for reservation more feasible than for quadrants 1 and 2 because of slower rates of transformation and (likely) lower land prices. Quadrant 4: the positions of areas here are likely to be stable and require least intervention, although monitoring of land use is advisable.

Interaction between reserve management and the location and design of reserves is inevitable. Decisions in the earlier stages of the planning process should, if possible, anticipate management issues. Key considerations include size and shape, alignment of boundaries with watersheds, avoidance of intrusive adjacent land uses, negotiations with neighbours, and the maintenance of migration routes. In turn, as the management needs of established reserves become apparent or as new needs emerge, it might be necessary to return to the selection stage (stage 4) to modify the design of individual reserves or the overall conservation network.

The outlook

There are many views about how best to identify priority conservation areas. To some extent this diversity is welcome as it arises from attempts by people with varying backgrounds to solve different problems in different parts of the world. This variety contributes usefully to an ongoing debate about appropriate planning approaches. But some of the divergence is less useful and seems to reflect different, poorly defined conservation goals and different, often implicit assumptions about the constraints under which conservation action will be applied. If these goals and assumptions were defined more explicitly, the relative roles and limitations of alternative approaches might be better understood and more attention could focus on addressing particular knowledge gaps and problems of implementation and management. Both clarity of purpose and productive debate would be achieved more readily if there was more direct interchange between groups working on conservation planning and between these groups and managers who face the daily challenges of staving off threats to biodiversity. Better communication depends inevitably on the interactions between individual researchers and managers, but more regular organized meetings specifically for conservation planning could also achieve much.

Conservation planning is also riddled with uncertainty. In the six stages of planning described here, uncertainty pervades the use of biodiversity surrogates, the setting of conservation targets, decisions about which kinds of land tenure can be expected to contribute to targets and for which features, and decisions about how best to locate, design, implement and manage new conservation areas in the face of limited resources, competition for other uses, and incursions from surrounding areas. New developments in all the planning stages will progressively reduce, but never eliminate, these uncertainties. One implication is that planners, rather than proceeding as if certain, must learn to deal explicitly with uncertainty in ways that minimize the chances of serious mistakes.

An urgent need is for more precision in the measurement of biodiversity and more consistency in mapping it across regions and biomes. In part this can be addressed by the allocation of more resources — funds, personnel and infrastructure — to the collection of field records of species and other biodiversity features. However, because all collections are samples, and as complete inventories of regions are not a realistic option for the foreseeable future, the design of data-collecting activities should be based soundly in ecological theory and should enable the application of proven statistical techniques to the modelling of wider spatial distribution patterns from the point locations that these field records were taken from³⁹.

Another need is for more effort to be applied to mapping patterns and monitoring rates of spread of threats to biodiversity, as it is such threats to which conservation planning should respond. A better understanding of the present and future distribution patterns of various threats will help focus limited conservation resources on areas and features most at risk. It will also clarify the extent to which conservation priorities overlap with priority areas for extractive and destructive uses. Some threats arise for reasons that can be understood only with the benefit of hindsight, but this is no reason not to improve foresight with refined predictions about the effects of extractive uses, urbanization and the spread of alien species.

More precise management prescriptions for the persistence of

biodiversity are also needed. So far, enough is known only about a select few species, mostly large vertebrates and vascular plants, for effective management prescriptions. Finally, and just as importantly, biologists and ecologists must participate more in real planning processes. This is the only sure way to understand fully where the need for new ecological and biological knowledge is and what the social and political constraints on effective planning really are. □

1. Kanowski, P. J., Gilmour, D. A., Margules, C. R. & Potter, C. S. *International Forest Conservation: Protected Areas and Beyond* (Commonwealth of Australia, Canberra, 1999).
2. Chandrasekara, U. M. & Sankar, S. Ecology and management of sacred groves in Kerala, India. *For. Ecol. Mgmt* **112**, 165–177 (1998).
3. Grove, R. H. Origins of western environmentalism. *Sci. Am.* **267**, 22–27 (1992).
4. Hanks, J. Protected areas during and after conflict: the objectives and activities of the Peace Parks Foundation. *Parks* **7**, 11–24 (1997).
5. World Conservation Union. *Guidelines for Protected Area Management Categories* (IUCN, Gland, Switzerland, and Cambridge, 1994).
6. Anon. *Global Biodiversity Strategy* (World Resources Institute, World Conservation Union, and United Nations Development Program, Washington DC, 1992).
7. Terborgh, J. *Requiem for Nature* (Island, Washington DC, 1999).
8. Austin, M. P. & Margules, C. R. in *Wildlife Conservation Evaluation* (ed. Usher, M. B.) 45–67 (Chapman & Hall, London, 1986).
9. Soulé, M. E. (ed.) *Viable Populations for Conservation* (Cambridge Univ. Press, Cambridge, 1987).
10. Shafer, C. L. National park and reserve planning to protect biological diversity: some basic elements. *Landscape Urban Plan.* **44**, 123–153 (1999).
11. Peres, C. A. & Terborgh, J. W. Amazonian nature reserves: an analysis of the defensibility status of existing conservation units and design criteria for the future. *Conserv. Biol.* **9**, 34–46 (1995).
12. Holling, C. S. (ed.) *Adaptive Environmental Assessment and Management* (International Institute for Applied Systems Analysis, and Wiley, Toronto, 1978).
13. Pressey, R. L. in *Ecology for Everyone: Communicating Ecology to Scientists, the Public and the Politicians* (eds Wills, R. & Hobbs, R.) 73–87 (Surrey Beatty, Sydney, 1998).
14. Cowling, R. M., Pressey, R. L., Lombard, A. T., Desmet, P. G. & Ellis, A. G. From representation to persistence: requirements for a sustainable reserve system in the species-rich Mediterranean-climate deserts of southern Africa. *Div. Distrib.* **5**, 51–71 (1999).
15. Davis, F. W., Stoms, D. M. & Andelman, S. Systematic reserve selection in the USA: an example from the Columbia Plateau ecoregion. *Parks* **9**, 31–41 (1999).
16. Nix, H. A. et al. *The BioRap Toolbox: A National Study of Biodiversity Assessment and Planning for Papua New Guinea. Consultancy Report to World Bank* (CSIRO Publishing, Melbourne, 2000).
17. Noss, R. F., Strittholt, J. R., Vance-Borland, K., Carroll, C. & Frost, P. A conservation plan for the Klamath-Siskiyou ecoregion. *Nat. Areas J.* **19**, 392–411 (1999).
18. Dobson, A. P., Rodriguez, J. P., Roberts, W. M. & Wilcove, D. S. Geographic distribution of endangered species in the United States. *Science* **275**, 550–553 (1997).
19. Aiken, S. R. Peninsular Malaysia's protected areas' coverage, 1903–92: creation, rescission, excision, and intrusion. *Environ. Conserv.* **21**, 49–56 (1994).
20. Pressey, R. L. et al. How well protected are the forests of north-eastern New South Wales?—Analyses of forest environments in relation to tenure, formal protection measures and vulnerability to clearing. *For. Ecol. Mgmt* **85**, 311–333 (1996).
21. Ranta, P., Blom, T., Niemela, J., Joensuu, E. & Siitonen, M. The fragmented Atlantic rain forest of Brazil: size, shape and distribution of forest fragments. *Biodiv. Conserv.* **7**, 385–403 (1998).
22. Sarkar, S. Wilderness preservation and biodiversity conservation—keeping divergent goals distinct. *BioScience* **49**, 405–412 (1999).
23. Anon. *National Forest Policy Statement: a New Focus for Australia's Forests* (Australian Government Publishing Service, Canberra, 1992).
24. Noss, R. F., O'Connell, M. A. & Murphy, D. D. *The Science of Conservation Planning: Habitat Conservation under the Endangered Species Act* (Island, Washington, 1997).
25. Pressey, R. L. & Logan, V. S. in *Conservation Outside Nature Reserves* (eds Hale, P. & Lamb, D.) 407–418 (Univ. Queensland Press, Brisbane, 1997).
26. Hansen, A. J., Garman, S. L., Marks, B. & Urban, D. L. An approach for managing vertebrate diversity across multiple-use landscapes. *Ecol. Applic.* **3**, 481–496 (1993).
27. Prendergast, J. R. et al. Rare species, the coincidence of diversity hotspots and conservation strategies. *Nature* **365**, 335–337 (1993).
28. van Jaarsveld, A. S. et al. Biodiversity assessment and conservation strategies. *Science* **279**, 2106 (1998).
29. Howard, P. C. et al. Complementarity and the use of indicator groups for reserve selection in Uganda. *Nature* **394**, 472–475 (1998).
30. McKenzie, N. L., Belbin, L., Margules, C. R. & Keighery, J. G. Selecting representative reserve systems in remote areas: a case study in the Nullarbor region, Australia. *Biol. Conserv.* **50**, 239 (1989).
31. Goldstein, P. Z. Functional ecosystems and biodiversity buzzwords. *Conserv. Biol.* **13**, 247–255 (1999).
32. Nix, H. A. in *Evolution of the Flora and Fauna of Australia* (eds Baker, W. R. & Greenslade, P. J. M.) 47–66 (Peacock, Adelaide, 1982).
33. Nix, H. A. in *Atlas of Elapid Snakes of Australia* (ed. Longmore, R.) 4–14 (Australian Government Publishing Service, Canberra, 1986).
34. Austin, M. P. Continuum concept, ordination methods and niche theory. *Annu. Rev. Ecol. Syst.* **16**, 39–61 (1985).
35. Austin, M. P., Nicholls, A. O. & Margules, C. R. Measurement of the qualitative realised niche: environmental niches of five *Eucalyptus* species. *Ecol. Monogr.* **60**, 161–177 (1990).
36. Wessels, K. J., Freitag, S. & van Jaarsveld, A. S. The use of land facets as biodiversity surrogates during reserve selection at a local scale. *Biol. Conserv.* **89**, 21–38 (1999).
37. Richards, B. N. et al. *Biological Conservation of the South-East Forests* (Australian Government Publishing Service, Canberra, 1990).
38. Ferrier, S. & Watson, G. *An Evaluation of the Effectiveness of Environmental Surrogates and Modelling Techniques in Predicting the Distribution of Biological Diversity* (Environment Australia, Canberra, 1997).
39. Margules, C. R. & Austin, M. P. Biological models for monitoring species decline: the construction and use of data bases. *Phil. Trans. R. Soc. Lond. B* **344**, 69–75 (1994).
40. Nelson, B. W., Ferreira, C. A. C., da Silva, M. F. & Kawasaki, M. L. Endemism centres, refugia and botanical collection intensity in Brazilian Amazonia. *Nature* **345**, 714–716 (1990).
41. Hutchinson, M. F. et al. *BioRap Volume 2. Spatial Modelling Tools* (<http://cres.anu.edu/biorap/tools.html>) (The Australian BioRap Consortium, Canberra, 1996).
42. Austin, M. P. & Meyers, J. A. Current approaches to modelling the environmental niche of *Eucalyptus*: implications for management of forest biodiversity. *For. Ecol. Mgmt* **85**, 95–106 (1996).
43. Deadman, P. J. & Gimblett, H. R. Applying neural networks to vegetation management plan development. *AI Applic.* **11**, 107 (1997).
44. Jennings, M. D. Gap analysis: concepts, methods, and recent results. *Landscape Ecol.* **15**, 5–20 (2000).
45. Pressey, R. L. & Logan, V. S. Size of selection units for future reserves and its influence on actual vs. targeted representation of features: a case study in western New South Wales. *Biol. Conserv.* **85**, 305–319 (1998).
46. Soulé, M. E. & Sanjayan, M. A. Conservation targets: do they help? *Science* **279**, 2060 (1998).
47. Commonwealth of Australia. *Nationally Agreed Criteria for the Establishment of a Comprehensive, Adequate and Representative Reserve System for Forests in Australia* (Australian Government Publishing Service, Canberra, 1997).
48. Margules, C. R. & Nicholls, A. O. in *Nature Conservation: The Role of Remnants of Native Vegetation* (eds Saunders, D. A., Arnold, G. W., Burbidge, A. A. & Hopkins, A. J. M.) 89–102 (Surrey Beatty, Sydney, 1987).
49. Balmford, A., Mace, G. M. & Ginsberg, J. A. in *Conservation in a Changing World* (eds Mace, G. M., Balmford, A. & Ginsberg, J. A.) 1–28 (Cambridge Univ. Press, Cambridge, 1998).
50. MacArthur, R. H. & Wilson, E. O. *The Theory of Island Biogeography* (Princeton, New Jersey, 1967).
51. Diamond, J. M. The island dilemma: lessons of modern biogeographic studies for the design of natural reserves. *Biol. Conserv.* **7**, 129 (1975).
52. Wilson, E. O. & Willis, E. O. in *Ecology and Evolution of Communities* (eds Cody, M. L. & Diamond, J. M.) 522–534 (Belknap, Cambridge, MA, 1975).
53. Higgs, A. J. Island biogeography and nature reserve design. *J. Biogeogr.* **8**, 117–124 (1981).
54. Sauer, J. D. Oceanic islands and biogeographical theory. *Geogr. Rev.* **59**, 585 (1969).
55. Davies, K. F., Margules, C. R. & Lawrence, J. F. Which traits of species predict population declines in experimental forest fragments? *Ecology* **81** (in the press).
56. Levins, R. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bull. Entomol. Soc. Am.* **15**, 237–240 (1969).
57. Holt, R. D. & Gaines, M. S. in *Patch Dynamics* (eds Levin, S. A., Powell, T. M. & Steele, J. H.) 260–276 (Springer, Berlin, 1993).
58. Gilpin, M. E. in *Viable Populations for Conservation* (ed. Soulé, M. E.) 126–139 (Cambridge Univ. Press, New York, 1987).
59. Bennett, A. F. *Linkages in the Landscape: the Role of Corridors and Connectivity in Wildlife Conservation* (IUCN, Gland, Switzerland, and Cambridge, 1998).
60. Thomas, C. D. et al. in *Conservation in a Changing World* (eds Mace, G. M., Balmford, A. & Ginsberg, J. R.) 107–138 (Cambridge Univ. Press, Cambridge, 1998).
61. Holt, R. D. in *Species Diversity in Ecological Communities* (eds Ricklefs, R. E. & Schluter, D.) 77–96 (Univ. Chicago Press, Chicago, 1993).
62. Lindenmayer, D. B. & Possingham, H. P. *The Risk of Extinction: Ranking Management Options for Leadbeater's Possum* (Centre for Resource and Environmental Studies, Australian National University, Canberra, 1995).
63. Pickett, S. T. A., & Thompson, J. N. Patch dynamics and the design of nature reserves. *Biol. Conserv.* **13**, 27–37 (1978).
64. Lamberson, R. H., Noon, B. R., Voss, C. & McKelvey, R. Reserve design for territorial species: the effects of patch size and spacing on the viability of the Northern Spotted Owl. *Conserv. Biol.* **8**, 185–195 (1994).
65. Burgman, M., Ferson, S. & Akçakaya, H. R. *Risk Assessment in Conservation Biology* (Chapman & Hall, New York, 1993).
66. Lindenmayer, D. B., Burgman, M. A., Akçakaya, H. R., Lacy, R. C. & Possingham, H. P. A review of three models for metapopulation viability analysis—ALEX, RAMAS/Space and VORTEX. *Ecol. Model.* **82**, 161–174 (1995).
67. Lambek, R. J. Focal species: a multi-species umbrella for nature conservation. *Conserv. Biol.* **11**, 849–856 (1997).
68. Dias, P. C. Sources and sinks in population biology. *Trends Ecol. Evol.* **11**, 326–330 (1999).
69. Braithwaite, L. W., Binns, D. L. & Nowlan, R. D. The distribution of arboreal marsupials in relation to eucalypt forest types in the Eden (NSW) Woodchip Concession Area. *Aust. Wildl. Res.* **10**, 231–247 (1988).
70. Saunders, D. A., Hobbs, R. J. & Margules, C. R. Biological consequences of ecosystem fragmentation: a review. *Conserv. Biol.* **5**, 18 (1991).
71. Kapos, V. Effects of isolation on the water status of forest patches in the Brazilian Amazon. *J. Trop. Ecol.* **5**, 173 (1989).
72. Didham, R. K., Hammond, P. M., Lawton, J. H., Eggleton, P. & Stork, N. E. Beetle species responses to tropical forest fragmentation. *Ecol. Monogr.* **68**, 295–323 (1998).
73. Margules, C. R., Milkovits, G. A. & Smith, G. T. Contrasting effects of habitat fragmentation on the scorpion, *Cercophonium squama* and an amphipod. *Ecology* **75**, 2033–2042 (1994).
74. Cochrane, M. A. et al. Positive feedbacks in the fire dynamic of closed canopy tropical forests. *Science* **284**, 1832–1835 (1999).
75. Yates C. J. & Hobbs, R. J. Temperate eucalypt woodlands: a review of their status, processes threatening their persistence and techniques for restoration. *Aust. J. Bot.* **45**, 949–973 (1997).
76. Frankel, O. H. & Soulé, M. E. *Conservation and Evolution* (Cambridge Univ. Press, Cambridge, 1981).
77. Rojas, M. The species problem and conservation: what are we protecting? *Conserv. Biol.* **6**, 170–178 (1992).
78. Vane-Wright, R. L., Humphries, C. J. & Williams, P. H. What to protect?—Systematics and the agony of choice. *Biol. Conserv.* **55**, 235–254 (1991).
79. Fieldsa, J. Geographic patterns for relict and young species of birds in Africa and South America and implications for conservation priorities. *Biodiv. Conserv.* **3**, 207–226 (1994).
80. Kiester, A. R. et al. Conservation prioritization using GAP data. *Conserv. Biol.* **10**, 1332–1342 (1996).
81. Kirkpatrick, J. B. An iterative method for establishing priorities for the selection of nature reserves: an example from Tasmania. *Biol. Conserv.* **25**, 127–134 (1983).
82. Stoms, D. M. GAP management status and regional indicators of threats to biodiversity. *Landscape Ecol.* **15**, 21–33 (2000).
83. Noss, R. F. Assessing and monitoring forest biodiversity: a suggested framework and indicators. *For.*

- Ecol. Mgmt* **115**, 135–146 (1999).
84. Williams, P. H. in *Conservation in a Changing World* (eds Mace, G. M., Balmford, A. & Ginsberg, J. R.) 211–249 (Cambridge Univ. Press, Cambridge, 1998).
 85. Faith, D. P. Phylogenetic pattern and the quantification of organismal biodiversity. *Phil. Trans. R. Soc. Lond. B* **345**, 45–48 (1994).
 86. Colwell, R. K. & Coddington, J. A. Estimating terrestrial biodiversity through extrapolation. *Phil. Trans. R. Soc. Lond. B* **345**, 101–108 (1994).
 87. Faith, D. P. & Walker, P. A. Environmental diversity: on the best-possible use of surrogate data for assessing the relative biodiversity of sets of areas. *Biodiv. Conserv.* **5**, 399–415 (1996).
 88. Belbin, L. Environmental representativeness: regional partitioning and reserve selection. *Biol. Conserv.* **66**, 223–230 (1993).
 89. Faith, D. P. & Norris, R. Correlation of environmental variables with patterns of distribution and abundance of common and rare freshwater macroinvertebrates. *Biol. Conserv.* **50**, 77–89 (1989).
 90. Williams, P. H. *et al.* Comparison of richness hotspots, rarity hotspots and complementary areas for conserving biodiversity, using British birds. *Conserv. Biol.* **10**, 155–174 (1996).
 91. Ferrier, S., Pressey, R. L. & Barrett, T. W. A new predictor of the irreplaceability of areas for achieving a conservation goal, its application to real-world planning, and a research agenda for further refinement. *Biol. Conserv.* (in the press).
 92. Faith, D. P., Margules, C. R., Walker, P. A., Hutchinson, M. & Nix, H. A. in *Science for Pacific Posterity: Environments, Resources and Welfare of the Pacific People* (ed. Anon) 153 (Univ. of New South Wales Press, Sydney, 1999).
 93. Faith, D. P., Walker, P. A., Ive, J. R. & Belbin, L. in *Conserving Biological Diversity in Temperate Forest Ecosystems—Towards Sustainable Management* (ed. Anon) 74–75 (Centre for Resource and Environmental Studies, Australian National University, Canberra, 1994).
 94. Faith, D. P. & Walker, P. A. in *BioRap Volume 3. Tools for Assessing Biodiversity Priority Areas* (eds Faith, D. P. & Nicholls, A. O.) 63–74 (The Australian BioRap Consortium, Canberra, 1996).
 95. Faith, D. P. & Walker, P. A. Integrating conservation and development: effective trade-offs between biodiversity and cost in the selection of protected areas. *Biodiv. Conserv.* **5**, 417–429 (1996).
 96. Pressey, R. L. in *National Parks and Protected Areas: Selection, Delimitation and Management* (eds Pigram, J. J. & Sundell, R. C.) 337–357 (Univ. of New England, Centre for Water Policy Research, Armidale, 1997).
 97. Myers, N. Threatened biotas: hotspots in tropical forests. *The Environmentalist* **8**, 178–208 (1988).
 98. Mittermeier, R. A., Myers, N., Thomsen, J. B., da Fonseca, G. A. B. & Olivieri, S. Biodiversity hotspots and major tropical wilderness areas: approaches to setting conservation priorities. *Conserv. Biol.* **12**, 516–520 (1998).
 99. Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B. & Kent, J. Biodiversity hotspots for conservation priorities. *Nature* **403**, 853–858 (2000).
 100. Dinerstein, E. & Wikramanayake, E. D. Beyond “hotspots”: how to prioritize investments to conserve biodiversity in the Indo-Pacific region. *Conserv. Biol.* **7**, 53–65 (1993).
 101. Balmford, A. & Long, A. Avian endemism and forest loss. *Nature* **372**, 623–624 (1994).
 102. Sisk, T. D., Launer, A. E., Switky, K. R. & Erlich, P. R. Identifying extinction threats: global analyses of the distribution of biodiversity and the expansion of the human enterprise. *BioScience* **44**, 592–604 (1994).
 103. Ricketts, T. H. *et al.* *Terrestrial Ecoregions of North America: A Conservation Assessment* (Island, Washington DC, 1999).
 104. Myers, N. *The Sinking Ark: A New Look at the Problem of Disappearing Species* (Pergamon, Oxford, 1979).
 105. James, A. N. Institutional constraints to protected area funding. *Parks* **9**, 15–26 (1999).
 106. Stolton, S. & Dudley, N. A preliminary survey of management status and threats in forest protected areas. *Parks* **9**, 27–33 (1999).
 107. Caughley, G. & Sinclair, A. R. E. *Wildlife Management and Ecology* (Blackwell Science, Cambridge, MA, 1994).
 108. Hockings, M. & Phillips, A. How well are we doing?—Some thoughts on the effectiveness of protected areas. *Parks* **9**, 5–14 (1999).
 109. Faith, D. P. & Walker, P. A. in *National Parks and Protected Areas: Selection, Delimitation and Management* (eds Pigram, J. J. & Sundell, R. C.) 297–314 (Univ. New England Press, Armidale, 1997).

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