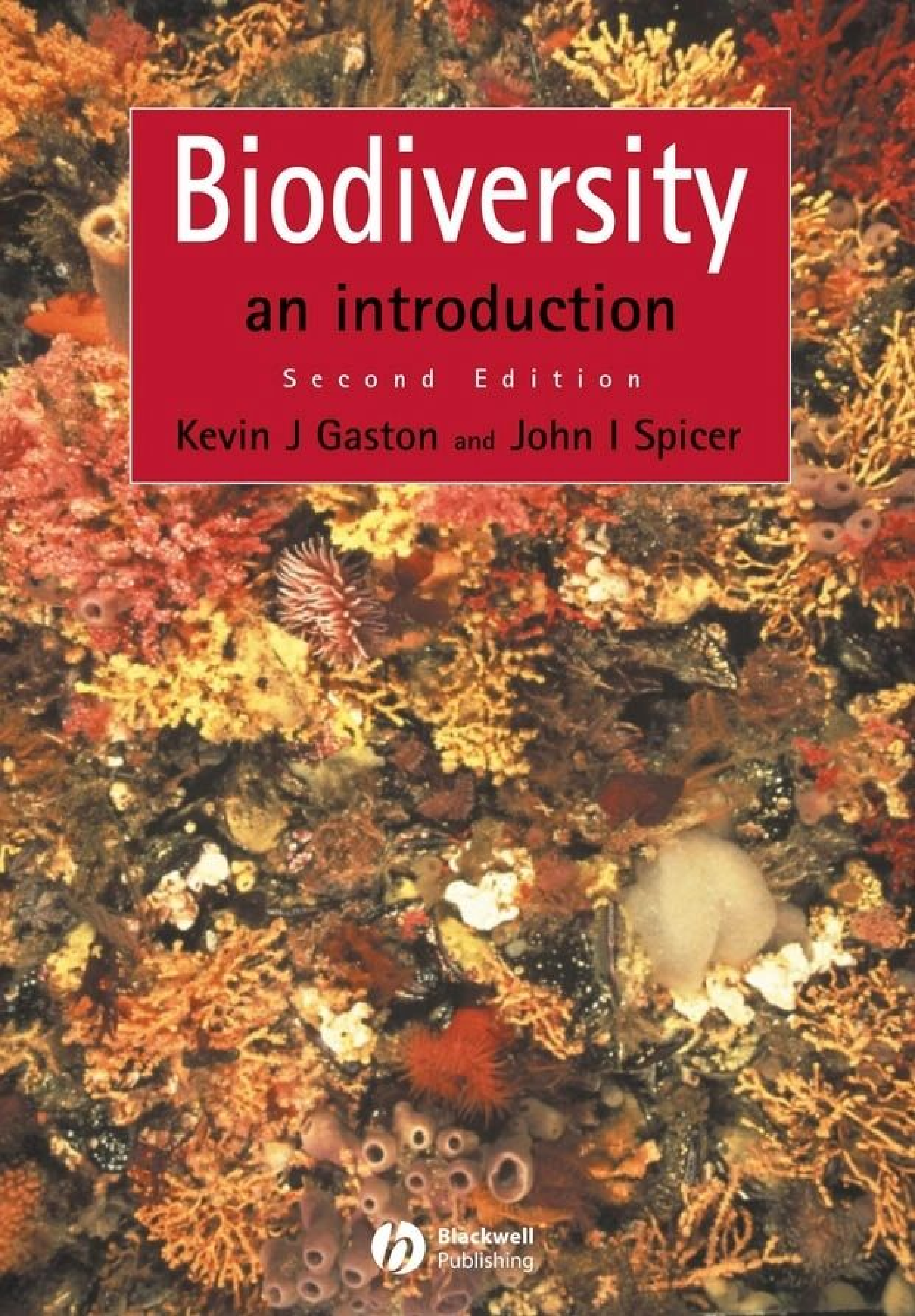

Biodiversity

an introduction

Second Edition

Kevin J Gaston and John I Spicer

Blackwell
Publishing

BIODIVERSITY: AN INTRODUCTION

Biodiversity: An Introduction

SECOND EDITION

Kevin J. Gaston
Professor of Biodiversity and Conservation
Department of Animal & Plant Sciences
University of Sheffield

and

John I. Spicer
Reader in Marine Biology and
Physiological Ecology
School of Biological Sciences
University of Plymouth

Blackwell
Publishing

350 Main Street, Malden, MA 02148-50120, USA
108 Cowley Road, Oxford OX4 1JF, UK
550 Swanston Street, Carlton, Victoria 3053, Australia

First edition published 1998
Second edition published 2004

Library of Congress Cataloging-in-Publication Data

Gaston, Kevin J.
Biodiversity: an introduction/
Kevin J. Gaston and John I. Spicer. – 2nd ed.
p. cm.
Includes bibliographical references and index.
ISBN 1-4051-1857-1 (pbk.: alk. paper)
1. Biological diversity. I. Spicer, John I. II. Title.
QH541.15.B56G37 2004
333.95′11—dc21 2003011788

A catalogue record for this title is available from the British Library.

Set in 10/13pt Berkeley Old Style
by Graphicraft Limited, Hong Kong
Printed and bound in the United Kingdom
by TJ International, Padstow, Cornwall

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Preface

This is the second edition of *Biodiversity: An Introduction*. Our goal in writing the first edition was to provide a text that both gave an introduction to biodiversity – what it is, how it arose, how it is distributed, why it is important and what should be done to maintain it – and present an entry point into the wider literature on biodiversity. That remains the goal here. However, much has occurred in the intervening years. First, understanding of many key issues has developed rapidly, with important new models having been developed, experiments having been conducted, and measurements made. Some controversies have been settled, and others have arisen. In short, the study of biodiversity remains vibrant and stimulating. Second, and as a consequence of these advances, the literature on biodiversity has continued to blossom with, for example, few issues of some of the major science journals (e.g. *Nature*, *Science*) now passing without containing one or more papers of relevance. Third, there has been a marked change in the structure of botanical, zoological and ecological courses taught in universities, away from inclusion of the more traditional taxonomically centred surveys of different groups of organisms, and towards an approach centred instead on the concept of biodiversity. Fourth, and most importantly, there has been little, if any, reduction in the degree of threat faced by the variety of life on Earth; if anything, there is now a sharpened awareness of how acute that threat is and how pervasive are its implications.

These developments have led us to revise *Biodiversity: An Introduction* substantially. Much of the book has been rewritten, updated and extended. The six chapters address the nature of biodiversity (Chapter 1), the history of biodiversity (Chapter 2), the spatial distribution of biodiversity (Chapter 3), the value of biodiversity (Chapter 4), human impacts on biodiversity (Chapter 5), and the future maintenance of biodiversity (Chapter 6). In each case, we have sought to draw out the major issues and provide actual examples. All the figures in the book can be downloaded from the Blackwell Publishing website (www.blackwellpublishing.com/gaston). Reference is made throughout the text to relevant papers and books, where possible with an emphasis on those that are more readily accessible. In addition, each chapter concludes with suggestions for further reading. These are sources, usually books, that we hope readers will find useful for exploring particular themes in greater detail, but which have often not been cited elsewhere in the chapter.

Many people have generously provided guidance in this endeavour, commenting on drafts of the first edition of *Biodiversity: An Introduction*, suggesting ways in which the published version could be improved and developed, commenting on drafts of chapters for the second edition, and responding to multifarious queries and requests. In particular, we are grateful to Dave Bilton, Steven Chown, Andy Foggo, Sian Gaston, Alison Holt, Rhonda Snook, Richard Thompson, Mick Uttley and Clare Vincent. We would also like to thank the students who have taken module *APS215 Biodiversity* at the University of Sheffield, Tim Caro and the students on his conservation biology course, Lee Hannah, Claudia Moreno and Ana Rodrigues. Rosie Hayden, Cee Pike, Katrina Rainey and Sarah Shannon of Blackwell Publishing cajoled, encouraged and helped steer this volume to its conclusion, with good humour and insight. We are grateful for their assistance.

As before, we dedicate this book to Megan, Ben, Ethan and Ellie, with the desire that their generation is kinder to biodiversity than our own has been.

K.J.G. & J.I.S.
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1 What is biodiversity?

1.1 Marion Island

The biotas of a few sites around the world have received disproportionate attention from biologists. One such is Marion Island, the larger of the two islands that make up the Prince Edward archipelago. Small (c. 290 km^2) and remote (c. 2300 km southeast of Cape Town, South Africa), and with no permanent human population, the principal attractions that have led numerous scientists to conduct studies here in the midst of the vast Southern Ocean have been the, often charismatic, birds and mammals that are present. Marion Island is home to breeding populations of about 50,000 elephant seals and fur seals, and perhaps a million seabirds, including penguins, albatrosses, petrels and shearwaters. But these are just some of the more obvious inhabitants, and closer inspection reveals many more kinds of organisms. There are about 150 known species of invertebrates, including 44 species of insects and about 69 species of mites. And then there are, of course, the plants. There are 24 naturally occurring and 13 introduced species of vascular plants on Marion Island, and over 80 species of mosses, 45 species of liverworts, and 100 species of lichens have been identified.

Even given the intensity of study that Marion Island has received much remains unknown. No one has studied the nematode worms, although there seem likely to be more than 50 species present. The protists, bacteria

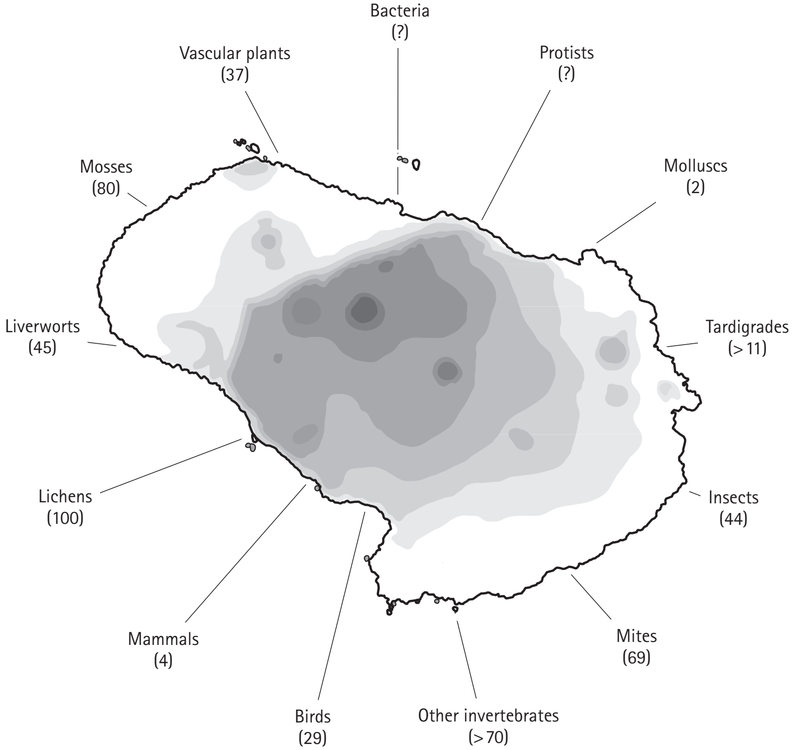

Fig. 1.1 The breeding species of sub-Antarctic Marion Island, one of the two remote Prince Edward Islands. Grey scales indicate variation in elevation. (Data from a variety of sources, including Gremmen 1981; Hänel & Chown 1999; Gaston et al. 2001; Øvstedal & Gremmen 2001; S.L. Chown pers. comm.)

and viruses also remain largely unexamined. Many of the species occurring on the island doubtless have associated parasites, but these also are mostly unknown. Indeed, there is a total of more than 500 species inhabiting Marion Island (Fig. 1.1).

Each of these species embraces a diverse range of evolutionary history, genetics, morphology, physiology and ecology. Each typically also comprises many tens of thousands of individuals, sometimes considerably less, but sometimes orders of magnitude more. For the majority, rather few of these individuals actually occur on Marion Island itself (although there are some species that occur nowhere else), but are scattered over the land- or seascape across many hundreds of square kilometres. Most of these individuals will have a unique genetic make-up, and, if only in the fine details, a unique morphology, physiology and ecology.

Such variety is echoed time and again across the Earth. Indeed, although it is important because some species found there occur nowhere else, and because of the large breeding populations of birds and mammals, Marion

Island would scarcely register on any league table of biological variation. It is by most standards a very depauperate place – as well as being small and remote, it is also cool (mean annual air temperature c. 5°C), wet (annual rainfall > 2.5 m), windy (gale-force winds blow for at least 1 h on nearly a third of all days) and was extensively covered in ice during recent periods of glaciation, a combination that would not predispose it to 'Eden-like' tendencies. Many areas have many more species, individuals of which exhibit greater diversities of form and function. For example:

- 173 species of lichens have been recorded on a single tree in Papua New Guinea (Aptroot 1997);
- 814 species of trees have been recorded from a 50 ha study plot in Peninsular Malaysia (Manokaran et al. 1992);
- 850 species of invertebrates are estimated to occur at a sandy beach site in the North Sea (Armonies & Reise 2000);
- c. 1300 species of butterflies have been recorded on five field trips, averaging less than 3 weeks each, to an area of < 4000 ha in Brazil (Robbins & Opler 1997);
- 245 resident species of birds have been recorded holding territories on a 97 ha plot in Peru (Terborgh et al. 1990);
- > 200 species of mammals may occur at some sites in the Amazonian rain forest (Voss & Emmons 1996);
- 55–135 animal species have been recorded in individual 30 × 30 cm cores of ocean floor sediment from 2100 m depth (Grassle & Maciolek 1992).

1.2 What is biodiversity?

Most straightforwardly, biological diversity or biodiversity is 'the variety of life', and refers collectively to variation at all levels of biological organization. Thus, one can, for example, speak equally of the biodiversity of some small or large part of Marion Island, of the island as a whole, of the islands of the Southern Ocean, of a continent or an ocean basin, or of the entire Earth. Many more formal definitions of biological diversity or biodiversity (we shall use the two terms interchangeably) have been proposed, which develop this simple one (DeLong 1996 reviewed 85 such definitions!). Of these, perhaps the most important and far-reaching is that contained within the Convention on Biological Diversity (the definition is provided in Article 2). This landmark treaty was signed by more than 150 nations on 5th June 1992 at the United Nations Conference on Environment and Development, held in Rio de Janeiro, and came into force approximately 18 months later (we shall subsequently refer to it simply as 'the Convention', although elsewhere you will commonly find it referred to by its acronym, CBD).

The Convention states that:

> *'Biological diversity' means the variability among living organisms from all sources including,* inter alia, *terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems.*

['*inter alia*' means 'among other things'.] Biodiversity is the variety of life, in all of its many manifestations. It encompasses all forms, levels and combinations of natural variation and thus serves as a broad unifying concept.

For the purposes of the exploration of biodiversity embodied in this book we will amplify the full definition from the Convention in one way. At present it does not obviously take into account the tremendous variety of biological life that occurred in the past, some of which is preserved in the fossil record. However, we will want to trace the origins of present-day biodiversity and this will necessitate delving into the past (Chapter 2). To avoid any possible confusion therefore, we will explicitly interpret the definition to embrace the variability of all organisms that have ever lived, and not simply those that are presently extant.

The actual definition of biodiversity, as given above, is neutral with regard to any importance it may be perceived to have. The Convention is, in contrast, far from a neutral document, as amply revealed by its objectives (Article 1), which are:

> *. . . the conservation of biological diversity, the sustainable use of its components and the fair and equitable sharing of the benefits arising out of the utilization of genetic resources, including by appropriate access to genetic resources and by appropriate transfer of relevant technologies, taking into account all rights over those resources and to technologies, and by appropriate funding.*

Likewise, much of the usage of the term 'biodiversity' is value laden. It carries with it connotations that biodiversity is *per se* a good thing, that its loss is bad, and that something should be done to maintain it. Consequently, it is important to recognize that there is rather more to use of the term than a formal definition in the Convention, or for that matter elsewhere, and its application often reveals just as much about the values of the person using it (see Section 1.4.2 and Chapter 4). This should always be borne in mind when interpreting what is being said about biodiversity, particularly now that the term has become a familiar feature of news programmes and papers, and importance is attached to it by environmental groups, political decision-makers, economists and ordinary citizens alike. Many users assume everyone shares the same intuitive definition, but this is not necessarily the case.

Table 1.1 Elements of biodiversity. (Adapted from Heywood & Baste 1995.)

Ecological diversity	Genetic diversity	Organismal diversity
Biomes		Domains or Kingdoms
Bioregions		Phyla
Landscapes		Families
Ecosystems		Genera
Habitats		Species
Niches		Subspecies
Populations	Populations	Populations
	Individuals	Individuals
	Chromosomes	
	Genes	
	Nucleotides	

1.3 Elements of biodiversity

The variety of life is expressed in a multiplicity of ways. Some sense of this variety can begin to be made by distinguishing between different key elements. These are the basic building blocks of biodiversity. They can be divided into three groups: (i) genetic diversity; (ii) organismal diversity; and (iii) ecological diversity (Table 1.1). Genetic diversity encompasses the components of the genetic coding that structures organisms (nucleotides, genes, chromosomes) and variation in the genetic make-up between individuals within a population and between populations. Organismal diversity encompasses the taxonomic hierarchy and its components, from individuals upwards to species, genera and beyond. Ecological diversity encompasses the scales of ecological differences from populations, through niches and habitats, on up to biomes. Although presented separately, the groups are intimately linked, and in some cases share elements in common (e.g. populations appear in all three).

Some of these elements are more readily, and more consistently, defined than are others. When we consider genetic diversity, nucleotides, genes and chromosomes are discrete, readily recognizable, and comparative units. Things are not quite so straightforward and neat when we move up to individuals and populations, with complications being introduced by, for example, the existence of clonal organisms and difficulties in identifying the spatial limits to populations. When we come to organismal diversity most of the elements are perhaps best viewed foremost simply as convenient human constructs for grouping evolutionarily related sets of individuals (although they do not always manage to do so). For instance, debate persists over exactly how many taxonomic kingdoms of organisms there should be, with a three domain natural classification being increasingly widely accepted (Bacteria and Archaea (prokaryotes), and Eukarya (eukaryotes)). When we refer to orders, families, genera or species of different groups we are not necessarily comparing like with like, although within a group examples of a given taxonomic level (e.g. different genera) may be broadly comparable. Thus, some species placed in different genera of cichlid fishes last shared common ancestors within the last few thousand years, some species placed in different families of primates diverged within the last few million years, and some species in the genus *Drosophila* diverged more than 40 million years ago (Fig. 1.2). Even the reality and recognition of species, for long considered one of the few biologically meaningful elements, has been a recurrent theme of debate for many decades, and a broad range of opinions and viewpoints have been voiced (Table 1.2; Section 1.4.4). Finally, and perhaps most problematic, is exactly how we define the various elements of ecological diversity. In most cases these elements constitute useful ways of breaking up continua of phenomena. However, they are difficult to distinguish without recourse to what ultimately constitute some essentially arbitrary rules. For example, whilst it is helpful to be able to label different habitat types, it is not always obvious precisely where one should end and another begin, because no such beginnings and endings really exist.

While many of the elements of biodiversity may be difficult to define rigorously, and in some cases may have no strict biological reality, they remain useful and important tools for thinking about and studying biodiversity. Thus, the elements of biodiversity, however defined, are not independent. Within each of the three groups of genetic, organismal and ecological diversity, the elements of biodiversity can be viewed as forming nested hierarchies (see Table 1.1); which serves also to render the complexity of biodiversity more tractable. For example, within genetic diversity, populations are constituted of individuals, each individual has a complement of chromosomes, these chromosomes comprise numbers of genes, and genes are constructed from nucleotides. Likewise, within organismal diversity kingdoms, phyla, families, genera, species, subspecies, populations and individuals form a nested sequence, in which all elements at lower levels belong to one example of each of the elements at higher levels. Along with the evolutionary process, this hierarchical organization of biodiversity reflects one of the central organizing principles of modern biology.

Whether any one element of biodiversity, from each or all of the three groups, can be regarded in some way as the most fundamental, essential or even natural is a contentious issue. For some, genes are the basic unit of life. However, in practice, it is often the species that is treated as the most fundamental element of biodiversity. Whether or not such an approach is useful, never mind correct, we will return to shortly (Section 1.4.4).

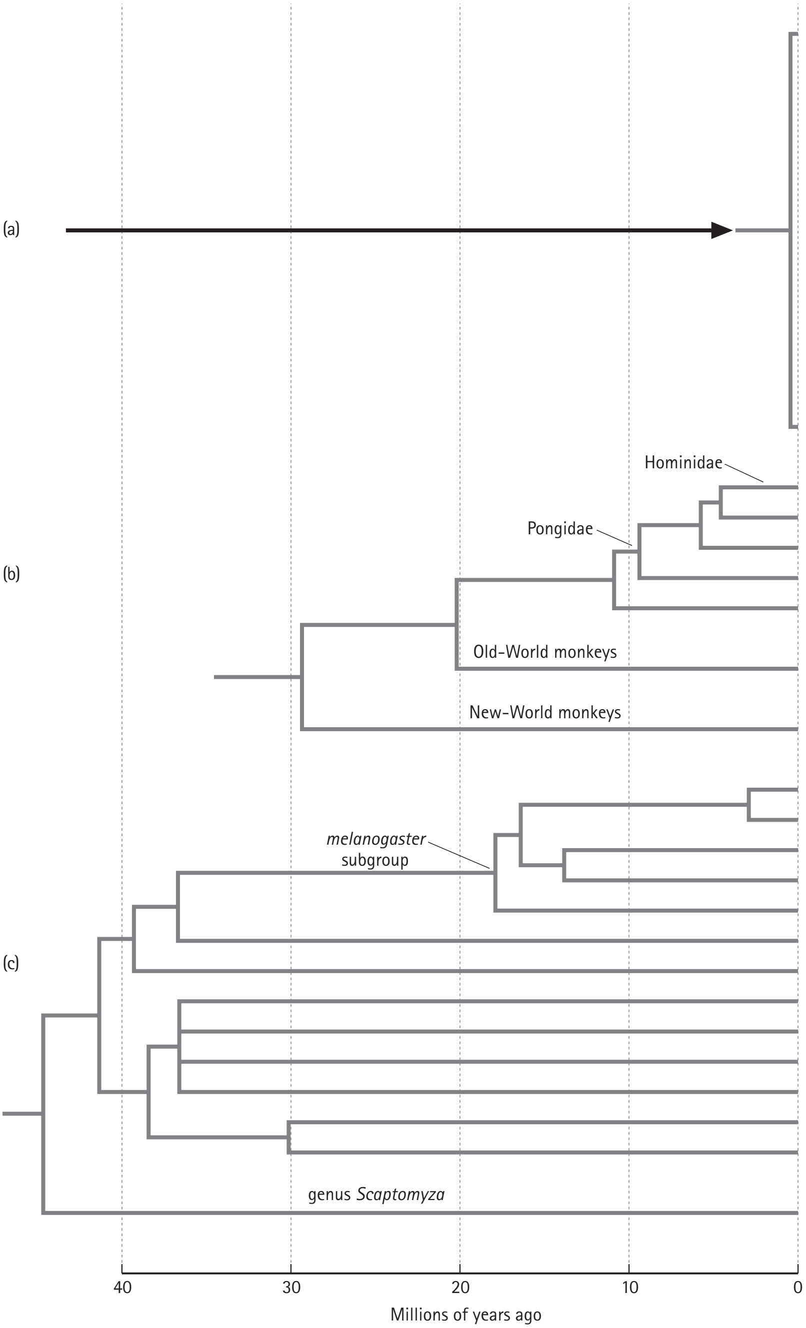

Fig. 1.2 Examples of disparities of taxonomic assignments in classifications of representatives of: (a) cichlid fish in Lake Victoria (14 species in nine genera); (b) anthropoid primates (seven species of several families); and (c) the genus *Drosophila* (13 species). (From Avise & Johns 1999.)

Table 1.2 (a) Species concepts; and (b) their strengths and weaknesses. (Adapted from Bisby 1995.)

(a)

Species concept	Definition
Biological species	A group of interbreeding natural populations that do not successfully mate or reproduce with other such groups (and, some would add, which occupy a specific niche)
Cohesion species	The smallest group of cohesive individuals that share intrinsic cohesive mechanisms (e.g. interbreeding ability, niche)
Ecological species	A lineage which occupies an adaptive zone different in some way from that of any other lineage in its range and which evolves separately from all lineages outside its range
Evolutionary species	A single lineage of ancestor–descendant populations which is distinct from other such lineages and which has its own evolutionary tendencies and historical fate
Morphological species	The smallest natural populations permanently separated from each other by a distinct discontinuity in heritable characteristics (e.g. morphology, behaviour, biochemistry)
Phylogenetic species	The smallest group of organisms that is diagnostically distinct from other such clusters and within which there is parental pattern of ancestry and descent
Recognition species	A group of organisms that recognize each other for the purpose of mating and fertilization

(b)

Species concept	Practical application	Strengths/weaknesses
Biological	Difficult	Popular, irrelevant to asexual organisms, complicated by natural hybridization, polyploidy, etc.
Cohesion	Difficult	Cohesion is difficult to recognize
Ecological	Difficult	Adaptive zones difficult to define, assumes two species cannot occupy same niche for even a short period
Evolutionary	Difficult	Criteria vague and difficult to observe
Morphological	Common	Morphological criteria may not reflect actual links that hold organisms together into a natural unit
Phylogenetic	Increasing	Will give rise to recognition of many more species than more traditional concepts
Recognition	Difficult	Determining if a feature is used to recognize potential mates is difficult or impossible in many populations

1.4 Measuring biodiversity

1.4.1 Number and difference

For many purposes the concept of biodiversity is useful in its own right, as it can provide a valuable shorthand expression for what is a very complex phenomenon. However, for more general applicability, one needs to be able to measure biodiversity – to quantify it in some way. Only then can one address such fundamental questions as how biodiversity has changed through time, where it occurs, and how it can be maintained.

From the definition alone, it is clear that no single measure of biodiversity will be adequate. Indeed, given its great complexity, it would be foolish to believe that the variety of life in an area, however small or large that area might be, could be captured in a single number. Measures of diversity in general, and not solely of biodiversity, are commonly found in basic ecological texts. Essentially, many of these measures have two components: (i) the number of entities; and (ii) the degree of difference (dissimilarity) between those entities. For example, species richness (the number of species) places emphasis on the number of elements. But, weighting each of these species by, say, the numbers of individuals, would be one way of incorporating a metric of the differences between them into a measure (Fig. 1.3). In the case of biodiversity the entities are one of its elements.

In measuring biodiversity, the breadth of ways in which differences can be expressed is potentially infinite. Think, for example, of the ways in which one could discriminate between just two species. These might include facets of their biochemistry, biogeography, evolutionary history, genetics, morphology or physiology, or perhaps the ecological role they play in a particular community (shredder, decomposer, predator, etc.) (cf. Table 1.2). As a result of the variety of elements of biodiversity, and of differences between them, there is no single all-embracing measure of biodiversity – nor will there ever be one! This means that it is impossible to state categorically what is the biodiversity of an area or of a group of organisms. Instead, only measures of certain components can be obtained, and even then such measures are only appropriate for restricted purposes.

Whilst one may feel uncomfortable with this notion, it is important to realize that it also applies, though perhaps not so obviously, in making many other concepts operational. For example, the topic of complex systems is attracting wide interest across a spectrum of fields of research (including physics), but there is no single measure of complexity (or simplicity for that matter). Instead there are many measures, none necessarily any more correct than the others, and which quantify rather different

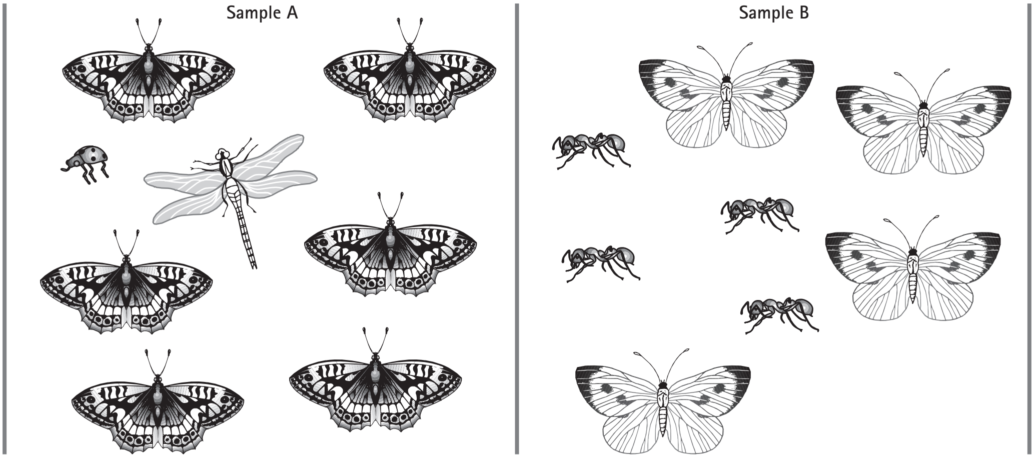

Fig. 1.3 Two samples of insects from different locations, illustrating two of the many different measures of biodiversity: species richness and species evenness. Sample A could be described as being the more diverse as it contains three species to sample B's two. However, in sample B there is less chance than in sample A that two randomly chosen individuals will be of the same species. (From Purvis & Hector 2000.)

components of complexity. To take an example closer to home, the concept of body size is utilized widely in biology. For example, one can recognize that relationships exist between body size and latitude (the biggest butterflies are found in the tropics) or between body size and abundance (elephants are rarer than many species of mice). And yet there is no such thing as the body size of an organism. Rather, size can be (and is) expressed in a variety of ways, none of which has any obvious logical precedence. Consider two individuals similar in body mass, but differing in linear dimensions. Which is the larger?

1.4.2 Value

Measures of biodiversity are commonly used as bases for making decisions about conservation action, or for planning more generally. It should now be clear that the choice of measure employed might not be neutral with regard to the outcome of such decisions. Different measures of biodiversity may suggest different answers. Moreover, it is important to remember that concentration on a particular element of biodiversity essentially places differential value on that facet of the variety of life. Both what you are measuring and how you are measuring it reveal something about what you most value. For example, if we use measures of ecological diversity as a basis for decision-making this implies that this is the dimension of biodiversity that is of most importance to us.

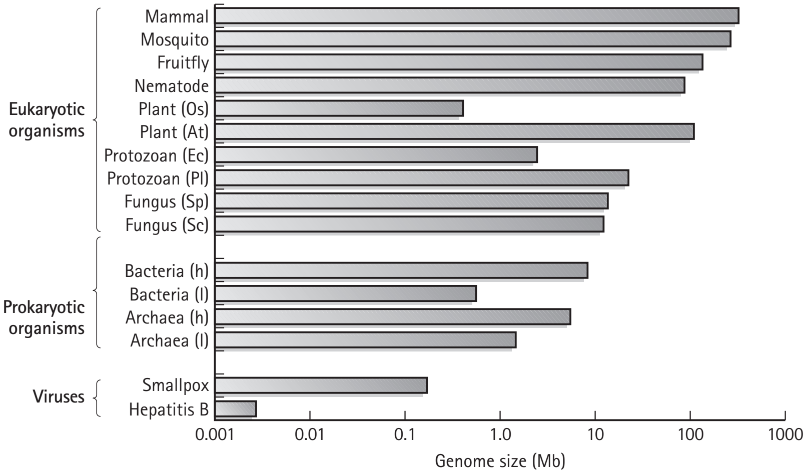

Fig. 1.4 Genome size for a range of organisms and viruses for which there are complete sequences (data derived from Genome Monitoring Table at http://www2.ebi.ac.uk/genomes/mot and Genomes online database at http://wit.integratedgenomics.com/GOLD). Abbreviations: l, lowest value for the grouping; h, highest value for the grouping; Os, *Oryza sativa*; At, *Arabidopsis thaliana*; Ec, *Encephalitozoon cuniculi*; Pl, *Plasmodium falciparum*; Sp, *Schizosaccharomyces pombe*; Sc, *Saccharomyces cerevisiae*.

1.4.3 Genetic diversity as a critical component

Few would disagree that genetic diversity is a critical component of biodiversity. This can be measured both directly (identifying and cataloguing variation in nucleotides, genes and chromosomes; see Table 1.1) or indirectly (quantifying variation in phenotypic features shown – or often just assumed – to have a genetic basis). Genes are constructed from strings of nucleotides (DNA). The total number, position and identity (there are four different types) of the nucleotides are all critical in the coding of biological information. Thus, determining nucleotide sequences is arguably one of the strongest measures of genetic diversity, although a large number of other techniques involving DNA analysis are also prevalent (restriction fragment length polymorphism (RFLP), DNA fingerprinting, random amplified polymorphic DNAs (RAPDs), microsatellite variation), their usage being dependent on the precise question being addressed.

Huge variation is encountered in the size and composition of the small, but steadily increasing, number of genomes sequenced to date (Fig. 1.4). Generally, multicellular organisms tend to have more DNA than single-celled organisms but there are exceptions. Similarly, although there appears to be an overall trend of increasing genome size with increasing morphological complexity, this is not invariant. For example, the lungfish (which still has not been fully sequenced) seems to have approximately

40 times more DNA than the mammal example in Fig. 1.4. This said, many of these discrepancies can be accounted for if comparison is limited to functional portions of DNA, those that encode for functional RNA and proteins. The species with the greatest amount of DNA has about 100,000 times as much as that with the least, but the species with the largest number of genes has only 20 times as many genes as that found in many bacteria. In other words, much of the variation in genomes is attributable not to differences in the number of functional genes, but in the amounts of non-coding DNA. One of the most striking findings from comparative genomics is that there are many 'universal' gene segments (e.g. those that code for ATP-binding sites), suggesting the existence of an ancient minimal set of DNA sequences that all cells must have. There is some evidence that nucleotide sequence divergence increases with increasing taxonomic diversity.

Nucleotide variation may give rise to changes in the character of the actual protein coded for. Until recently allelic variation determined in this way was one of the most commonly used (and cheapest) measures of genetic diversity. It was assessed using allozyme electrophoresis that identifies protein alleles, as different forms of a protein migrate at different rates on a gel. Allozyme electrophoresis has revealed an enormous amount of variation at all hierarchical levels.

Genes are located on chromosomes. All eukaryotic cells contain chromosomes, and their number, size and shape in an individual is referred to as the karyotype. Variation in karyotype has been investigated in detail mainly within species of plants, insects, amphibians and mammals. Most eukaryotes possess between 10 and 50 chromosomes, but there is huge variation both within and between groupings, with the overall range being from one to more than 200 (Fig. 1.5). There is no obvious relationship between chromosome number and any other measure of genetic diversity.

It is difficult to see at present how the various measures of genetic diversity discussed above map onto, or relate to, other measures of biodiversity, and how they could be employed as the primary measures of biodiversity. In the former case, much of the difficulty lies in the limited understanding of how genetic diversity matches up with the results of its expression, phenotypic diversity, although great strides are being made in this area. In the latter case, the difficulty rests in the limited amount of data that are available on genetic diversity through time and space, although the quantity is growing rapidly and the means of obtaining it are becoming more rapid.

1.4.4 Species richness as a common currency

Whilst biodiversity can be measured in a host of ways, in practice it tends most commonly to be measured in terms of species richness, the number of species. There are several reasons why this is so.

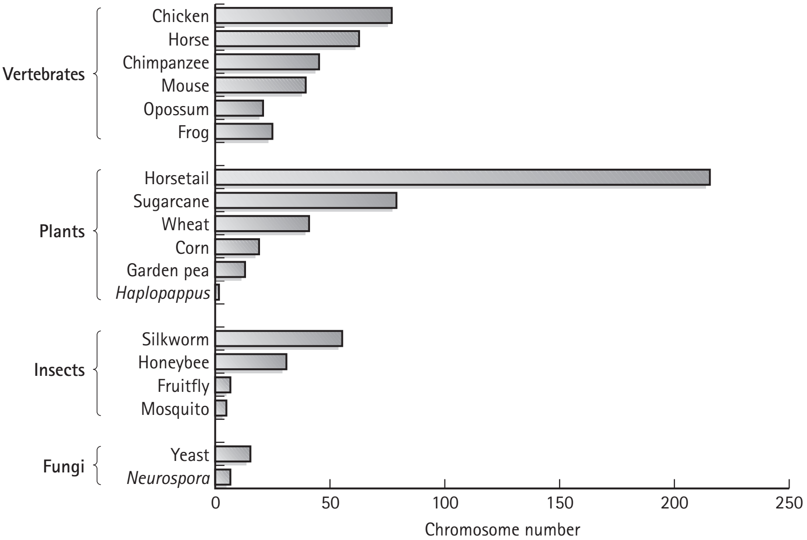

Fig. 1.5 Chromosome number for a range of organisms. (Data from various sources.)

1 *Practical application*. Species richness has proven to be measurable in practice, at least to the point where different workers will provide much the same estimation of the number of species of a given status (e.g. present, breeding, wintering) in a given taxon in a given area at a given time.
2 *Existing information*. A substantial amount of information already exists on patterns in species richness, and this has been made available in the scientific literature. Moreover, further information on this can readily be extracted from existing museum collections (which globally comprise many millions of biological specimens) and their associated literature (many millions of volumes), particularly as greater efforts are made to catalogue these collections in computerized databases that are accessible from remote locations.
3 *Surrogacy*. Species richness acts as a surrogate measure for many other kinds of variation in biodiversity. In general, as long as the numbers involved are at least moderate, greater numbers of species tend to embody more genetic diversity (in the form of a greater diversity of genes through to populations), more organismal diversity (in the form of greater numbers of individuals through to higher taxa), and greater ecological diversity (from representatives of more niches and habitats through to more biomes) (Fig. 1.6).
4 *Wide application*. The species unit is commonly seen as the unit of practical management, of legislation, of political discourse, and of tradition (folk taxonomies have frequently been found to conform closely to modern ones). For a wide range of people, variation in biodiversity is pictured as variation in species richness.

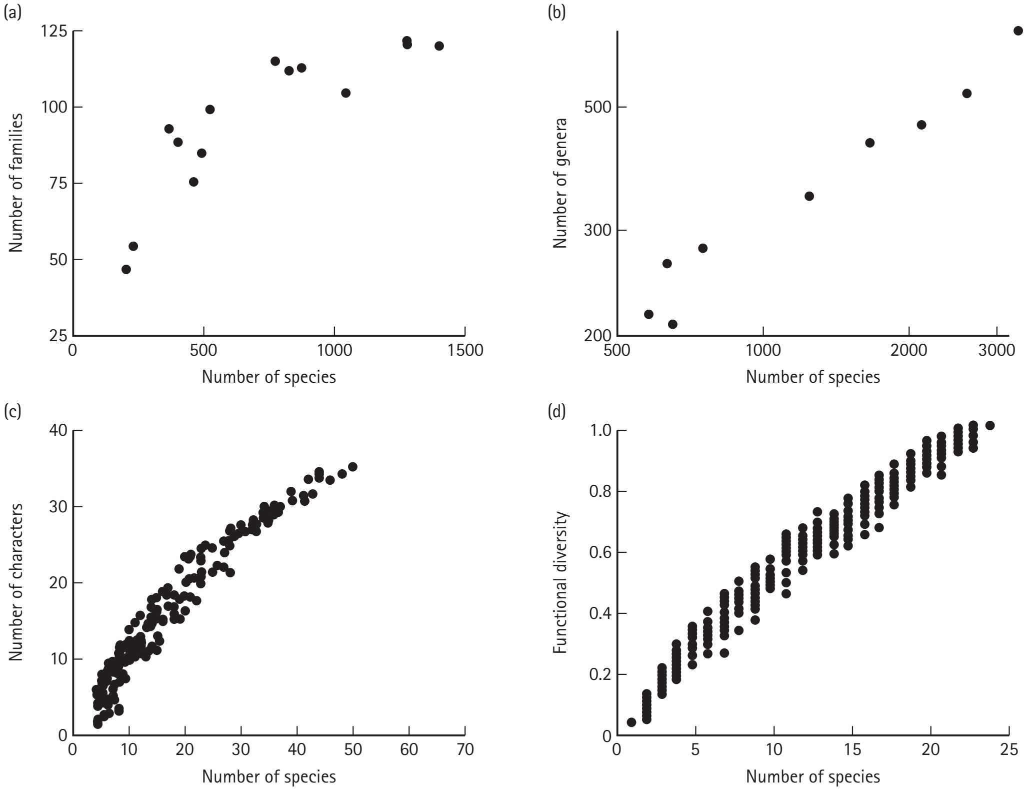

Fig. 1.6 Relationships between species richness and: (a) family richness for eastern Pacific benthic molluscs in different latitudinal bands; (b) generic richness for macromycete fungi for areas of the UK; (c) character richness for bumblebees among 611,000 km^2 grid cells; and (d) functional diversity (a measure of the extent of functional differences amongst a set of species) for Patagonian forbs. (a, From Roy et al. 1996; b, from Balmford et al. 2000; c, from Williams & Humphries 1996; d, from Petchey & Gaston 2002.)

The above said, the measurement of biodiversity in terms of species richness does have some significant limitations:

- *Definition of species*. The foremost difficulty is the lack of agreement as to precisely what constitutes a species. In major part this results because species can to a large extent be regarded as hypotheses, opinions or concepts, as much as real robust entities. There are at least seven major species concepts, each with their own strengths and weaknesses, from either theoretical or practical perspectives (see Table 1.2). The application of these different concepts can lead to the recognition of different numbers of species. For example, populations of seemingly coherent morphospecies (species separated on the basis of distinct discontinuities in one or more heritable characteristics, such as morphological features) may actually exhibit levels of genetic divergence typical of different species identified on this alternative basis, and thus constitute so-called cryptic species. Likewise, using a biological species concept, 40–42 species of birds-of-paradise (Paradisaeidae) have been distinguished in Australasia, but using a phylogenetic species concept pushes this figure up to 90 (Cracraft 1992). In practice, such problems are, however, commonly not as severe as this might seem to imply. As the vast majority of groups of organisms have been, and are still being, described based on collections of preserved specimens using differences in morphological characteristics, references to species richness more often than not concern 'morphological' species richness or are very close to estimates based on such a species concept (with some particular level of morphological difference being regarded as sufficient to confer species status). Fortunately, this method of defining a species continues to be relatively effective for most needs (although it may be woefully inadequate for groups such as prokaryotes). There is general consensus amongst appropriate specialists as to the overall numbers of species in a reasonably well-studied group occurring in an area or globally, and radical shifts in the number of species recognized do not tend to occur.

- *Different kinds of diversity*. An additional limitation of species richness as a measure of biodiversity has frequently been illustrated with reference to the issue of whether an assemblage of a small number of closely related species, say two species of mouse, is more or less biodiverse than an equivalent sized assemblage of more distantly related species, say a species of mouse and a species of shrimp. While the latter assemblage would, intuitively, seem to be the more diverse (in terms of morphological variation, differences in evolutionary history, etc.), in terms of species richness the assemblages are equally diverse. The extent to which this is a weakness of using species richness as a measure of biodiversity depends, however, perhaps less on the outcomes of such simple scenarios than on scenarios more typical of studies of biodiversity, which commonly involve assemblages numbering at least tens, if not hundreds or thousands, of species. Here, it seems that species richness is often strongly positively correlated with many other measures of biodiversity; i.e. it is a good surrogate (Gaston 1996a).

Species richness has, in some sense, become the common currency of much of the study of biodiversity. If one wishes to explore and discuss the origin, patterns and maintenance of biodiversity, such a currency certainly makes the task manageable. Although we will also have recourse to some other measures, throughout the rest of this book we will essentially treat species richness as equivalent to biodiversity, notwithstanding the facts that it remains only one among many measures, and retains some significant and important limitations. In so doing, we do not wish to imply that the problems associated with using this one measure are either trivial or unimportant. However, progress can be made using it, provided one remains alert to its limitations.

1.5 Summary

1 Biodiversity is the variety of life, in all its manifestations.
2 Key elements of this variety can be recognized, comprising three nested hierarchies of genetic, organismal and ecological diversity.
3 Because the variety of life can be expressed in a multiplicity of ways, there is no single overall measure of biodiversity, rather there are multiple measures of different facets.
4 The measure of biodiversity chosen may influence the findings of a particular study, and may reveal something about the values placed on a particular facet of the variety of life by an investigator.
5 Whilst it has some significant limitations, species richness has become the common currency of much of the study of biodiversity, and has proven valuable for many heuristic and practical purposes.

Further reading

For this chapter

Carroll, S., Grenier, J. & Weatherbee, S. (2001) *From DNA to Diversity: Molecular Genetics and the Evolution of Animal Design*. Blackwell Science, Oxford. (*An excellent advanced undergraduate text that genuinely tries to link genetic diversity to morphology and evolutionary diversity*.)

Claridge, M.F., Dawah, H.A. & Wilson, M.R. (eds.) (1997) *Species: The Units of Biodiversity*. Chapman & Hall, London. (*An in-depth exploration of the meaning of species.*)

Gaston, K.J. (1996) What is biodiversity? In: *Biodiversity: A Biology of Numbers and Difference* (ed. K.J. Gaston), pp. 1–9. Blackwell Science, Oxford. (*Takes a different view from the one proffered here, distinguishing between biodiversity as a concept, a measurable entity, and a social/political construct*.)

Hawksworth, D.L. (ed.) (1995) *Biodiversity: Measurement and Estimation*. Chapman & Hall, London. (*An important, if somewhat eclectic, set of papers*.)

Hey, J. (2001) *Genes, Categories and Species*. Oxford University Press, Oxford. (*An unusual, at times erratic, but interesting book*.)

Magurran, A.E. (1988) *Ecological Diversity and its Measurement*. Croom Helm, London. (*Lucid review, and a good point of entry into this field.*)

Noss, R.F. (1990) Indicators for monitoring biodiversity: a hierarchical approach. *Conservation Biology* 4, 355–364. (*Distinguishes an alternative hierarchical organization to biodiversity, based on composition, structure and function.*)

General texts on biodiversity

Dobson, A.P. (1996) *Conservation and Biodiversity*. Scientific American, New York. (*Beautifully produced and reasonably comprehensive, with a good bibliography – very accessible.*)

Gaston, K.J. (ed.) (1996) *Biodiversity: A Biology of Numbers and Difference*. Blackwell Science, Oxford. (*A wide-ranging, but far from comprehensive, examination of the measurement of temporal and spatial patterns in, and the conservation and management of, biodiversity*.)

Groombridge, B. & Jenkins, M.D. (2002) *World Atlas of Biodiversity: Earth's Living Resources in the 21st Century*. University of California Press, London. (*A wide-ranging overview, with lots of maps, tables and graphs*.)

Heywood, V.H. (ed.) (1995) *Global Biodiversity Assessment*. Cambridge University Press, Cambridge. (*A major review of the different facets of biodiversity, from characterization to economic importance. A formidable tome*!)

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Wilson, E.O. & Perlman, D.L. (2000) *Conserving Earth's Biodiversity* (CD-ROM). Island Press, Washington, DC. [Demonstration version at http://www.islandpress.org/wilsoncd/index.ssi] (*There are surprisingly few CD-ROM and other such resources available on the topic of biodiversity; this is perhaps the best general one*.)

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World Conservation Monitoring Centre (comp.), Groombridge, B. (ed.) (1994) *Biodiversity Data Sourcebook*. World Conservation Press, Cambridge. (*An update and expansion of some of the information in the World Conservation Monitoring Centre (1992) volume*.)

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Surfing the World Wide Web (WWW)

'Biodiversity' on a search engine throws up a whole load of material; some useful, and much not. To save you time there are some lists of biodiversity WWW sites (http://www.groms.de/data/zoology/riede/taxalinks.html; http://biodiversity.uno.edu; http://www.biodiversity.org.uk/ibs/other/env/biodiv.htm). However, there are three web sites that call for special mention:

1 The Convention on Biological Diversity and all of the material associated with it is accessible at http://www.biodiv.org/.

2 The World Resources Institute (WRI) web site (http://wri.igc.org/wri/biodiv) is a valuable source of biodiversity facts and figures.

3 The UNEP-World Conservation Monitoring Centre (UNEP-WCMC) is an internationally recognized body for collation of information on conservation and sustainable use of biodiversity. Visitors to their web site (http://www.unep-wcmc.org) will find good general information and also fairly detailed information in the form of statistics and maps, generated from their databases. These include details of protected areas, national biodiversity strategies and data on threatened species.

2 Biodiversity through time

2.1 Introduction

As well as being of inherent interest, it is not unreasonable to suppose that an understanding of how biodiversity has arisen, and how it has changed in the past, may be important in interpreting its present and future structure. In this chapter, we consider the temporal dynamics of biodiversity – that is, how biodiversity changes with time. We begin by considering the sources of information on which this understanding is founded. We then give a brief overview of the history of life and of the principal historical patterns in the magnitude of biodiversity. We next turn to the major processes that give rise to these patterns, particularly diversification and extinction. Finally, we consider one product of these dynamics, namely the numbers of extant species.

Throughout this chapter, we will be concerned with the broad sweep of history. Those relatively recent, in geological terms, changes in biodiversity that have resulted as a direct or indirect product of human activities will be addressed at some length in Chapter 5.

2.2 Sources of information

Knowledge of the history of biodiversity derives from two primary sources. The first is analyses of data from the fossil record, and the second is analyses of molecular data.

2.2.1 Fossil record

Much of the modern-day geological landscape owes its origins to past biodiversity, which has left behind a rich fossil record. This has provided extraordinary insights into the history of life on Earth. However, working with the fossil record to understand this history is an important constraint for three reasons. First, as recognized by Darwin when marshalling evidence for his theory of evolution, this record is far from perfect or even. The record is much better for some periods than for others, and estimates of the numbers of species leaving a fossil record range from less than one to, at most, a few per cent of those that have ever lived (e.g. Sepkoski 1992). Second, of this fossil record, only a tiny fraction has actually been recovered. Third, the record, and that portion of it that has been recovered, is biased towards the more abundant, the more widespread, and the longer lived species, and more towards some groups of organisms than others. For instance, soft-bodied organisms, such as some cnidarians (jellyfish, sea anemones) are rarely fossilized and are exceptional in the fossil record, whereas the number of individual fossils of brachiopods, which are hard-bodied organisms, has been estimated to be in the billions. Some of the major soft-bodied animal groupings have left no fossil remains: animals like the Platyhelminthes (flatworms, flukes and tapeworms). The fossil record for animals with hard body parts, such as the brachiopods and molluscs, echinoderms and vertebrates, while often much better, is still far from complete and not always representative: 95% of all fossil species are marine animals while 85% of today's recorded plants and animals are terrestrial. In short, many of the pages of the history of biodiversity written in the fossil record are missing, and those that have been obtained only capture a biased portion of that history.

The paucity of the fossil record, even with regard to individual taxa, is well illustrated by a group that possesses hard body parts and is relatively well researched, having caught the attention and imagination of people of all ages and from all walks of life: the dinosaurs. Although something of the history of this group is familiar even to many primary/elementary school children, it remains based on a remarkably small window on the past. As of 1990, 900–1200 genera of dinosaurs were estimated to ever have lived (Dodson 1990). Of these, only 285 (336 species) were known from fossils, and nearly half of these were from only a single specimen; complete skulls and skeletons were known from only 20% of known genera. Similarly, it has been estimated that no more than 7% of all the primate species that have existed are known from fossils (Tavaré et al. 2002).

While it is clear that the documented fossil record is far from complete, in many different ways, it still provides an invaluable pictorial history of life on Earth, where many of the major events in that history have left their mark in, or on, the rocks. Notwithstanding its limitations, it is still possible to construct an understanding of changes in biodiversity through geological time using the fossil record (for recent analyses of the robustness of the fossil record, see Benton et al. 2000; Alroy et al. 2001; Smith 2001). However, because of the constraints referred to above, it will often be necessary to make recourse, throughout this chapter, to the temporal dynamics of numbers of higher taxa rather than of species because these are less vulnerable to the constraints. This should not pose too much of a problem, for not only do numbers of higher taxa act as a surrogate for numbers of species (cf. Section 1.4.4), but it is also true that they act as a measure of biodiversity in their own right (see Table 1.1).

2.2.2 Molecular evidence

Whilst the fossil record continues to provide the bulk of insights into the history of biodiversity, molecular evidence is playing an increasingly significant role. Comparison of molecular data for different organisms enables the generation of branching trees representing hypotheses of their patterns of phylogenetic relatedness, with those organisms with sequences that are more different being assumed to have diverged earlier in the evolutionary process. If assumptions are made about the rate at which molecular sequences diverge (a 'molecular clock'), then the timings of different evolutionary events can be estimated.

Fossil and molecular evidence do not always agree, particularly over the dates of first appearance of groups. For example, molecular evidence suggests that at least six animal phyla originated deep in the Precambrian, more than 400 million years (Myr) earlier than their first appearance known from the fossil record (Wang et al. 1999). Likewise, molecular data suggest that primates diverged from other placental mammals c. 90 Myr ago whereas the oldest known fossil primates are from c. 55 Myr ago (Tavaré et al. 2002). The fossil record is always liable to underestimate dates of first appearance, because the likelihood of such early individuals being fossilized and the fossils recovered is low. Equally, of course, the accuracy of first appearances estimated from molecular evidence rests on the interpretation of the molecular divergence data and particularly on the assumptions about the nature and dynamics of the molecular clock. However, together, fossil and molecular evidence provide a powerful combination for unlocking many of the secrets of the past.

2.3 A brief history of biodiversity

2.3.1 Principal features, from the Beginning to the present day

Drawing on insights provided by the fossil record and molecular evidence, some of the major events of life on Earth, together with their

Table 2.1 Geological eras, periods, and the major events associated with them. (Adapted from Schopf 1992.)

Era	Period	Myr ago	Major events
Precambrian	(PC)	4500	Origin of life, first multicellular organisms
Palaeozoic	Cambrian (C)	550	All of the major phyla present in fossil record, including first vertebrates (jawless fish)
	Ordovician (O)	500	First jawed fish
	Silurian (S)	440	Colonization of land by plants and arthropods
	Devonian (D)	410	Diversification of teleosts (bony fish). First amphibians and insects
	Carboniferous (Crb)	360	Extensive forests of vascular plants, origin of reptiles, amphibians dominant
	Permian (P)	290	Mass extinction of marine invertebrates, origins of mammal-like reptiles and 'modern insects'
Mesozoic	Triassic (Tr)	250	Origin and diversification of ruling reptiles, origin of mammals, gymnosperms dominant
	Jurassic (Jur)	210	Dominance of ruling reptiles and gymnosperms, origin of birds
	Cretaceous (Cret)	140	Origin of angiosperms (flowering plants), ruling reptiles and many invertebrate groups go extinct towards end of period
Cenozoic	Tertiary (Tert)	65	Diversification of mammals, birds, pollinating insects and angiosperms. Late Tertiary/early Quaternary – the zenith of biodiversity
	Quaternary (Q)	1.8	Origin of humankind

chronology, are presented in Table 2.1. It is likely that all known organisms originated from a single common ancestor. Self-evidently, biodiversity has increased between this inception, estimated to be about 3.5–4.0 billion years ago (the Earth itself is thought to be more than 4.5–5.0 billion years old, and thus life has been present throughout most of its existence), and the present time – otherwise we would not see the wealth of organisms that we do today. At first this increase appears to have been very slow.

One of the key innovations, which opened the door to a major increase in biodiversity, was the advent of multicellularity (i.e. the appearance of individual organisms being composed of numerous cells, differentiated for the performance of different functions). Multicellular organisms did not begin to diversify until perhaps 1.4 billion years ago, when nearly 60% of the history of life had already passed. Multicellular animals (metazoans) specifically did not begin markedly to diversify until approximately

600 Myr ago, by which time about 80% of the history of life had passed. None of these first fossil metazoans possessed any hard parts and most were no more than a few millimetres long. There are a few tantalizing glimpses of relatively large soft-bodied metazoans in late Precambrian (also known as Vendian) rocks, for example in the Ediacaran fauna in Australia, which has been referred to as comprising either ancestral metazoans, or a parallel unsuccessful metazoan experiment.

It is only with the beginning of the Palaeozoic Era (early life), and in rocks of the Cambrian period (550 Myr ago), that we see the sudden appearance of the first sizeable metazoans with hard parts (as exemplified by the *Wonderful Life* (Gould 1989) of the Burgess Shale fauna from Canada). Not only are the fossils plentiful, but there is a bewildering array of different body plans present, some 'experimental' (or, with hindsight, novel), and relatively short-lived (300 + Myr), but others surviving and remaining to the present. It has been estimated that if the Cambrian explosion of biodiversity had continued at a constant rate to the present day the oceans would be occupied by 10^{60} families of metazoan organisms, instead of the 10^3 there actually are (Sepkoski 1997). In fact, by the end of the Cambrian all of today's major animal groupings (or phyla) are present in the fossil record.

The diversity of body plans displayed by the different phyla belies some important underlying conservatism in their genetic make-up, particularly in the homeotic genes, those genes that regulate the expression of other genes. Some of the best understood are the *Hox* genes. Homologous *Hox* genes are present in nearly all organisms. They have a precise role in the definition of anterior/posterior regional identity. Mutation in a *Hox* gene, or the development of even one novel *Hox* gene, can have profound morphological consequences. Not surprisingly such events have been suggested as providing a mechanism for initial rapid evolution of body plans, leading to the increase in the diversity of phyla around and before the Cambrian period. Figure 2.1 illustrates the relative timing of the major events in *Hox* gene evolution mapped onto a phylogenetic tree of metazoans for which there are data. Cnidarians possess only anterior and posterior *Hox* genes. The remaining animal phyla examined show an expansion of central *Hox* genes (with further specialization accompanying the origin of moulting animals – the ecdysozoans), with echinoderms and chordates being characterized by a further expansion of the posterior *Hox* genes. Vertebrates show duplication of *Hox* genes: sharks and jawless fish possess more than two *Hox* complexes; teleost fish have 5–7 complexes; and the tetrapods have four complexes.

A list of all of the present-day phyla as recognized by one authority is presented in Table 2.2. This is based on a five kingdom system of higher classification, although a three domain system has also been proposed (Woese et al. 1990). Other surveys recognize greater or smaller numbers

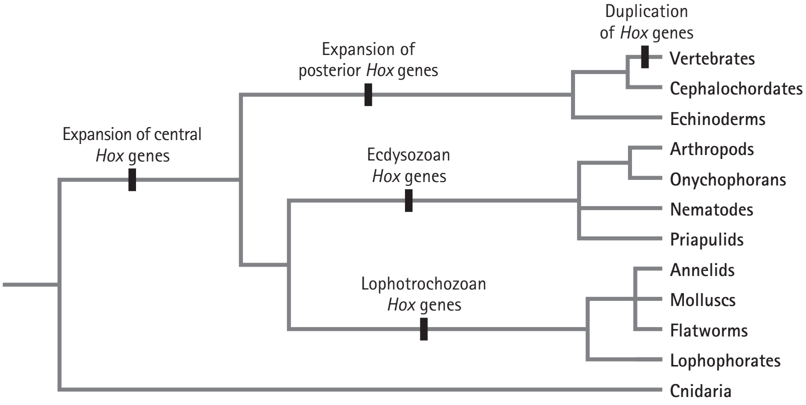


Fig. 2.1 Major events in the evolution of metazoan *Hox* genes. (Data from Rosa et al. 1999.)

Table 2.2 A survey of present-day phyla, based on the classification of Margulis and Schwartz (1998).

		Marine	Freshwater	Terrestrial
Superkingdom: **Prokarya**				
Kingdom: **Bacteria**				
Subkingdom: **Archaea**				
Euryarchaeota	Methanogens and halophils	√	√	√
Crenarchaeota	Thermoacidophils	√	√	
Subkingdom: **Eubacteria**				
Proteobacteria	Purple bacteria	√	√	√
Spirochaetae		√	√	√
Cyanobacteria	Blue-green bacteria and chloroxybacteria, grass green	√	√	√
Saprospirae	Fermenting gliders	√	√	√
Chloroflexa	Green non-sulphur phototrophs		√	√
Chlorobia	Anoxygenic green sulphur bacteria	√	√	√
Aphragmabacteria	Mycoplasmas			√
Endospora	Endospore-forming and related low-G + C Gram-positive bacteria	√	√	√
Pirellulae	Proteinaceous-walled bacteria and relatives		√	
Actinobacteria	Actinomycetes, actinomycota and related high-G + C Gram-positive bacteria		√	√

(*cont'd*)

Table 2.2 (*cont'd*)

		Marine	Freshwater	Terrestrial
Deinococci	Radiation-resistant or heat-resistant Gram-positive bacteria		√	
Thermotogae	Thermophilic fermenters	√	√	√
Superkingdom: **Eukarya**				
Kingdom: **Protoctista**				
Archaeprotista		√	√	√
Microspora	Microsporida			√
Rhizopoda	Amastigote amoebas and cellular slime moulds	√	√	√
Granuloreticulosa		√	√	
Xenophyophora		√		
Myxomycota	Myxogastria, plasmodial slime moulds			√
Dinomastigota	Dinoflagellata, Dinophyta	√	√	
Ciliophora	Ciliates	√	√	
Apicomplexa	Sporozoa, Telosporidea			√
Haptomonada	Prymnesiophyta, Haptophyta, coccolithophorids	√	√	
Cryptomonada	Cryptophyta	√	√	
Discomitochondria	Flagellates, zoomastigotes, zooflagellates	√	√	√
Chrysomonada	Chrysophyta	√	√	
Xanthophyta		√	√	√
Eustigmatophyta		√	√	
Diatoms	Bacillariophyta	√	√	√
Phaeophyta	Brown algae	√	√	
Labyrinthulata	Slime nets and thraustochytrids	√		
Plasmodiophora				√
Oomycota	Oomycetes, oomycotes		√	√
Hyphochytriomycota			√	√
Haplospora		√		
Paramyxa		√		
Myxospora	Myxozoa, myxosporidians	√	√	
Rhodophyta	Red algae	√	√	√
Gamophyta	Conjugaphyta, conjugating green algae		√	
Actinopoda		√	√	√
Chlorophyta	Green algae	√	√	
Chytridiomycota			√	√
Zoomastigota	Zoomastigotes, zooflagellates	√	√	√

(*cont'd on p. 26*)

Table 2.2 (*cont'd*)

		Marine	Freshwater	Terrestrial
Kingdom: **Animalia**				
Placozoa	Trichoplaxes	√		
Porifera	Sponges, poriferans	√	√	
Cnidaria	Cnidarians, hydras, jellyfish, sea anemones, corals	√	√	
Ctenophora	Comb jellies	√		
Platyhelminthes	Flatworms	√	√	√
Gnathostomulida	Jaw worms	√		
Rhombozoa	Rhombozoans	√		
Orthonectida	Orthonectids	√		
Nemertea	Ribbon worms, nemertines, Rhynchocoela	√	√	√
Nematoda	Nematodes, thread worms, round worms	√	√	√
Nematomorpha	Gordian worms, horsehair worms, nematomorphs	√	√	√
Acanthocephala	Thorny-headed worms	√	√	√
Rotifera	Rotifers, wheel animals	√	√	√
Kinorhyncha	Kinorhynchs	√		
Priapulida	Priapulids	√		
Gastrotricha	Gastrotrichs	√	√	
Loricifera	Loriciferans	√		
Entoprocta	Entoprocts	√		
Chelicerata	Chelicerates, spiders, scorpions, ticks, mites	√	√	√
Mandibulata (Uniramia)	Mandibulates, mandibulate arthropods	√	√	√
Crustacea	Crustaceans	√	√	√
Annelida	Annelid worms, true worms	√	√	√
Sipuncula	Sipunculans, sipunculids, peanut worms	√		
Echiura	Spoon-worms, echiurans, echiurids	√		
Pogonophora	Beard worms, pogonophorans, tube worms	√		
Mollusca	Molluscs	√	√	√
Tardigrada	Water bears, tardigrades	√	√	√
Onychophora	Velvet worms, onychophorans, peripatuses			√
Bryozoa	Ectoprocta, ectoprocts, moss animals	√	√	
Brachiopoda	Lampshells, brachiopods	√		

(*cont'd*)

Table 2.2 (*cont'd*)

		Marine	Freshwater	Terrestrial
Phoronida	Phoronids	√		
Chaetognatha	Arrow worms	√		
Hemichordata	Acorn worms, pterobranchs, enteroptneusts, tongue worms	√		
Echinodermata	Echinoderms	√		
Urochordata*	Tunicates, sea squirts, ascidians, larvaceans, salps	√		
Cephalochordata*	Lancelets, Acrania	√		
Craniata*		√	√	√
Kingdom: **Fungi**				
Zygomycota	Zygomycotes, zygomycetes		√	√
Basidiomycota	Basidiomycotes, basidiomycetes		√	√
Ascomycota	Ascomycotes, ascomycetes	√	√	√
Kingdom: **Plantae**				
Bryophyta	Mosses		√	√
Hepatophyta	Liverworts		√	√
Anthocerophyta	Hornworts			√
Lycophyta	Club mosses, lycophytes, lycopods		√	√
Psilophyta	Psilophytes, whisk fern			√
Sphenophyta	Sphenophytes, Equisetophyta, horsetails			√
Filicinophyta	Pterophyta, Pterodatina, Pteridophyta, ferns		√	√
Cycadophyta	Cycads			√
Ginkgophyta				√
Coniferophyta	Conifers			√
Gnetophyta	Gnetophytes			√
Anthophyta	Angiospermophyta, Magnoliophyta, flowering plants	√	√	√

*These phyla comprise the chordates.

of phyla, and different sets thereof (the listing does not include viruses, which are minute and mostly parasitic sub-organisms derived, in many cases it has been suggested, from the nuclear material of organisms). Moreover, new phyla continue to be found. In 1998 alone, some authorities reported more than 20 new divisions of bacteria at the phylum, and possibly higher, level (Fuhrman & Campbell 1998). At the time of writing, the most recent to be discovered has been named the Nanoarchaeota, with as yet a single species, a nano-sized hyperthermophilic microorganism obtained from a submarine hot vent (Huber et al. 2002).

Gould (1989) suggests that anatomical diversity reached a maximum around the time of the Cambrian explosion in biodiversity. The colonization of land by animals and plants (440 Myr ago), and their subsequent diversification, lagged far behind the emergence of multicellular organisms in the oceans. So animal life has gone from a position of relatively few species encompassing many different body plans in the Cambrian ('early experimentation . . .'), up to the present day where we see considerably more species but fewer body plans ('. . . and later standardisation') (Gould 1989).

Broadly speaking, there were relatively few species during the Palaeozoic and early Mesozoic eras (although this has been a matter of some controversy; Signor 1990). However, starting just over 100 Myr ago there was a progressive and substantial increase in biodiversity that culminated at the end of the Tertiary and beginning of the Quaternary (Pleistocene) in there being more extant species and higher taxa of animals and plants (both marine and terrestrial) than at any time before or, indeed, since (Signor 1990). The ancestors of the human lineage emerged from the apes about 5 Myr ago in Africa, the genus *Homo* about 2 Myr ago, and anatomically modern humans 100,000–200,000 years ago. We are living in the Quaternary (Holocene) in a time of decreasing diversity, which is correlated with change in climate and the advent of organized and large-scale human activity (Chapter 5).

There is no consensus as to whether in broad outline the path from one species to many can be explained in terms of a simple mathematical model, and if so what that model might be. Part of the difficulty lies in the fact that once diversification began to occur on a major scale (Cambrian to the present day) it was not, as we have seen above, continuous. Rather, there were periods of dramatic increase, interspersed by some times of major setbacks or periods of relative stasis (or at least no marked directional trend in diversity). Consequently, the history of biodiversity is often presented as one of radiations and stabilizations, punctuated by mass extinctions (Signor 1990; Sepkoski 1992).

Growth in numbers of families of marine organisms exhibits three main phases of diversification (in the early Cambrian, in the Ordovician, and through the Mesozoic and Cenozoic), two main phases of approximate stabilization of diversity (in the mid to late Cambrian, and through most of the Palaeozoic), and five major mass extinctions (Late Ordovician, Late Devonian, Late Permian, Late Triassic, end-Cretaceous) (Fig. 2.2). This has been explained using two sequential S-shaped (logistic) curves, each consisting of an initially slow period of increase, followed by a rapid one, with a final slow approach to an asymptote (Courtillot & Gaudemer 1996). It has also been explained using an underlying exponential curve,

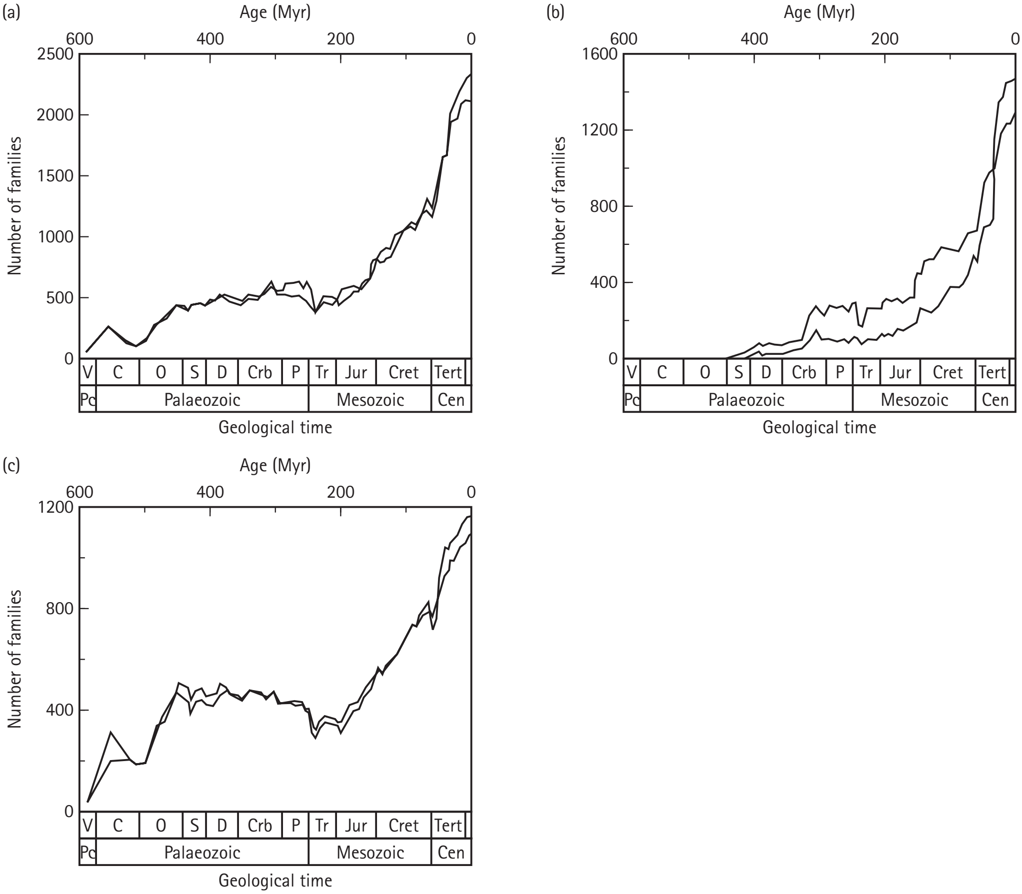


Fig. 2.2 Temporal dynamics of the number of families of: (a) all organisms; (b) continental organisms; and (c) marine organisms. In each case a maximum and minimum curve is shown, based on a combination of stratigraphic and habitat-preference information. C, Cambrian; Cen, Cenozoic; Crb, Carboniferous; Cret, Cretaceous; D, Devonian; Jur, Jurassic; O, Ordovician; P, Permian; Pc, Precambrian; S, Silurian; Tert, Tertiary; Tr, Triassic; V, Vendian. (From Benton 1995.)

about which there is considerable variation in numbers of families (Hewzulla et al. 1999). Growth in numbers of families of continental organisms, and of all organisms (marine + continental) show more continuous patterns of increase (Fig. 2.2; Benton 1995, 1997). These have been explained using exponential curves, with a regular doubling of family numbers within fixed units of time. In none of these cases is there evidence of an obvious long-term limit to the diversity of life that can inhabit the Earth. Presumably, if diversification were to continue, at some point an ultimate ceiling would be attained, but it is not difficult to see that many more different species than are presently extant might be packed onto the Earth before that ceiling was attained. This is important because

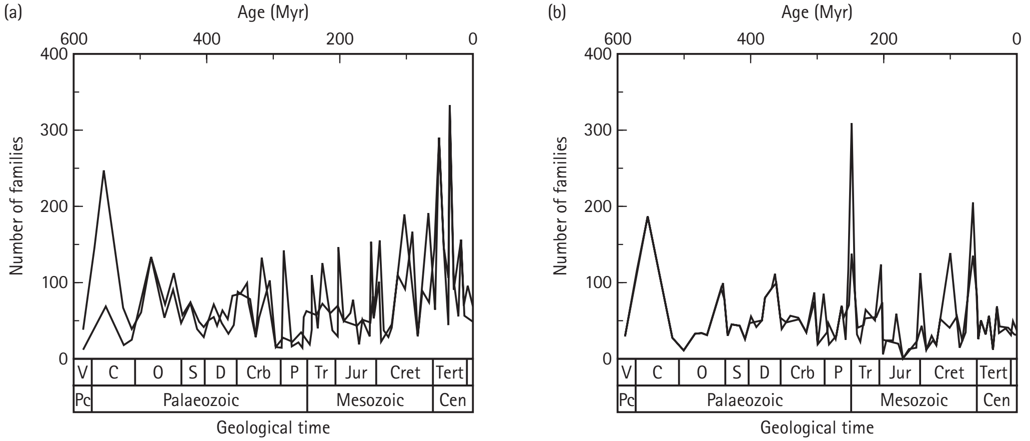


Fig. 2.3 Temporal dynamics of the numbers of family (a) originations and (b) extinctions for all organisms. Maximum and minimum curves are shown and abbreviations are as in Fig. 2.2. (From Benton 1995.)

many models of patterns of species richness both in time and space assume, conversely, that this richness has attained equilibrium.

The number of families in any one period is the number in the preceding period, plus the number of new ones that have appeared, minus the number from the preceding period that have become extinct. The patterns of these originations and extinctions are complex (Fig. 2.3), and numerous studies have sought to identify underlying regularities. The patterns seem to be driven both by internal dynamics of the diversification process and by the influence of external factors.

The broad patterns of temporal change are, to a first approximation, reflected both in global and regional biodiversity and in local biodiversity (Fig. 2.4). This is both interesting and informative, as it means that as biodiversity has increased on a global scale it has tended also to do the same locally. The alternative scenario would have been that biodiversity remained approximately constant locally, with the global increase having resulted solely from a growing differentiation between the occupants of different localities.

Given that there is a pattern of overall increase in biodiversity through time, the obvious question is why? The answer, quite simply, is that we do not know. A number of different factors have been suggested as effecting this increase: external factors such as the break-up of the continents and their subsequent drift (increasing the differentiation between assemblages on different continents and in different ocean basins), and changing climatic conditions and intrinsic factors such as the occupation, through evolutionary time, of more and more of the potential niche space open to organisms (associated with evolutionary 'break-throughs'), and perhaps

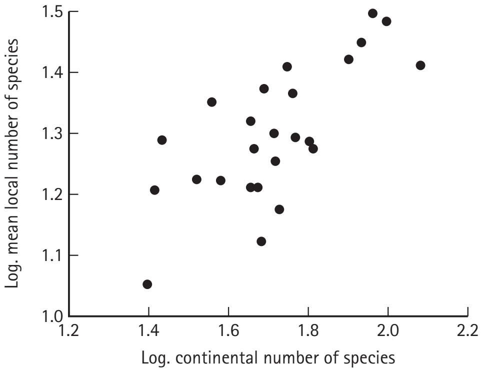


Fig. 2.4 Relationship between local and continental species richness through time for large mammalian carnivore and herbivore species in North America over the last 44 Myr (divided into 25 time intervals, each data point is for one time interval). (From Van Valkenburgh & Janis 1993.)

finer subdivision of this space. The move onto land, for example, opened up many more opportunities for speciation than had previously existed.

2.3.2 Diversification

The overall pattern of diversification is not a product of synchronous changes in the biodiversity of all the component groups of organisms. Rather, some groups underwent differential diversification in particular time periods, often associated with the invasion of new habitats or following major extinction events. Moreover, different groups diversified in different ways (Benton 1997). Some radiated quickly and later also underwent rapid decline in diversity, perhaps to extinction. Some radiated very slowly, and persisted at low diversity. Others continued to radiate at moderate to high rates for very long periods.

This can clearly be seen with reference to land plants and to vertebrate tetrapods. Amongst the land plants, the dominance of primitive vascular plants gave way to pteridophytes (ferns) and lycopsids (club mosses), which in turn gave way to a predominance of gymnosperms (spore bearers), which finally were overtaken by the angiosperms (flower bearers) (Fig. 2.5); there is some evidence that the angiosperms continue their diversification through the present. Amongst vertebrate tetrapods, the early amphibians and reptiles gave way to a number of successful reptile groups (including dinosaurs), which in turn gave way to the modern amphibians and reptiles, the birds and the mammals (Fig. 2.6). It is tempting to interpret these successions as cases of competitive replacement or improvement, with one group being driven out by the growing numbers of species of the ascendant group. However, there is no reason that this interpretation need be correct, and the reasons for these patterns are almost always considerably more complex, and associated with changing environmental conditions and the shifting opportunities associated with these.

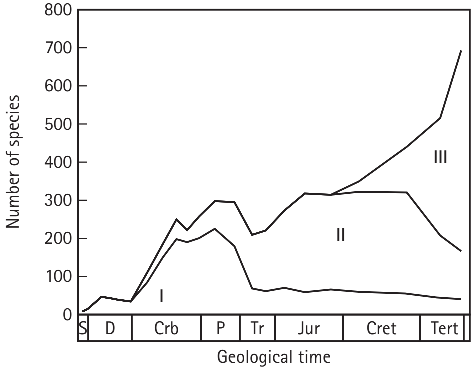


Fig. 2.5 Temporal dynamics of the numbers of fossil species of vascular land plants. I, pteridophytes; II, gymnosperms; III, angiosperms. Abbreviations are as in Fig. 2.2. (From Niklas 1986.)

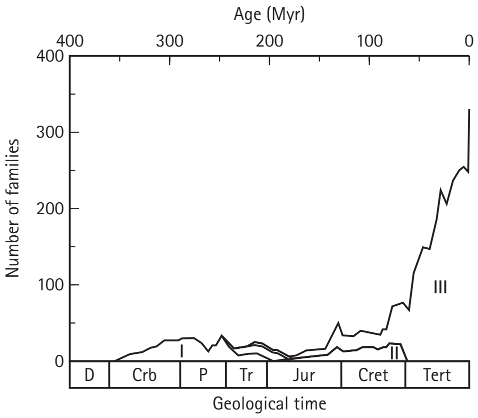


Fig. 2.6 Temporal dynamics of the numbers of families of terrestrial tetrapods. I, early amphibians, early reptiles (anapsids), mammal-like reptiles; II, early diapsids (reptiles), dinosaurs, flying lizards; III, 'modern groups' – amphibians (salamanders and frogs), reptiles (turtles, lizards, snakes and crocodiles), birds and mammals. Abbreviations are as in Fig. 2.2. (From Benton 1985.)

It has been suggested that the rise and fall in the diversity of different groups can, mass extinctions and other such disruptions aside, be reasonably well modelled by a modification of a logistic model, in which a group diversifies initially rather slowly and then more quickly, at some point attaining a peak in richness, and then declines slowly to extinction over some longer period (Fig. 2.7). How general is such a model remains unclear.

Notwithstanding the relatively large number of major body plans, or phyla (see Table 2.2), at any one time much of biodiversity is contributed by just a few groups of organisms, whilst most groups are simply not very diverse. This pattern is repeated at all taxonomic levels. Thus, for example, most species are in the kingdom Animalia, most of the species in the Animalia are in the Arthropoda, most of the species in the Arthropoda are in the class Insecta, and most of the species in the Insecta are in the orders Diptera (the flies), Hymenoptera (the ants, bees and wasps) and Coleoptera (the beetles). Likewise, the largest number of species in the class Mammalia are in the order Rodentia (the rodents), most of the species in the Rodentia are in the family Muridae, and a high proportion of species in the Muridae are in the largest genus in that group.

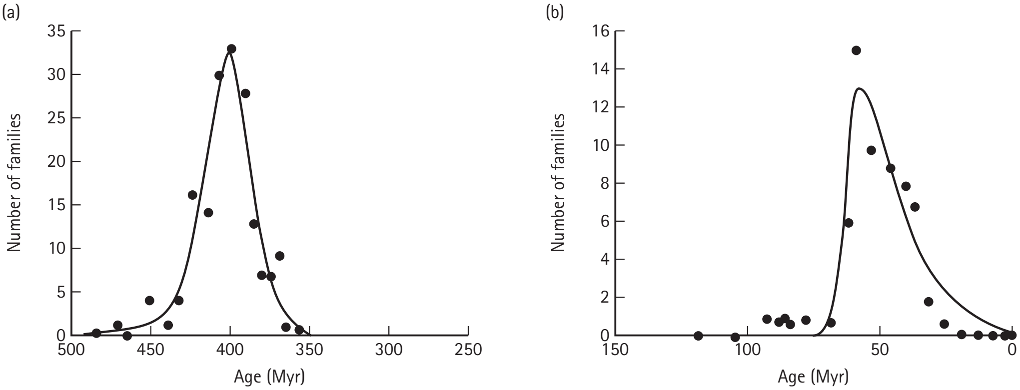


Fig. 2.7 Numbers of families occurring every 1 Myr for: (a) agnathans (jawless vertebrates related to modern lampreys and hagfish); and (b) Cimolesta (small dog-like animals). (From Boulter 2002.)

Three main explanations have been proposed for this clumped pattern of diversity. First, it is possible that this could merely be an artefact of the process of classifying organisms into groups, and may have no biological basis. There is little evidence that this is actually true, because the differences between many groups of organisms are clearly real and reflective of their evolutionary relationships; although curiously, humans do tend to organize sets of differing inanimate objects into a few large groups and many small ones!

Second, the patterns could simply be a matter of chance. Indeed, a pattern in which many groups have a few species and one or a few groups contain a high proportion of species is a likely product of a model of random speciation and extinction. Consider the circumstances in which lineage splitting leads from one ancestral species to four descendant species, and in which at all branching points one ancestral species gives rise to two descendants (dichotomous splitting; Fig. 2.8). Initially an ancestral species splits to give two distinct species. Depending on which of these two speciates, two possible three-species outcomes exist, and depending on which of these three species subsequently speciates, six possible four-species outcomes may result. Of these patterns of phylogeny of four species, only one third (2/6) are symmetrical; an uneven distribution of species is the more likely outcome. Such a pattern is repeated for progressively larger and larger numbers of species (although the possible number of evolutionary trees grows very rapidly; for example by the same set of rules, there are 87,178,291,200 possible trees giving rise to 15 species!). Indeed, models of random speciation and extinction take us a long way towards understanding patterns of diversification, but are not always sufficient. Some groups still have disproportionately more species than would be expected by chance.

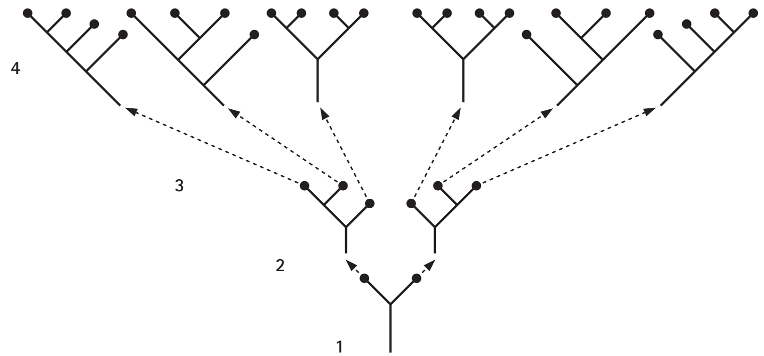


Fig. 2.8 A diagrammatic representation of the possible routes by which lineage splitting leads from one ancestral species to four. (From Slowinski & Guyer 1989.)

This leads us to the third possible reason for the observed pattern, which is that some groups have features that predispose them to diversify disproportionately. Thus, it has been proposed that dispersal by animals has promoted the diversification of some vascular plant groups, the ability to fly has promoted the diversification of some insect groups, and small body size has promoted the diversification of some bird groups. Such suggestions have proven much more difficult to test than was long supposed, and there are many 'just-so' stories (a phrase used by Gould & Lewontin (1979), borrowed from Rudyard Kipling's 1902 book of the same name, to describe a clever explanation of why a given species has a particular trait which is either untested or untestable) for why one group is more diverse than another, with no sound empirical support. Nonetheless, it would seem likely that the evolution of some traits opened up opportunities for some groups to diversify disproportionately more than others. Thus, there is quantitative evidence that the adoption of phytophagy ('plant eating') has been associated with disproportionate diversification in insect groups (Mitter et al. 1988), whilst the adoption of a carnivorous parasitic lifestyle has not (Wiegmann et al. 1993). Much of the history of diversification has been one of specialization in interspecific interactions, be these based on consumption, pollination or dispersal (Thompson 2002).

2.3.3 Extinction

The overall pattern of temporal change in biodiversity results from the difference between rates of speciation (adding species) and rates of extinction (taking species away). If species are being generated faster than they are becoming extinct, then the level of biodiversity will rise. When the rate of extinction equals that of speciation an overall pattern of stability (stasis) will result. Hence if, or when, stasis is observed in the level of

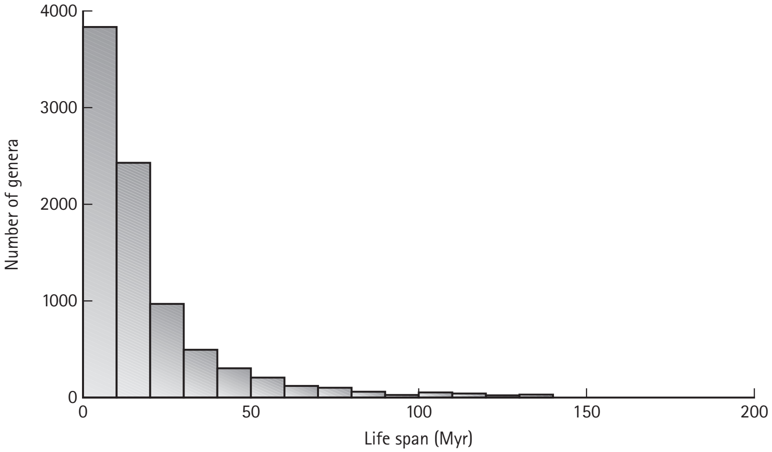


Fig. 2.9 Life spans of c. 17,500 extinct genera of marine animals (vertebrate, invertebrate and microfossil). (From Raup 1994.)

biodiversity this does not necessarily mean that nothing is happening; turnover in the identities of taxa through time could, and frequently will, still be high. When the level of extinction exceeds that of speciation then biodiversity will decline, and if this persisted for a sufficient period then life would ultimately be expunged from the Earth.

Over the history of life on Earth, in excess of 90% of all species (and perhaps closer to 98%) are estimated to have become extinct. Based on evidence from a variety of groups (both marine and terrestrial), the best present estimate is that the average species has had a life span (i.e. from the time a particular species appears in the fossil record until the time it disappears) of around 5–10 Myr (May et al. 1995). Again using a higher taxonomic unit to reduce the sampling problems, Raup (1994) found that the recorded life spans of 17,500 genera of fossil marine animals were strongly right-skewed (Fig. 2.9). Most genera persisted for a relatively short time, whilst a few persisted for a very long period. The real pattern is probably even more skewed, as the very short-lived are unlikely even to be recorded in the fossil record. The pattern is also likely to apply to species. Compared with the duration of life on Earth, however, no genus survived for very long. The longest-lived persisted for about 160 Myr, or about 5% of the history of life.

Some groups tend to have characteristically higher rates of extinction than do others. Thus, there is substantial variation in the estimated periods for which, on average, species in different taxonomic groups persist (Table 2.3). Indeed, natural extinctions tend to be taxonomically clumped, often disproportionately within species-poor groups, which may mean that more genetic diversity is lost than would be expected by chance. Extinctions resulting from human activities tend also to be

Table 2.3 Estimated mean duration (Myr) of fossil species. (From McKinney 1997.)

	Duration (Myr)
Marine	
Reef corals	25
Bivalves	23
Benthic foraminiferans	21
Bryozoa	12
Gastropods	10
Planktonic foraminiferans	10
Echinoids	7
Crinoids	6.7
Non-marine	
Monocotyledonous plants	4
Horses	4
Dicotyledonous plants	3
Freshwater fish	3
Birds	2.5
Mammals	1.7
Insects	1.5
Primates	1

clumped (parrots, pheasants and primates are all disproportionately threatened at present). Such differences may reflect extrinsic factors. Thus, for example, in the fossil record marine groups seem to have lower rates of extinction than do terrestrial groups (Table 2.3), which may perhaps reflect the greater buffering of marine systems to environmental change. However, the differences may also reflect intrinsic factors that make some species more vulnerable to extinction than others, with the relationship between the intrinsic characteristics of species and the likelihood of extinction depending fundamentally on the extrinsic factors that are posing the threat to continued persistence.

The intensity of extinction has varied markedly over time, with comparatively low levels during the majority of periods and high levels during the minority, and an overall right-skewed frequency distribution (Fig. 2.10). The right-hand tail of this continuum comprises what have come to be known as the mass extinctions (the other periods comprise background extinctions), albeit that they clearly do not represent a distinct subset of periods. Although in these short intervals 75–95% of species alive at that time are estimated to have become extinct (Jablonski 1995), in sum the mass extinctions only account for about 4% of all extinctions in the last 600 Myr (Raup 1994). Their importance therefore lies not in their contribution to total extinctions, but in the disruptive effect they have had on the patterns of development of biodiversity. They

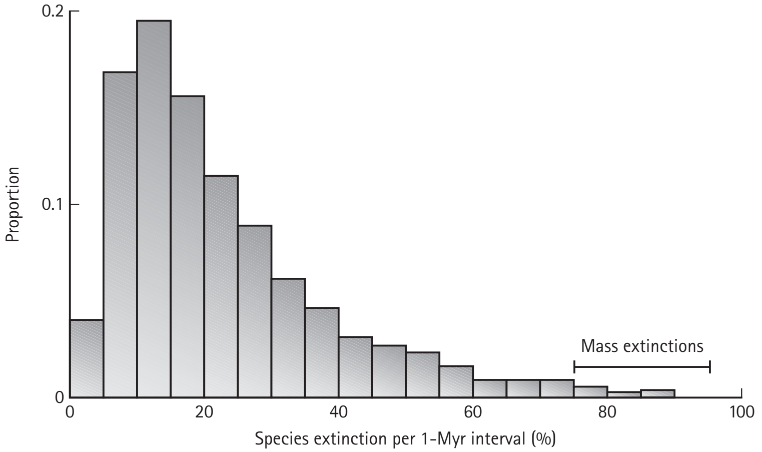


Fig. 2.10 Proportion of 1-Myr intervals during the past 600 Myr with different intensities (percentage of species) of extinction. Mass extinctions occur in the extreme of the right-hand tail. (From Raup 1994.)

reveal that marine and terrestrial biotas are not infinitely resilient but can in some senses be pushed beyond their limits by certain environmental stresses leading to dramatic collapses in diversity (Jablonski 1991). When levels of biodiversity recover, they often have a markedly different composition to those that preceded a mass extinction, with those groups which were previously highly successful in terms of species richness being lost entirely or persisting at reduced numbers.

Although they are the tail of a continuum, the mass extinctions were not simply the result of the chance coincidence of extinctions of very large numbers of species. Indeed, the ‘big five’ mass extinctions are believed to have had rather different causes (Erwin 2001).

1 *Late Ordovician (440 Myr ago)*. Global climates during the Ordovician were warm, causing a decline in vertical circulation in the oceans, and thence depletion of oxygen in deep waters. The movement of a large amount of continental area near to the South Pole resulted in climatic cooling and the onset of glacial conditions. Sea levels decreased, causing the extinction of marine, particularly deep-water, groups. The end of the glaciation led to a second phase of extinction, with rising sea levels being associated with the spread of low oxygen conditions, leading to the loss of shallow-water groups.

2 *Late Devonian (360 Myr ago)*. Many processes have been suggested to have given rise to this extinction event, including extraterrestrial impact, sea-level fluctuations and spread of anoxic waters, climatic changes and global cooling. There is insufficient evidence to attribute the event solely to any of these, and it may have arisen from a combination of factors.

3 *Late Permian (250 Myr ago)*. Again, the cause of this extinction event, the largest of all (extinguishing 95% of all marine species and 70% of species on land), is debatable. There is evidence that the event coincided with low oxygen levels in the oceans, sea-level rise, and climatic change, some or all of which may have been triggered by other processes.
4 *Late Triassic (210 Myr ago)*. Attempts to explain this event have focussed on extraterrestrial impact, marine anoxia and volcanism (the last giving rise to rapid climatic shifts, volcanic gases and acid rain). Again, however, the patterns of causality are unclear.
5 *End-Cretaceous (65 Myr ago)*. Explanations of this extinction event, best known for the extinction of the dinosaurs, pterosaurs and marine reptiles, have focussed on consequences of the impact of an extraterrestrial object, in particular the global cooling that may have followed from subsequent changes to the atmosphere (particularly dust, smoke, water vapour and sulphur dioxide).

The fossil record reveals that overall levels of biodiversity may recover from mass extinction events very rapidly (for example, the families of marine organisms in Fig. 2.2) on an evolutionary time scale, but the recovery and the re-establishment of some communities still typically requires 2–10 Myr (Jablonski 1995; Erwin 1998). Whilst some lineages may pass on to attain high diversity, others surviving a mass extinction event may fail ever to recover markedly, suggesting an impact that may extend well beyond the actual extinction event itself (a pattern that has been termed ‘dead clade walking’; Jablonski 2002). If substantial extinctions occur in the near future, as seems likely if not inevitable (Chapter 5), then the species will not be replaced in short order.

2.4 How many extant species are there?

If the diversity of life has increased through evolutionary time, how many species are presently extant? Although it has received substantial attention, the importance of this question perhaps has less to do with the usefulness of the actual answer than with the challenge it poses to an understanding of how biodiversity is distributed amongst different groups of organisms and across the Earth. It is one of the basic descriptors of life on the planet, to which we should be able to provide a reasonably accurate answer.

On the face of it, the best way of finding out how many extant species there are would simply be to count them! However, the diversity of life is so great that this presents a truly formidable task, and one that has never risen high enough up the agenda of humankind to be given serious consideration. The question of how insurmountable the obstacle would be if substantial resources, technology and ingenuity were brought to bear remains unanswered. Some believe that it is attainable in a matter of decades, but most are unconvinced.

Given the enormity of such a task, all of the many attempts at estimating how many extant species there are have employed indirect measures, and, in the process, have made major assumptions of one kind or another (for reviews, see May 1988, 1990, 1994a; Hammond 1995; Pimm et al. 1995a; Stork 1997). Five main methods have been used to estimate the numbers of extant species in large taxonomic groups or all groups, based on extrapolations from:

1 *Canvassing experts*. This involves estimating overall numbers of species based on the opinions of those experts who have studied particular groups of species over long periods and have gained an understanding of the numbers that are unknown to science. This makes the entirely untestable assumption that these experts know these groups sufficiently well to make reliable estimates.

2 *Patterns of species description*. Overall numbers of species in some groups have been estimated by extrapolating into the future the growth in the cumulative numbers of taxonomically described species through time. This assumes that past patterns of description indicate future patterns.

3 *Proportion of undescribed species*. This approach involves estimating overall numbers of species from the ratio of previously unknown to previously known species in large samples of specimens, and then extrapolating from the overall numbers of known species. This assumes that the samples are representative.

4 *Well-studied areas*. Overall numbers of species globally or in very large regions have been estimated by extrapolating from those few (predominantly temperate) areas for which numbers of species are reasonably well known. This assumes that the areas for which overall species numbers are well known are representative of those for which they are not.

5 *Well-studied groups*. This involves estimating overall numbers of species based on the global numbers in well-known groups and estimates of the ratio of the numbers of species in these groups to others in those few regions where the latter are reasonably well known. This assumes that these ratios of numbers of species in well-known and other groups remain reasonably constant across space.

The assumptions of all of these approaches are seldom precisely met. All also require extrapolation beyond the bounds of available data, something that statisticians, quite correctly, always caution against.

A widely quoted working estimate of extant species numbers, integrating what is presently known based on large numbers of studies, is one of around 13.5 million, with upper and lower estimated numbers of about 3.5 and 111.5 million species, respectively (Table 2.4) (Hawksworth & Kalin-Arroyo 1995; see also World Conservation Monitoring Centre 1992; Hammond 1995). The upper boundary appears wildly improbable,

Table 2.4 Approximate numbers of described species (in thousands) currently recognized, and estimates of possible species richness for groups with more than 20,000 described species and/or estimated to include in excess of 100,000 species. The reliability of all estimates is likely to vary greatly, and a crude indication of the likely accuracy is given. (From Hawksworth & Kalin-Arroyo 1995.)

	Described species	Number of estimated species		Working figure	Accuracy of working figure
		High	Low		
Viruses	4	1000	50	400	Very poor
Bacteria	4	3000	50	1000	Very poor
Fungi	72	2700	200	1500	Moderate
'Protozoa'	40	200	60	200	Very poor
'Algae'	40	1000	150	400	Very poor
Plants	270	500	300	320	Good
Nematodes	25	1000	100	400	Poor
Arthropods					
Crustaceans	40	200	75	150	Moderate
Arachnids	75	1000	300	750	Moderate
Insects	950	100,000	2000	8000	Moderate
Molluscs	70	200	100	200	Moderate
Chordates	45	55	50	50	Good
Others	115	800	200	250	Moderate
Totals	1750	111,655	3635	13,620	Very poor

if for no other reason than that it is not obvious where all the 'missing' species are to be found! Evidence in support of the working estimate or a figure somewhat lower is becoming increasingly convincing, albeit categorical demonstrations of its validity do not exist. Thirteen and a half million species is difficult to visualize. It is about one species for every 450 people in the world, but it is debateable how much that helps to comprehend this extraordinary level of diversity.

The major uncertainties in the overall numbers of species remain in estimates for particular taxonomic groups (e.g. viruses, bacteria, fungi, nematodes, mites, insects), functional groups (e.g. parasites), and habitats or biomes (e.g. soils, tropical forest canopies, deep-ocean benthos; see Section 3.3.5). Indeed, the relative contribution of some groups compared with others continues to be, sometimes vigorously, debated (e.g. see Hammond 1995).

- *Bacteria*. Understanding of the numbers of species of bacteria (and microbes more generally) is complicated by frequent difficulties in applying standard species concepts to these creatures (resort is usually made to operational taxonomic units, OTUs), by the difficulty of culturing the vast majority of these organisms and thereby applying classical identification techniques, and by the unimaginable numbers of individuals that exist (the global number of prokaryotes is estimated to be $4\text{–}6 \times 10^{30}$ cells, with a production rate of 1.7×10^{30} cells yr^{-1}; Whitman et al. 1998). The numbers of species estimated to occur in even very small areas can vary by several orders of magnitude, depending on the approach taken to estimation (Curtis et al. 2002; Ward 2002). Globally, it is clear that the diversity of bacteria, both in terrestrial and marine systems, may be far larger than many had previously imagined (Fuhrman & Campbell 1998; Torsvik et al. 2002), and may number millions of taxa.

- *Protozoa.* Whilst even very small samples of sediment may contain many species of Protozoa, it is becoming clear that at least in some groups most of these have large geographic ranges and that this local richness may not therefore be indicative of high global richness (Finlay 2002). Thus, of 85 ciliate species found in a volcanic crater-lake in Australia none were unique to the continent (Finlay & Fenchel 1999). Free-living ciliate species have been estimated to perhaps number just 3000, with the number of extant free-living Protozoa totalling perhaps 12,000–19,000 (Fenchel et al. 1997; Finlay et al. 1998; Finlay & Fenchel 1999).
- *Fungi.* A working figure of 1.5 million species of fungi, based primarily on extrapolation from temperate studies, has been widely cited (Hawksworth 1991). On the one hand, some tropical studies suggest that this may constitute a substantial underestimate (Fröhlich & Hyde 1999; Arnold et al. 2000). On the other hand, it has been argued that the frequency of discovery of previously unknown species in areas whose fungi are not well studied suggests that the figure may be a substantial overestimate. Regardless, the scale of fungal diversity may be suggested by the discovery that just three individual plant leaves (two dicotyledonous and one palm leaf) from the Neotropics together supported 108 foliicolous lichen species, 25% of all the taxa known from the region (Lücking & Matzer 2001); lichens comprise a mutualistic relationship between a fungus and an alga or cyanobacterium.
- *Nematodes.* Cobb (1914) observed that 'If all matter in the universe except the nematodes were swept away, our world would still be dimly recognisable, and if, as disembodied spirits, we could then investigate it, we should find its mountains, hills, vales, rivers, lakes and oceans represented by a film of nematodes'. The figure 10^{19} has been suggested as a conservative estimate of the global number of individuals of free-living nematodes (Lambshead, in press). How this vast abundance translates into numbers of species remains unclear. Figures of 1 million to 100 million extant species have been suggested (for a review, see Lambshead, in press), although recent analyses have cast severe doubt on the more extreme upper estimates.

- *Mites*. The mites have long been regarded as a hyperdiverse group of organisms, and studies in the tropics are revealing a richness comparable to that of many insect taxa (Walter & Proctor 1998; Walter et al. 1998; Walter & Behan-Pelletier 1999). Of an estimated total of at least some hundreds of thousands, less than 50,000 species of mites have been described (World Conservation Monitoring Centre 1992; Walter & Behan-Pelletier 1999).
- *Insects*. The total number of all species depends in major part on the number of extant species of insects (because they constitute such a high proportion of all species), for which estimates have ranged particularly widely (see Table 2.4). A number of recent analyses have strongly suggested that the higher estimates are not tenable (e.g. Bartlett et al. 1999; Ødegaard et al. 2000; Dolphin & Quicke 2001; Novotny et al. 2002a), but they continue to be championed in some quarters. Much of the uncertainty rests on the numbers of species that are to be found in the tropical rain forest canopy, the proportion that are restricted to this environment, and the degree of host specificity of herbivorous insects in such forests, which was assumed to be much higher than is actually the case, implying a fine subdivision of plant resources and thereby inflating estimated numbers of insect species (Novotny et al. 2002a,b). Debate continues to surround the issue of which order of insects is most speciose. Evidence that the Coleoptera (beetles) are a more tropical group than some of the others would seem to bolster their claim, but empirical support is quite sparse.

A feature common to most of these groups is that many of their species are parasites. This has led to a lively debate as to whether parasitism is the most common lifestyle on Earth, and whether the majority of species are parasitic rather than free-living (e.g. May 1992a; Poulin 1996; Windsor 1998). Given that parasites are, and will doubtless remain, more poorly known than free-living species, these are important issues in understanding the overall biodiversity of life on Earth. Given that most free-living species harbour many species of parasites, that some of these species are commonly host specialists, and that parasites frequently themselves provide hosts for other parasites, the significance of the parasitic way of life to the global total number of species is indisputable. If you remain unconvinced, then consider that humans alone play host to probably several hundred parasitic species (including microbes).

Significant debate over numbers of extant species also persists for some of what are regarded as better known taxonomic groups. Thus, for example, it appears that the widely quoted figure of c. 250,000 species of angiosperms (seed plants) is a substantial underestimate, with suggestions that there may in fact be 300,000 or even more than 400,000 (Prance et al. 2000; Govaerts 2001; Bramwell 2002). Whilst reliable figures exist for small areas and regions, global estimates are still largely based on extrapolation and assumptions about the overlap in the occurrence of species in different biogeographic regions.

The construction of an inventory of the Earth's species is hampered severely by the fact that only a fraction of the total number of species have been formally taxonomically described. Even determining how large a fraction is complicated by the absence of a definitive listing of all described species and their status (e.g. whether they are presently regarded as valid species or not). There have been several attempts to establish an international programme to generate such a catalogue, but to date these have foundered for lack of the substantial funding that is required. A widely quoted working estimate is that approximately 1.75 million living species have been described, that is about 13% of an estimated total number of extant species of 13.5 million, with the percentage of species in some particular groups that have been described thought to be much smaller (see Table 2.4).

Lists of described species are prone to two kinds of errors. First, the same species name may have been attributed to more than one species, so-called homonymy. Second, more than one species name may have been attributed to the same species, so-called synonymy. For example, of the 59 new species of mammals described from the Neotropics between 1992 and 1998, two (*Coendou koopmani* and *Thryoptera robusta*) were already deemed by 1997 to be synonyms of previously known species (Patterson 2000). Most synonyms take much longer to be recognized, often many decades. The balance of these two kinds of errors seems to lean strongly towards synonymy, with many thousands of species names thought to be synonyms. For example, 20% of extant insect species names may be synonyms, with the proportion being higher for groups that have been intensively studied, have larger geographic ranges and exhibit conspicuous individual variation (Gaston & Mound 1993), and high proportions are also becoming apparent for some better studied or easily collected groups of fungi and molluscs (Altaba 1996; Aptroot 1997; Bouchet 1997). A similar problem plagues lists of fossil species, with analyses of North American fossil mammal species predicting that 24–31% of currently accepted names will prove invalid (Alroy 2002). This suggests two things. First, a substantially smaller total number of species have been described than the number of presently valid species names implies. Second, substantially less than 13% of the estimated total numbers of extant species may have been described. This is less clear, however, because estimates of global numbers of extant or fossil species that are based on extrapolation from lists of known species will also be inflated by these difficulties.

In fact, the situation is yet more dynamic than even this may seem to imply. For example, perhaps reducing the overestimation, recognized synonyms may be reinstated as full species names if subsequent work shows that they did indeed originally refer to genuinely distinct species

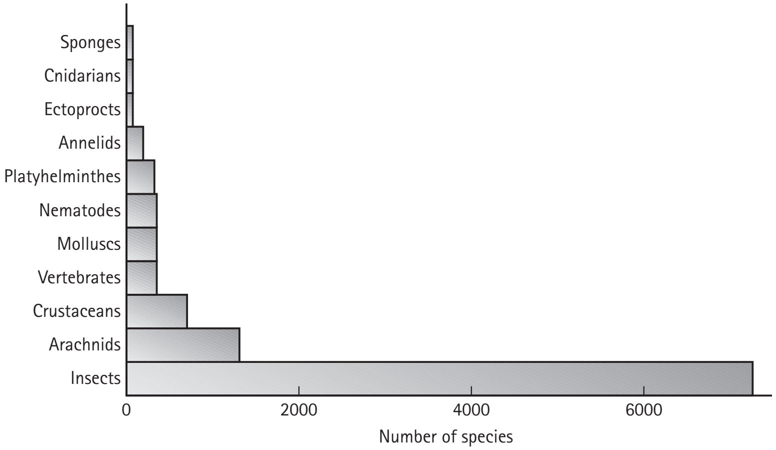


Fig. 2.11 Average number of species described per annum between 1978 and 1987 for major animal groups. (Data from World Conservation Monitoring Centre 1992.)

and not to previously described ones. Thus, since 1982, for the Neotropics, 57 new mammal species have been described, 57 species have been synonymized, and about 150 species have been resurrected from previous synonymy, resulting in a net increase of about 150 species (Patterson 2000).

Additional species are being formally described at a rate of about 13,000 per annum, or about 36 species on the average day (both figures based on formal published descriptions of new species); the breakdown for major groups of animals is given in Fig. 2.11. This rate has remained remarkably constant over past decades (Hawksworth & Kalin-Arroyo 1995). However, the particular group of organisms a taxonomist chooses to study is on the one hand a matter of serendipity and personal choice, and on the other is driven by practical concerns such as the significance of the group in human affairs (e.g. agriculture, medicine) and the availability of funding for research (in some major groups fossil species are being described at higher rates than extant species; Bouchet 1997). Consequently, the catalogue of biodiversity has grown in a somewhat haphazard fashion. Even within those better studied groups, the species that have been described are far from a random subset of all species. On average they are larger-bodied, more abundant (locally or regionally), more widely distributed, occupy a larger number of habitats or life zones, and derive disproportionately from temperate zones (for some groups, rates of description from the tropics appear to have collapsed; e.g. Bouchet 1997). Where species have been formally described, this should not be taken to mean that much is known about them. For example, one estimate suggests that about 40% of described species of beetles are each known from only a single locality (May et al. 1995), usually reflecting the fact that they were captured on just one occasion, often many decades ago (meaning that their present status is unclear; Section 5.2.2).

Inevitably, with so many new species continuing to be found and described, extant representatives of major lineages that were previously unknown continue also to be discovered. The discovery of new phyla has previously been mentioned (Section 2.3.1); other recent examples include a new order of insects (named the Mantophasmatodea; Klass et al. 2002) and a new family of beetles (named the Aspidytidae; Ribera et al. 2002).

Typically, through time the cumulative number of species described in a taxon follows, albeit often only very approximately, an S-shaped function. It increases slowly at first, then goes through a period of rapid growth, before approaching an asymptote when all of the species are known. Such a pattern can be disrupted by changes in the species concept that is generally being employed (see Section 1.4.4), and by variation in the numbers and output of the taxonomists studying a group, but the overall shape is reasonably robust. For well-known groups of organisms the full shape of the function has been revealed, for poorly known ones only the early parts have thus far been attained (Fig. 2.12).

The gap between the number of described animal species and the estimated total number of extant species is due predominantly to ignorance of small-bodied invertebrate taxa; the majority of species are small-bodied. However, it should not be forgotten that numbers of new vertebrate species continue to be discovered. New fish species are described at the rate of about 130–160 each year (Berra 1997). In Africa alone, between 1946 and 1995 some 48 new species of birds were discovered (Fig. 2.13). Globally, from 1980 to mid-2002, 151 extant or recently extinct species of birds were newly described, an average of 6–7 per annum, with several others awaiting description (van Rootselaar 1999, 2002). The majority of these species have been identified using classical taxonomic techniques. However, molecular studies are revealing the existence of many more bird species than had been apparent from morphological studies alone (Martin 1996; Price 1996). Many previously recognized subspecies, races and disjunct populations are as distinct in terms of their degree of molecular divergence as previously recognized species, albeit this may not be as obvious in other regards. This has led to the speculation that there may be 20,000 extant species of birds, twice the present generally accepted number.

Sixteen new, living species of large mammals alone were described during the period 1937 to the early 1990s, about three per decade (Pine 1994). These were two porpoises (*Lagenodelphis hosei*, *Phocoena sinus*), four beaked whales (*Tasmacetus shepherdi*, *Mesoplodon ginkgodens*, *M. carlhubbsi*, *M. peruvianus*), a wild pig (*Sus heureni*), a peccary (*Catagonus wagneri*), four deer (*Mazama chunyi*, *Moschus fuscus*, *Muntiacus atherodes*,

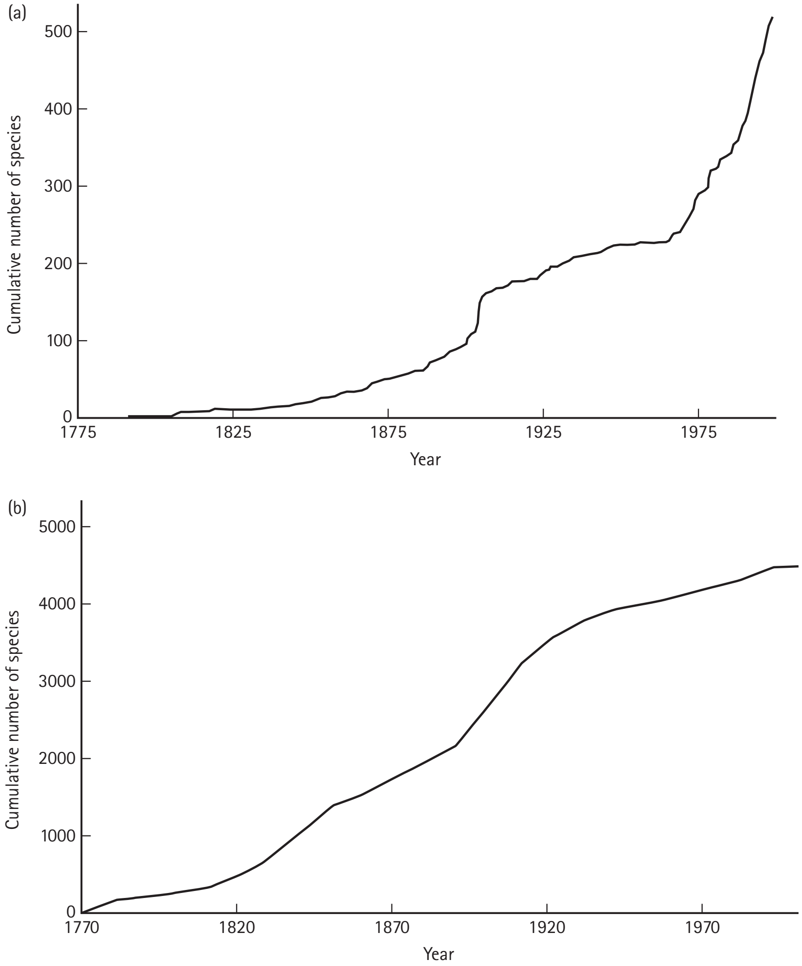


Fig. 2.12 Growth in the cumulative numbers of species described for: (a) thalassinid shrimps; and (b) mammals. (a, From Dworschak 2000; b, from Wilson & Reeder 1993.)

Muntiacus gongshanensis), the kouprey (*Bos sauveli*), a gazelle (*Gazella bilkis*), a wild sheep (*Pseudois schaeferi*) and a 'bovid' (*Pseudoryx nghetinhensis*). Based on historical patterns of species accumulation, Medellín and Soberón (1999) estimate that by the year 2032 an additional 247 mammal species will have been described above the 1992 total of 4628 species. The majority of the new species will be small (< 100 g) and will be in the orders Insectivora, Chiroptera and Rodentia. Given the present rate of loss of biodiversity, it is not unlikely that many presently extant species of mammal will become extinct even before they are described (Chapter 5).

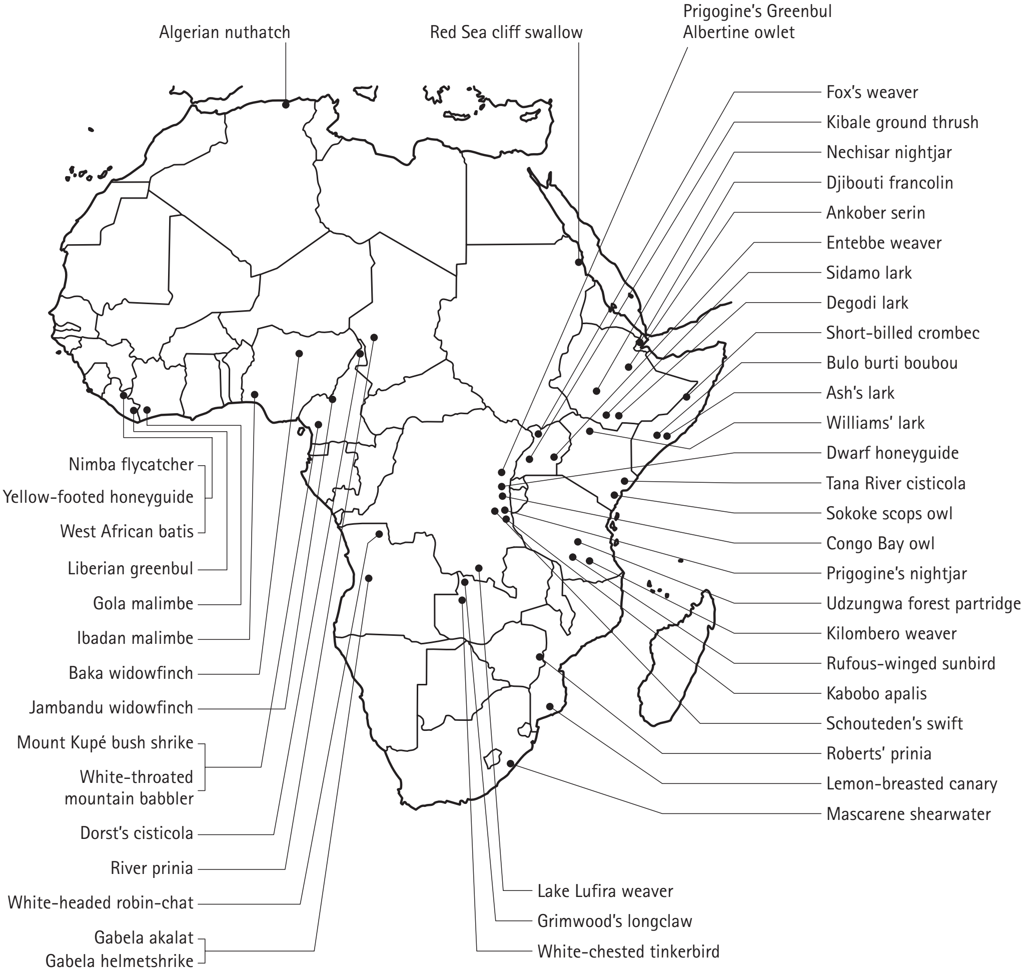


Fig. 2.13 Sites of the discoveries of 47 of the 48 new species of birds recorded from Africa between 1946 and 1995 (in addition, Forbes-Watson's swift was also described from the island of Socotra). (From Hockey 1997a,b.)

There is no likelihood that in the foreseeable future the disparity between the total number of extant species and the number of species that have been described will be markedly closed. This is simply because the taxonomic workforce does not exist to perform the task. In fact, the present workforce is actually in decline (Gaston & May 1992). In the face of this lamentable state of affairs, fulfilment of the task of describing all species will remain a far-distant prospect. What is required is a planned targeting of key groupings, taxa and geographical areas for taxonomic description designed to give a better understanding of the important questions in the study of biodiversity and other fields, rather than the *ad hoc* accumulation of taxa seen at present.

2.5 Summary

1 There has been an overall pattern of increase in biodiversity, from the appearance of the first organism up to the present day, despite the fact that more than 90% of all species that have existed have become extinct.

2 Although it has been described in terms of some simple mathematical models, this increase has not been continuous but is composed of radiations and stabilizations, punctuated by mass extinctions of different taxonomic groups at different times.

3 The mass extinctions are the tail of a continuum of levels of extinction in different periods. Although accounting only for a small proportion of extinctions, they have major disruptive effects on the patterns of development of biodiversity.

4 At any one time, the bulk of biodiversity is contributed by only a relatively few taxonomic groups of organisms; most groups are not particularly diverse.

5 The total number of extant species has been estimated using a variety of extrapolations. The best estimate is that there are approximately 13.5 million species, with only 1.75 million of these currently described. However, there are large potential errors in both these figures.

Further reading

Archibald, J.D. (1996) *Dinosaur Extinction and the End of an Era: What the Fossils Say*. Columbia University Press, New York. (*A readable book, especially for the non-specialist, on the extinction of dinosaurs and other vertebrates*.)

Benton, M.J. (1997) Models for the diversification of life. *Trends in Ecology and Evolution* **12**, 490–495. (*A valuable summary*.)

Brooks, D.R. & McLennan, D.A. (2002) *The Nature of Diversity: An Evolutionary Voyage of Discovery*. University of Chicago Press, Chicago, IL. (*Develops the thesis that historical contingency is vital to understanding the origin of biodiversity*.)

Crawley, M.J. (1997) Biodiversity. In: *Plant Ecology*, 2nd edn. (ed. M.J. Crawley), pp. 595–632. Blackwell Science, Oxford. (*A very useful overview of the biodiversity of plants, with sections on temporal dynamics and aliens*.)

Drury, S. (2001) *Stepping Stones: The Makings of Our Home World.* Oxford University Press, Oxford. (*A short history of the geological and biological origins of our planet*.)

Gee, H. (1996) *Before the Backbone: Views on the Origin of the Vertebrates*. Chapman & Hall, London. (*Extremely well written, state-of-the-art, discussion of vertebrate origins*.)

Hammond, P.M. (1994) Practical approaches to the estimation of the extent of biodiversity in speciose groups. *Philosophical Transactions of the Royal Society, London B* **345**, 119–136. (*A particular viewpoint on estimating the species richness of the very largest groups.*)

Howard, D.J. & Berlocher, S.H. (eds.) (1999) *Endless Forms. Species and Speciation*. Oxford University Press, New York. (*Group of essays presenting current critical thinking on what constitutes a species.*)

Magurran, E.A. & May, R.M. (eds.) (1999) *Evolution of Biological Diversity*. Oxford University Press, Oxford. (*A collection exploring a variety of aspects of the generation of biodiversity.*)

Margulis, L. & Schwartz, K.V. (1998) *Five Kingdoms: An Illustrated Guide to the Phyla of Life on Earth*, 3rd edn. W.H. Freeman & Co., New York. (*The standard work on the higher taxa.*)

Minelli, A. (1993) *Biological Systematics: The State of the Art*. Chapman & Hall, London. (*An accessible overview of biological systematics, including the state of taxonomy of major groups.*)

Raup, D.M. (1994) The role of extinction in evolution. *Proceedings of the National Academy of Sciences, USA* **91**, 6758–6763. (*Simply a great paper.*)

Rosenzweig, M.L. (1995) *Species Diversity in Space and Time*. Cambridge University Press, Cambridge. (*A major review of some of the principal patterns, and the mechanisms which underpin them.*)

Schopf, J.W. (ed.) (1992) *Major Events in the History of Life*. Jones & Bartlett, Boston, MA. (*Contains some very good chapters, written by experts but mainly pitched at undergraduate level, introducing the oldest fossils (chapter 2), the evolution of the earliest animals (chapter 3) and diversification of the vertebrates (chapter 5).*)

Tokeshi, M. (1999) *Species Coexistence: Ecological and Evolutionary Perspectives*. Blackwell Science, Oxford. (*A wide-ranging treatment of the patterns and processes of species diversity and coexistence, unusually blending palaeobiological and contemporary perspectives.*)

3 Mapping biodiversity

3.1 Introduction

Biodiversity is not distributed evenly across the Earth, or through the media (e.g. air, soil, water) that blanket it. Rather, species numbers form a richly textured surface of highs and lows, and species composition (the particular set of species) changes in spatially complex ways. Attempts to understand the distribution of biodiversity have focussed particularly on the identification of general spatial patterns in species richness that transcend this complexity, and on the mechanisms that have given rise to these patterns. Inevitably, such efforts have largely concerned the small number of better known taxa, especially plants, birds and mammals in the terrestrial realm, and molluscs and fish in the marine one. Very little empirical information is available about spatial patterns in the biodiversity of most of the highly speciose groups, such as the bacteria, fungi and insects. For no geographic area, even if only of moderate size, do we as yet have a completed count of all of the species (across all taxa) that occur there.

In this chapter, we do four things. First, we address some issues regarding the effects of spatial scale on observed levels of biodiversity. Second, we identify spatial patterns in the occurrence of areas of extremely high and low biodiversity. Third, we identify spatial gradients in biodiversity, and the mechanisms that have been purported to give rise to them. Finally, we discuss spatial congruence in the biodiversity of different groups, and the prospects for determining the big picture that will allow further generalizations to be made about the distribution of life on Earth.

Throughout this chapter, a distinction is drawn between species richness at local and at regional or large spatial scales. Elsewhere, a distinction is commonly made between alpha, beta and gamma diversities, with alpha diversity being the number of species found within local assemblages or communities, beta diversity being the turnover of species identities between communities, and gamma diversity being the number of species occurring across a region (for a review, see Whittaker et al. 2001).

3.2 Issues of scale

Observed levels of species richness are dependent on spatial scale. There are two principal manifestations of this dependence, species–area relationships and local–regional richness relationships.

3.2.1 Species–area relationships

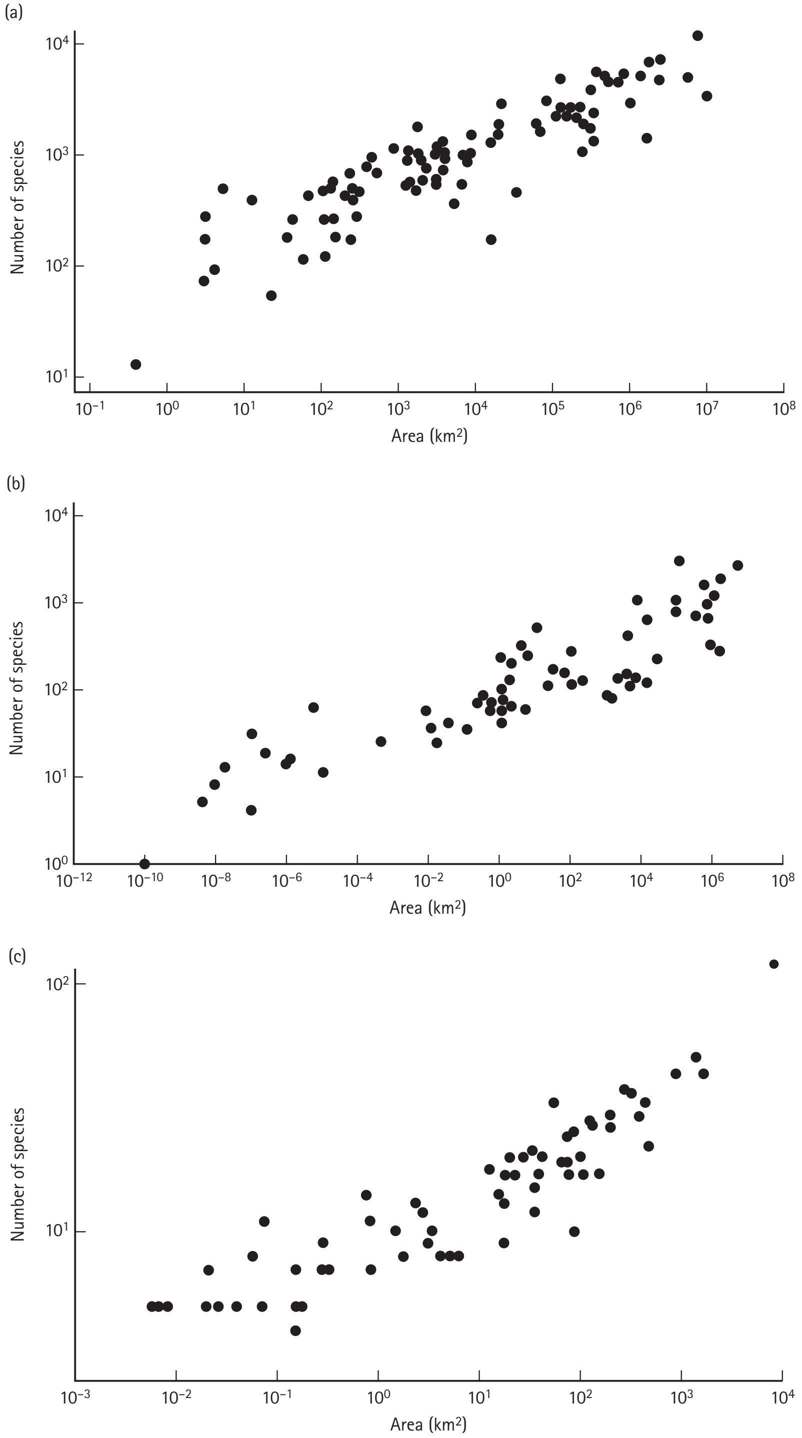
On average, as the size of an area increases, so does the number of species which it contains (Fig. 3.1; MacArthur & Wilson 1967; Williamson 1988; Rosenzweig 1995). Although other models better fit some data sets, the relationship between species richness and area can commonly be approximated as:

$$S = cA^z$$

or

$$\log S = \log c + z \log A$$

where S is the number of species, A is the area, and z and c are constants (known as the Arrenhius relationship). Relationships of this type characteristically explain more than 50% of the variation in species richness between different areas. The slope of the relationship, z, is commonly found to be about 0.25 to 0.30 (although values span the range 0 to 0.5). This roughly suggests that the loss of 90% of the habitat in an area (i.e. a 10-fold reduction in its extent) will result in the loss of 50% of the species that live exclusively in that habitat. Likewise, the loss of 99% of the habitat will lead to the extinction of 75% of the species. z may vary markedly with whether areas are nested or not (smaller areas lying within the confines of progressively larger ones), whether they are islands or parts of continents, with their latitude, and with the range of sizes of areas (e.g. Palmer & White 1994; Rosenzweig 1995; Crawley & Harral 2001; Lomolino & Weiser 2001; Lyons & Willig 2002).


(a)
Number of species
10^4
10^3
10^2
10^1
10^{-1}
10^0
10^1
10^2
10^3
10^4
10^5
10^6
10^7
10^8
Area (km²)
(b)
Number of species
10^4
10^3
10^2
10^1
10^0
10^{-12}
10^{-10}
10^{-8}
10^{-6}
10^{-4}
10^{-2}
10^0
10^2
10^4
10^6
10^8
Area (km²)
(c)
Number of species
10^2
10^1
10^{-3}
10^{-2}
10^{-1}
10^0
10^1
10^2
10^3
10^4
Area (km²)

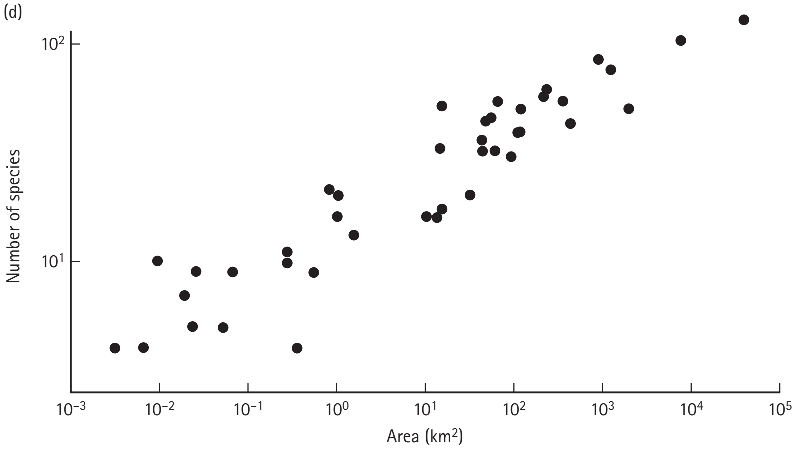


Fig. 3.1 Species–area relationships for: (a) native plant species at sites around the world; (b) benthic macrofaunal species in areas of the Arctic; (c) land snails on Aegean islands; and (d) birds on the Bismarck Islands. (a, From Lonsdale 1999; b, from Azovsky 2002; c, data from Welter-Schultes & Williams 1999; d, data from Mayr & Diamond 2001.)

Four primary reasons have been proposed to explain the species–area relationship.

1 *Sampling*. There may in fact be no underlying relationship between species number and area, with that observed being a statistical artefact of variations in sample size associated with areas of different sizes. More species are recorded from larger areas because more individuals are sampled from those areas.

2 *Habitat diversity*. Larger areas might contain more species because they contain more habitats, and thus more opportunities for different kinds of organisms to establish and persist. Larger areas may contain more habitats because they are topographically and environmentally more diverse.

3 *Colonization/extinction dynamics*. The number of species in an area may result from a dynamic balance between the number of species colonizing from the source pool (e.g. the mainland set of species for many islands), and those going extinct after colonization. Colonization rate is hypothesized to decline as the number of species increases, because there are fewer species remaining to colonize, and because the early colonizers will be those best suited to colonization (e.g. good dispersers). Extinction rate is hypothesized to increase with number of species, as each species has its own finite probability of extinction, and because negative interactions between species (competition, predation, etc.) are more likely when there are more species (although positive interactions may also increase, nullifying this latter effect). Therefore, as the number of species in an area increases, colonization rate declines and extinction rate increases.

4 *Speciation/extinction dynamics*. For very large areas, the influence of immigration on the numbers of species present is relatively small, and the balance between speciation (adding entirely new species) and extinction (removing species) is the most significant process. The larger the area, the larger, on average, are the potential geographic range sizes of the species that occur there. If species with larger geographic ranges have a greater probability of speciating (perhaps because barriers are more likely to subdivide their ranges) and also have a smaller likelihood of extinction (because they contain more individuals, and chance events are less likely to influence them all simultaneously), then more species will accumulate.

These different mechanisms vary in importance with different kinds and sizes of sets of areas. Thus, colonization/extinction dynamics are likely to be very important in genuine island systems, and speciation/extinction dynamics important at the scale of biogeographic provinces.

Differences in the sizes of areas have, with some important exceptions (e.g. see Section 3.3), a pervasive influence on most spatial patterns in biodiversity. This must be borne in mind in much of the subsequent discussion in this chapter. Indeed, species–area relationships will feature as possible explanations of several such patterns. However, the species–area relationship may sometimes be obscured or even reversed by some of the other spatial patterns in biodiversity, especially that with latitude (Section 3.4.1). For example, the small tropical country of Costa Rica (51,100 km^2) contains at least 218 species of reptiles, 796 species of birds and 203 species of mammals, whereas the large temperate country of Canada (9,970,610 km^2) contains 32 species of reptiles, 434 species of birds and 94 species of mammals (Medellín & Soberón 1999).

3.2.2 Local–regional richness relationships

Although it is true that smaller areas tend to contain fewer species than larger areas (Section 3.2.1), the species richness of a small area is not independent of that of the larger area in which it is embedded. Two theoretical types of relationship between the local richness an assemblage might attain and the species richness of the region in which that assemblage resides have been contrasted (Fig. 3.2; Cornell & Lawton 1992). First, 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 (Huston 1999; Lawton 1999; Srivastava 1999), most real systems, including marine, freshwater and terrestrial assemblages, seem to exhibit an underlying Type I relationship (Fig. 3.3; Cornell & Lawton 1992; Caley & Schluter 1997; Rex et al. 1997; Lawton 1999). Not uncommonly,

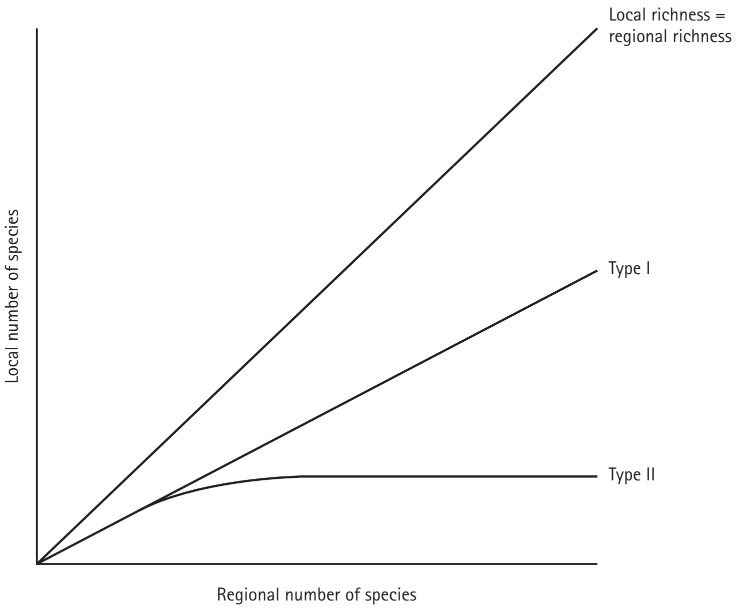


Fig. 3.2 Relationships between local and regional species richness, illustrating the form of Type I and Type II relationships and the limiting condition where local richness equals regional richness.

regional richness explains a large proportion (> 75%) of variance in local richness, and local richness constitutes a marked proportion (> 50%) of regional richness. The predominance of Type I relationships is supported by the observation that some spatial gradients in species richness (e.g. that with latitude) are documented both for localities and regions across those gradients.

The preponderance of examples of Type I relationships, particularly where habitat type has been kept constant, backed up with other evidence (e.g. the limited support for: (i) convergence of communities in comparable environments in regions with different numbers of species; (ii) density compensation among species in assemblages; and (iii) invasion resistance of assemblages), suggests that commonly there are not hard limits to levels of local richness (Cornell 1999). That is, local assemblages do not appear to be saturated with species, in the way one might have expected if ecological interactions (e.g. competition, predation, parasitism) limited local richness. This would fit with the observation that an historical limit has not been reached to the number of species that can be packed onto the Earth (Section 2.3.1).

If the majority of systems exhibit Type I local–regional richness relationships, then a prime driver of local richness appears to be the regional number of species. The importance of regional-scale phenomena for local-scale assemblage structure is a general one (Ricklefs & Schluter

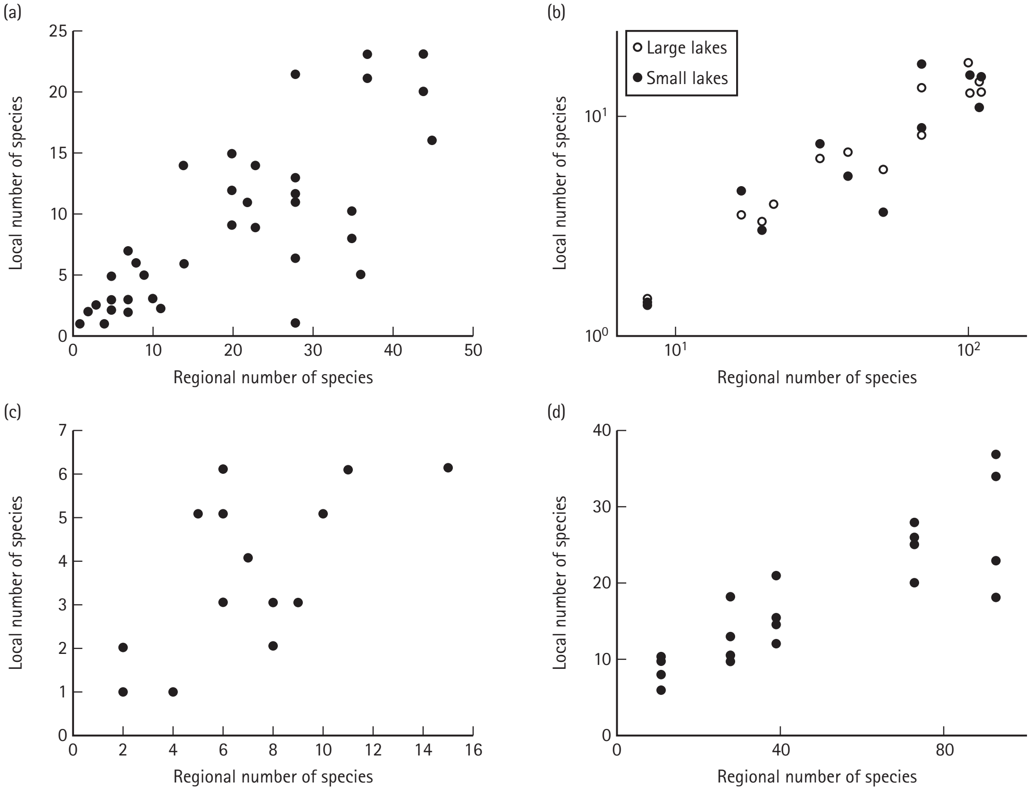


Fig. 3.3 Relationships between local and regional species richness for: (a) mangroves; (b) lacustrine fish in North America; (c) viperid snakes in South America; and (d) birds in the Caribbean. (a, From Ellison 2002; b, data from Griffiths 1997; c, from Bini et al. 2000; d, from Ricklefs 1987.)

1993). A local community is assembled from a regional pool of species (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, climate), and broad-scale ecological or evolutionary processes, such as species migrations, invasions, speciation and regional extinction (Huston 1999). They set the species composition and the abundance, body size and trophic structure of the pool from which local communities are drawn. However, whilst regional pools doubtless play an important role 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 biodiversity.

Species–area relationships and local–regional species relationships may be closely related, with some arguing that the latter are a direct consequence of the different forms that the former take (Rosenzweig & Ziv 1999). Whatever its causes, the relationship between local and regional biodiversity underpins the crucial observation that temporal changes in global and regional biodiversity tend to be reflected in local biodiversity, and vice versa (Section 2.3.1). Thus, changes in the numbers of species in local fossil assemblages can often be taken as indicative of the changes occurring at broader scales.

3.3 Extremes of high and low diversity

Some parts of the Earth are far richer or poorer in taxa than are others. Attention is paid particularly to the distribution of the peaks of diversity, partly because of a widespread fascination with why some areas contain large numbers of species, and partly because of the conservation implications.

3.3.1 Biological realms

The oceans cover about 67% and the land about 33% of the 511 million km^2 of the Earth's surface (Table 3.1). One would therefore expect that the oceans would have greater biodiversity. However, whether or not this is so depends on the taxonomic level being considered. Many more phyla are known from marine systems than from terrestrial ones (May 1994b). Of the 96 phyla recognized by Margulis and Schwartz (1998), about 69 have marine representatives and 55 have terrestrial ones (see Table 2.2). The greater diversity of marine systems is also true of some lower taxa, such as classes (Nicol 1971); Reaka-Kudla (1997) states that 90% of all known classes are marine. However, fewer than 15% of species currently named are marine, despite the vastly greater area covered by the

Table 3.1 The areas of different components of the Earth's surface (note some are subsets of others). (From Reaka-Kudla 1997.)

	Area (× 10^6 km^2)	Percentage of the Earth
Global surface area	511	100
Global land area	170.3	33.3
Global rain forests	11.9	2.3
Global oceans	340.1	66.7
Tropical seas	123	24
Global coastal zones	40.9	8
Tropical coastal zones	9.8	1.9
Coral reefs	0.6	0.1

oceans (May 1994b). The extent to which these proportions would change if all of the marine and terrestrial species had been described remains controversial (Section 2.4). Nevertheless, it seems unlikely that anything like parity in richness between the two would be achieved, and that marine systems are genuinely substantially poorer in species numbers.

Five sets of factors have been suggested that might help to explain the contrast in the diversities between land and sea (May 1994b).

1 *Life began in the sea*. This meant that the early diversification of form that led to the different higher taxa that are seen today took place in the sea, with only some of these groups subsequently being able to emerge onto land. Of itself, this does not explain, however, why there should be more species in the terrestrial realm.

2 *Continental environments are more heterogeneous than marine ones*. This observation has long been held to be true, although the complexities of marine environments are increasingly being recognized. The heterogeneity of continental environments would have tended to promote greater levels of speciation on land, especially when coupled with continental drift. The latter resulted in the evolution of sets of distinct floral and faunal assemblages on different land masses, often with species with different evolutionary origins filling similar roles.

3 *The ocean-bed environment is less architecturally elaborate than the terrestrial environment*. Again, if correct, this would tend to promote greater levels of speciation in the terrestrial realm relative to the marine one, although this might arguably be offset by the greater continuous area of the oceans.

4 *Patterns of herbivory differ between sea and land*. Herbivores in marine environments tend to be generalists, whilst those in terrestrial environments tend to be specialists, often feeding on just a single host-plant species and often on only a particular part thereof. Greater specialism gives opportunities for more speciation, but whether this is strictly a cause or a consequence of high species numbers is more debatable.

5 *There are differences in the body size distributions of marine and terrestrial species assemblages*. Primary production, herbivory and predation all tend to involve smaller species in the sea than they do on land (e.g. much of marine productivity results from the huge abundances of microscopic picoplankton). Smaller-bodied species may be able to maintain the contiguity of larger geographic ranges more readily, through having larger numbers of individuals and greater dispersal abilities, perhaps therefore reducing the likelihood of allopatric speciation (speciation by subdivision of the distributions of ancestral species) in marine systems.

The fact that life began in the sea seems to us to be likely to have played an important role in explaining why there are more higher taxa in marine systems than terrestrial ones. The heterogeneity and fragmentation of the land masses seem a likely explanation as to why there are more species in terrestrial systems than in marine ones.

Whilst freshwater systems are not usually regarded as comprising a strict biological realm in their own right, it is instructive to contrast their biodiversity with that of marine and terrestrial systems. There are approximately 55 phyla in freshwater systems, somewhat less than in terrestrial ones (see Table 2.2); however, the number of species is much smaller (70,000 species of freshwater invertebrates have been described, with perhaps another 100,000 awaiting discovery; Strayer 2001). This could simply be an area effect, with lakes and rivers estimated to cover just 1.5 million km^2 (another 16 million km^2 is under ice and permanent snow, and 2.6 million km^2 is wetlands, soil water and permafrost), although the high degree of habitat fragmentation, the wide variation in physical and chemical habitat characteristics, and the limited dispersal abilities of many freshwater organisms have doubtless led to many species having extremely restricted distributions.

3.3.2 Biogeographic regions

Moving down the spatial scales, there have been a number of attempts to divide the land surface of the Earth into broad biogeographic regions, which distinguish areas of marked dissimilarity in the composition of their biota. Comparison of the relative biodiversity of these regions gives a broad-scale picture of its spatial variation. First, of the six to eight biogeographic regions commonly recognized (Fig. 3.4a), the three 'tropical' regions (Neotropics, Indotropics, Afrotropics) perhaps contain two-thirds or more of all extant terrestrial species. Second, the Neotropics is generally recognized to be the region that contains the greatest overall levels of terrestrial biodiversity. Third, the three 'tropical' regions tend to decline in overall biodiversity from the Neotropics to the Indotropics to the Afrotropics. Levels of biodiversity in the first two are probably the more similar to one another, with the Afrotropics being relatively less diverse. In part, this is because the tropical forests of Africa are not as extensive, well developed or rich as those in the other two regions. Fourth, patterns in the biodiversity of different biogeographic regions may not be consistent amongst many groups of organisms. The distribution amongst regions of butterfly species richness, for example, appears to be more similar to that of birds than of mammals (Robbins & Opler 1997).

The different biogeographic regions have also been subdivided into smaller regions, employing a number of schemes, and variously terming the resultant areas as major habitats, vegetation types or biomes. The scheme of Olson et al. (2001) distinguishes 14 such types in the terrestrial realm, on the basis of the similarity of areas in terms of environmental conditions, habitat structure and patterns of biological complexity (Fig. 3.4).

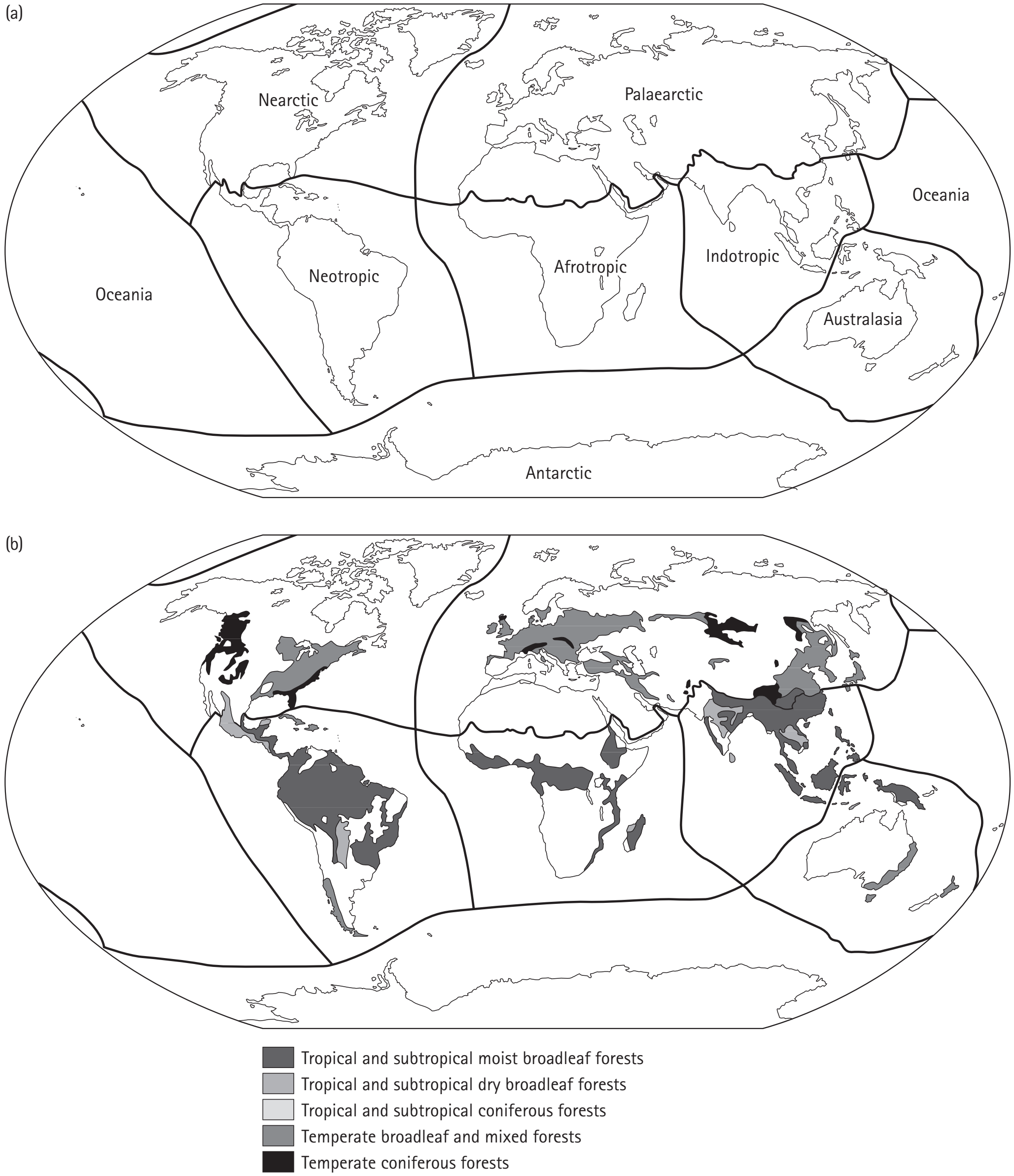


Fig. 3.4 Classification of the terrestrial realm into (a) eight biogeographic regions and (b)–(d) 14 biomes. (From Olson et al. 2001.) (*cont'd*)

These habitat types are: (i) tropical and subtropical moist broadleaf forests; (ii) tropical and subtropical dry broadleaf forests; (iii) tropical and subtropical coniferous forests; (iv) temperate broadleaf and mixed forests; (v) temperate coniferous forests; (vi) boreal forests/taiga; (vii) tropical and subtropical grasslands, savannahs and shrublands; (viii) temperate grasslands, savannahs and shrublands; (ix) flooded grasslands and savannahs; (x) montane grasslands and shrublands; (xi) tundra; (xii)

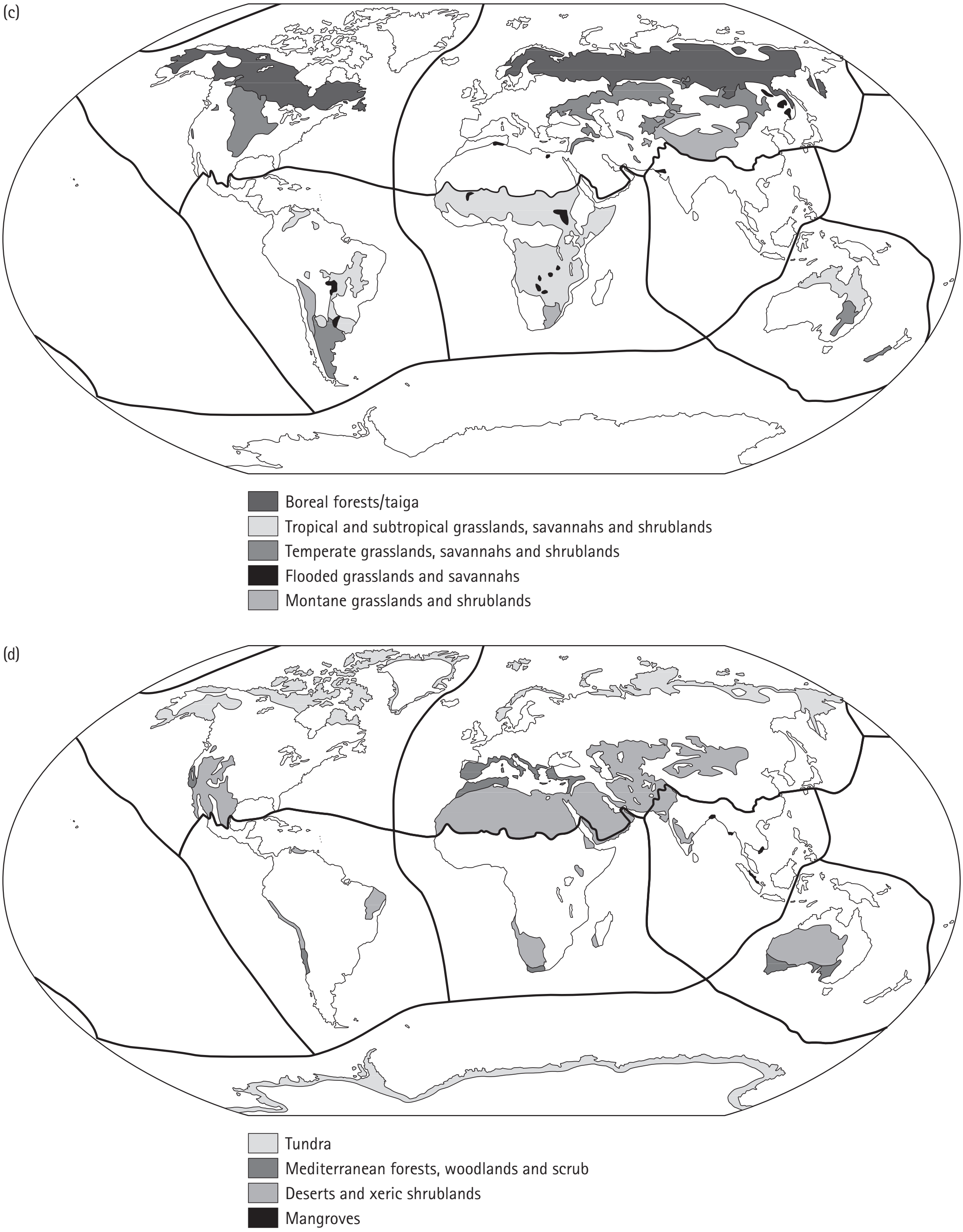


Fig. 3.4 (*cont'd*)

Mediterranean forests, woodlands and scrub; (xiii) deserts and xeric shrublands; and (xiv) mangroves. Nested within these, Olson et al. (2001) recognize 867 ecoregions, representing distinct biotas, and reflecting the distributions of a broad range of flora and fauna (Fig. 3.5).

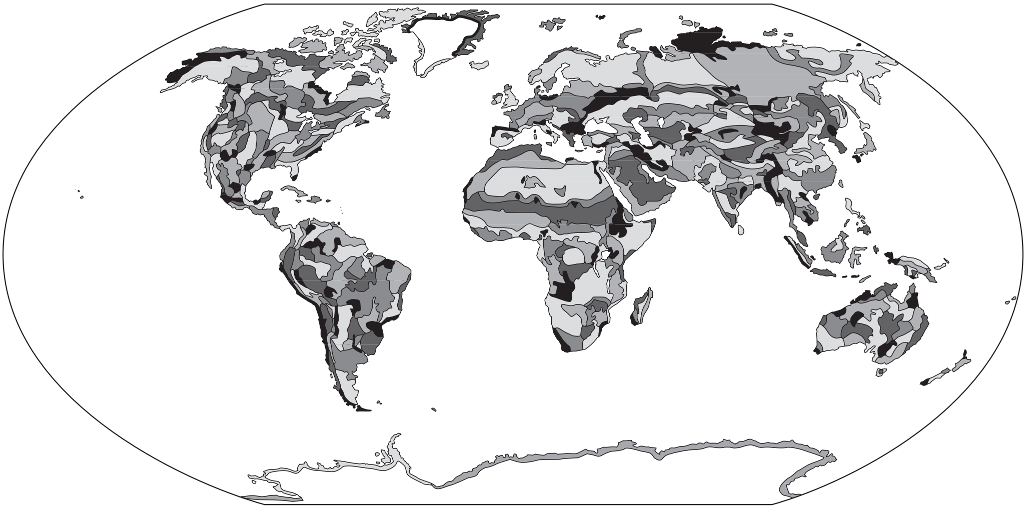


Fig. 3.5 Classification of the terrestrial realm into 867 ecoregions. (From Olson et al. 2001.)

Dividing the marine realm into biogeographic regions has proven much more problematic than has been the case for the terrestrial realm, and arguably the floristic and faunistic discontinuities remain only rather sketchily understood. Much of the problem lies in the enormous extent of the oceans, their three-dimensional complexity, the fact that biological life is found at all depths, from the marine intertidal down to about 11 km, and the associated paucity of sampling, particularly of the sea bed (see below). Of all the species that live in the sea, only about 2% live in mid-water, the remainder living on, or in, the sea bed.

As a result of these difficulties, the marine realm has tended to be divided into regions on the basis of physical characteristics (e.g. temperature regimes, surface currents; Couper 1983; Hayden et al. 1984), but more recently divisions have been recognized in large part on the basis of the algal ecology of the pelagic open ocean (Longhurst 1998). This latter scheme distinguishes four primary biomes: (i) polar; (ii) westerlies; (iii) trades; and (iv) coastal boundary. These biomes are then further subdivided, on the basis principally of biogeochemical features, into 51 provinces (Fig. 3.6).

Relating known patterns of species richness to such schemes for dividing the oceans is not easy. However, marine biodiversity is thought to be highest in the Indo-western Pacific (World Resources Institute 1996; Roberts et al. 2002). Briggs (1996) used data for echinoderms, molluscs, some crustaceans, reef corals, and fish, to show that shelf faunas belonging to the four great tropical regions increased in diversity in the sequence: eastern Atlantic, eastern Pacific, western Atlantic, and Indo-western

Pacific. With a shelf area of 6,570,000 km^2, the diversity of the Indo-western Pacific exceeds the total of the other three, with more than 6000 species of molluscs, 800 species of echinoderms, 500 species of hermatypic (reef-forming) corals and 4000 species of fish (Briggs 1999). This region has been argued to be a centre for the evolutionary radiation of many groups, partly as a consequence of its large area, and because richness declines with distance away from this centre (see also Findley & Findley 2001).

3.3.3 Hotspots

The identification of areas of high biodiversity at yet more moderate scales than those of biogeographic regions has been a topic of some concern, particularly to conservation biologists. Most data at these scales tend to refer to geopolitical units (e.g. states, countries), whose boundaries often do not coincide with biologically meaningful entities, but do reflect an important scale at which many decisions regarding the exploitation and preservation of biodiversity take place (Chapter 6).

The distribution of biodiversity amongst countries is highly skewed, with a few containing a disproportionately large number of species, and most containing a disproportionately small number (Fig. 3.7). For example, Brazil alone contains 50,000–56,000 species of plants, > 3000 species of freshwater fish, 517 species of amphibians, 468 species of reptiles, 1622 species of birds and 524 species of mammals (Mittermeier et al. 1997). Indeed, a set of mega-diversity countries have come to be recognized, comprising the 17 countries which are believed to harbour 66–75% of the world's biodiversity, expressed in terms of species richness (Mittermeier et al. 1997). The list comprises Brazil, Indonesia, Colombia, Mexico, Australia, Madagascar, China, Philippines, India, Peru, Papua New Guinea, Ecuador, USA, Venezuela, Malaysia, South Africa and Democratic Republic of Congo. Much of the variation in biodiversity between countries inevitably results from the dramatic differences in their areas, but it also reflects such characteristics as their latitude, topographical and habitat diversity, and their human history.

Such assessments are based almost exclusively on data for plants and vertebrates. Estimates of the total numbers of species to be found in countries are extremely scarce. Nonetheless, figures have been ventured of 750,000 species for the USA and > 88,000 for the UK (Anon. 1994; Pimentel et al. 1997). Most countries have rather poor inventories of the flora and fauna that lie within their bounds, let alone details of their occurrence. For example, even for those whose faunas have been reasonably well studied, inventories of insect species may remain substantially incomplete (e.g. Japan 29–41% estimated to have been inventoried, Canada 55%, Finland 84%; Gaston 1996a). Moreover, the pattern of

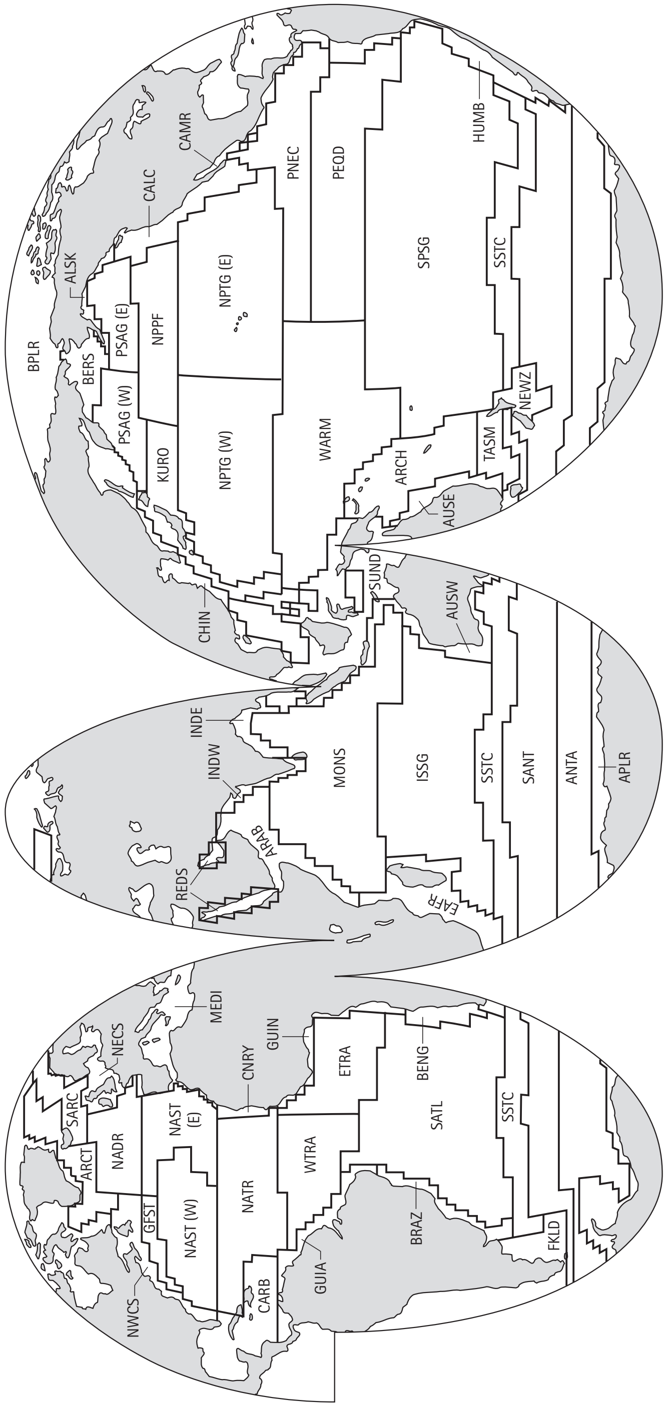

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Fig. 3.6 Biomes and provinces of the oceans, the former recognized on the basis of algal ecology, and the latter on the basis principally of biogeochemical features. **Antarctic Polar Biome**: ANTA, Antarctic Province; APLR, Austral Polar Province. **Antarctic Westerly Winds Biome**: SANT, Subantarctic Water Ring Province; SSTC, South Subtropical Convergence Province. **Atlantic Coastal Biome**: BENG, Benguela Current Coastal Province; BRAZ, Brazil Current Coastal Province; CNRY, Eastern (Canary) Coastal Province; FKLD, Southwest Atlantic Shelves Province; GUIA, Guianas Coastal Province; GUIN, Guinea Current Coastal Province; NECS, Northeast Atlantic Shelves Province; NWCS, Northwest Atlantic Shelves Province; BPLR, Boreal Polar Province; SARC, Atlantic Subarctic Province. **Atlantic Trade Wind Biome**: CARB, Caribbean Province; ETRA, Eastern Tropical Atlantic Province; NATR, North Atlantic Tropical Gyral Province; SATL, South Atlantic Gyral Province; WTRA, Western Tropical Atlantic Province. **Atlantic Westerly Winds Biome**: GFST, Gulf Stream Province; MEDI, Mediterranean Sea, Black Sea Province; NADR, North Atlantic Drift Province; NAST, North Atlantic Subtropical Gyral Province. **Indian Ocean Coastal Biome**: ARAB, Northwestern Arabian Upwelling Province; AUSW, Australia–Indonesia Coastal Province; EAFR, Eastern Africa Coastal Province; INDE, Eastern India Coastal Province; INDW, Western India Coastal Province; REDS, Red Sea, Persian Gulf Province. **Indian Ocean Trade Wind Biome**: ISSG, Indian South Subtropical Gyre Province; MONS, Indian Monsoon Gyres Province. **Pacific Coastal Biome**: ALSK, Alaska Downwelling Coastal Province; AUSE, East Australian Coastal Province; CALC, California Current Province; CAMR, Central American Coastal Province; CHIN, China Sea Coastal Province; HUMB, Humboldt Current Coastal Province; NEWZ, New Zealand Coastal Province; SUND, Sunda–Arafura Shelves Province. **Pacific Polar Biome**: BERS, North Pacific Epicontinental Sea Province. **Pacific Trade Wind Biome**: ARCH, Archipelagic Deep Basins Province; NPTG, North Pacific Tropical Gyre Province; PEQD, Pacific Equatorial Divergence Province; PNEC, North Pacific Equatorial Countercurrent Province; SPSG, South Pacific Subtropical Gyre Province; WARM, Western Pacific Warm Pool Province. **Pacific Westerly Winds Biome**: KURO, Kuroshio Current Province; NPPF, North Pacific Transition Zone Province; PSAG, Pacific Subarctic Gyres (East and West) Province; TASM, Tasman Sea Province. (From Longhurst 1998.)

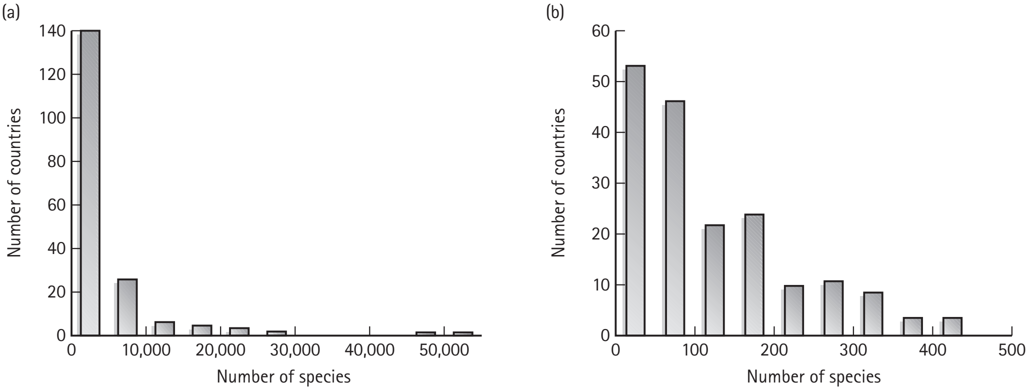


Fig. 3.7 Numbers of species of: (a) flowering plants; and (b) mammals in different countries for which data are available. (Data from World Conservation Monitoring Centre 1994.)

growth in knowledge often does not reflect the distribution of biodiversity. Thus, whilst most species occur in the tropics, as many species of insects are presently being described per unit area from temperate regions as from tropical ones (Gaston 1994).

Besides countries, other schemes have been employed to recognize areas of disproportionately high biodiversity. The most important of these is the identification of 25 biodiversity hotspots (Fig. 3.8), based on areas that contain exceptional concentrations of endemic species and are undergoing exceptional loss of habitat (and are thus facing particularly high threat; Myers et al. 2000; Myers 2001). These areas comprise only 1.4% of the land surface of the Earth, but constitute the remaining habitats for about 135,000 plant species (45% of all extant plant species) and about 9650 vertebrate species (35% of all extant vertebrate species). They also harbour greater amounts of evolutionary history than expected on the basis of species numbers alone (Sechrest et al. 2002). Despite their importance to the maintenance of biodiversity on Earth, knowledge about these areas remains, however, extremely variable, with even the basic summary descriptors of their composition in some cases being little more than best approximations.

3.3.4 Endemism

A taxon is endemic to an area if it occurs there and nowhere else. The area of endemism can either be relatively large (e.g. the three extant species of monotremes, the echidnas *Tachyglossus aculeatus* and *Zaglossus bruijni*, and the platypus *Ornithorhynchus anatinus*, are confined to Australia and New Guinea) or it can be very small (e.g. the 'water bear' *Thermozodium esakii* [Phylum: Tardigrada] is found only in a single Japanese hot spring).

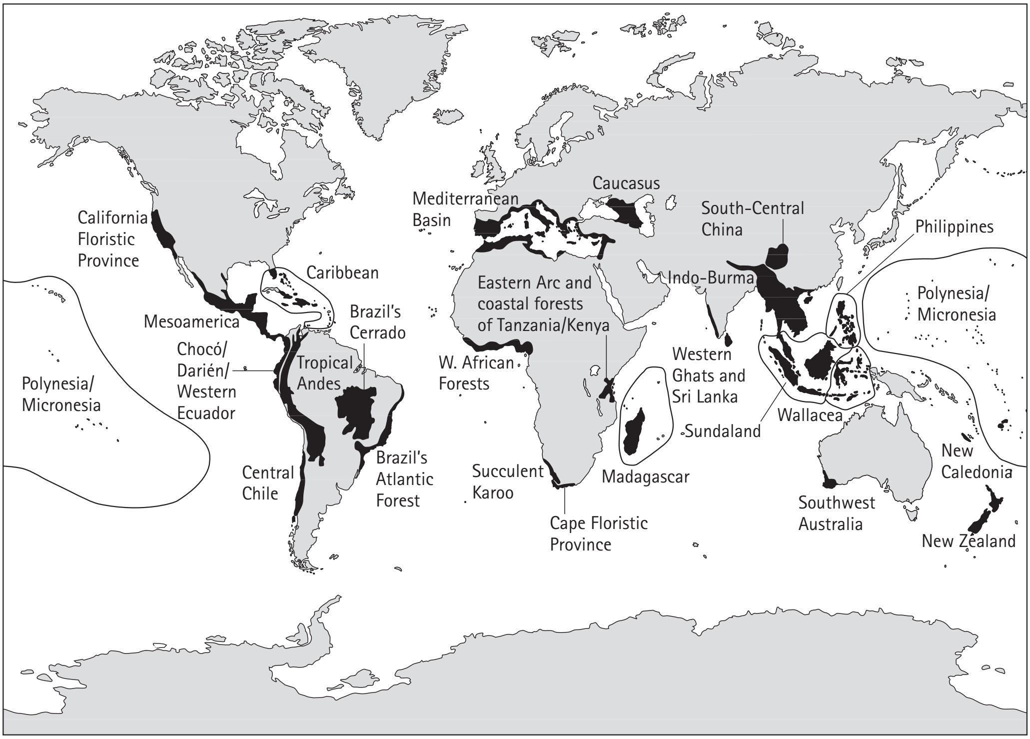


Fig. 3.8 The 25 global hotspots where exceptional concentrations of endemic species are undergoing exceptional habitat loss. (From Myers et al. 2000.)

Some small areas, particularly oceanic islands, can have very high levels of endemism (e.g. Hawaii). Two groups of endemics are commonly recognized. Neoendemics are taxa that have evolved relatively recently, and palaeoendemics are those that may be regarded as evolutionary relicts.

Levels of endemism tend to show patterns of variation with the following:

- *Area*. On average, the number and proportion of taxa that are endemic to a locality or region tends to be an increasing function of area, though such species–area relationships are usually considerably weaker than those based on the sum of all species whether endemic or otherwise (Major 1988; Anderson 1994; McKinney 2002). For example, the number of plant species that are endemic to each of 52 biogeographic provinces (distributed across all major biomes on all continents) tends to increase with their area, and the number of mammal species that are endemic to different countries tends to increase with their area (Fig. 3.9).
- *Latitude*. More importantly, and more markedly, the number of endemics tends to increase towards lower latitudes (Fig. 3.10; Major 1988; Cowling & Samways 1995). This has been graphically demonstrated in a study of birds (Fig. 3.11), which has identified 218 Endemic Bird Areas,

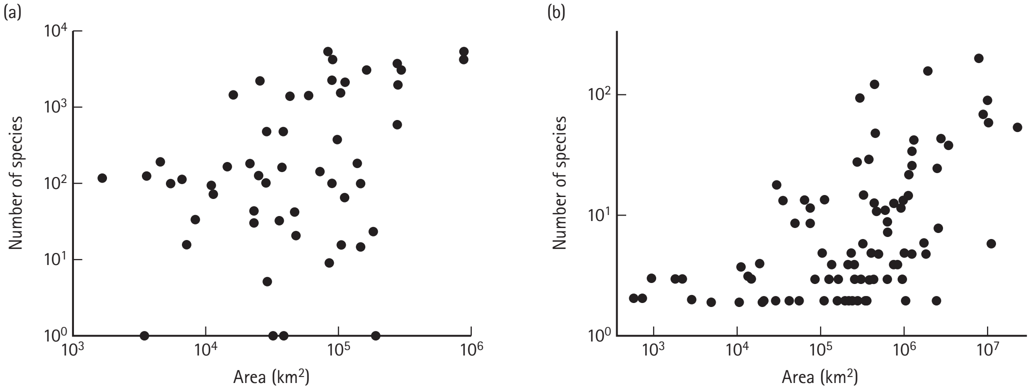


Fig. 3.9 Relationships between number of endemic species and area for: (a) plants in regions on continental land masses; and (b) land mammals in 155 countries. (a, From Cowling & Samways 1995; b, from Ceballos & Brown 1995.)

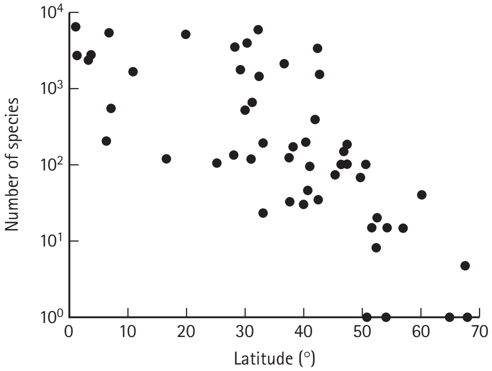


Fig. 3.10 Relationship between number of endemic species and latitude for plants in regions on continental land masses. (From Cowling & Samways 1995.)

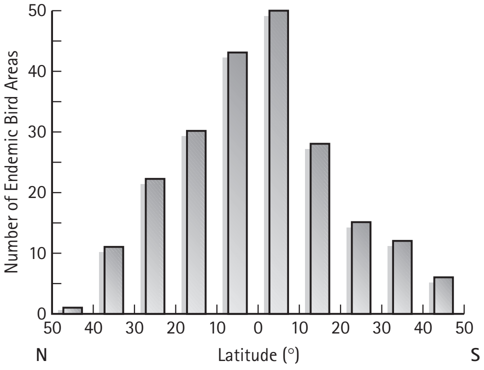


Fig. 3.11 Latitudinal distribution of Endemic Bird Areas (areas supporting two or more species with geographic ranges of < 50,000 km^2). (From Stattersfield et al. 1998.)

defined as areas supporting two or more species with restricted ranges (< 50,000 km^2). In total, these areas occupy a mere 4.5% of the Earth's land surface and contain 73% of all globally threatened bird species; 2649 land bird species (27% of all birds) have breeding ranges of 50,000 km^2 or

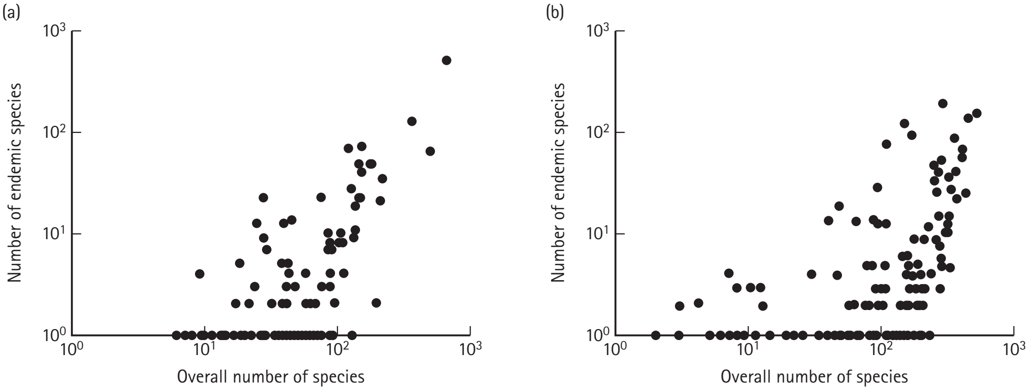


Fig. 3.12 Relationships between numbers of endemic species and overall numbers of species in different areas for: (a) fish in river basins of the northern hemisphere; and (b) land mammals in 155 countries. (a, From Oberdorff et al. 1999; b, from Ceballos & Brown 1995.)

less (Long et al. 1996). Latitudinal gradients in endemism contribute to broader latitudinal trends in the geographic range sizes of species, with the mean range sizes of those present in an area tending to decline particularly from high to intermediate latitudes, and especially in the northern hemisphere (Stevens 1989; Gaston et al. 1998).

- *Species richness*. Levels of endemism and of species richness are not infrequently positively correlated (Fig. 3.12; Balmford & Long 1995). However, there are many exceptions here, with oceanic islands for example tending to have high levels of endemism but relatively low overall numbers of species, and continental peaks of endemism often not being coincident with peaks of species richness (e.g. Seymour et al. 2001; de Klerk et al. 2002).

Reasons given for the occurrence of areas of high levels of endemism are typically: (i) unusual environmental conditions – these may select for independent evolution of local adaptations that enable species to persist under these conditions but prevent them from occurring more widely; (ii) isolation – the separation either by distance or other barriers of individuals from conspecifics enables independent evolution that may give rise to endemic taxa; and (iii) historical – changing environmental conditions (both biotic and abiotic) can constrain previously more widespread species to limited areas (Kruckeberg & Rabinowitz 1985; Major 1988). On continents, high levels of endemism may particularly be associated with areas that have exhibited long-term ecoclimatic stability, enabling populations to survive periods of major global climatic change (e.g. Fjeldså et al. 1999). Such areas may also be evolutionary hotspots, in which multiple evolutionary events have occurred over a significant period (McLennan & Brooks 2002). Historical processes seem to be particularly important, such that the richness of endemics is generally thought to be more difficult to explain in terms of prevailing environmental conditions than is the richness of taxa more generally, although some recent analyses have challenged this notion (Johnson et al. 1998).

3.3.5 Particular environments

The biodiversity associated with different kinds of environments has attracted much interest from biologists. Some of these environments have for practical reasons proven hard to access, and thus important features of this biodiversity continue to be discovered. The following are given by way of a few examples:

- *Tropical forest canopies*. Termed 'the last biotic frontier' (Erwin 1983), despite their large extent (more than 11 million km^2), tropical forest canopies long remained poorly explored. However, their mysteries are now rapidly being exposed through the application of a variety of techniques that have enabled much improved access to this environment (e.g. rope-climbing techniques, aerial walkways, cranes, balloons). These have revealed much higher levels of richness of some groups than had been anticipated, and lower richness of others, but have overall served to confirm the significance of tropical forests for global species numbers.
- *Soils*. Soils have been termed 'the poor man's tropical forest', in homage to the huge numbers of individual organisms that may occur per square metre (Groffman 1997). The small body size of many of the associated species, and the poor efficiency of many extraction methods, have served, however, severely to limit understanding of soil biodiversity, leading to dramatic underestimations both of the local densities of individuals and of species richness (André et al. 2002). Spatial turnover in species composition remains poorly explored, so the basis for estimations of regional or global species richness and patterns is largely lacking.
- *Coral reefs*. The global area covered by coral reefs is only about 600,000 km^2 (c. 0.18% of the total area of oceans). Nonetheless, it has been estimated that up to one quarter of all marine species and one fifth of known marine fish species live in coral reef ecosystems, leading it to be seen as the marine equivalent of tropical forests. Thus, for example, a detailed study involving 400 person-days of collecting at 42 sample stations in a 295 km^2 coral reef complex at a site off New Caledonia yielded 2738 species of molluscs, and a predicted total number of species of more than 3000 (Bouchet et al. 2002). As with all environments that are typically species rich, there are examples of areas of coral reef that naturally are not so, and the 10 richest centres of endemism cover 15.8% of the world's coral reefs but include approximately one half of the species of corals, snails, lobsters and reef fish with restricted ranges (Roberts et al. 2002).

- *Deep ocean*. The biodiversity of the deep ocean remains one of the great imponderables, and a topic of some debate. Areas at depths below 1 km cover more than half of the planet. Some recent studies on the fauna of deep-sea floors in the Atlantic and Pacific have uncovered a high level of species richness (Grassle 1991; Grassle & Maciolek 1992; Poore & Wilson 1993), and it has been suggested that there may be 10 million species in the deep sea (Grassle & Maciolek 1992). Whilst this seems likely to be a marked overestimate (May 1992b), it is undoubtedly the case that large numbers remain to be discovered. For example, knowledge of the sediment-dwelling infauna of the deep sea derives from study of less than 2000 quantitative cores, an estimated area of 500 m^2 (Paterson 1993), and for the meiofauna (the very small animals living between and around the grains of the sediment) alone the area is estimated to be less than 5 m^2 (Lambshead et al. 2000). With the improved access that sophisticated technologies have provided (remotely operated vehicles, bottom landers, submarines, sonar, video), several new kinds of communities of organisms have been identified, such as hydrothermal vents, cold seeps and cold-water coral reefs. Along with seamounts, whilst not especially diverse, these communities are often hotspots of endemism (Tunnicliffe 1991; de Forges et al. 2000; van Dover 2000, 2001).

For reviews of biodiversity in other particular environments: see Marmonier et al. (1993) for ground water; see Körner (2001) for alpine ecosystems; see Convey (2001) for Antarctic ecosystems; see Callaghan et al. (2001) for Arctic ecosystems; and see Hogarth (2001) for mangrove ecosystems.

3.4 Gradients in biodiversity

As has already been observed, spatial variation in biodiversity across the Earth is complex. To aid in understanding this complexity, attention has particularly focussed on how species richness changes along gradients of latitude, elevation and depth, and additionally across peninsulas and bays. Patterns that are manifest along these gradients are abstractions from the broader spatial variation, and need to be interpreted as such. This is particularly so when considering the mechanisms that may give rise to changes in richness with latitude and other such variables. If these mechanisms correctly explain these changes, then they should also explain the wider patterns of variation in species numbers.

3.4.1 Latitude

Perhaps the boldest signature of spatial variation in biodiversity is that associated with latitude. As has long been acknowledged (e.g. Humboldt

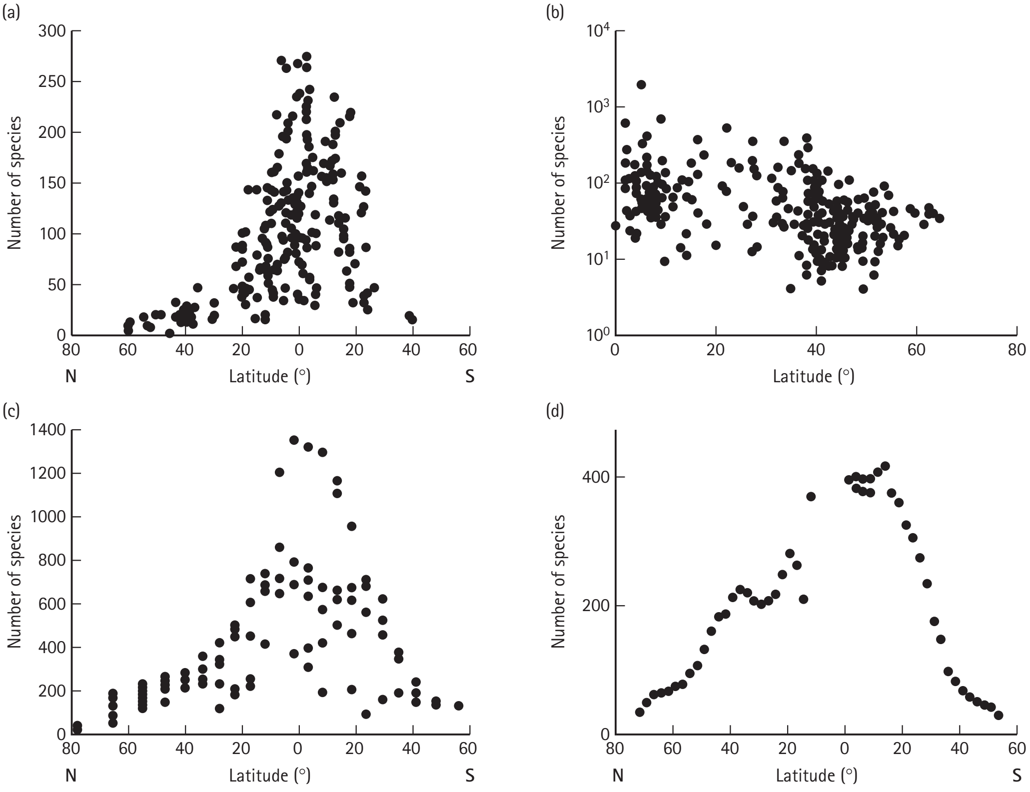


Fig. 3.13 Variation in terrestrial/freshwater species richness with latitude for: (a) trees per 0.1 ha at sites across the Earth; (b) freshwater fish in rivers across the Earth; (c) birds across the New World (grid cells of ~ 611,000 km^2); and (d) mammals across the New World (latitudinal bands of 2.5°). (a, From Enquist & Niklas 2001; b, from Oberdorff et al. 1995; c, adapted from Gaston & Blackburn 2000; d, from Kaufman & Willig 1998.)

& Bonpland 1807; Wallace 1853; Bates 1862), the species richness of most groups of organisms increases from high (temperate) to low (tropical) latitudes (Figs. 3.13 & 3.14). A similar pattern is also frequently observed for the richness of higher taxa, such as genera and families (Fig. 3.15). It is typically manifest whether diversity is determined at local sites, across large regions, or is determined cumulatively across entire latitudinal bands.

Four features of the latitudinal gradient of increasing biodiversity towards lower latitudes are of note.

1 It has been a persistent feature of much of the history of life on Earth. This has been elegantly demonstrated for flowering plants (angiosperms) by Crane and Lidgard (1989), who have shown that the pattern was maintained throughout much of the Cretaceous (Fig. 3.16). Studies of Foraminifera and molluscs suggest that for these groups at least, the

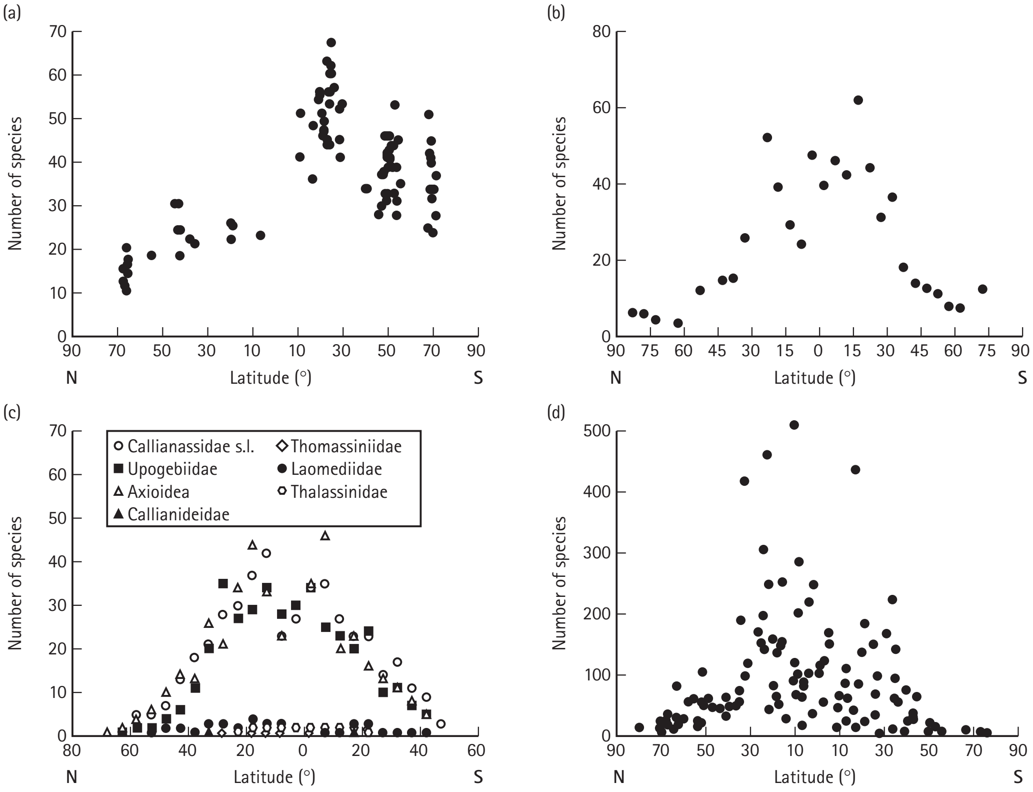


Fig. 3.14 Variation in marine species richness with latitude for: (a) deep-sea benthic Foraminifera; (b) tintinnids (planktonic ciliates); (c) thalassinid shrimp superfamilies; and (d) marine bivalves (at different localities). (a, From Culver & Buzas 2000; b, from Dolan & Gallegos 2001; c, from Dworschak 2000; d, from Flessa & Jablonski 1995.)

gradient may, nonetheless, have become steeper through time (Crame 2001, 2002; Buzas et al. 2002).

2 The peak of diversity is seldom actually at the equator. Rather, it seems often to have an inflection point somewhat further north, often at 20–30°N (e.g. Roy et al. 1998; Crame 2000).

3 The gradient is commonly, though far from universally, asymmetrical about the equator. That is, the pattern of diversity across the Earth is more like a pear (increasing rapidly from northern regions to the equator and declining slowly from the equator to southern regions) than an egg (Platnick 1991, 1992). This is well illustrated by the numbers of genera of termites (Fig. 3.17). In some cases, such effects have been found to result from latitudinal variation in land area (e.g. Kaufman & Willig 1998).

4 The steepness of the gradient may vary markedly. Thus, butterflies are more tropical than birds. Although there are approximately two species of butterflies for every species of bird worldwide, birds greatly outnumber

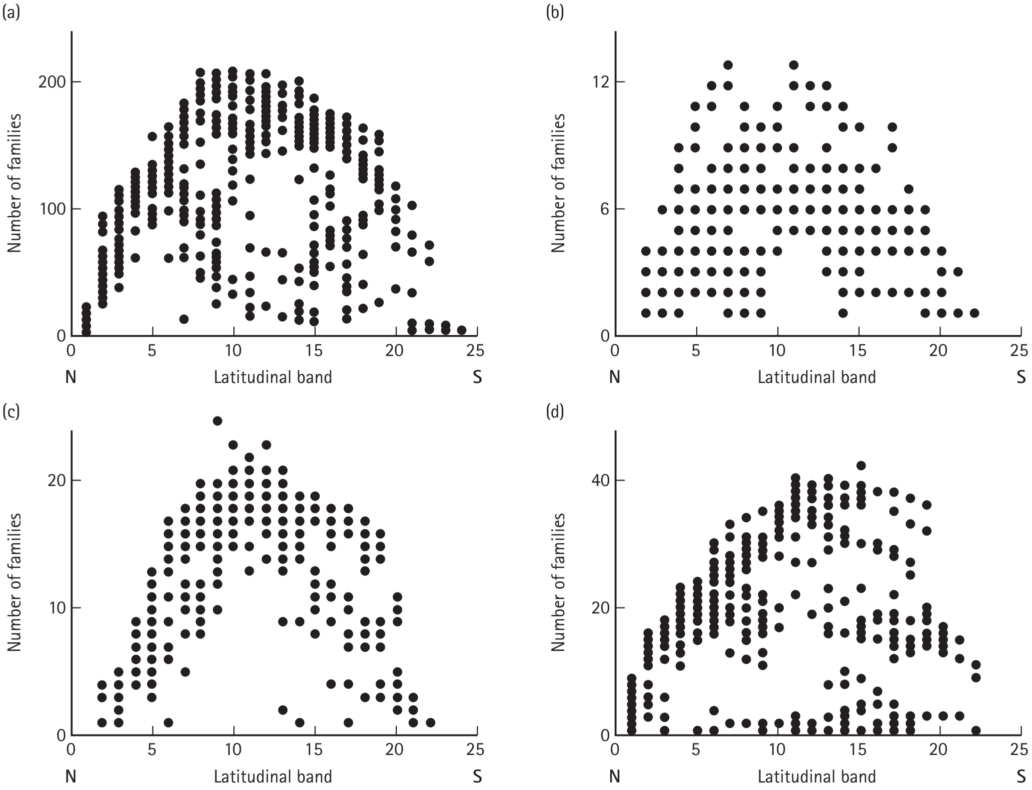


Fig. 3.15 Latitudinal gradients in family richness for: (a) seed plants; (b) amphibians; (c) reptiles; and (d) mammals. Each data point represents the number of species in a cell of a grid of 611,000 km^2 squares, and latitudinal bands run from the north of the northern hemisphere (1) to the south of the southern hemisphere (24). (From Gaston et al. 1995.)

butterflies in the Arctic, have about equal numbers of species in temperate North America, and are outnumbered by butterflies in the Neotropics (Robbins & Opler 1997).

Terrestrial and freshwater systems

The latitudinal gradient in biodiversity is best established for terrestrial and freshwater systems (see Fig. 3.13). Here, exceptions are relatively scarce. They include a variety of usually comparatively minor but sometimes quite major taxa, such as polypore fungi, sawflies, ichneumonid and braconid wasps, aphids and galling insects (Fig. 3.18; Kouki et al. 1994; Reid 1994; Price et al. 1998; Wright & Samways 1998; Kouki 1999). There are also exceptions for some taxonomic groups in some regions of the world or in particular habitat types (e.g. North American grasshoppers, Australian butterflies, breeding birds of eastern USA,

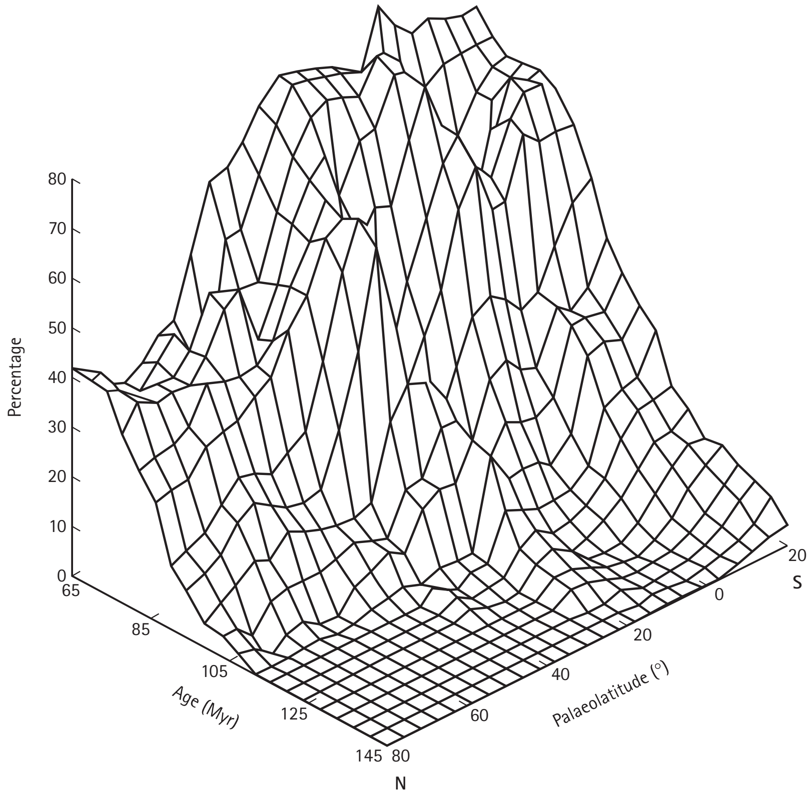
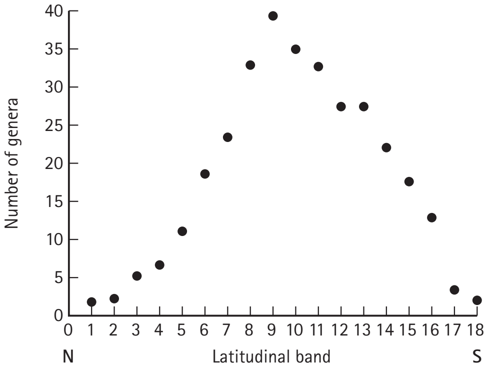


Fig. 3.16 Estimated percentage representation of flowering plants at different geological times and at different palaeolatitudes within Cretaceous palynofloras. (From Crane & Ligard 1989.)

Fig. 3.17 Mean generic richness of termites across areas (each of 611,000 km^2) in different latitudinal bands running from the north of the northern hemisphere (1) to the south of the southern hemisphere (18). (From Eggleton 1994.)



Australian forest mammals; Rabenold 1993; Davidowitz & Rosenzweig 1998; Johnson 1998; Dingle et al. 2000). Although these cases may turn out to apply somewhat more widely, they pose little threat to the generality of the underlying increase in richness towards the tropics.

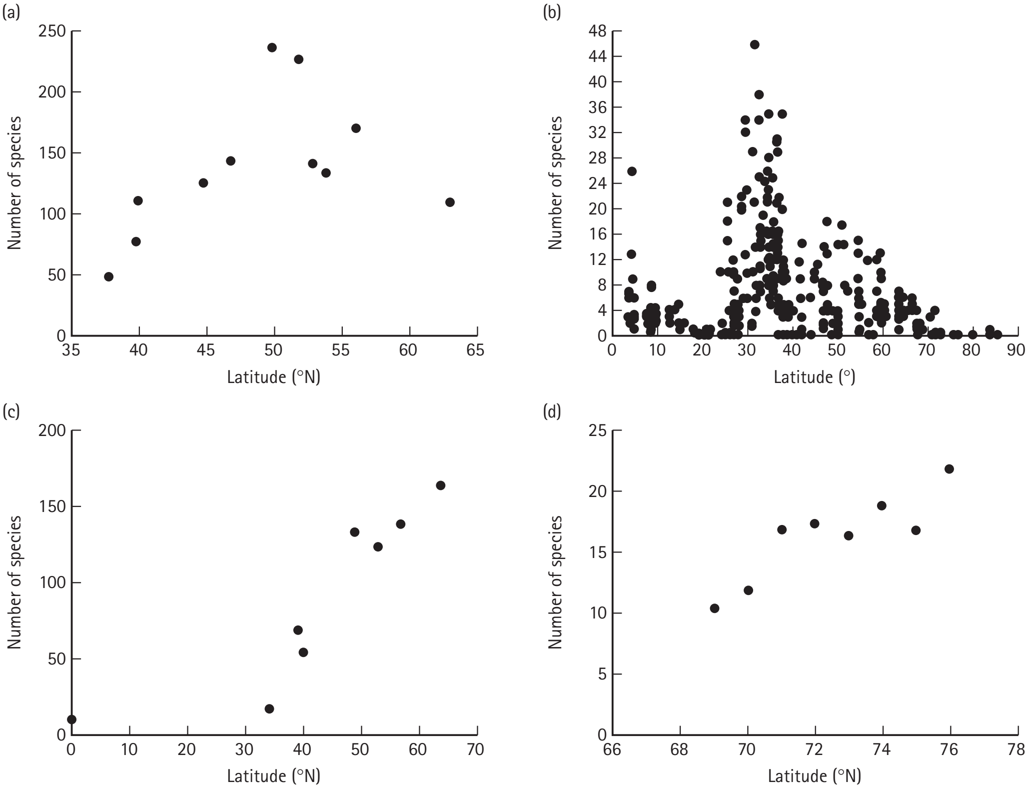


Fig. 3.18 Examples in which decreases in terrestrial species richness with latitude have not been documented: (a) aphid species in areas of 1000 km^2; (b) galling insect species in vegetation samples; (c) sawfly species in areas of 1000 km^2; and (d) breeding bird species on Finnish flark fens. (a, From Dixon et al. 1987; b, from Price et al. 1998; c, from Kouki et al. 1994; d, from Järvinen et al. 1987.)

Curiously, latitudinal gradients in terrestrial systems have also been documented for the diversity of human languages and human ethnic groups, which also tend to increase in number with temperature and rainfall (Mace & Pagel 1995; Cashdan 2001; Collard & Foley 2002).

Marine systems

The question of whether there are latitudinal gradients in biodiversity in marine systems that parallel those in terrestrial ones has given rise to much debate. The detection of latitudinal patterns in these environments has been hampered by the confounding effects of depth (Section 3.4.2) and by the problems of attaining adequate levels of sampling (Section 3.3.5).

Most contention surrounds patterns in shallow waters. Here it seems that whilst there are clear clines of increasing diversity towards lower latitudes for some groups of organisms, most notably molluscs and fish (Rohde 1978, 1992; Vincent & Clarke 1995; Clarke & Crame 1997; Roy et al. 1998), there are not for others (e.g. Kendall & Aschan 1993; Lambshead 1993; Dauvin et al. 1994; Boucher & Lambshead 1995; Vincent & Clarke 1995; Lambshead et al. 2000; Ellingsen & Gray 2002). The reasons for these differences are unclear. However, they may in part result from differences in the way in which comparisons are made. Most of the studies failing to find declines in richness towards high latitudes are for taxa from soft sediments, and are based on point samples. Conversely, most of those studies documenting such patterns are based on pooling data from records of species occurrences across regions. For bryozoans, common benthic organisms, where both analytical approaches have been employed, studies based on local samples failed to find any latitudinal gradient, whilst studies based on regional pools did find them (Clarke & Lidgard 2000), apparently at odds with the existence of any marked local–regional richness relationship (see Section 3.2.2).

Whatever the overall latitudinal pattern of species richness on the continental shelves, it is evident that benthic richness in Antarctic waters may be surprisingly high (Brey et al. 1994; Clarke & Crame 1997). This may, at least in part, result from groups that originally evolved in this region.

In contrast, patterns in the deep sea seem reasonably clear. Latitudinal diversity gradients have been reported in the North Atlantic, and strong inter-regional variation in the South Atlantic, for deep-sea bivalves, gastropods and isopods (Rex et al. 1993, 2000). Poore and Wilson (1993) find a similar pattern for deep-sea isopods, and Culver and Buzas (2000) document decreases in the species richness of deep-sea benthic Foraminifera in both the North and South Atlantic (see Fig. 3.14). These trends were unexpected, as it had long been assumed that the depth of the overlying water would buffer deep-sea assemblages from the environmental variation thought to be associated with such gradients. However, large-scale environmental gradients at the surface may in practice influence deep-sea diversity through, for example, the influence on the pattern and rate of descent of organic matter; with the exception of vent and seep habitats, basal food supply in the deep sea is entirely of extrinsic origin.

Pelagic assemblages also appear to exhibit a latitudinal gradient in richness, though again not necessarily a simple one. For example, declining species richness towards higher latitudes has been documented for ostracods, euphausiids, decapods and fish in the water column to a depth of 2000 m, at a set of stations in the northeast Atlantic (Angel 1993, 1994a). Such gradients may be stepped rather than smooth, as a result of discontinuities such as the polar front and the subtropical convergences (Angel 1994b). The number of species of planktonic Foraminifera peaks at mid-latitudes in all oceans, with tropical latitudes tending to be more species rich than high latitudes (Rutherford et al. 1999). McGowan and Walker (1993) argue that the number of species of pelagic plankton is low at high latitudes, but rather than a regular, systematic increase towards the equator exhibits a sharp gradient at about 40°N. Diversity is high at mid-latitudes, but in the central and eastern Pacific drops to intermediate levels in the equatorial zone. Diversity increases in the South Pacific, and drops to a minimum near Antarctica.

In summary, conflicting evidence and apparently complex patterns in latitudinal clines in the sea mean that these patterns continue to constitute a challenge to the generality of the statement that diversity increases from temperate to tropical regions. However, there is ample evidence that such patterns do exist.

Mechanisms

A large number of possible mechanisms for latitudinal gradients in biodiversity have been proposed (Pianka 1966; Stevens 1989; Rohde 1992; Colwell & Hurtt 1994; Rosenzweig 1995; Turner et al. 1996). These include the effects of competition, mutualism, predation, patchiness, environmental stability, environmental predictability, productivity, area, number of habitats, ecological time, evolutionary time and solar energy (Rohde 1992). At present no consensus view on the cause of the pattern seems to be emerging. However, attention has focussed on three principal mechanisms.

1 *Area effects*. Latitudinal gradients result from the tropical regions having a larger area than temperate ones, and consequently higher rates of speciation and lower rates of extinction (Rosenzweig 1992). The debate as to the evidence for and against this mechanism provides a valuable insight into some of the difficulties that surround identifying the determinants of large-scale patterns in biodiversity (see Rosenzweig 1992, 1995; Blackburn & Gaston 1997; Rohde 1997, 1998; Rosenzweig & Sandlin 1997; Ruggerio 1999; Chown & Gaston 2000; Hawkins & Porter 2001). In this case, there are two critical issues of contention: the first is the most appropriate way in which to divide the world into zones which are biologically meaningful in this sense and whose areas can then be determined; and the second is how differences in these areas influence speciation rates.

2 *Energy availability*. Latitudinal gradients result from higher levels of available energy in low-latitude regions, providing a wider resource base and allowing more species to occur there (Wright 1983; Currie 1991; Wright et al. 1993; Turner et al. 1996). In support of this mechanism, in general those environmental factors that are related to the supply of usable energy (food or limiting nutrient availability, productivity) explain

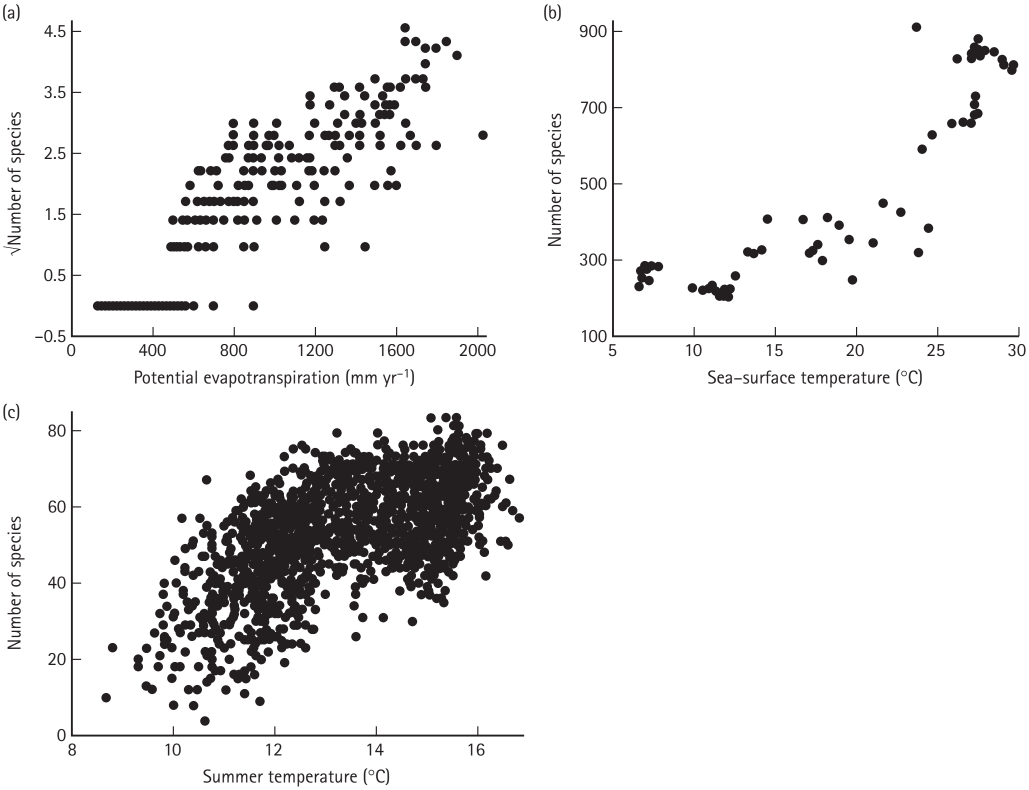


Fig. 3.19 Species–energy relationships for: (a) potential evapotranspiration (mm yr^{-1}) and richness of *Epicauta* beetles (Meloidae) in North America (grid cells of 2.5° × 2.5° south of 50°N, 2.5° × 5° north of 50°N); (b) mean annual sea-surface temperature (°C) and richness of eastern Pacific marine gastropods (bands of 1° latitude); and (c) mean monthly summer temperature (°C) and richness of breeding birds in Britain (grid cells of 10 km × 10 km). (a, From Kerr & Packer 1999; b, from Roy et al. 1998; c, from Lennon et al. 2000.)

more variation in species richness than do those that are not (Wright et al. 1993). However, latitudinal patterns in energy availability may not be simple, and whilst some studies have found relationships between energy and species richness to be broadly positive at large regional scales (particularly across temperate zones) (Fig. 3.19), others have found them to be hump-shaped, with richness declining towards high energy levels (Guégan et al. 1998; Kerr et al. 1998; Chown & Gaston 1999; Kerr & Currie 1999; Balmford et al. 2001). Much may rest on identifying those measures that best reflect available energy and account for temporal patterns in its availability.

3 *Time*. Latitudinal gradients result from the greater length of effective evolutionary time that has been available in the tropics for species

to evolve to fill habitats and niches in those regions (Wallace 1878; Rohde 1992). That is, large-scale environmental perturbations (e.g. glaciation, climatic drying) have been less frequent in the tropics, and so have provided more time for the evolutionary process (and perhaps lower rates of extinction), with the emphasis on effective evolutionary time (the product of absolute time and the rate at which this process occurs) rather than simply on absolute time, and the supposition that tropical climates increase the rate of the evolutionary process. Unfortunately, it is as yet unclear whether evolutionary rates are faster in the tropics, and there is substantial evidence that tropical climates have been considerably more unstable than was commonly supposed, and that much of the richness of tropical assemblages may have resulted from quite recent diversification (given that some regions may have been covered in tropical vegetation for more than 100 million years). Thus, for example, the Neotropical tree genus *Inga* appears to be species rich not because it gradually accumulated species over a long geological period but because it underwent rapid diversification in the past 10 Myr (Richardson et al. 2001).

There is no logical reason why any of these mechanisms need operate in isolation. Indeed, there are potentially close links between each of them, suggesting that the prevalence of the latitudinal gradient in species richness may result because different mechanisms all pull in the same direction. Moreover, the effects of any of these mechanisms are likely to be modified, and in some cases may be overridden, by a number of other factors, such as habitat heterogeneity (e.g. Kerr & Packer 1997; Kerr et al. 2001).

This said, ultimately, spatial variation in biodiversity is a product of patterns in rates of origination, immigration, extinction and emigration. At large spatial scales it will tend solely to be a product of origination and extinction. The tropics have thus variously been argued to represent a cradle of diversity exhibiting high origination rates, a museum of diversity with low extinction rates, or some combination of the two. Jablonski (1993), in an analysis of post-Palaeozoic marine orders, has found that there have been significantly more first appearances in tropical waters, whether defined latitudinally or biogeographically, than expected from sampling alone. This provides direct evidence that tropical regions have been a major source of evolutionary novelty.

3.4.2 Altitude and depth

In considering species–area relationships (Section 3.2.1) and latitudinal gradients in biodiversity (Section 3.4.1), very little allowance was made for the fact that, quite literally, the Earth is not flat; its surface, above and below water, is moulded into mountains and valleys both by local and global geological processes. Whilst for some purposes it may be useful to refer to the Earth's surface using measures of area, the three-dimensional structure of land- and seascapes means that sometimes one should really be dealing in volumes.

Altitude

In the terrestrial realm, the third spatial dimension is commonly construed as the altitude or elevation of land. Altitude could arguably be ignored when considering large areas, because its magnitude is small compared with those of longitude or latitude (mean elevation is 840 m, Mt Everest is 8848 m high). However, it must be remembered that a moderate increase in altitude has, for example, an associated temperature change corresponding to a latitudinal separation perhaps of several hundred kilometres; a change of 2–3°C is experienced over some 10° of latitude or approximately 700 m of altitude in the hills of northern Britain (Whittaker & Tribe 1996).

In terrestrial systems, it is generally accepted that species richness declines towards high elevations (Fig. 3.20; Rahbek 1995; Sanders 2002). However, the details of this pattern are quite variable. Some groups apparently show a relatively simple decline. Others show a pronounced hump-shaped relationship in which richness at first increases from low to mid-elevations and then declines towards high elevations; although even here, diversity at low elevations almost invariably exceeds that at the highest ones.

Elevational gradients in species richness are typically explained in terms of one or more of four principal factors (Lomolino 2001; Sanders 2002).

1 *Area*. Land area varies with elevation, thus it is possible that observed patterns in richness may be driven by the same processes as give rise to species–area relationships (Section 3.2.1). Certainly, accounting for variation in area can change observed relationships between richness and elevation, confirming that area does exert an influence. Thus, Rahbek (1995, 1997) has shown, for example, that when data are not standardized for differences in area then South American tropical land birds exhibit a steady decline in richness with elevation, but when these same data are standardized for area a hump-shaped pattern emerges (Fig. 3.21).

2 *Energy availability*. Just as variation in energy availability may contribute to latitudinal gradients in species richness, it may also explain altitudinal gradients in species numbers. Energy availability may peak at low to intermediate elevations, particularly because day-time temperatures enable higher rates of photosynthesis and cool evenings enable

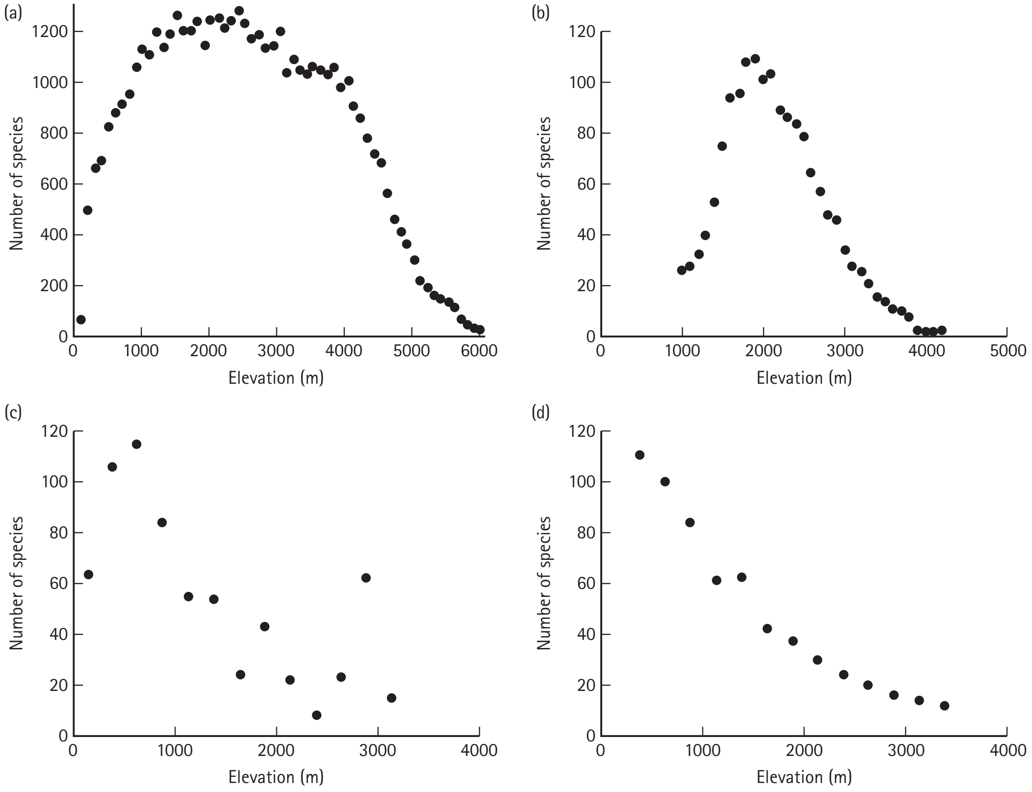


Fig. 3.20 Variation in number of species with elevation for: (a) flowering plants in Nepal; (b) ants in Colorado; (c) treehoppers in Colombia; and (d) bats in Manu National Park & Biosphere Reserve, Peru. (a, From Grytnes & Vetaas 2002; b, from Sanders 2002; c, data from Olmstead & Wood 1990; d, from Patterson et al. 1998.)

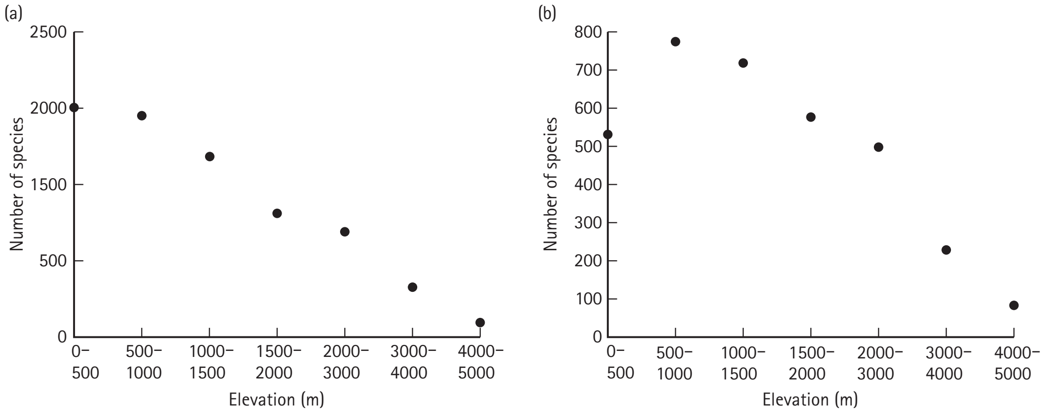


Fig. 3.21 Altitudinal gradient in the species richness of South American tropical land birds, based on data: (a) not standardized for elevational variation in area; and (b) standardized for such variation. (From Rahbek 1995.)

lower plant respiration, providing a wider resource base and allowing more species to co-occur.

3 *Isolation*. Higher elevations are, for most taxa, much more isolated from other areas of similar habitat (e.g. other mountain peaks) than those at low to intermediate elevations. This may make immigration less likely, increase the likelihood of speciation, and increase the likelihood of local extinction because of the reduced connectivity of populations. In consequence, higher elevations may have lower species richness, but commonly have higher levels of endemicity (although the pattern of endemism may be highly variable depending on the taxon considered; Kessler 2002). This does not explain, however, why intermediate elevations may be most species rich.

4 *Zonation*. Peaks in species richness at intermediate elevations may result from interactions and feedback among zonal communities, the transitions between which serve to inflate species numbers. This assumes elevational zonation in community structure, with marked changes in species composition occurring at some altitudes, rather than a continuous pattern of structural change.

As with latitudinal gradients, there is no necessity that these mechanisms be mutually independent, and present evidence suggests some role for each of them, at least, for different taxonomic groups and regions.

Below the Earth's surface

Life occurs beneath the Earth's surface as well as above it, for example in caves occurring at different depths. Little is known of the effect of this depth gradient on biodiversity. Certainly, the exciting discovery of endemic cave communities reliant on chemosynthetic (as opposed to photosynthetic) energy production, similar in function to those occurring in the deep sea at hydrothermal vent sites, is likely to prove of tremendous interest (Sarbu et al. 1996). However, life also occurs at even greater depths. Bacterial assemblages have been recovered from up to 4000 m underground, which has been noted as a cause of some concern regarding safety in the development of deep repositories for nuclear waste (Pedersen 1993). While their 'species' richness is not related to depth, such assemblages can consist of up to 62 different 'types' at any one depth (Flierman & Balkwill 1989).

Depth

In some sense, depth can be regarded as the marine equivalent of altitude. However, plainly there are limitations to this parallel because few species are able to achieve a purely aerial existence (although a few do spend the bulk of their lives airborne (e.g. swifts and some oceanic seabirds), no species is known to complete its life cycle in the air). Distinction must therefore be drawn between the effects of depth on benthic and pelagic marine assemblages. The oceans average c. 3.8 km in depth, but reach down more than 10 km. From the surface downwards, mean temperature and variability in that temperature decrease, hydrostatic pressure increases, and light and nutrient fluxes decline.

As it does with altitude, species richness tends to decline towards extreme depths, but again linear and hump-shaped relationships have been documented (Fig. 3.22). However, in both the pelagic and benthic realms, the species richness–depth relationship is generally held to be a hump-shaped one; richness commonly peaks at depths of 1000–1500 m for pelagic assemblages, and in many taxa increases with increasing depth to a maximum at 1000–2000 m for megabenthos and 2000–3000 m for macrobenthic infauna (Rex 1981; Etter & Grassle 1992; Angel 1993, 1994b; Rex et al. 1997; Pineda & Caswell 1998) (but cf. final section of Section 3.3.2). Indeed, a hump-shaped pattern of richness with depth may have been a persistent feature of life, with palaeontological examples having been documented (Tokeshi 1999). Whilst the same mechanisms as proposed to explain relationships between species richness and altitude may in modified form also explain those between species richness and depth, for benthic assemblages trends with depth may also be associated with changes in sediment characteristics, particularly particle-size diversity (Etter & Grassle 1992). For samples taken from the western North Atlantic from depths of 250–3029 m, species diversity of macrofauna was found to be positively related to sediment particle-size diversity, and when this effect was statistically controlled for there was no longer any relationship between species richness and depth.

The interplays between the various spatial patterns are important in generating the global landscape of biodiversity that is observed. Macpherson and Duarte (1994) examined the effect of both depth and latitude on (amongst other things) the species richness of benthic fish (Fig. 3.23). They found that species richness declined towards higher latitudes (Section 3.4.1) but at most latitudes species richness also varied with depth; species richness tended to peak at depths of 150–300 m.

3.4.3 Peninsulas and bays

The shapes of land masses and water bodies can have profound effects on the levels of biodiversity associated with them, by affecting environmental conditions and likelihoods of colonization and extinction, leading to gradients in that diversity. Thus, terrestrial species richness is often observed to decline towards the tips of peninsulas (the ‘peninsula effect’) and marine species richness to decline across bays with distance from the open sea (the ‘bay effect’) (Fig. 3.24). Exceptions to both patterns are,

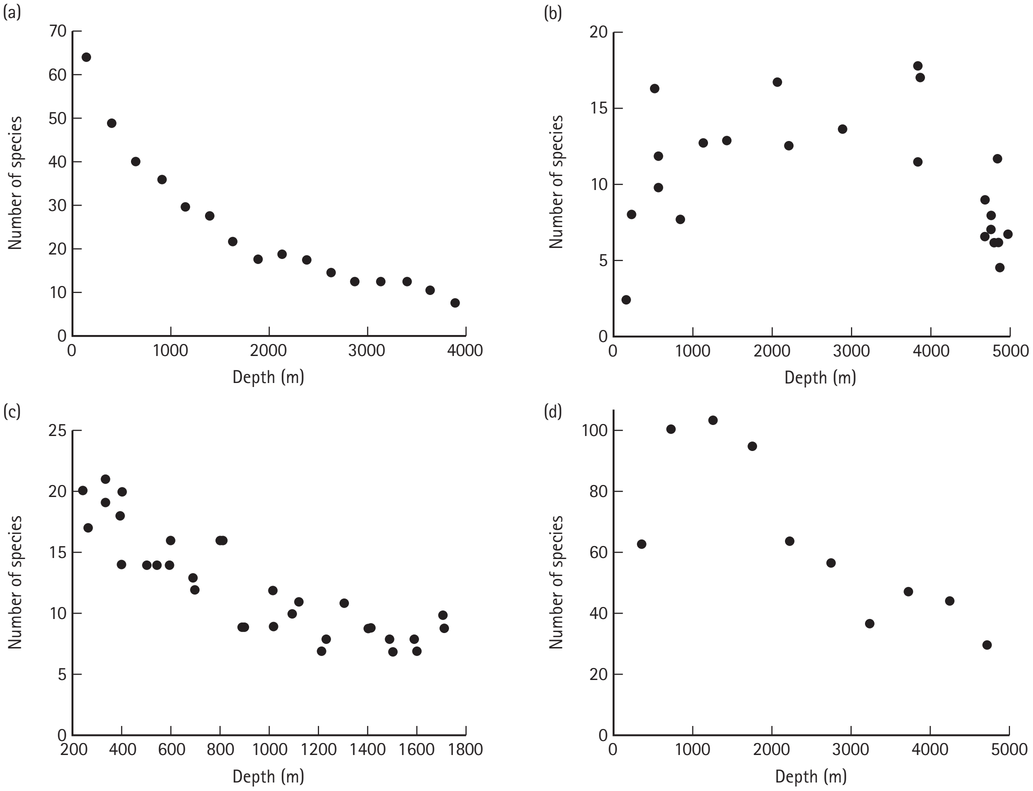


Fig. 3.22 Variation in species richness with depth for: (a) asellote isopod species in the northern seas; (b) gastropod species in the North American basin; (c) fish species on the continental slope of the Balearic Islands; and (d) megabenthos (summing fish, decapods, holothurians and asteroids) in the Porcupine Seabight region to the southwest of Eire. (a, From Svavarsson et al. 1993; b, from Rex et al. 1997; c, from Morenta et al. 1998; d, from Angel 1994b.)

however, not unusual (e.g. Seib 1980; Due & Polis 1986; Brown 1987; Tackaberry & Kellman 1996). Where they do exist, these trends may result from the effects of systematic changes in area or isolation.

3.5 Congruence

Most major terrestrial and freshwater groups are more speciose in tropical than in temperate regions, at low elevations than at high, and in forests than in deserts. Likewise, most major marine groups are more speciose in tropical than in temperate regions, at intermediate than at extreme depths, and in coral reefs than in the pelagic zone. One might, therefore, expect that within biological realms the regional richness of different groups of organisms would be positively correlated (areas in which they

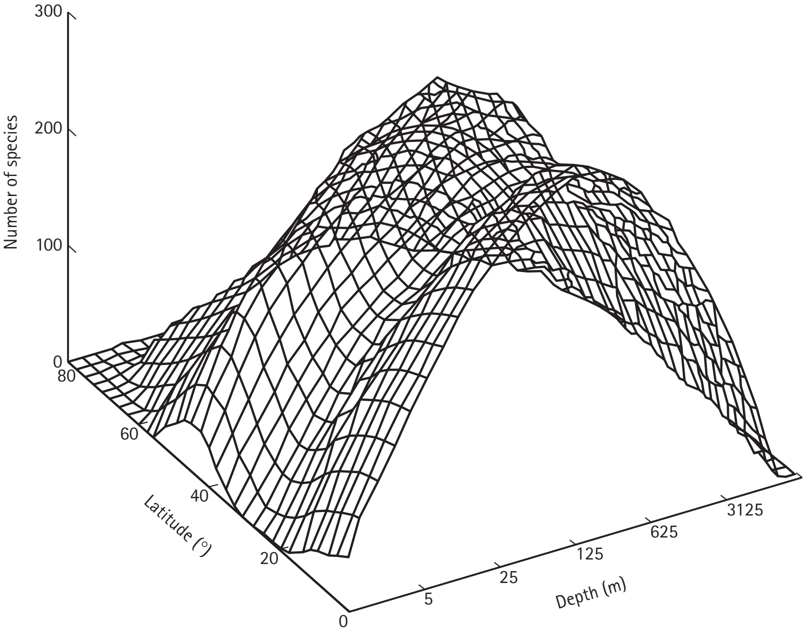


Fig. 3.23 Three-dimensional relationship between species richness, latitude and depth for benthic fish in the eastern Atlantic. (From Macpherson & Duarte 1994.)

are species poor coinciding and areas in which they are species rich coinciding) and, because of the positive local–regional richness relationship, local richness would do likewise. This would be important because it would greatly 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 taxonomic groups have often been observed (e.g. Flather et al. 1997; Kerr 1997; Virolainen et al. 2000). Thus, whilst for the taxonomic groups trees, tiger beetles, amphibians, reptiles, birds and mammals, the 5% of land area across the USA and southern Canada in which the highest levels of species richness are attained do overlap between some pairs of taxa, this pattern is not a general one (Flather et al. 1997). Likewise, although the numbers of species in different, large, 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 substantially explained by latitudinal gradients in diversity (Fig. 3.25; Currie 1991; Flather et al. 1997; Ricketts et al. 1999). These conclusions seem to hold at finer resolutions over more constrained areas. Thus, at a scale of 10 × 10 km squares, species rich areas for different taxa in Britain

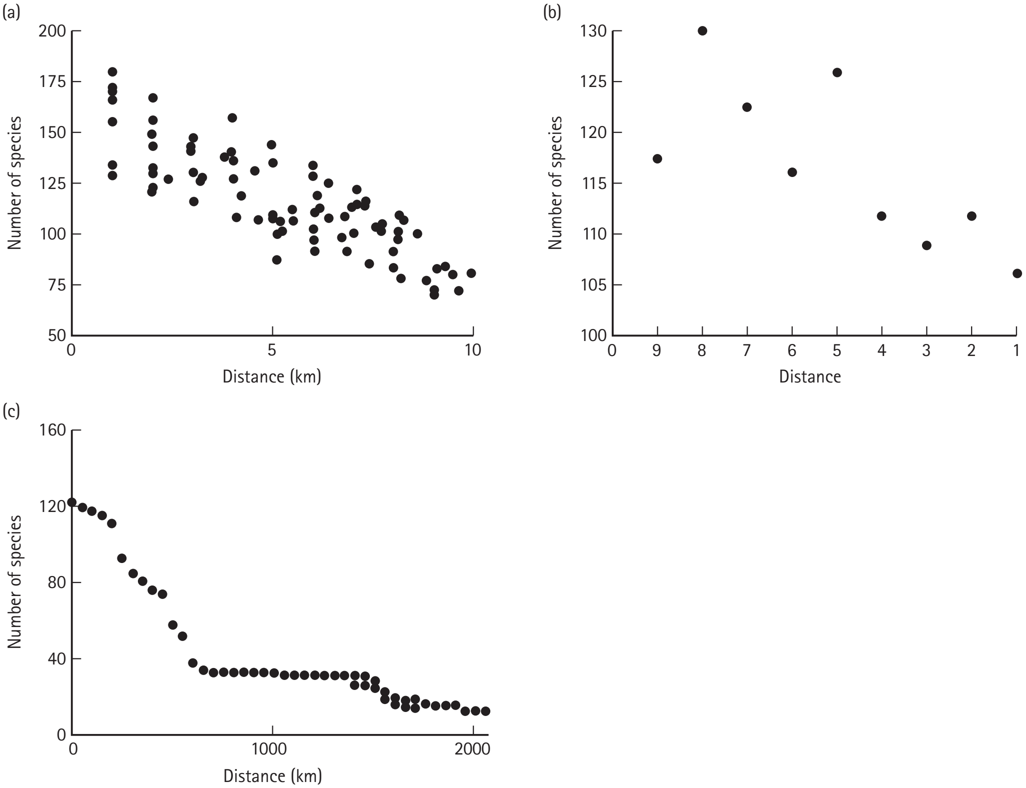


Fig. 3.24 Variation in species richness towards the tips of peninsulas and the shores of bays for: (a) butterflies on the Iberian peninsula, at different distances from the Pyrenees; (b) birds at different distances from the tip of Cornwall; and (c) fish in the Baltic Sea, at different distances from the Atlantic-Skagerrak mouth. (a, From Martin & Gurrea 1990; b, from Gaston & Blackburn 2000; c, from Rapoport 1994.)

frequently do not coincide (Prendergast et al. 1993). 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 Africa (van Jaarsveld et al. 1998).

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. More species of two groups may be recorded in some areas, and fewer in others, simply because greater efforts were made for both groups in the former. If the positive relationships are 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 (if there is a greater overall number of species in an area, then by chance there are likely to be more species of

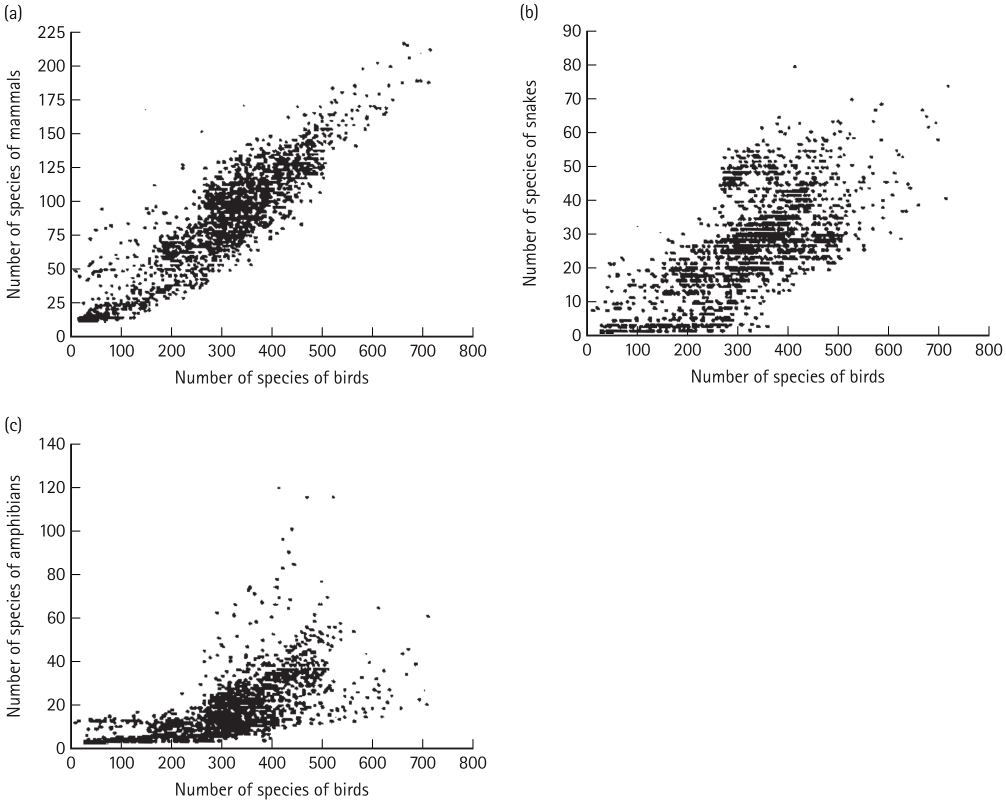


Fig. 3.25 Relationships between the species richness of birds and the species richness of: (a) mammals; (b) snakes; and (c) amphibians across 1962 1° grid cells in sub-Saharan Africa. (From Balmford 2002.)

each of the constituent groups), because groups share common determinants of richness (e.g. energy availability), or even because groups differ in determinants of richness but these determinants themselves exhibit spatial covariance (Gaston 1996b,c).

The frequent lack of strong positive covariance in the species richness of different 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 (like birds and mammals) to biodiversity at large. The latter is particularly important given that only c. 13% of the total number of species estimated to be extant have been formally taxonomically described, the distributions of the majority of these remain largely unknown (a high proportion are known from only a single locality; Andersen et al. 1997; Stork 1997), that species whose distributions are well documented are strongly biased with respect to their higher taxonomic affinities, and that they belong to groups whose potential for indicating patterns of biodiversity at large may in some cases be particularly poor (Ricketts et al. 1999). Such outcomes are, however, 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 (e.g. Section 3.4.1). Which particular patterns are and are not expressed by a given taxon rests on contingencies (e.g. physiology, dispersal ability, resource requirements, evolutionary history; Lawton 1999).

3.6 Summary

1 On average, as the size of a geographical area increases, so too does the number of species that it contains (the species–area relationship).
2 Local species richness tends to be positively correlated with regional species richness (the local–regional richness relationship).
3 There are more higher taxa in the marine realm than in the terrestrial one, but more species in the latter than in the former.
4 The tropical regions contain at least two-thirds of all extant terrestrial species, with the Neotropics containing the greatest overall levels. Marine biodiversity is thought to be highest in the Indo-western Pacific.
5 The distribution of terrestrial biodiversity between provinces is uneven, with 17 mega-diversity countries possessing 66–75% of the world's species.
6 The proportion of endemic taxa present tends, on average, to increase with the size of an area and with higher species richness, and the number of endemics increases towards lower latitudes.
7 Species richness in both marine and terrestrial realms tends to increase from temperate to tropical latitudes, although the generality of the pattern is more uncertain in the former. Latitudinal gradients in richness have been a persistent feature through much of the history of biodiversity.
8 In the terrestrial realm, species richness declines towards high elevations, often with a peak at intermediate elevations, whilst in the marine realm the relationship with depth is typically hump-shaped.
9 Mismatches in the spatial occurrence of peaks in the richness of different taxonomic groups have often been observed, and correlations between the numbers of species in different groups are frequently rather weak.

Further reading

Begon, M., Harper, J.L. & Townsend, C.R. (1996) *Ecology: Individuals, Populations and Communities*. Blackwell Science, Oxford. (*A superb treatment of ecology, including the ecological issues touched on in this chapter.*)

Brown, J.H. (1995) *Macroecology*. University of Chicago Press, Chicago, IL. (*An introduction to macroecology, by its chief proponent.*)

Brown, J.H. & Lomolino, M.V. (1998) *Biogeography*, 2nd edn. Sinauer Associates, Sunderland, MA. (*The best text on biogeography*.)

Gaston, K.J. (1994) *Rarity*. Chapman & Hall, London. (*A synthesis of what is known about rarity, much of it related to the patterns of biodiversity*.)

Gaston, K.J. & Blackburn, T.M. (2000) *Pattern and Process in Macroecology*. Blackwell Science, Oxford. (*A demonstration of how regional-scale processes influence local patterns of biodiversity and community structure.*)

Groombridge, B. & Jenkins, M.D. (2002) *World Atlas of Biodiversity: Earth's Living Resources in the 21st Century*. University of California Press, London. (*Lots of useful maps of patterns of biodiversity*.)

Hubbell, S.P. (2001) *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton, NJ. (*A development of island biogeography theory to explain biodiversity – a thought-provoking read.*)

Lawton, J.H. (2000) *Community Ecology in a Changing World*. Ecology Institute, Oldendorf/Luhe. (*An authoritative exploration of the determinants of community structure and the likely consequences.*)

Mittermeier, R.A., Myers, N., Gil, P.R. & Mittermeier, C.G. (1999) *Hotspots: Earth's Biologically Richest and most Endangered Terrestrial Ecoregions*. CEMEX/Conservation International, Mexico City. (*Impressive, but in our experience it is difficult to obtain a copy*.)

Myers, A.A. & Giller, P.S. (eds.) (1988) *Analytical Biogeography: An Integrated Approach to the Study of Animal and Plant Distributions*. Chapman & Hall, London. (*Remains perhaps the best single-volume treatment of many of the primary issues in biogeography*.)

Ormond, R.F.G., Gage, J.D. & Angel, M.V. (eds.) (1997) *Marine Biodiversity: Patterns and Processes*. Cambridge University Press, Cambridge. (*One of the only volumes dedicated to this topic.*)

Ricklefs, R.E. & Schluter, D. (eds.) (1993) *Species Diversity in Ecological Communities: Historical and Geographical Perspectives.* University of Chicago Press, Chicago, IL. (*A landmark text exploring the roles of large-scale spatial and temporal processes in generating and maintaining diversity*.)

Rosenzweig, M.L. (1995) *Species Diversity in Space and Time*. Cambridge University Press, Cambridge. (*An important overview, with a particular take on the processes that structure patterns of diversity*.)

Tokeshi, M. (1999) *Species Coexistence: Ecological and Evolutionary Perspectives*. Blackwell Science, Oxford. (*A wide-ranging treatment of the patterns and processes of species diversity and coexistence, unusually blending palaeobiological and contemporary perspectives.*)

Whittaker, R.J. (1998) *Island Biogeography*. Oxford University Press, Oxford. (*An up-to-date overview of a topic that has fascinated biologists for generations.*)

4 Does biodiversity matter?

4.1 Introduction

The variety of life is manifestly complex (Chapter 1), has changed dramatically through time (Chapter 2), and is unevenly distributed through space (Chapter 3). For some these observations may be interesting in their own right, and the study of biodiversity may be largely a heuristic exercise. Certainly, exploring such issues has attracted the attentions of generations of natural historians, palaeobiologists and ecologists. But this ignores a fundamental question that demands both an intellectual and a practical response. Does biodiversity matter? In this chapter we address this issue. We discuss the sorts of things that might be valued about biodiversity and why. In so doing, we use 'value' in the broadest sense and not simply as a shorthand for monetary worth. The values of biodiversity can be divided into two broad and largely self-explanatory groups: use values and non-use values. These categories are not always clear-cut, but they are still helpful as long as one is mindful of their limitations. We begin by considering the use value of biodiversity, taking in turn its two major components of direct-use and indirect-use value (Sections 4.2 & 4.3) and the relationships between biodiversity and ecosystem function (Section 4.3). We then move on to address non-use values, including option, bequest, existence and intrinsic values (Section 4.4).

The sequence in which these values are presented is not indicative of our perceptions of their relative importance. Nor are observations that will be made on the form and level of some kinds of use intended to imply any endorsement of their appropriateness. Plainly, some of the examples of the exploitation of biodiversity that we will discuss are distressingly unsustainable at present levels (see Section 5.4.1 for further discussion), and others would be regarded by some, and perhaps a substantial proportion, of the human population as unethical.

4.2 Direct-use value

Direct-use value derives from the direct role of biological resources in consumption or production. It essentially concerns marketable commodities. The scale of the direct-use exploitation of biodiversity is enormous and extremely multifaceted. To date it has eluded comprehensive evaluation. Under some broad headings, selected types of the direct-use value of biodiversity are for food, medicine, biological control, industrial materials, recreational harvesting and ecotourism. We will address each of these in turn.

4.2.1 Food

Biodiversity provides food for humans, and hence is the foundation of all our food industries and related services. This food takes forms that include vegetables, fruit, nuts, meat, and adjuncts to food in the form of food colourants, flavouring and preservatives. These may derive from wild or cultivated sources, but for the bulk of the human population the latter are, of course, predominant (in 1997, global agriculture provided 95% of all plant and animal protein and 99% of energy consumed by humans; United Nations Development Programme et al. 2000). The development of and subsequent improvements in agriculture enabled the continued expansion of the human population, from a global total of perhaps 4 million hunter–gatherers to the present 6 billion people (Cohen 1995). Current agricultural technology enables one person to be fed from the food grown on $\leq 2000\ m^2$ (Trewavas 2002), although inequities mean that some of the human population is obese, and much is malnourished or at or below the level of starvation.

Of the 300,000 or more species of flowering plants, about 12,500 are considered to be edible to humans, although occasional use may embrace a much larger number (Rapoport & Drausal 2001). Around 200 plant species have been domesticated for food. However, at present more than 75% of the food supply (in terms of energy intake) of the human population is obtained, directly or indirectly, from just 12 kinds of plants (bananas/plantains, beans, cassava, maize, millet, potatoes, rice, sorghum, soybean, sugar cane, sweet potatoes, wheat). Average global annual production of major food crops in 1996–98 totalled 2.7 billion tonnes (2.07 billion tonnes of cereals and 0.64 billion tonnes of roots and tubers; United Nations Development Programme et al. 2000). The total number of wheat stalks alone grown in 1994 exceeded 450 trillion, probably a record at that time (Myers 1997).

The diversity of animals that are exploited for food is more difficult to enumerate, although again whilst a wide range of species is consumed or provides products for consumption (e.g. milk), most consumption is concentrated on just a small proportion of these species. Animals of which use is made directly or indirectly include groups of insects (moths, beetles, wasps and bees), crustaceans (lobsters, crabs, shrimp), molluscs (bivalves, gastropods, squid), echinoderms (sea urchins, sea cucumbers) and vertebrates (fish, amphibians, reptiles, birds, mammals). The vast scale of the exploitation is readily apparent from just a few figures: (i) 3.39 billion livestock are maintained worldwide (1996–98) (1.33 billion cattle, 1.76 billion sheep and goats, 0.12 billion equines, 0.18 billion buffaloes and camels; United Nations Development Programme et al. 2000); (ii) average global annual meat production for 1996–98 was 215 million tonnes (United Nations Development Programme et al. 2000); and (iii) global fisheries land more than 80 million tonnes per year.

Whether of plants or animals, the diversity of organisms exploited for food remains rather narrow when compared with their overall diversity, leaving significant potential for further exploitation (although the characteristics necessary for domestication may be exhibited by a surprisingly small proportion of species; Diamond 2002). This gap is chiefly being closed indirectly, through the use of wild species and varieties to supply genes for the improvement of cultivated and domesticated species (increasing yields, tolerances, vigour and disease resistance); industrial-scale agriculture led to the loss of much of the previous local genetic variation in crops and livestock and their replacement by uniform varieties over often vast areas. Indeed, broadening the genetic base of some food species may perhaps be the only way in which our heavy reliance upon them can be maintained. Some of the most valuable genetic material may reside in particular wild populations of species that are exploited for food, or in their close relatives.

4.2.2 Medicine

As well as providing sustenance, biodiversity plays other vital direct roles in maintaining the health of the human population. Natural products have long been recognized as an important source of therapeutically effective medicines, and more than 60% of the world's human population relies almost entirely on plant medicine for primary health care (Harvey 2000). Of 520 new drugs approved between 1983 and 1994, 39% were natural products or were derived from them. Moreover, of the 20 best-selling non-protein drugs in 1999, nine were derived, directly or indirectly, from natural products, with combined annual sales of more than US$16 billion (simvastatin, lovastatin, enalapril, pravastatin, atorvastatin, augmentin, ciprofloxacin, clarithromycin, cyclosporin; Harvey 2000). Plant species that have proven of medical importance include willow trees (from which salicylic acid was originally obtained, and of which aspirin is a simple derivative), foxglove (digitoxin), belladonna (atropine) and poppy (codeine).

Animals also are extensively used in traditional remedies (with international trade in association with Oriental and other customary forms of medicine being substantial), as a source of a range of products in modern medicine (e.g. anticoagulants, coagulants, vasodilatory agents) and for models on which to test potentially useful drugs or techniques.

Examples of recently developed drugs (see Chivian 2001; Mateo et al. 2001 and references therein) include:

- *Taxol*. The Pacific yew tree *Taxus brevifolia* was routinely discarded by logging operations as being of no commercial value. However, it was found to contain the compound taxol, which kills cancer cells in a manner unlike that of other chemotherapeutic agents and has been shown to be one of the most promising drugs for the treatment of breast and ovarian cancer. It has become the best-selling anticancer agent ever (with sales exceeding US$1 billion annually). The taxol molecule, which has now been detected in other species, has been used as the basis for several synthetic compounds that are even more effective.
- *Cone snail venom*. A wide diversity of peptide compounds have been found to occur in the venoms of tropical reef cone snails. These compounds have been found to block a variety of ion channels, receptors and pumps in neuromuscular systems. One, omega-conotoxin, a calcium-channel blocker, has been found to be a potent analgesic and to provide a means of keeping nerve cells alive following ischaemia (insufficient flow of blood and oxygen to an organ). Advanced clinical trials are being conducted on its synthetic form for the prevention of nerve cell death following coronary artery bypass surgery, head injury and stroke, and for the treatment of chronic intractable pain associated with cancer, AIDS, and peripheral neuropathies. This synthetic form has 1000 times the analgesic potency of morphine, but does not lead to the development of tolerance or addiction, or to a clouding of consciousness.
- *Acetylcholinesterase (ACE)-inhibiting drugs*. ACE-inhibiting drugs such as enalapril, captopril, lisinopril and perindopril have been derived based on a peptide in the venom of the fer-de-lance (*Bothrops athrox* or *B. jararaca*), a Neotropical pit viper that kills its prey by causing a drop in blood pressure. These drugs have played a significant role in the decline of human deaths from stroke and heart attack.

The proportion of species that have been investigated for the potential derivation of drugs is quite small. For example, as of 1995, whilst about 37,500 species of plants had been studied phytochemically, only about 14,000 had been studied for at least one type of biological activity (Verpoorte 1998), and the number studied in detail for their medicinal properties is at best in the low thousands (Dobson 1995).

Despite advances in computer-assisted drug design, in molecular biology and in gene therapy, there remains a pressing need for new drugs to counteract drug-resistant pathogens, multidrug-resistant cancers, the emergence of new human diseases (particularly HIV/AIDS), the resurgence of older diseases such as tuberculosis, changes in the geographical distribution of diseases resulting from increased human movement and global climate change, and conditions associated with an aging population in much of the developed world (Dobson 1995; Munro et al. 1999). Perhaps the most efficient way to find them is to exploit the millions of generations of trial and error by natural selection that have given other creatures the means to healthy lives (Beattie & Ehrlich 2001). It has been suggested that one out of every 125 plant species studied has produced a major drug, whilst for synthesized chemicals the potential for finding major new drugs is of the order of one in 10,000 compounds tested (Dobson 1995). Thus, the search for useful compounds from biological material goes on (perhaps the most conspicuous example of what has come to be known as bioprospecting). For example, in the area of cancer treatment, clinical trials have been conducted using compounds derived from tunicates and a bryozoan, and preclinical trials on compounds from a sponge and a mollusc (Munro et al. 1999).

Clues to solutions to other medical problems faced by humans may also lie in other species. Thus, for example, new ways of preventing and treating osteoporosis may perhaps be found in bears, which are the only mammals in which the problem is thought not to occur (Chivian 2001). During the 3–7 months that black bears *Ursus americanus* den, they do not eat, drink, urinate or defecate, and yet they can deliver and nurse young, maintain their bone density and lean body mass, and do not become ketotic or uraemic.

4.2.3 Biological control

The use of natural enemies to control species regarded as problems is increasingly widespread and is often seen as an environmentally friendly alternative to the use of pesticides (but see Section 5.4.3). Biocontrol programmes have been attempted against several hundred species of plants and insects, with approximately 30% of weed biocontrol and 40% of insect biocontrol programmes being successful (Kunin & Lawton 1996). Biological control has included introductions of agents to control populations of pests in or on crops, populations of disease vectors (e.g. mosquitoes) and populations of invasive species.

The economic returns of biological control programmes can be huge, with the monetary values of annual gains in food or other crop production perhaps exceeding by many times the entire investment in control programmes. For example, the cost–benefit ratio for the control of cassava mealybug *Phenacoccus manihoti* by the encyrtid wasp *Epidinocarsis lopezi* in Africa was estimated to be 1 to 149 with annual savings as high as US$250 million (Norgaard 1988).

4.2.4 Industrial materials

A wide range of industrial materials, or templates for the production of such materials, have been derived directly from biological resources. These include building materials, fibres, dyes, resins, gums, adhesives, rubber, oils and waxes, agricultural chemicals (including pesticides) and perfumes. For wood alone, in 1989 the total worldwide value of exports was estimated to be US$6 billion (World Conservation Monitoring Centre 1992), and more than 3.8 billion cubic metres are estimated to be harvested annually worldwide, for fuel, timber and pulp (Kunin & Lawton 1996). Including agriculture, food processing, industrial chemical and pollution control sectors, the biotechnology industry made sales of US$10–12 billion in 1993 in the USA alone (these are projected to reach US$100 billion by 2035; Colwell 1997).

Biological materials have provided the models (biomimicry) for many industrial materials and structures. Thus, inspiration for the dome of the Crystal Palace in London came from the Amazonian water lily *Victoria amazonica*, for air-conditioning systems from the mounds constructed by termites, for Velcro fasteners from the seeds of burdock *Arctium* spp., for the echo-sounder from bats, and for infrared sensors from the thermosensitive pit organ of the rattlesnake (Beattie & Ehrlich 2001; Mateo et al. 2001). As is the case for food and medicine, the scope for exploitation of a far greater diversity of organisms for industrial materials is vast. Plants and other animals have already solved many of the problems and challenges facing humankind, often in what appear to us to be ingenious ways. The reasons that the potential for exploitation is so much greater than presently realized probably have as much to do with cultural factors (the devil you know) as they do with ignorance of natural products.

4.2.5 Recreational harvesting

Examples of recreational harvesting are multifarious but include hunting and fishing, the harvesting of animals (e.g. fish, reptiles, birds, mammals) for display and as pets, and the harvesting of plants for personal and private gardens.

Thus, for example, in the British Isles alone, 25,000 plant species are grown in botanic gardens, and some 65,000 named plant taxa are sold for horticulture, of which 14,000 represent distinct species grown out of doors (Crawley et al. 1996). Likewise, an estimated 14–30 million fish may be traded each year for aquaria, about two-thirds of the species of which are from coral reefs (Groombridge & Jenkins 2002).

The global international legal net trade in wildlife and wildlife products reported by the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) in 1997 included 26,000 live primates, 235,000 live parrots, 76,000 live tortoises, 948,500 live lizards, 259,000 live snakes, 344,000 wild orchids, 22,000 cat skins, 850,000 crocodile skins, 1,638,000 lizard skins and 1,458,000 snake skins (United Nations Development Programme et al. 2000). Species traded legally within national borders and illegal trade are not included in these figures, but run to billions of dollars annually. Recreational harvesting is of huge commercial value, both because of the scale of the trade, and because individual specimens of rare and otherwise sought after species can attract large sums (with the value often increasing as the species become progressively rarer). The illegal trade in wildlife has been argued to rank second in value only to the clandestine arms and drugs markets (Juniper 2002). In the late 1990s an illegally smuggled pair of Lear's macaws *Anodorhynchus leari* were gram for gram more valuable than heroin, fetching c. US$75,000 (Juniper 2002).

4.2.6 Ecotourism

Ecotourism is by definition founded on biodiversity, and has developed into a massive industry. Indeed, tourism as a whole is one of the fastest growing industries in the world. In 1988 an estimated 157–236 million people took part in international ecotourism (i.e. in countries of which they were not nationals), contributing between US$93 and US$233 billion to national incomes (Filion et al. 1994). However, international tourism is also estimated to account for perhaps only 9% of global tourism receipts (the rest is domestic), suggesting that these figures represent only a fraction of the scale and economic impact of ecotourism (Filion et al. 1994). In 1998, an estimated 9 million people went whale-watching alone, with expenditures on just this activity of US$1 billion (Hoyt 2000).

At a regional and local scale, ecotourism can be of economic significance. For example: (i) in Britain, at least US$7.5 billion is spent each year by urban visitors to the countryside in the course of more than 650 million day-visits (Pretty 1998); (ii) bird-watching contributes more than US$1500 million per annum to the economy of South Africa (Turpie &

Ryan 1999); and (iii) marine wildlife tourism contributes US$14 million per year to the Scottish Highlands and Islands (Everett 1998).

A single male black-winged stilt *Himantopus himantopus* that since 1993 has been resident at the Royal Society for the Protection of Birds (RSPB) reserve at Titchwell, UK has been argued to be the most watched bird in Britain, and is estimated to have been seen by more than half a million people.

4.3 Indirect-use value

The biota annually cycles gigatonnes (10^{15} g) of elements such as carbon, hydrogen, nitrogen, oxygen, phosphorus and sulphur, and teragrams (10^{12} g) of aerosols and particles among the atmosphere, hydrosphere (the waters) and lithosphere (the solid matter forming the Earth's crust; Naeem 2002). Such biogeochemical cycling modifies physical and chemical conditions, creating an environment that sustains life. Indeed, in the absence of life, Earth would be a very different place. In particular, it has been estimated that the atmospheric gas composition would be radically altered, and surface temperatures and pressures dramatically heightened (Table 4.1).

The indirect-use value of biodiversity derives from the many functions that it performs in providing services that are crucial to human wellbeing (Table 4.2; Westman 1977; Ehrlich & Ehrlich 1992; Chapin et al. 1997; Daily 1997). These services can in some sense be regarded as being 'free', in that they tend not to be the subject of direct trading in the marketplace, although such a perception has proven detrimental to their maintenance. Alongside those that are perhaps more readily recognized, such as nutrient cycling and soil formation, there are numerous other ecosystem

Table 4.1 Differences between the atmospheric gas composition, surface temperature and pressure of Venus, Earth as it is, and Mars, and estimations of what these would be like if Earth was without life. (From Lovelock 1989.)

	Venus	Earth as it is	Mars	Earth without life
Carbon dioxide	96.5%	0.03%	95%	98%
Nitrogen	3.5%	79%	2.7%	1.9%
Oxygen	Trace	21%	0.13%	0.0%
Argon	70 ppm	1%	1.6%	0.1%
Methane	0.0	1.7 ppm	0.0	0.0
Surface temperature (°C)	459	13	−53	240–340
Total pressure (bars)	90	1.0	0.0064	60

Table 4.2 Some ecosystem services provided by biodiversity.

Atmospheric regulation
Climatic regulation
Hydrological regulation
Nutrient cycling
Pest control
Photosynthesis
Pollination
Soil formation and maintenance

services. For example, many non-commercial species of marine molluscs and crustaceans may not be used directly themselves, but may nonetheless constitute an essential food source for many economically important fish species. The value of these invertebrates is indirect as they derive their value (in an economic sense) from the fish. Likewise, declines in the diversity and numbers of wild bees in many areas (often as a product of habitat destruction) have drawn attention to their agricultural significance as pollinators, and to the adverse effects on crop yields of these losses (O'Toole 1993).

Some natural environments have both a direct and an indirect value. Take, for example, a tropical forest. This may provide a number of direct-use values, including those of timber, medicinal plants, other forest products, hunting and fishing, recreation and tourism. It may also provide indirect-use values, including soil conservation and soil productivity, and watershed protection (with consequences for water supply and storage, flood control, climate, and carbon sequestration; Perrings 1995). The value of the forest for its indirect uses tends, however, vastly to exceed that for direct uses, giving it greater global than local value, and tending to make it more vulnerable to clearance by local people (Godoy et al. 2000). In practice, of course, ecosystem services are essential for the maintenance of all direct-use values.

Indirect-use values are more difficult to quantify or cost than direct-use values and in some cases it may be difficult to recognize, let alone explain, them. There have nonetheless been some, inevitably extremely contentious, attempts to estimate the aggregated annual value of nature's services (Costanza et al. 1997; Pimentel et al. 1997; see also Pimm 1997). These suggest figures similar in magnitude to, larger than, or a large proportion of, the global total annual gross national product, albeit there is nowhere one could purchase a replacement set of such services. The overall benefit : cost ratio of an effective programme for the conservation of remaining natural ecosystems has been estimated at, at least, 100 : 1 (Balmford et al. 2002).

The need to maintain biodiversity because of the services it provides was graphically illustrated in the Biosphere 2 experiments (Cohen & Tilman 1996). Biosphere 2 is the world's largest closed-environment facility, a 3.15 acre area, containing soil, air, water, plants and animals. Roughly US$200 million was invested in its design and construction, millions more in its operation (annual energy investments exceeded US$1 million), and it drew on immense technological resources and expertise. Nonetheless, it proved impossible to create a materially closed system that could support eight humans with adequate food, water and air, for 2 years. Surprise changes in the environment included a dramatic fall in oxygen levels and rise in carbon dioxide, a rise in nitrous oxide (N_2O) concentrations, overloading of water systems with nutrients, and the extinction of all pollinators. In short, with all human technology, ingenuity and unlimited (compared with normal science budgets) financial resources, a system could not be built that will provide eight humans, let alone humankind, with the life-supporting services that natural ecosystems provide for free.

Humans do not live within glasshouses, however large. But, a high proportion lives in cities. These draw on ecosystem services over large areas. Thus, the 29 largest cities in the Baltic Sea region have been estimated to draw ecosystem support services from areas at least 500–1000 times larger than the areas of the cities themselves (Folke et al. 1997). Average residents of North America, Europe, Japan and Australia require the biophysical output (an 'ecological footprint') of 5–10 ha of biophysically productive land and water each to support their consumer lifestyles (Rees 2001).

4.3.1 Biodiversity and ecosystem function

Whilst the importance of biodiversity for ecosystem functions is evident, it is less obvious how much biodiversity is required to provide those functions. Indeed, the relationship between levels of biodiversity and ecosystem functioning has emerged as a dominant issue in ecology (Chapin et al. 1998; Loreau et al. 2001). Numerous hypothetical ways have been identified in which varying levels of biodiversity may influence ecosystem functioning (Martinez 1996; Schläpfer & Schmid 1999). However, in addition to the null hypothesis of no effect, there are three principal ways in which ecosystem processes might respond to reductions in species richness (Lawton 1994; Johnson et al. 1996).

1 *Redundancy*. Beyond some minimum number of species necessary to carry out basic ecosystem processes, most species are equivalent and their loss of little significance (Fig. 4.1a).

2 *Rivet-popping*. Likening the species in an ecosystem to the rivets holding together an aeroplane, the loss of a few species may have no apparent effect, but beyond some threshold losses, the ecosystem processes will fail (Fig. 4.1b; Ehrlich & Ehrlich 1981).

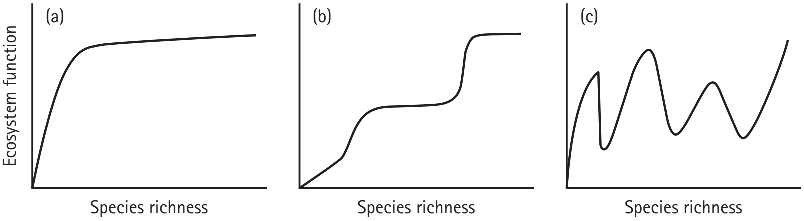


Fig. 4.1 Three possible relationships between species richness and ecosystem function: (a) redundancy; (b) rivet-popping; and (c) idiosyncrasy. (From Naeem 1998.)

3 *Idiosyncrasy*. As diversity changes so does ecosystem function, but the magnitude and direction of change is unpredictable because individual species have complex and varied roles (Fig. 4.1c; Lawton 1994).

There have been a large number of experiments conducted (in the laboratory and in the field) to differentiate amongst these possibilities, with the most common approach being to create replicate assemblages of different numbers of species and to measure the associated ecosystem functioning (Naeem et al. 1994, 1995; Tilman et al. 1996; Schwartz et al. 2000; Díaz & Cabido 2001). The design and the interpretation of the results of some of these studies have been extremely contentious. Although other outcomes have also been reported, a number of experiments have found that ecosystem functioning increases from assemblages of very small to small numbers of species, with the effect diminishing as species numbers increase further (Fig. 4.2), suggesting some degree of ecological equivalency amongst species (redundancy).

Three mechanisms have been proposed to explain why there should be a relationship between biodiversity and ecosystem functioning (Naeem 2002).

1 *Sampling effect*. If in a regional pool of a large number of species some have strong impacts on ecosystem processes, then the more species that are drawn from this pool to form a local assemblage the greater the probability that some of these strongly impacting species will be included.

2 *Species complementarity*. If species differ in their resource use, then the more species that are included in a local assemblage the more thoroughly will the available set of resources be exploited, with the actions of different species complementing one another.

3 *Positive interactions*. Increasing numbers of species in a local assemblage could result in increases in the number of mutual, facultative or positive indirect effects among them, increasing ecosystem functioning.

In practice, all three of these mechanisms may often be operating, with the research challenge being to find ways to determine their relative contribution to ecosystem functioning. Understanding the relationship between biodiversity and ecosystem functioning is, however, further

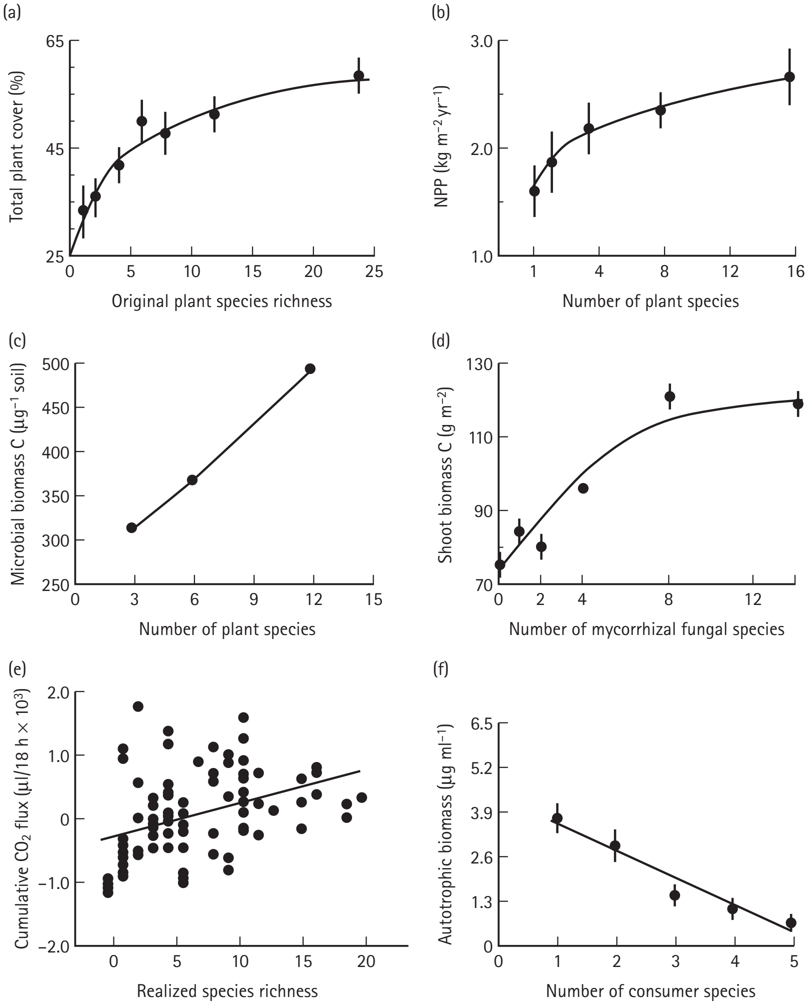


Fig. 4.2 Experimental evidence that biodiversity affects ecosystem processes. Relationships between: (a) plant species richness of experimental grassland plots in Minnesota and percentage of the ground covered with vegetation, a proxy for plant production; (b) plant species richness of experimental old-field ecosystems and net primary production (NPP); (c) plant species richness in Mediterranean herbaceous ecosystems and microbial biomass, a proxy for microbial production; (d) mycorrhizal fungal species richness and shoot biomass, a proxy for plant production; (e) microbial species richness in microcosms and carbon dioxide flux; and (f) heterotrophic protist richness (bacterivores, algavores, omnivores) in microcosms and autotrophic (green alga) biomass, a proxy for production. (From Naeem 2002; based on studies by Tilman et al. 1996, McGrady-Steed et al. 1997, Naeem & Li 1997, Chapin et al. 1998 and Van der Heijden et al. 1998.)

complicated by the temporal dynamics of ecological systems. This may mean that as conditions change different species become more or less important contributors to ecosystem functioning, with the importance of biodiversity lying not simply in how many species are present at a given time but in the maintenance of a pool of species that can buffer a system against the vagaries of an uncertain world (an insurance effect; McGrady-Steed et al. 1997). There seems little doubt that higher species richness increases both species redundancy and temporal resilience of ecosystem functioning, thereby increasing the reliability of that functioning (Naeem 1998).

4.4 Non-use value

Non-use value is that associated with biological resources even if they are not directly or indirectly exploited. Non-use value can be divided into at least four components: (i) option value; (ii) bequest value; (iii) existence value; and (iv) intrinsic value.

4.4.1 Option value

In addition to the necessity that biodiversity be maintained for its current direct- and indirect-use value, one might equally argue that it should be retained for the options for future use or non-use that it provides (Weisbrod 1964). There is, for example, huge unexploited potential for the use of biodiversity, particularly with the possible medicinal and industrial uses of much of the variety of life remaining unexplored. This potential should be valued, and may be vital as the problems faced by humanity change in nature and magnitude. Option value may include the knowledge (of practical or heuristic significance) embodied in organisms, in as much as the loss of a species represents the loss of information (Morowitz 1991).

4.4.2 Bequest value

Closely related, but distinct from option value, is bequest value. This is the value of passing on a resource, in this case biodiversity, intact (or as near as possible) to future generations (Krutilla 1967). The philosopher John Locke suggested that each generation should bequeath ‘enough and as good for others’ to future generations not just because they should, but because justice demands it. The modern version of this is the slightly more elaborated ‘justice as opportunity’ view that says we should compensate our children in the future for the loss of wealth, production or ecosystem services for which the present generation is responsible.

This notion is embodied in the final section of the Preamble to the Convention on Biological Diversity, which states that contracting parties are 'determined to conserve and sustainably use biological diversity for the benefit of present and future generations'.

4.4.3 Existence value

All of the values of biodiversity considered thus far in this chapter have been based, in one way or another, on marketable commodities and non-market goods and services. They assume that value is expressed solely in terms of the wellbeing of humanity. However, biodiversity may equally be seen as having value to people irrespective of the uses to which it may or may not be put. That is, value may be placed simply on its existence. For example, the continued persistence in the wild of many species of large-bodied mammals, such as the giant panda *Ailuropoda melanoleuca*, tiger *Panthera tigris* and killer whale *Orcinus orca*, is valued by sectors of the human population, despite the fact that these species are unlikely ever actually to be seen by many of these individuals. Indeed, substantial sums of money are contributed by them towards maintaining populations of such species. Wilson (1984) believes that humankind recognizes and has empathy with other bearers of life ('biophilia'), and that this naturally predisposes them to an appropriate care of, and for, biodiversity in all its multifaceted forms.

4.4.4 Intrinsic value

Direct- and indirect-use values, and option, bequest and existence non-use values rest on human judgements of worth. Whether from a philosophical perspective values can exist independently of such judgements is a contentious issue; however if they can, then biodiversity may be seen to have an intrinsic value. The view that such a value exists seems to be deeply rooted in many societies, cultures and faiths. Logically it leads to an absolute moral responsibility to protect other species, our only known living companions (deities aside) in the universe (Ehrlich & Wilson 1991). Indeed, the notion of an intrinsic value to biodiversity (or components thereof) is found in many regional and global treaties for conservation. The opening section of the Preamble to the Convention on Biological Diversity recognizes the 'intrinsic value of biological diversity and of the ecological, genetic, social, economic, scientific, educational, cultural, recreational and aesthetic values of biological diversity and its components'.

To some, listing intrinsic value first is a true reflection of its significance. Placing it last in this chapter is not intended to convey the converse message.

4.5 Summary

1 Direct-use values of biodiversity are concerned with the consumption or production of marketable commodities. These include food, medicine, use in biological control, industrial raw materials, recreational harvesting and ecotourism. Many present patterns of exploitation are not sustainable.

2 Indirect-use values of biodiversity are more difficult to quantify, not being subject to direct trading in the marketplace, but are nonetheless real and important, embracing the services provided by biodiversity which are crucial for human wellbeing.

3 It is not currently possible to build artificial systems that could provide us with the life-supporting systems that natural systems provide us 'for free'.

4 Ecosystem functioning increases from assemblages of very small to small numbers of species, with the effect diminishing as species numbers increase further, suggesting some degree of ecological equivalency amongst species.

5 Higher species richness increases both species redundancy and temporal resilience of ecosystem functioning, thereby increasing the reliability of that functioning.

6 Apart from present-day use values, biodiversity may have a variety of non-use values, including option value (for future use or non-use), bequest value (in passing on a resource to future generations), existence value (value to people irrespective of use or non-use) and intrinsic value (inherent worth, independent of that placed upon it by people).

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Pearce, D. (1998) *Economics and Environment. Essays on Ecological Economics and Sustainable Development*. Edward Elgar, London. (*Interesting, engaging and provocative view of environmental economics, even if you will not always agree with the views expressed.*)

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5 Human impacts

5.1 Introduction

Although it is essential to humankind, brings innumerable benefits, and has other important values, humans have had strong negative impacts on biodiversity. Indeed, whilst over geological time the general trend has been towards an overall net increase in biodiversity, the late Quaternary has been a period of marked decline, as both a direct and indirect consequence of human activities. This decline comprises all those changes that are associated with reducing or simplifying biological heterogeneity, from genes to ecosystems.

In this chapter we consider the negative human impacts on biodiversity, concentrating particularly on the loss of species. First, we address the level of those losses (Sections 5.2 & 5.3). Second, we examine the four principal proximate causes of the losses, namely overexploitation, habitat loss and degradation, introduced species, and extinction cascades (Section 5.4). Third, we consider the ultimate causes of the impacts of humans on biodiversity, namely the size of the human population, the growth in that population, and the scale of the human enterprise (Section 5.5).

5.2 Species extinctions

The best-known and most widely discussed impact of human activities on biodiversity has been that of the extinction of species. The loss of species seems to capture the public imagination, perhaps because of its irreversibility and the extraordinary nature of some of those species that have met their demise. In addition, species extinctions constitute the obvious, as well as a genuinely useful, barometer of change in biodiversity when this is measured in terms of species richness.

5.2.1 Prehistoric times

The impacts of humankind on other species have lasted for a long time, probably for much of the 100,000–200,000 years for which anatomically modern humans have existed. Although there remains some important debate on the issue, early humans may well have contributed significantly to the extinction of many large-bodied species of birds and mammals, and perhaps other groups, during the late Pleistocene (by some 10,000 years before the present (BP), all the major land masses except Antarctica had been colonized, some for a considerable period, and humans were exerting significant environmental effects). Apparently, broadly coincident with the arrival of humans in different major land masses, much of the megafauna disappeared, suggesting that they were either hunted to extinction (or perhaps close to the brink, with other factors finally tipping them over) or were brought to extinction by anthropogenic ecosystem disruption (Martin 1984, 2001; MacPhee 1999; Miller et al. 1999; Flannery 2001; R.G. Roberts et al. 2001; but see Grayson 2001; Brook & Bowman 2002). Doubtless, these extinctions were accompanied by many others, of which we remain unaware because of the inadequacies of the subfossil record.

The effects of early human activities on the biota are perhaps most graphically demonstrated by the large numbers of avian (and some other) extinctions that followed the colonization of tropical Pacific islands by prehistoric peoples, an expansion that began perhaps 30,000 years BP and was almost complete by 1000 years BP. The combined effects of resource exploitation, deforestation and the introduction of alien species led to roughly half the land bird species on each island group being exterminated (Milberg & Tyrberg 1993; Pimm et al. 1995b; Steadman 1995). The proportion of the avifauna on selected Pacific island groups that has recently become extinct, or is now endangered or in immediate danger of extinction, is less where human occupancy has been longest. This suggests that those areas colonized first have already lost most of the species that are sensitive to human activities (Fig. 5.1), although the time-lapse between human arrival and major extinction events was highly variable on oceanic islands (Steadman et al. 2002). A conservative estimate may be that an average of 10 sea- or land bird species or populations were lost from each of the approximately 800 islands of Oceania alone, giving an overall loss of 8000 species or populations (Steadman 1995). With one to

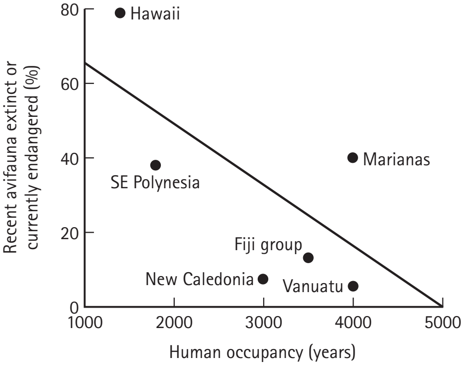

Fig. 5.1 Relationship between the percentage of the recent avifauna of Pacific islands that is extinct or currently endangered and the duration of human occupancy of those islands. The Marianas have an unusually high number of modern losses, as a result of recent colonization by the brown tree snake. (From Pimm et al. 1995b.)

four endemic rail species per island, 2000 species of rails may have been lost alone, which contrasts with the 133 extant species, a number of which are regarded as being highly threatened. It is not difficult to conceive that globally, perhaps a half of all recent bird species have already been driven extinct, at least in part as a consequence of human activities.

It is difficult to comprehend how differently the biota of Earth would have looked when all of these species were still extant. The diversity that we now find so impressive is, at least in terms of the vertebrates that attract so much attention, but a pale shadow of what it would have been without the losses that early humans directly and indirectly wrought. Some of these extinct species, and those which have subsequently been lost, doubtless contributed much to the shaping of environments and the communities associated with them, begging the question of what would truly natural assemblages have looked like? Whether terrestrial or marine, big animals, for example, may consume large quantities of vegetation or large numbers of smaller animals, and may physically disturb the habitat in profound ways. In terrestrial systems many of these big animals have been lost, and in marine ones they are now often ‘ecologically extinct’ (e.g. species of large sharks and rays, turtles, manatees and dugongs), in as much as their numbers have been reduced to the point where they no longer have major ecological impacts (Jackson & Sala 2001; Jackson et al. 2001).

5.2.2 1600 onwards

Species losses did not end when the primary phase of human colonization of the planet was largely complete. Since 1600 (a date after which the availability of contemporary information improves markedly) there have been over 1000 recorded extinctions of plant and animal species (see Table 5.1 for numbers in some groups). Roughly a half of these took place in the last century. There has been a significant rise in the rate of recorded

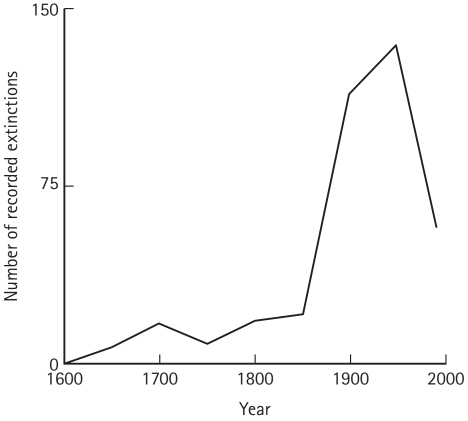

Fig. 5.2 The number of recorded global extinctions of animal species since c. 1600, for which a date is known. (From Smith et al. 1993.)

species extinctions for well-known groups of animals over the past 400 years, with a sharp increase in the 19th century coinciding with European colonial expansion (Fig. 5.2). A global decline in the recorded rate since about 1950 may perhaps in part reflect the growth of conservation activities, but more likely is due to the introduction of more stringent criteria for deciding that a species is genuinely extinct (rather than that it has simply gone unrecorded). For example, the present IUCN (The World Conservation Union) (1994) criteria define a species as extinct 'when there is no reasonable doubt that the last individual has died' and as extinct in the wild when the species is 'known only to survive in cultivation, in captivity or as a naturalised population (or populations) well outside the past range. A taxon is presumed extinct in the wild when exhaustive surveys in known and/or expected habitat, at appropriate times (diurnal, seasonal, annual) throughout its historic range have failed to record an individual'. Thus considerable time and effort is required to substantiate an extinction, particularly where the potential habitat for a species is extensive or difficult to access.

Interesting as the data on recorded extinctions may be, they undoubtedly underestimate the true levels of species losses. There are several reasons for believing this to be so.

1 Available information on extinctions is strongly biased towards higher plants, birds and mammals, which have been better studied, and away from groups such as fungi, lower plants and invertebrates, which have been more poorly studied. For example, most extant species of birds and mammals have host-specific lice and fleas, and probably in many cases also specific microbial symbionts. Thus, presumably the extinction of every avian and mammalian species has been accompanied by the loss of at least one other species. However, these so-called coextinctions have tended to pass undocumented (Stork & Lyal 1993), and despite the recognition of 128 bird and 83 mammal species extinctions, the IUCN

2000 Red List (Hilton-Taylor 2000) includes no extinct lice or flea species. Whilst different taxa may genuinely have suffered rather different recent rates of extinction, the wide disparities that are observed in numbers of recorded extinctions represent an artefactual distortion (McKinney 1999).

2 Available information on extinctions is strongly biased towards islands (71.6% of mammalian species extinctions since 1500 are for island species; MacPhee & Flemming 1999) and developed nations. In both cases this is in part because such extinctions have been easier to document, given the high levels of endemism commonly associated with islands and the longer period of formal study of the biotas of developed nations. It is also because island biotas may be more vulnerable to processes that drive extinctions (in the face of threatening processes, island endemic species may have no refuges), and the biotas of developed nations tend to be relatively species poor and to have experienced the consequences of that human development (extant species may simply be those that were more resilient to extinction).

3 Available information on extinctions is strongly biased towards terrestrial and freshwater species, and away from marine ones. Few marine species have been documented as having been lost. On the one hand, the paucity of documented extinctions of marine species could be because they are genuinely less likely to become extinct, perhaps because of the greater contiguity of the oceans compared with the continents and the resultant larger geographic ranges of marine species. On the other hand, this could be because extinctions in the oceans are hard to document. Both explanations are probably true, as evidenced by the longer average duration of marine species in the fossil record compared with terrestrial ones (McKinney 1998).

4 It is almost invariably assumed that a described species is extant unless sufficient evidence is accrued to show that it is extinct. Museum collections, for example, contain specimens of many species that have not been seen since they were originally collected or at least for a number of decades, and yet because no active search has been made to find them it is assumed that they are extant. Presumably, many of these have actually been lost, given that often the original habitat in the areas they were collected has entirely disappeared. Diamond (1987) observed that at that time (doubtless things have changed a little since), if one followed the assumption ‘extant unless proven extinct’ then one bird species has recently gone extinct in the Solomon Islands, but if one followed the assumption ‘extinct unless proven extant’ then up to 12 species may be extinct or endangered, with the latter figure likely to be closer to the real one.

5 Unless a species is known to science, then its extinction will pass unrecorded. Because the majority have remained undescribed (Section

2.4) and much severe habitat loss has taken place in regions for which biological inventories were previously poorly developed, then it follows that many particularly localized species may have become extinct without us being aware even of their existence (Hughes et al. 1997; Prance et al. 2000).

5.2.3 The future

Merely recording numbers of extinctions that have thus far occurred may underestimate the effects of past human activity on species losses, through a process known as extinction debt. Individuals of large-bodied species, for example, may persist after the populations to which they belong have ceased to be viable (they can no longer be self-sustaining), because they are long-lived. The species is effectively extinct; it just doesn't know it yet! Brooks and Balmford (1996) document an example of extinction debt in the Atlantic forests of South America. Here, whilst nearly 90% of the forest has been cleared, no bird species has so far been shown to have become extinct as a result, contrary to the predictions of species–area relationships (Section 3.2.1). However, the number of species presently recognized as being highly threatened with extinction is similar to that predicted to become extinct from deforestation. It would seem that without immediate conservation action these species will inevitably soon be lost.

More generally, information on the numbers of species that have been listed as being threatened with global extinction in the near future provides one of the bases for estimating the scale of impending extinctions (although given the time required for sufficient evidence of extinction to accumulate, some of these species are certainly already extinct). The most recent figures for plants and animals are given in Table 5.1. These are again highly biased, and in much the same ways as are those of recorded extinctions. Only for birds and mammals has the threat status of virtually all extant species been evaluated. In the former case, more than 10% of species have been identified as at threat of global extinction; in the latter case, about 25% have been recognized as such. An estimate for plants has suggested that as many as a half of extant species may qualify as threatened with extinction were it possible to evaluate them (Pitman & Jørgensen 2002).

As discussed earlier (Section 2.3.3), the average life span of any species in the fossil record is estimated to be around 5–10 Myr. For birds and mammals, rates of documented extinction over the past century correspond to species life spans of around 10,000 years (May et al. 1995). Although the calculations are inevitably very rough and ready, projection of impending extinctions, if current trends continue, suggest a life span for bird and mammal species of 200–400 years! These figures may

Table 5.1 Summary of the numbers of species in each of the plant and animal taxonomic classes which are listed as extinct, extinct in the wild (the species has been extirpated from its natural habitat), or globally threatened with extinction. (Adapted from Hilton-Taylor 2000.)

	Extinct	Extinct in the wild	Threatened
Plants			
Bryopsida	2	0	36
Anthocerotopsida	0	0	2
Marchantiopsida	1	0	42
Coniferopsida	0	1	140
Ginkgoopsida	0	0	1
Magnoliopsida	69	14	5099
Liliopsida	1	2	291
Total	**73**	**17**	**5611**
Animals			
Anthozoa	0	0	2
Turbellaria	1	0	0
Enopla	0	0	2
Gastropoda	260	12	846
Bivalvia	31	0	92
Polychaeta	0	0	1
Oligochaeta	0	0	5
Hirudinoidea	0	0	0
Onychophora	3	0	6
Merostomata	0	0	0
Insecta	72	1	555
Crustacea	8	1	408
Chilopoda	0	0	1
Arachnida	0	0	10
Echinoidea	0	0	0
Sarcopterygii	0	0	1
Actinopterygii	80	11	709
Elasmobranchii	0	0	39
Cephalaspidomorphi	1	0	3
Amphibia	5	0	146
Reptilia	21	1	296
Aves	128	3	1183
Mammalia	83	4	1130
Total	**693**	**33**	**5435**

perhaps be regarded as representative of a broad range of organisms, in which case impending extinction rates are at least three to four orders of magnitude faster than background rates seen in the fossil record. To put this into perspective, consider the following analogy (modified from Dunning 1997). Human death rates in populations not subject to war or famine are often in the range of 10–20 deaths per 1000 individuals per annum (in a stable population, average life span = 1/death rate, so this equates to life spans of 50–100 years). If that rate were increased by 1000 times, then everyone would die in the first year.

By comparison with most of those species that have been driven extinct or to the brink of extinction, *Homo sapiens* is a rather recent addition to the Earth. Species that have existed for millions of years are being erased by one that has existed for a fraction of that time.

5.3 Populations, individuals and genetic diversity

The listing of a species as having a significant risk of extinction in the near future is commonly associated with it having suffered a decline in population or geographic range size. In other words, it has undergone a loss of local populations, a decline in the numbers of individuals in remaining populations, or both. Such losses and declines are being experienced by huge numbers of species, whether these are sufficient for them to be listed as threatened by global extinction or not. For example, amphibian population declines are a global problem, with causes that may include ultraviolet radiation, predation, habitat modification, environmental acidity and toxicants, diseases, changes in climate or weather patterns, and interactions among these factors (Alford & Richards 1999; Houlahan et al. 2000). Concerns have similarly been expressed about declines in the abundances of species in a wide range of groups, such as trees (Oldfield et al. 1998), sharks (Manire & Gruber 1990) and birds (Terborgh 1989). Hughes et al. (1997) estimate that in tropical forests, 1800 populations may be being destroyed per hour, 16 million annually. Gaston and Blackburn (2003) estimate that land-use change alone may have caused the overall global bird population to decline by a fifth to a quarter from pre-agricultural levels.

The extinction of individual local populations and declines in species' local abundances both represent potentially insidious forms of erosion of biodiversity (Ehrlich & Daily 1993; Ehrlich 1995; Ceballos & Ehrlich 2002). Population losses, in particular, will tend to reduce the taxonomic, genetic and functional diversity of sites (see Table 1.1), and perhaps the performance of ecosystems (Section 4.3), without initially necessarily contributing to the global species extinctions that attract the bulk of attention.

5.4 Threats to biodiversity

Species losses, and other declines in biodiversity, result from four main causes, namely: (i) direct exploitation; (ii) habitat loss and degradation; (iii) introduced species; and (iv) extinction cascades. These have been termed 'the evil quartet' (Diamond 1984). Whilst reasonably well characterized, the patterns and rates at which these drivers are changing are less well understood.

5.4.1 Direct exploitation

The most obvious way in which humans can cause the extinction of species is by exploiting their populations, either down to the last individual or down to such low numbers that they have a very high likelihood of becoming extinct by chance. The scale of human exploitation of some species is incredibly high, and is not sustainable. Here we give three examples.

1 *Bush meat*. Hunting of wildlife in tropical forests, principally for subsistence or commerce, is ubiquitous (Redford 1992). Indeed, for many species it is difficult to ascertain what their natural abundances would be in the absence of such pressure, because places without the pressure do not exist. For example, 9.6–23.5 million reptiles, birds and mammals, or 67–165 thousand tonnes, have been estimated to be consumed per annum in the Brazilian Amazon (Peres 2000). Demand is increasing as tropical forests become more accessible to hunters, effective human population densities increase, people become more sedentary, traditional hunting practices change, the meat trade becomes more commercial, and demand increases from urban centres for wild meat (Robinson & Bodmer 1999). The use of mathematical models demonstrates that this harvest is not sustainable, particularly because of the low annual production rates of large mammals in tropical forests. Fa et al. (2002) estimate that the mammal production rates in the Congo Basin and the Amazon Basin are about 2.1 and 1.8 million tonnes per year, with extraction rates being 4.9 and 0.15 million tonnes per year respectively. This means that Congo Basin mammals must annually produce 93% of their body mass to balance current extraction rates, whereas Amazonian mammals must produce only 4%. **2** *Fuelwood*. More than 2 billion people (about a third of the present total) are estimated to depend directly for their primary or sole source of energy on biomass fuels, including woodfuels (fuelwood, charcoal, etc.), agricultural residues, and animal wastes (United Nations Development Programme et al. 2000). Of these, fuelwood is the dominant form of biomass energy in many, predominantly developing, countries. Supplies have decreased significantly in many areas in recent decades, with members of some communities having to travel substantial distances to obtain material. Although globally this has to some degree been offset by pro-

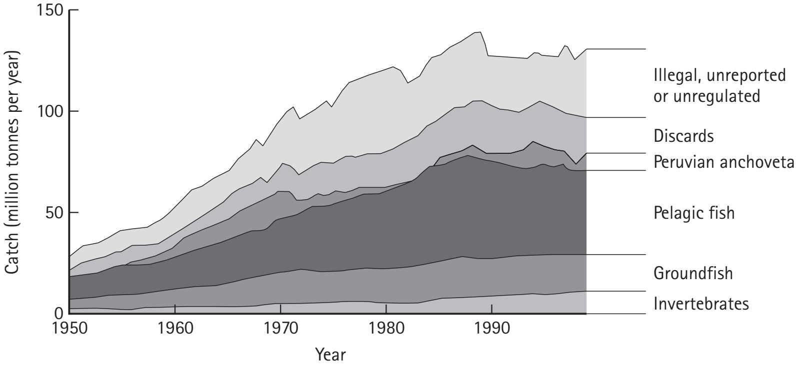

Fig. 5.3 Estimated global fish landings for 1950–99. (Note that the estimates for illegal, unreported or unregulated fish landings are very tentative.) (From Pauly et al. 2002.)

grammes of tree planting, woodfuel demand by 2010 is forecast to be 2.4–4.3 billion m^3 compared with an estimated availability of 2.3–2.4 billion m^3 of fuelwood and charcoal combined.

3 *Marine fisheries*. The 1950s and 1960s saw a huge increase in global fishing effort, fuelled in large part by its industrialization, which gave rise to rapid increases in catches (Fig. 5.3). The first major stock collapse was that of the Peruvian anchoveta *Engraulis ringens* in 1971–72, which was accompanied by declining catches elsewhere, which accelerated in the late 1980s and early 1990s when cod *Gadus morhua* stocks off New England and eastern Canada collapsed (Pauly et al. 2002). Global fishing effort, nonetheless, continued to expand, such that by the mid-1990s a high proportion of stocks had collapsed or were being exploited beyond sustainability (Fig. 5.4). Reported world fisheries landings have been declining slowly since the late 1980s by about 0.7 million tonnes per annum (Watson & Pauly 2001; Pauly et al. 2002). Fisheries have increasingly been 'fishing down marine food webs', as large long-lived predatory fish have been removed and those at lower trophic levels exploited (Pauly et al. 1998). They have changed the evolutionary characteristics of populations through size-selective harvesting (Conover & Munch 2002) and have placed the future persistence of some target species at risk (Hilton-Taylor 2000). Evidence suggests that although the effects of overfishing may be reversible, the time for stocks to recover may be considerable (Hutchings 2000). With declines of fisheries stocks in shallow waters, increasing emphasis has been directed towards deep-water fisheries, which are even less robust to such impacts (Roberts 2002). In addition to those on the stocks of target species, fishing has wider impacts, through: (i) the wholesale reorganization of the structure of remaining species assemblages as trophic interactions are disturbed; (ii) the huge amounts of by-catch of non-target species that are typically simply discarded (by-catch is

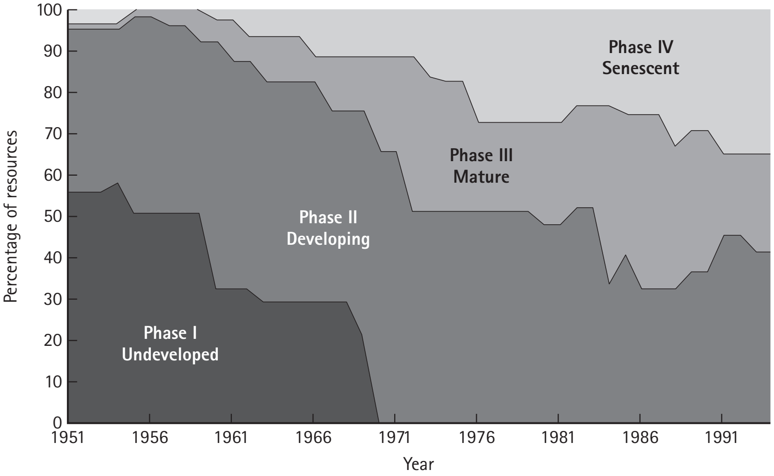

Fig. 5.4 Percentage of major marine fish resources in various phases of fishery development. In 1994 (the last data point shown), about 35% of the 200 major fishery resources were 'senescent' (showing declining yields), about 25% were 'mature' (plateauing at a high exploitation level), 40% were 'developing', and none remained undeveloped (at a low exploitation level). (From Grainger & Garcia 1996.)

in excess of 25 million tonnes per annum); (iii) the incidental capture and killing of other species (including seabirds, turtles, sea snakes, marine mammals, many of which are particularly vulnerable because they are long-lived and have low reproductive rates); (iv) the habitat destruction generated by some of the techniques employed (e.g. bottom-trawling); and (v) the environmental consequences of fishing debris (e.g. lost nets; Dayton et al. 1995).

Perhaps above all, the history of human exploitation of resources teaches us that the populations of even initially extremely abundant species can be reduced to low levels remarkably rapidly, and that the ease with which this can be achieved has grown with the march of technology. Unfortunately, in the short-term, from a strictly economic standpoint ('knowing the cost of everything and the value of nothing'?), non-sustainable use can in some cases still be regarded as a viable option. For example, from this perspective, the best harvesting strategy for biological populations with relatively low growth rates (e.g. whales) may be to exploit them to extinction. The revenue generated by this harvest when invested could conceivably yield a greater cash return than that generated by the sustainable harvest from the population (Clark 1981; Lande et al. 1994; May 1994c). Of course, this ignores both the direct- and indirect-use value (which may both be vital to sustain human populations) and the non-use value of biological resources, both in the short- and the long-term (we cannot conceive of the value that the continued existence of particular species may have in the future).

5.4.2 Habitat loss, fragmentation and degradation

Dramatic reshaping of the distribution of habitats or vegetation types has been a feature of much of the history of humankind, with habitat change as a consequence of the activities of prehistoric populations having been reported on numerous occasions (McGlone 1983; Kershaw 1986; McGlone & Basher 1995; Diamond 1998; Krech 1999; Pudjoarinto & Cushing 2001). Indeed, it has repeatedly been discovered that what had been held to be 'natural' landscapes had actually been much transformed by earlier human activities (for discussion see e.g. Isenberg 2000; Wilcove 2000).

At a broad scale, compared with an estimation of their extent before significant human disturbance, forest/woodland has declined in area by 29%, steppe/savannah/grassland by 49%, shrubland by 74%, and tundra/hot desert/ice desert by 14% (Fig. 5.5; Klein Goldewijk 2001). Cropland now covers 11% of the land surface, and pasture 23%. Human disturbance is evident in every biome on Earth, and in terrestrial systems is most marked in temperate broadleaf and evergreen sclerophyllous forests (< 6.5% relatively undisturbed; Table 5.2). Perhaps some of the most graphic evidence of such changes comes from contrasting the extent of the most speciose terrestrial environment, tropical forest, at different times, in particular areas of the world (Fig. 5.6). Most such forest clearance arises from pressures that are external to the ecosystem, particularly an undervaluing of the forest resource that encourages liquidation of the

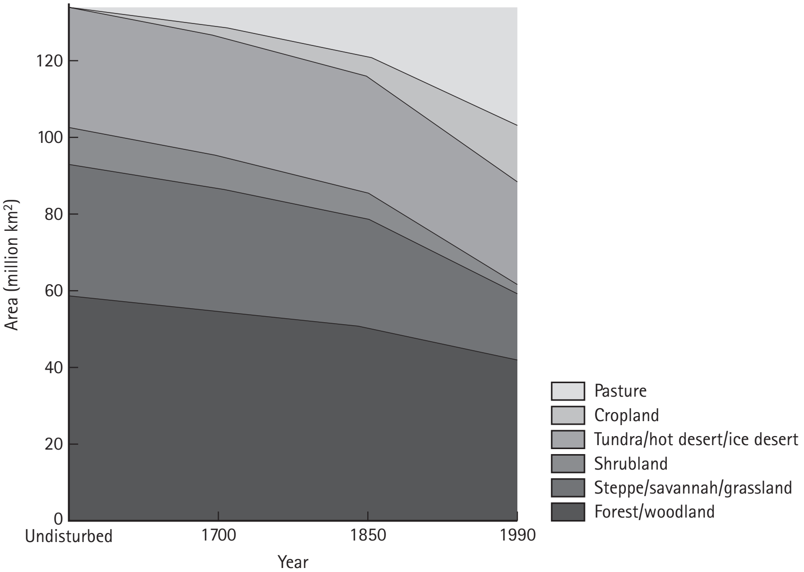

Fig. 5.5 Changes in the area of different land-use types from before significant human impact ('undisturbed') to the present. (Data from Klein Goldewijk 2001.)

Table 5.2 The pattern of human disturbance amongst biomes. Undisturbed areas have a record of primary vegetation and no evidence of disturbance, combined with a very low human population density. Partially disturbed areas have a record of shifting or extensive agriculture, evidence of secondary vegetation, livestock over carrying capacity or other evidence of human disturbance. Human dominated areas have a record of permanent agriculture or urban settlement, removal of primary vegetation or record of desertification or other permanent degradation. (From Hannah et al. 1995.)

Biome	Total area (km^2)	Percentage of undisturbed areas	Percentage of partially disturbed areas	Percentage of human dominated areas
Temperate broadleaf forests	9,519,442	6.1	12.0	81.9
Evergreen sclerophyllous forests	6,559,728	6.4	25.8	67.8
Temperate grasslands	12,074,494	27.6	32.0	40.4
Subtropical and temperate rain forests	4,232,299	33.0	20.9	46.1
Tropical dry forests	19,456,659	30.5	41.1	28.4
Mixed mountain systems	12,133,746	29.3	45.0	25.6
Mixed island systems	3,256,096	46.6	11.6	41.8
Cold deserts/semi-deserts	10,930,762	45.4	46.1	8.5
Warm deserts/semi-deserts	29,242,021	55.8	32.0	12.2
Tropical humid forests	11,812,012	63.2	11.9	24.9
Tropical grasslands	4,797,090	74.0	21.3	4.7
Temperate needleleaf forests	18,830,709	81.7	6.4	11.8
Tundra and Arctic desert	20,637,953	99.3	0.7	0.3

natural capital it provides and its replacement with agricultural systems that yield quicker returns (Noble & Dirzo 1997). This situation is acute in regions where immediate needs predominate, and future income is discounted at a high rate.

As predicted from species–area relationships (Section 3.2.1), land-use changes have brought about the loss of many species, and are the primary cause of species being listed as at high risk of extinction in the near future. Thus, globally 71% of freshwater fish species (excluding Lake Victoria cichlids, because of the complexity of their situation) that have recently become extinct have apparently done so for this reason (Harrison & Stiassny 1999), and 85% of bird and 47% of mammal species (not including most of the small mammals, because of insufficient data) are listed as being at risk on the same grounds (BirdLife International 2000; Mace & Balmford 2000). More than 100 species of birds are at threat as a result, at least in part, of each of 13 causes of habitat loss: selective logging/cutting, smallholder farming, plantations, clear-felling, arable farming/horticulture, livestock farming, infrastructure development, human

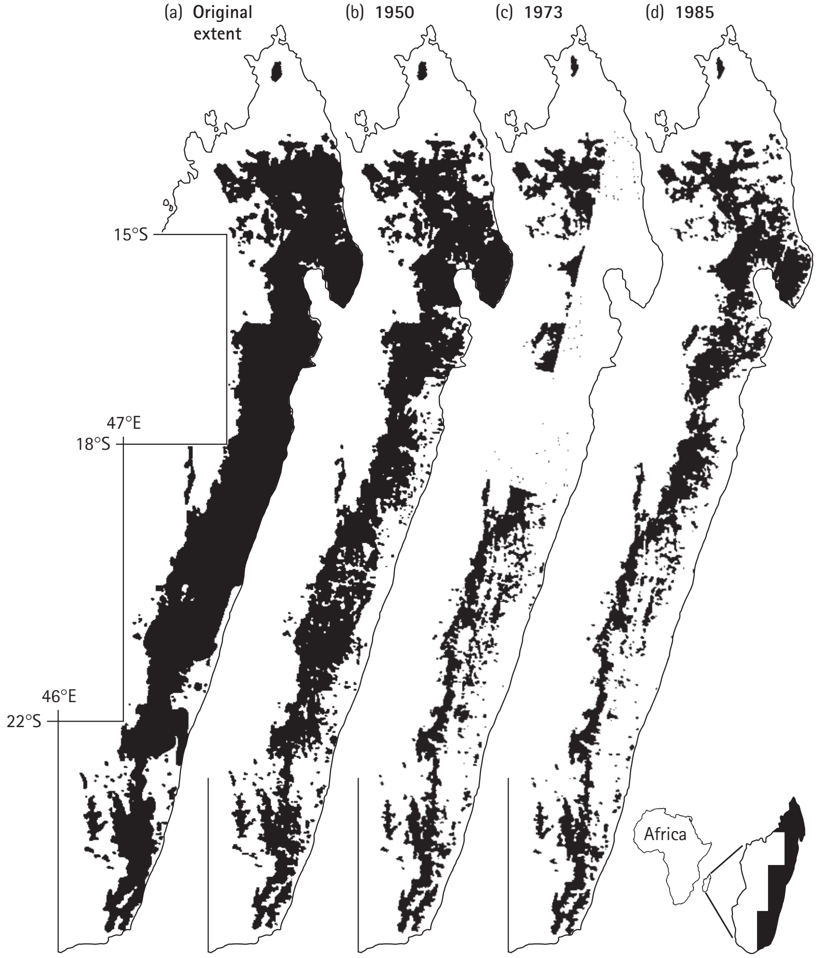

Fig. 5.6 Maps of the distribution of wet tropical forest in eastern Madagascar through time (extensive cloud cover permitted only partial mapping in 1973). The original cover of 11.2 million ha was reduced to 7.6 million ha by 1950, and to 3.8 million ha by 1985 (34% of the original). (From Green & Sussman 1990.)

settlement, grazing, shifting agriculture, deforestation with unknown causes, timber (firewood), and mining (BirdLife International 2000).

Substantial land-use change is predicted to continue into the future, not simply as a consequence of direct human activities, but also as a consequence of anthropogenic global climate change. The global average surface temperature has increased by approximately 0.6°C over the past 100 years, with most of the warming occurring during two periods, 1910–45 and 1976–2000 (Houghton et al. 2001). This temperature is projected to increase by from 1.4°C to 5.8°C over the period 1990–2100, based on a number of climate models, a rate much higher than observed during the 20th century and likely to be without precedent during at least the last 10,000 years (Houghton et al. 2001).

In large part, these changes result because human activities add carbon dioxide (CO_2) to the atmosphere by mining and burning fossil fuels, and by converting forests and grasslands to agricultural and other low biomass ecosystems (Vitousek et al. 1997a). Carbon dioxide is the principal 'greenhouse gas', although others make a contribution, including methane (CH_4), the chlorofluorocarbons (CFCs), ozone (O_3) and nitrous oxide (N_2O). Analysis of air bubbles extracted from ice cores from Antarctica and Greenland reveal that the atmospheric concentration of CO_2 was more or less stable for thousands of years, until about 1800, since when it has increased exponentially.

The distributions of a large number of species currently seem to be shifting in response to climate change (Kozár & Dávid 1986; Frey 1992; Parmesan 1996; Cannon 1998; Hill et al. 1999; Parmesan et al. 1999; Thomas & Lennon 1999; Burton 2001; McLaughlin et al. 2002), and many more are predicted to do so in the future (e.g. Beerling 1993; Huntley 1994; Brereton et al. 1995; Jeffree & Jeffree 1996; Nakano et al. 1996; Rogers & Randolph 2000). Other responses to climate change are also being documented. Thus, although there is regional variation, common shifts in phenology in Europe and North America include earlier breeding or first singing of birds, earlier arrival of migrant birds, earlier appearance of butterflies, earlier choruses and spawning in amphibians, and earlier shooting and flowering of plants (Walther et al. 2002; Root et al. 2003 and references therein).

Many of the changes that humans are making to the landscape involve not simply the reduction of the areas of some vegetation types and the expansion of others, but also the fragmentation of vegetation. This generates a landscape consisting of (often small) remnant areas of native vegetation embedded in a matrix of agricultural and developed land. Fragmentation results in change in the physical environment within patches (e.g. in fluxes of radiation, water and nutrients), in part because the size of areas of vegetation influences local climate, and because of the greater ratio of edge to area for smaller patches of vegetation which increases the potential for penetration by, and influence from, events and processes in the surrounding landscape. Changes in edge to area ratios may also increase pressure from invasive species, and other direct (e.g. hunting) and indirect (e.g. pollution) consequences of human activities. In addition, fragmentation causes biogeographic changes (e.g. in isolation and connectivity), which like its other consequences may be important influences on the size and composition of the biotas of the remnant patches (Saunders et al. 1991).

As well as changes in the pattern of coverage of different vegetation types, those areas that remain may for other reasons be degraded in terms

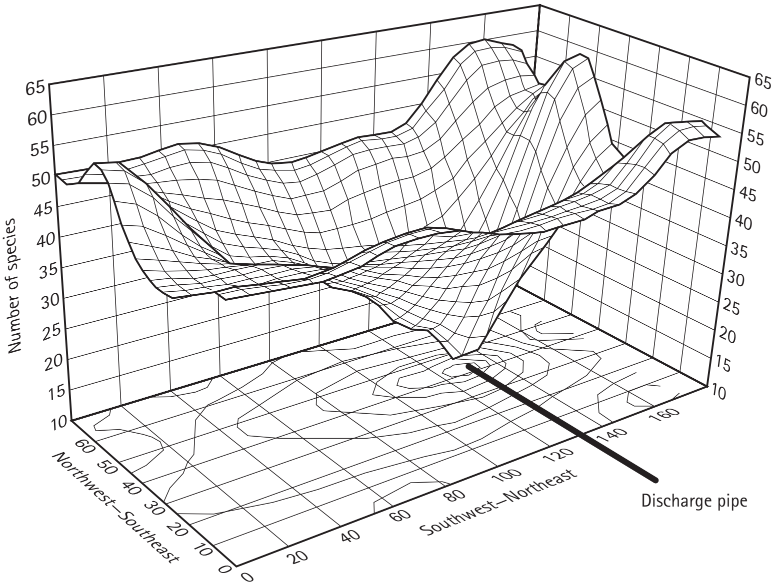

Fig. 5.7 A three-dimensional plot showing the depression of the numbers of microscopic sediment-dwelling species of meiofauna associated with an industrial effluent discharged to the outer reaches of a British estuary. The area shown is approximately 1.7 × 1.7 km. (From Anon. 1994.)

of their capacity to support populations of naturally occurring species (Fig. 5.7). That degradation may take many forms, including changes in the occurrence and abundance of many materials. For example, human activity has markedly altered the global nitrogen cycle, by fixing N_2 (combining it with carbon, hydrogen or oxygen), either deliberately (for fertilizer) or as a by-product of other actions (fossil fuel combustion). Now this activity adds at least as much fixed N to terrestrial ecosystems as do all natural sources combined (Vitousek et al. 1997a). The consequences include increasing atmospheric concentrations of the greenhouse gas N_2O, increasing fluxes of reactive N gases, contribution to acid rain and photochemical smog, increases in productivity of ecosystems where fixed N was in short supply resulting in losses of N and cations from soil, eutrophication of aquatic systems, and loss of biodiversity.

The sheer pervasiveness of such influences is well illustrated by the spread of materials that do not occur naturally. For example, brominated flame retardants are used in electronic equipment, such as computers and television sets, in textiles, cars and many other applications. They have been found to be present in sperm whales *Physeter macrocephalus* that normally stay and feed in deep water, suggesting that these compounds have reached these locations (de Boer et al. 1998).

Table 5.3 The numbers of native and established alien vascular plant species in selected continental and island floras. (Adapted from Vitousek et al. 1997b.)

Region	Native species	Alien species	Percentage of alien species
Russian Arctic	1403	104	6.9
Europe	11,820	721	5.7
USA	17,300	2100	10.8
Southern Africa	20,573	824	3.9
Australia	15,638	1952	11.1
British Isles	1225	945	42.9
Hawaii	1143	891	43.8
New Zealand	2449	1623	39.9

5.4.3 Introduced species

Since prehistoric times, human actions have served, intentionally or accidentally, to introduce non-domesticated species to areas in which they would not naturally have occurred, breaching many natural barriers to their dispersal. Ignoring domesticated species, the earliest known instance involves the introduction of a marsupial, the gray cuscus *Phalanger orientalis*, to New Ireland about 19,000 years ago (Grayson 2001). Perhaps some 400,000 species have now been introduced (Pimentel 2001). Often these constitute a high proportion of the species that occur in a given area (Table 5.3), and they continue to grow in number (Fig. 5.8). Introduced species are now widespread even in many nature reserves (e.g. Lonsdale 1999; Stadler et al. 2000; Pyšek et al. 2002; Sax 2002).

Such movements of species have been brought about by a multiplicity of routes, including intentional introduction for cultivation or sport, the transport of soil and ballast, the connection of waterways through canals, and the release or escape of pets. They reflect our choices as consumers, travellers, gardeners, and so on (Baskin 2002). Not infrequently, the numbers of introduced species in an area increase with the size of the human population, the duration of human occupation, and the numbers of visitors, all of which tend to increase the levels of such activities, and hence the likelihood and frequency with which individuals of given species arrive (Rapoport 1993; Chown et al. 1998; Lonsdale 1999; McKinney 2001). The numbers of introduced species in an area tend also commonly to be positively related to the number of native species, probably because the successful establishment of species of both groups responds to similar factors (e.g. Pyšek et al. 2002; Sax 2002).

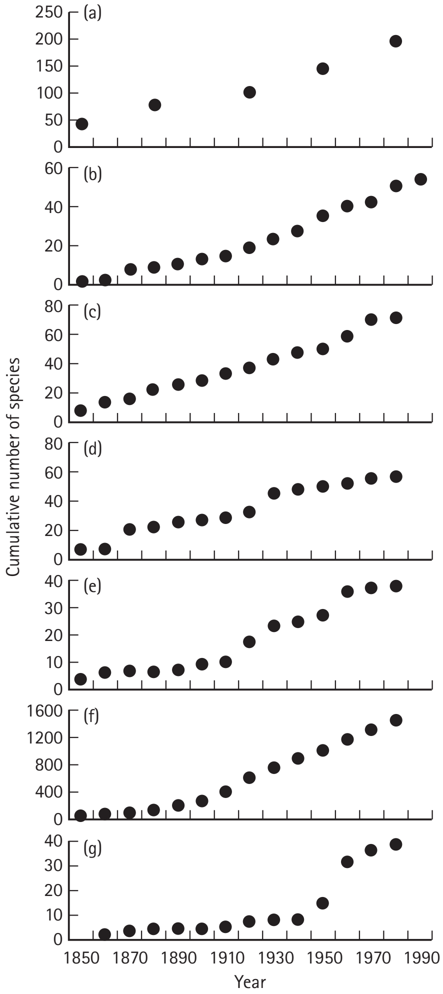

Fig. 5.8 Cumulative numbers of introduced species by decade of introduction for: (a) Illinois plants; (b) Great Lakes animals; (c) Great Lakes plants; (d) San Francisco Bay invertebrates; (e) Hawaiian birds; (f) North American insects; and (g) USA fish. (From Ruesink et al. 1995.)

Some introductions have enriched human existence and most invaders have minor consequences; Williamson (1996) suggests that as a useful rule of thumb, 10% of introduced invaders become established, and 10% of those established become pests. Unfortunately, the negative effects can be very large, and introductions have been described as constituting 'one of the great historical convulsions in the world's fauna and flora' (Elton 1958, p. 31). Introduced species can alter nutrient regimes, fire regimes, hydrology, or energy budgets, change vegetation or habitat, and drive changes in the abundance and distribution of native species, ultimately to extinction (Williamson 1996). Drawn from a wide diversity of groups (Table 5.4), they have thus become major agents of global change. Nearly a half of the threatened species of the USA, for example, are at risk at least in part because of the effects of alien species (Wilcove et al. 1998).

Table 5.4 One hundred of the world's worst invasive alien species. These were chosen according to their adverse effects on biodiversity and/or human activities and their illustration of important issues surrounding biological invasion. (From Baskin 2002.)

Disease agents	
Avian malaria	*Plasmodium relictum*
Banana bunchy top	Banana bunchy top virus
Chestnut blight	*Cryphonectria parasitica*
Crayfish plague	*Aphanomyces astaci*
Dutch elm disease	*Ophiostoma ulmi*
Frog chytrid fungus	*Batrachochytrium dendrobatidis*
Phytophthora root rot	*Phytophthora cinnamomi*
Rinderpest	Paramyxovirus
Aquatic plants	
Caulerpa seaweed	*Caulerpa taxifolia*
Common cordgrass	*Spartina anglica*
Wakame seaweed	*Undaria pinnatifida*
Water hyacinth	*Eichhornia crassipes*
Land plants	
African tulip tree	*Spathodea campanulata*
Black wattle	*Acacia mearnsii*
Brazilian pepper tree	*Schinus terebinthifolius*
Chromolaena (Siam weed, triffid weed)	*Chromolaena odorata*
Cluster pine	*Pinus pinaster*
Cogon grass	*Imperata cylindrica*
Fire tree	*Myrica faya*
Giant reed	*Arundo donax*
Gorse	*Ulex europaeus*
Hiptage	*Hiptage benghalensis*
Japanese knotweed	*Polygonum cuspidatum*
Kahili ginger	*Hedychium gardnerianum*
Koster's curse	*Clidemia hirta*
Kudzu	*Pueraria lobata*
Lantana	*Lantana camara*
Leafy spurge	*Euphorbia esula*
Leucaena	*Leucaena leucocephala*
Melaleuca	*Melaleuca quinquenervia*
Mesquite	*Prosopis glandulosa*
Miconia	*Miconia calvescens*
Mile-a-minute weed	*Mikania micrantha*
Mimosa (giant sensitive plant)	*Mimosa pigra*
Prickly pear cactus	*Opuntia stricta*
Privet	*Ligustrum robustum*
Pumpwood	*Cecropia peltata*
Purple loosestrife	*Lythrum salicaria*
Quinine	*Cinchona pubescens*
Shoebutton ardisia	*Ardisia elliptica*
Strawberry guava	*Psidium cattleianum*
Tamarisk (saltcedar, Athel pine)	*Tamarix ramosissima*

(*cont'd*)

Table 5.4 (*cont'd*)

Wedelia (Singapore daisy)	*Wedelia trilobata*
Yellow Himalayan raspberry	*Rubus ellipticus*
Aquatic invertebrates	
Chinese mitten crab	*Eriocheir sinensis*
Comb jelly	*Mnemiopsis leidyi*
Green crab	*Carcinus maenas*
Marine clam	*Potamocorbula amurensis*
Mediterranean mussel	*Mytilus galloprovincialis*
Northern Pacific seastar	*Asterias amurensis*
Spiny water flea	*Cercopagis pengoi*
Zebra mussel	*Dreissena polymorpha*
Land invertebrates	
Argentine ant	*Linepithema humile*
Asian long-horned beetle	*Anoplophora glabripennis*
Asian tiger mosquito	*Aedes albopictus*
Big-headed ant	*Pheidole megacephala*
Common wasp	*Vespula vulgaris*
Crazy ant	*Anoplolepis gracilipes*
Cypress aphid	*Cinara cupressi*
Flatworm	*Platydemus manokwari*
Formosan subterranean termite	*Coptotermes formosanus shiraki*
Giant African snail	*Achatine fulica*
Golden apple snail	*Pomacea canaliculata*
Gypsy moth (Asian and European)	*Lymantria dispar*
Khapra beetle	*Trogoderma granarium*
Little fire ant	*Wasmannia auropunctata*
Malaria mosquito	*Anopheles quadrimaculatus*
Red imported (tropical) fire ant	*Solenopsis invicta*
Rosy wolf snail	*Euglandina rosea*
Sweet potato whitefly	*Bemisia tabaci*
Amphibians	
Bullfrog	*Rana catesbeiana*
Cane toad	*Bufo marinus*
Caribbean tree frog	*Eleutherodactylus coqui*
Fish	
Brown trout	*Salmo trutta*
Common carp	*Cyprinus carpio*
Large-mouth bass	*Micropterus salmoides*
Mosquito fish	*Gambusia affinis*
Mozambique tilapia	*Oreochromis mossambicus*
Nile perch	*Lates niloticus*
Rainbow trout	*Oncorhynchus mykiss*
Walking catfish	*Clarias batrachus*
Reptiles	
Brown tree snake	*Boiga irregularis*
Red-eared slider turtle	*Trachemys scripta*

(*cont'd on p. 128*)

Table 5.4 (*cont'd*)

Birds	
Indian myna	*Acridotheres tristis*
Red-whiskered bulbul	*Pycnonotus cafer*
Starling	*Sturnus vulgaris*
Mammals	
Black or ship rat	*Rattus rattus*
Brushtail possum	*Trichosurus vulpecula*
Cat	*Felis catus*
Crab-eating macaque monkey	*Macaca fascicularis*
European rabbit	*Oryctolagus cuniculus*
Fox	*Vulpes vulpes*
Goat	*Capra hircus*
Gray squirrel	*Sciurus carolinensis*
Mouse	*Mus musculus*
Nutria (coypu)	*Myocastor coypus*
Pig	*Sus scrofa*
Red deer	*Cervus elaphus*
Small Indian mongoose	*Herpestes auropunctatus*
Stoat	*Mustela erminea*

Introduced species have most frequently caused species extinctions through predation/parasitism. Perhaps some of the best-documented examples have concerned the introduction of exotic predators to lakes and islands and the consequent extinction of plants and animals that had evolved no defences against them. Thus, numbers of species of fish, many endemic, from the lakes of the East African Rift Valley may be extinct as a result of the intentional introduction of the Nile perch *Lates niloticus*, a voracious predator (although other factors have also contributed; Harrison & Stiassny 1999 and references therein). Likewise, the accidental introduction of the brown tree snake *Boiga irregularis* to the island of Guam around 1950 resulted, directly or indirectly, in the loss of perhaps 12 species of an original fauna of 22 native birds (three pelagic species and perhaps nine forest ones, some endemic to the island), the reduction of most of the remaining forest species to small remnant populations, and the loss of 3–5 species of an original fauna of 10–12 reptiles (Fritts & Rodda 1998). In both cases, the catholic tastes of the generalist predators involved has been important, enabling them to maintain high abundances even when one of their prey species has been driven scarce.

The potential for introduced species to predate native species highlights the need for great caution in employing biological control of pest species (Section 4.2.3). Whilst this can be exceedingly beneficial in economic terms, potential biological control agents need to be very carefully screened to ensure that they will not have negative impacts on other species. A growing number of cases have been documented in which sufficient caution has not been exercised (Simberloff & Stiling 1996; Henneman & Memmott 2001; Louda & O'Brien 2002).

Introduced species may also cause species extinctions, at least locally, through competition. Thus, the introduction of some ant species, such as the red fire ant *Solenopsis invicta*, the Argentine ant *Linepithema humile*, and the big-headed ant *Pheidole megacephala*, has often caused dramatic reductions in native ant assemblages through aggressive interactions (e.g. Holway 1999; Mack et al. 2000). Likewise, the tropical alga *Caulerpa taxifolia* spread dramatically around the coastline of the Mediterranean, carpeting large areas and excluding many other species (Meinesz 1999).

The economic costs of introductions may be vast. Pimentel et al. (2000) estimate that the approximately 50,000 non-indigenous species in the USA alone result in economic damage and control estimated at US$137 billion per annum.

The net effect of species extinctions and of the introduction of species into areas in which they would not naturally occur is to homogenize biotas across the globe, making them more similar to one another (Lockwood & McKinney 2001); in the extreme we would be left with biota comprising pests and weeds. For example, on average, pairs of states in the continental USA now have 15.4 more fish in common than before European settlement of North America (Rahel 2000).

5.4.4 Extinction cascades

The extinction of one species may lead to the extinction of others. Indeed, this is inevitable where this species provides critical resources for others, such as specialist herbivores, parasites or predators, or perhaps itself acts as a specialist pollinator or dispersal agent. Thus, for example, in New Zealand, the giant eagle *Harpagornis moorei* almost certainly preyed on the large flightless moas, and its extinction likely resulted when these declined in numbers as a result of the hunting by the Maori that led to their demise (Cassels 1984; Worthy 1997; Holdaway 1999; Holdaway & Jacomb 2000). More complex sets of interactions may also result in cascades of extinctions, as evidenced by the dramatic, and often extensive, changes in floral and faunal composition that can result from changes in the abundance and occurrence of key species (e.g. large-bodied predators and herbivores; Terborgh 1988; Owen-Smith 1989; Crooks & Soulé 1999; Jackson 2001; Terborgh et al. 2001). For example, the loss of large-bodied predator species may be accompanied by meso-predator release, in which somewhat smaller predators escape the population controls that were previously imposed on them, and as a result they exert increased predation pressure on their prey species, reducing their abundance and perhaps driving them locally or even globally extinct.

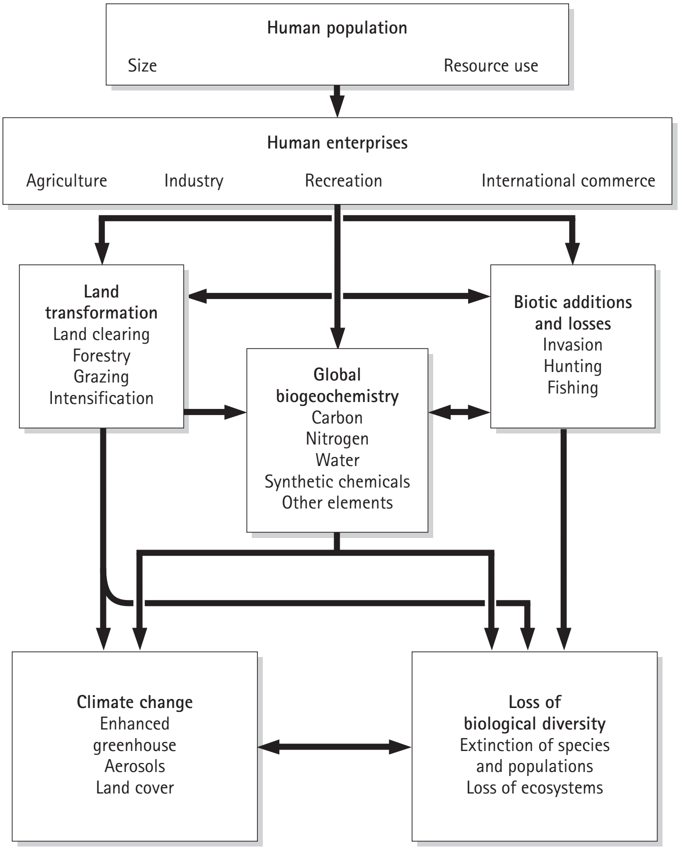

Fig. 5.9 A conceptual model illustrating humanity's direct and indirect effects on the Earth system. (From Vitousek et al. 1997a.)

5.5 The scale of the human enterprise

In some sense all of the above causes of species extinction and threat to biodiversity are proximate. The ultimate causes concern the size of the human population, growth in that population, and what has been termed the scale of the human enterprise (Fig. 5.9; Ehrlich 1995). The facts are stark.

1 *Population size and growth*. The world's human population is estimated to have reached a total of about 6.1 billion individuals in mid-2000. This compares to figures for the other great apes, our closest relatives, of 10,000–25,000 for the bonobo *Pan paniscus*, 100,000–150,000 for the chimpanzee *Pan troglodytes*, 40,000–65,000 for the gorilla *Gorilla gorilla*, and about 38,500 for the orang-utan *Pongo pygmaeus* (Cincotta & Engelman 2000).

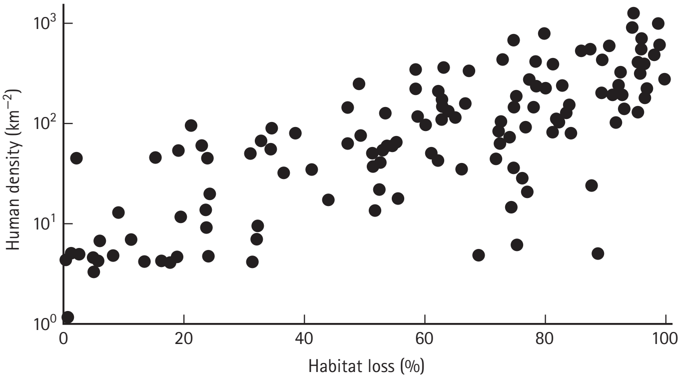

Fig. 5.10 Relationship between human population density and habitat loss for forest ecoregions of the Indo-Pacific. (From Wikramanayake et al. 2002.)

Generally, at a crude spatial resolution, there seems to be a marked positive correlation between the numbers of species found in an area and human density. Balmford et al. (2001) have shown this for sub-Saharan Africa, and it seems to occur because both species numbers and numbers of people show similar relationships with primary productivity, finding similar kinds of areas good for multiplication. Indeed, the human population is distributed such that more than 1.1 billion individuals live within the 25 global biodiversity hotspots (see Section 3.3.3), which constitute some of the most important and threatened areas for other forms of life (Cincotta & Engelman 2000; Cincotta et al. 2000). The density of people in these hotspots is about 73 per km^2, compared with a global average of 42 per km^2.

Levels of habitat loss in areas are commonly correlated with the numbers of people, even at relatively coarse spatial resolutions (Fig. 5.10), but the conflict between people and biodiversity becomes more obvious at finer spatial resolutions (here, of course, positive relationships between numbers of people and species richness tend rapidly to break down – highly urbanized areas may have few native species). Thus, the number of previously native scarce plant species that have not been recorded from areas of Britain since 1970 is an increasing function of the human population density of those areas (Thompson & Jones 1999), and the occurrence and persistence of a number of large-bodied vertebrate species declines with human population density, even when these species are in protected areas and this density is measured in the surrounding areas (Figs. 5.11 & 5.12; Hoare & du Toit 1999; Woodroffe 2000; Parks & Harcourt 2002; Walsh et al. 2003).

The extent of such conflicts will, of course, almost inevitably grow. The human population is currently increasing at an annual rate of 1.2% (about

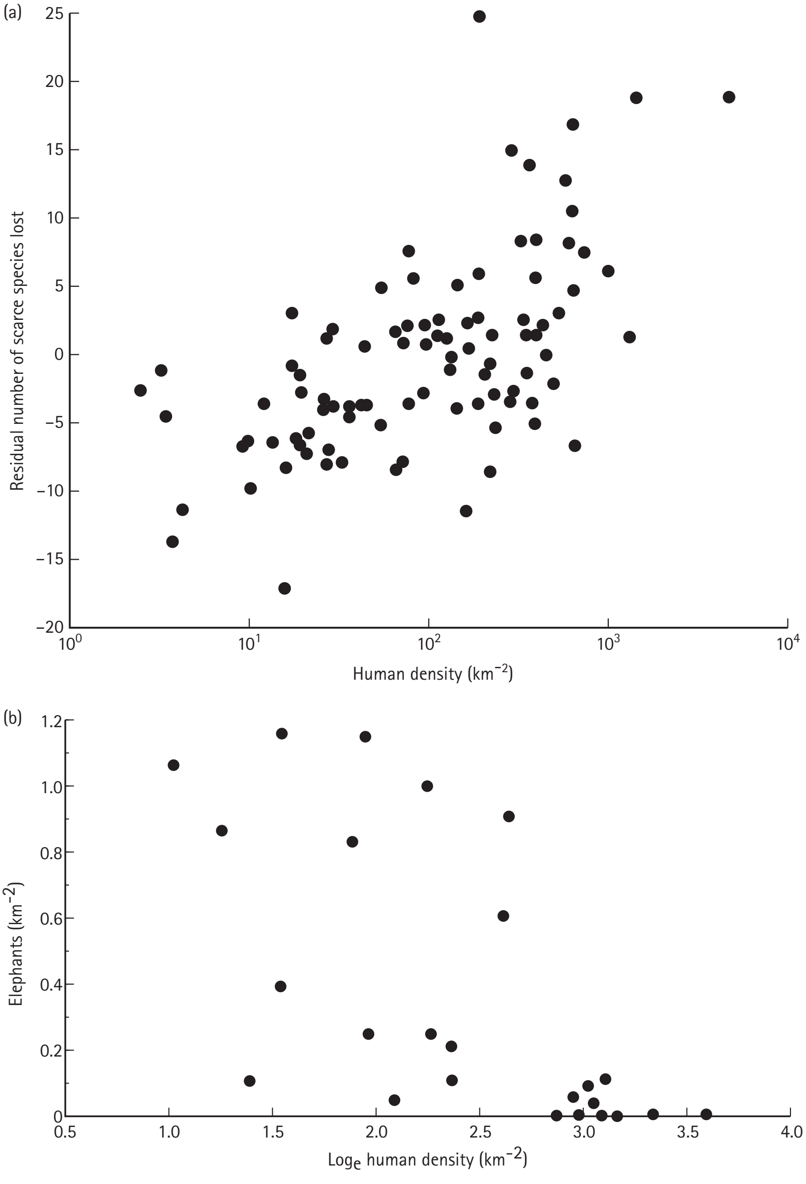

Fig. 5.11 Relationships between human density and: (a) number of scarce plant species lost, after the effects of the original number are corrected for, for vice counties (small geopolitical units) in Britain; and (b) number of elephants for 25 wildlife wards in the Sebungwe region, Zimbabwe. (a, From Thompson & Jones 1999; b, from Hoare & du Toit 1999.)

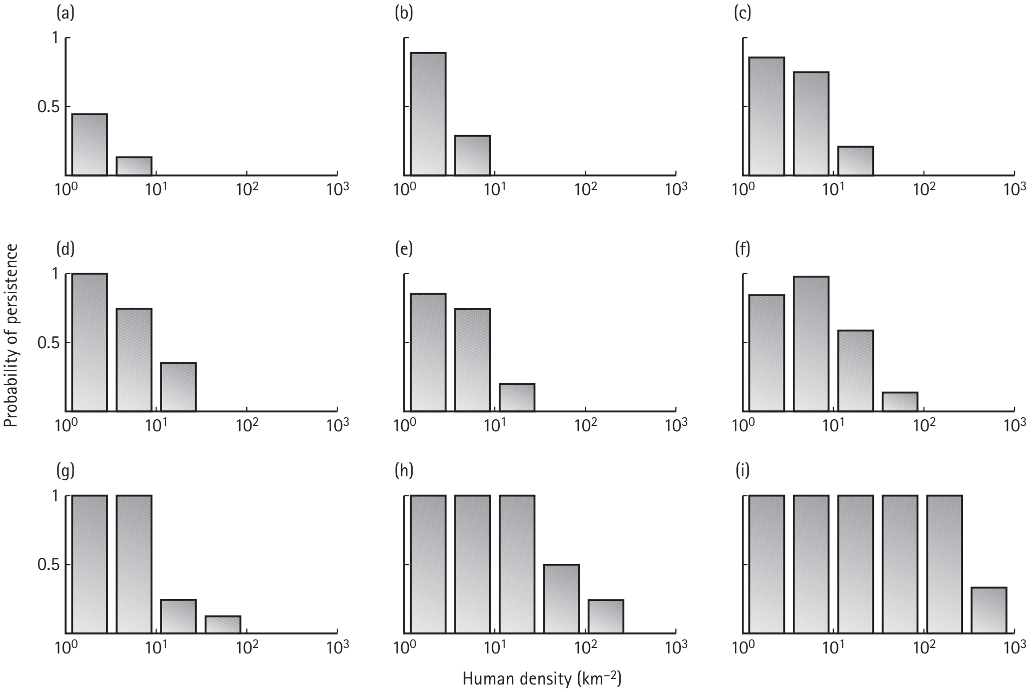

Fig. 5.12 Relationships between human density and probability of persistence for: (a) African wild dog in Southern Africa; (b) grizzly bear in USA; (c) African wild dog in Kenya; (d) mountain lion in USA; (e) wolf in USA; (f) cheetah in Kenya; (g) jaguar in Brazil; (h) spotted hyaena in Kenya; and (i) leopard in Kenya. (From Woodroffe 2000.)

80 million people annually, or nearly a quarter of a million people each day), and by 2050 is expected to be between 7.9 billion and 10.9 billion, with a medium variant of predictions of 9.3 billion (United Nations 2001). Population growth has been slow for most of human existence but over the past 200 years the rate has increased dramatically (Fig. 5.13). In 19 of the global biodiversity hotspots, the human population is growing more rapidly than it is globally, and in most of the hotspots located in developing countries it is projected to grow for several more decades (Cincotta et al. 2000).

The interaction between human population growth and species extinction may perhaps be epitomized by silphion *Ferula historica*, a herb in the carrot family (Riddle & Estes 1992; Cincotta & Engelman 2000). It once grew in abundance in the hills near Cyrene on the coast of what is now Libya, and was apparently highly valued as an antifertility drug in the classical world, in effect an oral contraceptive. It became one of the principal commodities of Cyrene's trade, and became very valuable. Indeed, coupled with the failure of attempts to cultivate the plant, its

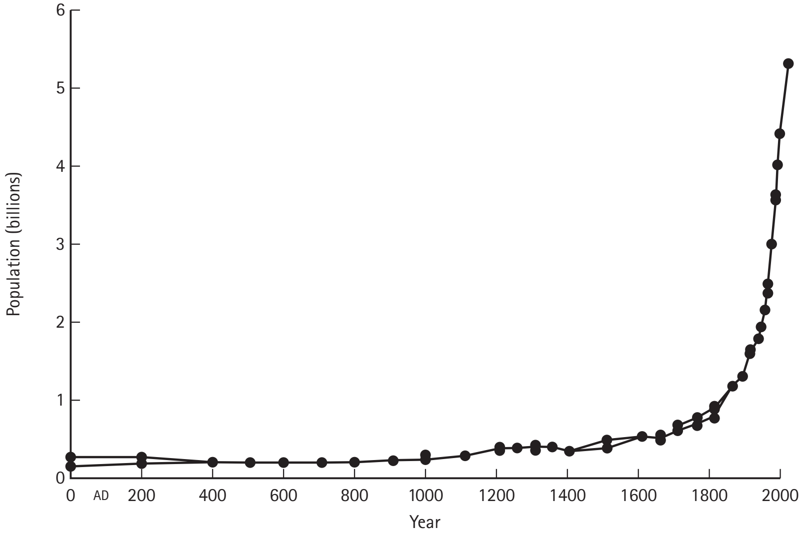

Fig. 5.13 Estimated human population from AD 1 to the present. Different lines represent estimates from different sources. (From Cohen 1995.)

value was such that it was overharvested, and in the 2nd or 3rd centuries AD, it disappeared.

2 *Primary production*. Humans use, co-opt or destroy approximately 35–40% of all potential terrestrial net primary productivity (the net accumulation of organic carbon resulting from the surplus of fixation over respiration; Vitousek et al. 1986; Pimm 2001; but see Rojstaczer et al. 2001 for discussion of the uncertainties in such estimates). The equivalent figure for aquatic systems is 8% of primary production, but with the proportion for nearshore and freshwater systems being much higher and close to that for terrestrial systems (Pauly & Christiansen 1995).

3 *Energy use*. Ehrlich (1995) estimates that from before the agricultural revolution to the present time, total power consumption by humanity multiplied roughly 7000–13,000-fold, from 0.001–0.002 terawatts (1 TW = 10^{12} watts) to 13 TW. Global commercial energy production in 1993 reached 338 exajoules (1 exajoule = 10^{18} joules, or about 163 million barrels of oil), 40% greater than in 1973. Total energy consumption rose to 326 exajoules, 49% greater than 20 years before (World Resources Institute 1996).

4 *Water*. Humanity uses more than a quarter of the 69,600 $km^3\ yr^{-1}$ of terrestrial evapotranspiration and more than a half of the 12,500 $km^3\ yr^{-1}$ of runoff that is geographically and temporally accessible (Postel et al. 1996). Of global water use, 42% is attributable to agriculture and 14% to industry. Freshwater is scarce in many regions, increasing ecological degradation, limiting production of agriculture and industry, impacting on human health, and increasing international tensions.

5 *Global economy*. For many decades global increases in consumption have outpaced increases in the human population. For 1980–97, the global economy nearly tripled to some US$29 trillion, although over the same period the population only increased by a third (United Nations Development Programme et al. 2000). Per capita consumption levels are rising in many nations as their economies develop.

It is inconceivable that an enterprise of this scale would not have major detrimental impacts on biodiversity.

5.6 Summary

1 Biodiversity loss, as epitomized by species extinctions, has been taking place as a consequence of human activities for a long time, initially associated with the colonization of some areas of the world by prehistoric peoples.

2 Since 1600 there have been over 1000 recorded extinctions of plant and animal species.

3 Impending extinction rates are estimated to be orders of magnitude greater than the background rates seen in the fossil record.

4 The principal proximate causes of biodiversity loss are: (i) direct exploitation; (ii) habitat loss, degradation and fragmentation; (iii) the effects of introduced species; and (iv) extinction cascades.

5 The ultimate causes of biodiversity loss concern the size of the human population, the rate of human population growth and the scale of the human enterprise.

Further reading

Baskin, Y. (2002) *A Plague of Rats and Rubbervines: The Growing Threat of Species Invasions*. Island Press, Washington, DC. (*A popular account of the invasions problem.*)

BirdLife International (2000) *Threatened Birds of the World*. Lynx Edicions and BirdLife International, Barcelona & Cambridge. (*The authority on the lamentable state of the global avifauna.*)

Brown, L.R. (2001) *State of the World 2001*. Earthscan, London. (*More applied and environmental slant than the WRI book (United Nations Development Programme et al. 2000) covering the same period.*)

Caughley, G. & Gunn, A. (1996) *Conservation in Theory and Practice*. Blackwell Science, Oxford. (*Includes a useful set of case studies of the decline or extinction of particular species.*)

Cincotta, R.P. & Engelman, R. (2000) *Nature's Place: Human Population and the Future of Biological Diversity*. Population Action International, Washington, DC. (*An interesting analysis of the relationship between biodiversity hotspots and human population.*)

Cohen, J.E. (1995) *How Many People can the Earth Support?* Norton, New York. (*Everything you wanted to know about the human population, and much that you had never thought to ask.*)

Committee on Recently Extinct Organisms. http://creo.amnh.org/. (*Lots of good information on extinctions in recent times.*)

di Castri, F. & Balajii, V. (eds.) (2002) *Tourism, Biodiversity and Information*. Backhuys Publishers, Leiden. (*A lot of interesting information – particularly if you travel a lot.*)

Ehrlich, P. (1997) *A World of Wounds: Ecologists and the Human Dilemma*. Ecology Institute, Oldendorf/Luhe. (*If you don't understand why you should do anything to help maintain biodiversity, read this book.*)

Flannery, T. & Schouten, P. (2001) *A Gap in Nature: Discovering the World's Extinct Animals*. William Heinemann, London. (*Beautiful paintings of many recently extinct species.*)

Fuller, E. (2000) *Extinct Birds*. Oxford University Press, Oxford. (*A fascinating compendium of what is known about recently extinct species of birds.*)

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Houghton, J.T., Ding, Y., Griggs, D.J., Noguer, M., van der Linden, P.J. & Xiaosu, D. (eds.) (2001) *Climate Change 2001: The Scientific Basis*. Cambridge University Press, Cambridge. (*Together with the other two volumes in this three-volume set, the definitive work on climate change.*)

Jennings, S., Kaiser, M.J. & Reynolds, J.D. (2001) *Marine Fisheries Ecology*. Blackwell Science, Oxford. (*An outstanding overview of fisheries exploitation, biology, conservation and management.*)

Kurlansky, M. (1997) *Cod: A Biography of the Fish that Changed the World*. Walker, New York. (*Perhaps not a promising title, until you have read a few pages. . . .*)

Lawton, J.H. & May, R.M. (eds.) (1995) *Extinction Rates*. Oxford University Press, Oxford. (*A landmark volume on extinction.*)

Leakey, R. & Lewin, R. (1996) *The Sixth Extinction: Biodiversity and its Survival*. Phoenix, London. (*Good basic introduction to many of the issues.*)

Levin, S.A. (2000) *Fragile Dominion: Complexity and the Commons*. Perseus Publishing, Cambridge, MA. (*One of the leading mathematical ecologists explains how the natural world is organized, and the consequences.*)

Lockwood, J.L. & McKinney, M.L. (eds.) (2001) *Biotic Homogenization: The Loss of Diversity through Invasion and Extinction*. Kluwer Academic/Plenum, New York. (*A mixed bunch, but includes some good contributions on an important topic.*)

Mackay, R. (2002) *The Atlas of Endangered Species*. Earthscan, London. (*Lots of maps and facts suitable for first-year undergraduates.*)

MacPhee, R.D.E. (ed.) (1999) *Extinctions in Near Time: Causes, Contexts, and Consequences*. Kluwer Academic/Plenum, New York. (*An important text, especially if you are interested in what the extant mammal fauna should look like.*)

McCarthy, J.J., Canziani, O.F., Leary, N.A., Dokken, D.J. & White, K.S. (eds.) (2001) *Climate Change 2001: Impacts, Adaptation, and Vulnerability*. Cambridge University Press, Cambridge. (*Together with the other two volumes in this three-volume set, the definitive work on climate change.*)

Meinesz, A. (1999) *Killer Algae: The True Tale of a Biological Invasion*. University of Chicago Press, Chicago, IL. (*A depressing story of government inaction and failure to prevent the spread of an aggressive introduced species.*)

Metz, B., Davidson, O., Swart, R. & Pan, J. (eds.) (2001) *Climate Change 2001: Mitigation*. Cambridge University Press, Cambridge. (*Together with the other two volumes in this three-volume set, the definitive work on climate change.*)

Moore, P.D., Chaloner, B. & Stott, P. (1996) *Global Environmental Change*. Blackwell Science, Oxford. (*A nice overview of lots of contentious topics.*)

Pimm, S.L. (2001) *The World According to Pimm: A Scientist Audits the Earth*. McGraw-Hill, New York. (*A fascinating, and very accessible, discussion of the scale of appropriation of productivity by humans and its implications.*)

Robinson, J.G. & Bennett, E.L. (eds.) (2000) *Hunting for Sustainability in Tropical Forests*. Columbia University Press, New York. (*Information on human hunting practices, the issues confronting conservationists and the use of tropical rain forests.*)

Safina, C. (1997) *Song for the Blue Ocean: Encounters along the World's Coasts and beneath the Seas*. Henry Holt, New York. (*A well-written, but depressing, account of the state of the oceans.*)

Terborgh, J. (1999) *Requiem for Nature*. Island Press, Washington, DC. (*A depressing lesson on the state of the natural world. Read it!*)

United Nations Development Programme, United Nations Environment Programme, World Bank & World Resources Institute (2000) *World Resources 2000–2001: People and Ecosystems: The Fraying Web of Life*. Elsevier Science, Amsterdam. (*A regular publication, providing valuable appraisals and data on the state of the environment.*)

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6 Maintaining biodiversity

6.1 Introduction

Use of the term 'biodiversity' arose in the context of, and has remained firmly wedded to, concerns over the loss of the natural environment and its contents. The importance of this connection cannot be overstated. In defining biodiversity in this book, we have relied heavily on the Convention on Biological Diversity (Section 1.2). This was not solely as a matter of convenience. It underscores our belief that, for better or for worse, and with its many flaws, this remains perhaps the single most important international step towards the long-term maintenance of biodiversity. The Convention constituted an historic commitment by nations of the world (though sadly not all of them, including the USA, have ratified or even signed). It was the first time that biodiversity was comprehensively addressed in a binding global treaty, the first time that genetic diversity was specifically covered, and the first time that the conservation of biodiversity was recognized as the common concern of humankind (Glowka et al. 1994). So, having examined the main features and patterns of biodiversity (Chapters 1, 2 & 3), the value placed on it (Chapter 4), and the threats that it faces (Chapter 5), we now turn to the relevant Articles contained in the Convention to provide a useful framework in which to discuss its maintenance into the future (as well as providing a valuable lesson in how such treaties are formulated). Whether or not one regards the Convention as having major significance, this provides a much broader canvas than that obtained by simply focussing on issues traditionally associated with the field of conservation biology. It draws attention to the fact that the maintenance of biodiversity touches on many facets of human activities, and concerns much more than how to prevent individual species from becoming extinct, or the provision of nature reserves and other protected areas for conservation.

The Convention is comprised of 42 Articles (Table 6.1), concerning issues ranging from its objectives, the practical obligations of each signatory, the policies to be followed, and the use of terms. Below we take various Articles in turn, and use these as a starting point to discuss the relationship of particular issues to the maintenance of biodiversity. Each of the Articles chosen is reproduced in full, followed by some commentary. We would encourage readers not to be deterred by the legal language (with its multiple caveats and sub-clauses) of the sections of the Convention that are quoted. This highlights the need to view any serious attempt to maintain biodiversity in a broader societal context; the obfuscation was necessary to achieve a document that so many countries could sign up to. Although at times rather formidable, the underlying ideas remain simple to understand and are amplified in the accompanying text.

6.2 Objectives of the Convention

The objectives of the Convention (Article 1) are threefold:

> *The conservation of biological diversity, the sustainable use of its components, and the fair and equitable sharing of the benefits arising from the utilization of genetic resources.*

(To avoid possible confusion, ‘sustainable use’ is defined (in Article 2) as ‘the use of components of biological diversity in a way and at a rate that does not lead to the long-term decline of biological diversity, thereby maintaining its potential to meet the needs and aspirations of present and future generations’ – to many minds, this is unhelpfully vague.)

This is the heart of the Convention, establishing the framework and context for the subsequent Articles, and its overall sense of direction. Indeed, right at the outset the Convention recognizes some of the main strands that must be involved in the future interaction of humanity with biodiversity. Biodiversity must be maintained, if only because to fail to do so would be to imperil human existence through the consequences for direct and indirect use (cf. Chapter 4). This can only be achieved through sustainable use, and only if the benefits arising from the use are fairly and equitably distributed. This reflects a general acceptance that there are social contexts to conservation actions.

Table 6.1 The 42 Articles of the Convention on Biological Diversity.

1	Objective
2	Use of terms
3	Principle
4	Jurisdictional scope
5	Cooperation
6	General measures for conservation and sustainable use
7	Identification and monitoring
8	*In-situ* conservation
9	*Ex-situ* conservation
10	Sustainable use of components of biological diversity
11	Incentive measures
12	Research and training
13	Public education and awareness
14	Impact assessment and minimizing adverse impacts
15	Access to genetic resources
16	Access to and transfer of technology
17	Exchange of information
18	Technical and scientific cooperation
19	Handling of biotechnology and distribution of its benefits
20	Financial resources
21	Financial mechanism
22	Relationship with other international conventions
23	Conference of the Parties
24	Secretariat
25	Subsidiary Body on Scientific, Technical and Technological Advice
26	Reports
27	Settlement of disputes
28	Adoption of protocols
29	Amendment of the Convention or protocols
30	Adoption and amendment of annexes
31	Right to vote
32	Relationship between this Convention and its protocols
33	Signature
34	Ratification, acceptance or approval
35	Accession
36	Entry into force
37	Reservations
38	Withdrawals
39	Financial interim arrangements
40	Secretariat interim arrangements
41	Depository
42	Authentic texts

The emphasis on equitable sharing of benefits arising from the utilization of genetic resources reflects concerns that in the past such resources belonging to one nation have been exploited by one or more others, with no recompense. Although examples usually relate to the exploitation of the genetic resources of developing nations by developed ones, where its consequences are at their most severe, the problem is more widespread. Thus, for instance, Svarstad et al. (2000) relate how the hyphomycete fungus *Tolypocladium inflatum* was collected in soil samples by a biologist during his holiday in Norway in 1969, within an open access regime. Best-selling medicines based on cyclosporin A (an immunosuppressant, and essential in the transplant of human organs), a biochemical produced by the fungus, were subsequently developed by a pharmaceutical company. Two per cent royalties on sales might have been a reasonable claim if there had been benefit-sharing with the source country (although the fungus has subsequently been found to be distributed across many countries), and in 1997 alone these would have amounted to US$24.3 million.

6.3 General measures for conservation and sustainable use

This, Article 6, is perhaps one of the most far-reaching and significant Articles in the Convention, and reads as follows:

Each Contracting Party shall, in accordance with its particular conditions and capabilities:
(a) Develop national strategies, plans or programmes for the conservation and sustainable use of biological diversity or adapt for this purpose existing strategies, plans or programmes which shall reflect, inter alia*, the measures set out in this Convention relevant to the Contracting Party concerned; and*
(b) Integrate, as far as possible and as appropriate, the conservation and sustainable use of biological diversity into relevant sectoral or cross-sectoral plans, programmes and policies.

In short, the conservation and sustainable use of biodiversity are not expected to emerge fortuitously in each nation. Indeed they will not do so, as the recent history of biodiversity testifies. Biodiversity is under great pressure from human activities, with many species being threatened with extinction (Section 5.2.3), and much of the use being unsustainable (Section 5.4.1).

The Convention obliges nations to establish mechanisms for bringing about the conservation and sustainable use of biodiversity, or for developing these mechanisms if they already exist. Strategies, plans and programmes can be seen as a chronological series of steps whereby specific recommendations are turned into methods of achieving those ends and thence into action on the ground (Glowka et al. 1994). They will inevitably have to be dynamic, and under continual refinement and development, in order to respond to the changing circumstances of biodiversity in a particular nation. If they are to be effective, then these national strategies, plans and programmes will not be easy to formulate, as they will have to touch on multiple (perhaps even most) human activities. They will thus have to be integrated with policies in fields as diverse as agriculture, education, employment, energy, health, industry and transport. If they are to be truly effective, then the strategies, plans and programmes for conserving and sustainably using a nation's biological diversity will have to become central to the way in which that nation's affairs are conducted.

A striking example of the ways in which this is not presently occurring concerns so-called perverse subsidies (Myers 1998; Myers & Kent 1998). These are subsidies that are adverse in the long run to both the economy and the environment, and include support for: (i) agriculture – may cause overloading of croplands, leading to soil erosion, pollution from synthetic fertilizers and pesticides, and release of greenhouse gases; (ii) fossil fuels and nuclear energy – may increase pollution, smog and global warming, and creates waste-disposal problems; (iii) road transport – promotes pollution, excessive road-building and resultant habitat loss; (iv) water – encourages greater use and misuse of supplies; and (v) fisheries – support overharvesting. The scale of perverse subsidies is vast, totalling perhaps US$1450 billion per annum, and often exceeding the value in the marketplace of the goods that are generated from a given industrial sector. For example, global subsidies to marine fisheries exceed the market value of the fish that are landed. Myers (1998) observes that a US citizen pays taxes of at least US$2000 a year to fund perverse subsidies and pays almost the same amount through the increased costs of consumer goods and through environmental degradation.

In accordance with Article 6, a number of countries have developed national Biodiversity Strategies (general policy instruments to identify strategic needs) or Action Plans (practical documents that identify what is to be done and who is to do what) (Miller et al. 1995). For example, publication of the UK Action Plan (Anon. 1994) represents such a direct governmental response to Article 6. Its goal, principles and objectives are listed in Table 6.2. At their best, such documents can identify how the ways in which societies operate will be restructured, so as to bring about the conservation and sustainable use of biodiversity. More frequently, they reflect aspirations with little indication of how these will be met, and fail to recognize the fundamental nature of what needs to be done.

Table 6.2 The goal, principles and objectives of the UK Action Plan (Anon. 1994).

Overall goal

To conserve and enhance biological diversity within the UK and to contribute to the conservation of global biodiversity through all appropriate mechanisms

Underlying principles

1 Where biological resources are used, such use should be sustainable
2 Wise use should be ensured for non-renewable resources
3 The conservation of biodiversity requires the care and involvement of individuals and communities as well as Governmental processes
4 Conservation of biodiversity should be an integral part of Government programmes, policy and action
5 Conservation practice and policy should be based upon a sound knowledge-base
6 The precautionary principle should guide decisions

Objectives for conserving biodiversity

1 To conserve and where practicable to enhance:
  (a) the overall populations and natural ranges of native species and the quality and range of wildlife habitats and ecosystems;
  (b) internationally important and threatened species, habitats and ecosystems;
  (c) species, habitats and natural and managed ecosystems that are characteristic of local areas;
  (d) the biodiversity of natural and semi-natural habitats where this has been diminished over recent past decades
2 To increase public awareness of, and involvement in, conserving biodiversity
3 To contribute to the conservation of biodiversity on a European and global scale

6.4 Identification and monitoring

In order to know whether strategies, programmes and plans for conservation and sustainable use are appropriate and are working effectively, it will be necessary to gather suitable information. Article 7 places such an obligation on signatories to the Convention (Annex I is given in Table 6.3):

Each Contracting Party shall, as far as possible and as appropriate, in particular for the purposes of Articles 8 to 10:
(a) Identify components of biological diversity important for its conservation and sustainable use having regard to the indicative list of categories set down in Annex I;
(b) Monitor, through sampling and other techniques, the components of biological diversity identified pursuant to subparagraph (a) above, paying particular attention to those requiring urgent conservation measures and those which offer the greatest potential for sustainable use;
(c) Identify processes and categories of activities which have or are likely to have significant adverse impacts on the conservation and sustainable use of

Table 6.3 Annex I of the Convention on Biological Diversity.

Identification and monitoring

1 Ecosystems and habitats: containing high diversity, large numbers of endemic or threatened species, or wilderness; required by migratory species; of social, economic, cultural or scientific importance; or, which are representative, unique or associated with key evolutionary or other biological processes;

2 Species and communities which are: threatened; wild relatives of domesticated or cultivated species; of medicinal, agricultural or other economic value; or social, scientific or cultural importance; or importance for research into the conservation and sustainable use of biological diversity, such as indicator species; and

3 Described genomes and genes of social, scientific or economic importance

biological diversity, and monitor their effects through sampling and other techniques; and
(d) Maintain and organize, by any mechanism data, derived from identification and monitoring activities pursuant to subparagraphs (a), (b) and (c) above.

The combination of the paucity of knowledge of biodiversity and the extraordinary magnitude of the variety of life (see Chapters 2 & 3) make it impossible to identify or monitor all of the components of biodiversity that lie within a nation's borders. The Article and its associated Annex therefore concentrate these undertakings in two directions: first on those components that are considered to be important for the conservation and sustainable use of biodiversity; and second on those activities which are likely to have the most substantial impacts on this conservation and use. Much of this will require the acquisition of entirely new information, while it will be possible to use some existing data (see Chapters 1, 2 & 3), perhaps freshly collated. Combined, this will have benefits far beyond the Convention, serving to improve overall understanding of biodiversity. This will be facilitated by the final clause of this Article.

The ease with which nations can begin to fulfil the requirements of this Article will vary dramatically, on the basis of existing knowledge alone (cf. final comments on Article 8). However, it is important that attempts to improve knowledge are not used as an excuse for failing to undertake action in other spheres of activity. This has been a recurrent problem in the fields of conservation and sustainable use.

6.5 *In-situ* conservation

Article 8 embodies the principal obligations for the conservation of biological diversity. Although it is one of the longer Articles in the Convention, and thus may appear especially daunting, it is so important that we

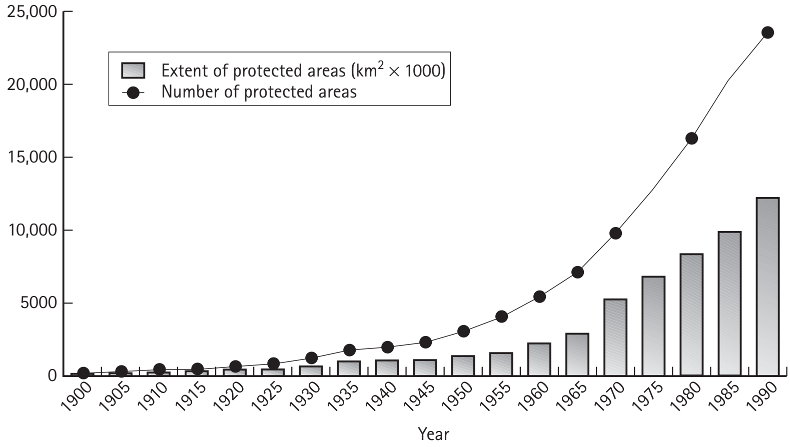


Fig. 6.1 Cumulative growth in the number and extent of protected areas (1900–94). (From Green & Paine 1997.)

must consider all of it. However, to make the task a little less onerous we will divide it into manageable sections.

Each Contracting Party shall, as far as possible and appropriate:
(a) Establish a system of protected areas or areas where special measures need to be taken to conserve biological diversity;
(b) Develop, where necessary, guidelines for the selection, establishment and management of protected areas or areas where special measures need to be taken to conserve biological diversity;

Protected area systems or networks are required to be established as a central plank of a national strategy for conserving biodiversity. More than 20,000 existing protected areas, spread amongst virtually all countries in the world, are recognized by the IUCN (The World Conservation Union) Commission on Parks and Protected Areas, covering an estimated 13.2 million km^2 (Fig. 6.1); marine reserves cover about 1.3 million km^2 of this total. However, this network suffers from a number of severe limitations.

1 Most protected areas are extremely small (Fig. 6.2), typically of a size that is far below that required to maintain viable populations of large vertebrates (Newmark 1987, 1996; Gurd et al. 2001). The severity of this size constraint may be reduced if protected areas are linked by corridors, but in practice with a few notable exceptions this has not happened, and there are both pros and cons to the creation of corridors. Potential benefits include increased immigration rates, and the provision of increased or alternative refugia; potential disadvantages include facilitated transmission of fire, disease and predators, and reduction in between-population

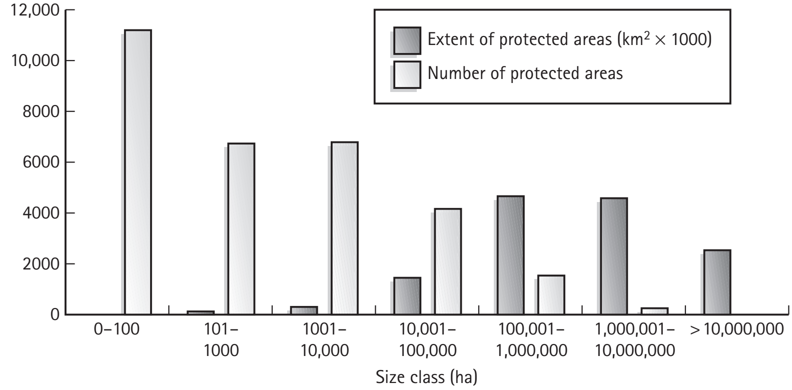


Fig. 6.2 Frequency distribution of protected area sizes. (From Green & Paine 1997.)

genetic variation (Saunders & Hobbs 1991; Newmark 1993; Gaston et al. 2002). The overall number of protected areas continues to increase, but the average size of those declared in any given period has tended to decline through time.

2 Protected areas tend to be biased towards lands of low economic value, experiencing less competition from alternative forms of land use, and towards the limits of geopolitical units (e.g. county, state and country boundaries, where they may serve as buffer zones). In consequence, they do not adequately represent patterns of natural vegetation or species occurrences (Scott et al. 2001; Pressey et al. 2002). Models of the changes in the distributions of species that are likely to result reveal that this situation is likely to be further exacerbated by climate change (e.g. Erasmus et al. 2002).

3 Many areas that have been formally designated for conservation in practice receive no, little or limited protection (and have often been termed 'paper parks'). Thus, for example, Grønne Ejland in Greenland was declared a Ramsar site (a protected area designated under the Ramsar Convention on Wetlands of International Importance) in 1987, with special reference to the presence of the world's largest colony of Arctic terns *Sterna paradisaea* (c. 1950 estimates suggested 50,000–80,000 breeding pairs). This designation never had any practical significance, and in the summer of 2000 not a single breeding pair of terns was recorded as remaining (Hansen 2002). The effectiveness of many other protected areas has been much debated (see Bruner et al. 2001a,b; Vanclay 2001). Ultimately, this will often depend on the level of management activities (e.g. enforcement of park boundaries, anti-poaching patrols). Funds for this are insufficient in much of the world. US$6 billion is presently spent globally on protected areas for conservation (James et al. 1999, 2001). This compares with US$2.1 billion for the cost of a replacement space

shuttle in 1991, US$6 billion spent to resolve property damage following Hurricane Floyd in 1999, US$15 billion agreed in 2002 for a single order of fighter aircraft by the UK government, and US$50 billion spent each year globally on methods of dieting.

4 The overall extent of the existing conservation network is too small. IUCN (1993) advocates that at least 10% of the land area of each nation be set aside for conservation. The expansion of the global network of protected areas to meet a target of 15% has been estimated to carry a global price-tag of US$20 billion–28 billion per annum (Balmford et al. 2002). In practice, even a network covering 15% of different regions is likely to be woefully inadequate to represent all species, especially in the tropics. Substantially larger percentages may be required for ecosystems or nations with higher levels of species richness and/or endemism (Rodrigues & Gaston 2001). The proportion of the land area set aside for conservation may be too small, but the proportion of the marine environment set aside for these purposes is much lower (c. 0.5% of ocean area). Nonetheless, existing evidence strongly supports the notion that designating protected areas of ocean has enormous benefits both for biodiversity within and without those areas, and hence for exploitation of the latter (Dugan & Davis 1993; Bohnsack 1998; Mosquera et al. 2000; C.M. Roberts et al. 2001; Halpern & Warner 2002). Estimates suggest that an initiative to generate a globally effective network covering 30% of the area of the oceans would cost c. US$23 billion per annum in recurrent costs, plus c. US$6 billion per annum (over 30 years) in start-up costs (Balmford et al. 2002).

5 The existing conservation network has been conceived along rather static lines, and is not well equipped to cope with the changes in the distributions of species that are being brought about by global climate changes (Section 5.4.2). These changes would normally cause shifts in the distributions of species, typically with expansions along some range boundaries and contractions along others. However, as protected areas become progressively more like islands of natural vegetation in a matrix of modified environments, often isolated from one another by considerable distances, the possibility for species to respond by such movements becomes increasingly constrained.

There have been a number of attempts to identify priority areas for conservation, to guide thinking in the location of future protected areas and the exercise of other conservation measures. These are based on the principles that biodiversity is unevenly distributed across the planet, that it is under more immediate threat in some areas than others, and that resources for conservation action are limiting. They include approaches based on hotspots of biodiversity, endemism and threat, and on the most outstanding examples of different habitat types, such as Birdlife International's Endemic Bird Areas, Conservation International's Hotspots, Conservation International's Major Tropical Wilderness Areas, World Resource Institute's Frontier Forests, World Wide Fund for Nature and World Conservation Union's Centres of Plant Diversity, and World Wildlife Fund-USA's Global 200 ecoregions (e.g. Davis et al. 1994, 1995, 1997; Bryant et al. 1997; Olson & Dinerstein 1998; Stattersfield et al. 1998; Myers et al. 2000; Olson et al. 2001). Particularly at regional scales, increasing attention is being paid to maximizing the complementarity between different areas (including the largest number of species in a network of a given total extent, cost, etc.; Pressey et al. 1993).

A key issue in identifying priority areas for conservation is the extent to which areas chosen on the basis of one taxonomic group are also appropriate for the maintenance of the biodiversity of others in a region (this is related to, although not the same as, the issue of how well the patterns of species richness of different groups are correlated; Section 3.5). Whilst there are some important similarities, there are also significant differences, which caution against assuming that planning based on those groups that we know well will suffice for those that we do not (e.g. Brooks et al. 2001).

(c) Regulate or manage biological resources important for the conservation of biological diversity whether within or outside protected areas, with a view to assuring their conservation and sustainable use;
(d) Promote the protection of ecosystems, natural habitats and the maintenance of viable populations of species in natural surroundings;
(e) Promote environmentally sound and sustainable development in areas adjacent to protected areas with a view to furthering protection of these areas;

Of course, whether on land or in the ocean, protected areas, whilst vital, are not sufficient in themselves for the conservation of biodiversity. First, they are not isolated from events beyond their boundaries, and the more degraded conditions become outside, the greater the reduction of population viability within. Second, they are often vulnerable to threats and accidents emanating from outside, such as resource exploitation and chemical contamination. Thus, for example, extinction rates of large mammals in protected areas in West Africa have been shown to increase with human density in the surrounding areas, presumably reflecting the increased hunting pressures that they face (Brashares et al. 2001). Third, much biodiversity will not be contained within protected areas. For example, an unknown but doubtless large proportion of species is unrepresented within protected areas, and large numbers of some flagship species occur outside their boundaries; 80% of Africa's elephants live outside protected areas (Ginsberg 2002). Fourth, many fundamental processes, such as migration and population replenishment (especially in marine systems), occur at scales much larger than those protected areas

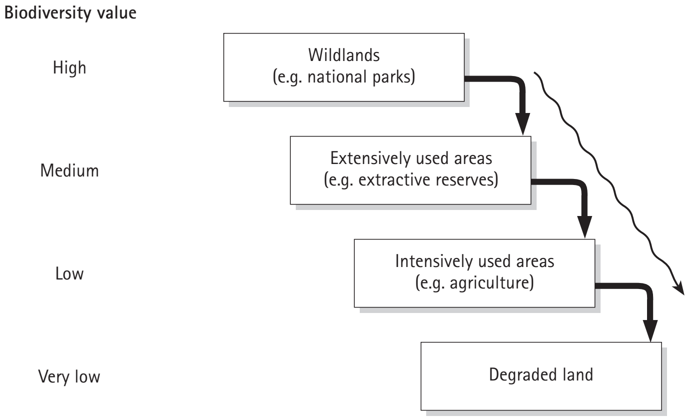


Fig. 6.3 The land-use cascade. (From Terborgh 1999.)

can reasonably attain. Fifth, climate change may make conditions within the boundaries of existing protected areas untenable for some of the species they were intended to conserve. These paragraphs of Article 8 therefore require the management of biological resources both within protected areas and outside of them (i.e. the general protection of ecosystems and populations wherever they occur), and so ensure that development in areas adjacent to protected areas does not undermine the capacity of those protected areas to conserve biodiversity.

Some attempt has been made to estimate what might be the cost of protecting biodiversity in the matrix of landscapes beyond reserves. Thus, it has been suggested that biodiversity remediation costs might be US$34 billion per annum for the forestry sector, US$1 billion for freshwater and US$14 billion for coastal and marine systems (United Nations 1993). Biodiversity conservation in the farming sector would cost far more, with one estimate of US$240 billion per annum, giving an overall annual total of about US$290 billion (James et al. 1999). This is a fraction of the sums presently spent on perverse subsidies (Section 6.3).

(f) Rehabilitate and restore degraded ecosystems and promote the recovery of threatened species, inter alia*, through the development and implementation of plans or other management strategies;*

The conservation of biodiversity is not simply about maintaining things the way they presently are. As we have seen, few (if any) areas are pristine and untouched, directly or indirectly, by human hand, and many are severely degraded (see Table 5.2). A creative approach to restoration is thus also required, which can reverse the slide of lands from wild to degraded (Fig. 6.3). This has given rise to the emergence of the science of restoration ecology (Jordan et al. 1990; Pywell & Putwain 1996; Perrow

& Davy 2002a,b). Many innovative and cost-effective approaches to restoration have been developed, which harness natural ecosystem processes (Dobson et al. 1997). Agricultural and industrial development, whilst it may be curtailed, cannot be stopped, so restoration provides a means of reducing the time for which habitat remains in a degraded state.

(g) Establish or maintain means to regulate, manage or control the risks associated with the use and release of living modified organisms resulting from biotechnology which are likely to have adverse environmental impacts that could affect the conservation and sustainable use of biological diversity, taking also into account the risks to human health;
(h) Prevent the introduction of, control or eradicate those alien species which threaten ecosystems, habitats or species;

The impacts on biodiversity and the environment associated with the introduction of alien species have already been mentioned (Section 5.4.3) and, plainly, actions to ameliorate these effects are a necessary part of an effective conservation strategy. Prevention of invasions is much less costly than is their control once they become established, and so effective quarantine measures are vital, although presently adopted by very few nations. Eradication of established introductions is sometimes possible, particularly from islands and small areas, where action can be taken early in the invasive process, where measures can be persistently applied often over long periods (temptations to reduce efforts in response to initial success in reducing numbers must be resisted), and where there is public support for such campaigns. In some cases the, often high, costs associated with eradication may be more economic than the ongoing year-on-year expenses associated with control programmes that serve solely to contain the distribution or reduce the abundance of an alien species. However, in most cases the latter steps are the only ones that are practical, and may require a great deal of commitment and diligence (Mack et al. 2000).

The need to combat the possible risks associated with the intentional use and release of living 'modified' organisms (which include genetically modified organisms) has been particularly highlighted in this Article. There is, of course, vigorous debate as to how severe these risks are.

(i) Endeavour to provide the conditions needed for compatibility between present uses and the conservation of biological diversity and the sustainable use of its components;
(j) Subject to its national legislation, respect, preserve and maintain knowledge, innovations and practices of indigenous and local communities embodying traditional lifestyles relevant for the conservation and sustainable use of biological diversity and promote their wider application with the approval and involvement

of the holders of such knowledge, innovations and practices and encourage the equitable sharing of the benefits arising from the utilization of such knowledge, innovations and practices;

Intuitively, support for the conservation of biological diversity will be less when necessary changes conflict with present uses (see Section 4.2). The first of these paragraphs requests that Parties to the Convention should minimize these conflicts, although plainly this will often be difficult and, at times, impossible. This issue begs the question of whether it is better to exploit smaller areas intensively, or to exploit less intensively over larger areas. Conventionally, the latter has been viewed as being better for the maintenance of biodiversity. However, evidence from studies both of forestry and fisheries suggests the converse may well be the case (Noble & Dirzo 1997). The long-term sustainability and environmental consequences of intensive agriculture are, however, of great concern. Locally, intensification of agricultural systems can increase erosion, lower soil fertility, and reduce biodiversity; regionally, it may pollute ground waters and cause eutrophication of rivers and lakes; globally, it may change the atmosphere and climate (Matson et al. 1997).

The second paragraph of this part of the Article recognizes that the knowledge, innovations and practices of indigenous and local communities may be pertinent to the conservation and sustainable use of biodiversity, and that this cultural relevance should be promoted, to the benefit of its custodians.

(k) Develop or maintain necessary legislation and/or other regulatory provisions for the protection of threatened species and populations;
(l) Where a significant adverse effect on biological diversity has been determined pursuant to Article 7, regulate or manage the relevant processes and categories of activities; and
(m) Cooperate in providing financial and other support for in-situ *conservation outlined in subparagraphs (a) to (l), particularly to developing countries.*

These paragraphs all concern mechanisms for conserving biodiversity, including the development of appropriate legislation, the regulation and management of processes and activities which from the gathering of suitable information (as outlined in Article 7, above) have been found to be detrimental to biodiversity, and the provision of financial and other support to developing countries. The final paragraph reflects a recurrent theme of the Convention, in recognizing that the resources available for the conservation and sustainable use of biodiversity are not evenly distributed, and that the poorer countries will require support from the richer if these ends are to be achieved.

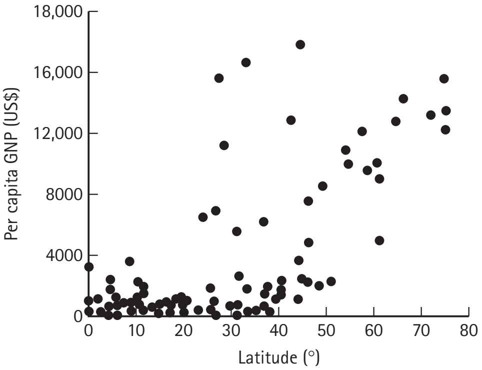


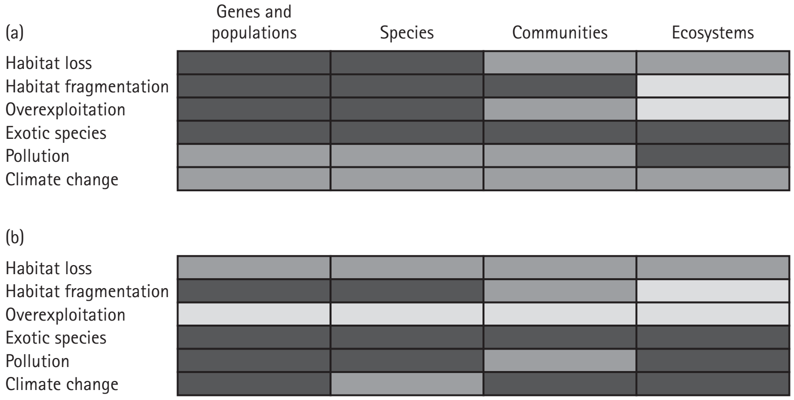
Fig. 6.4 Latitudinal gradient in the per capita gross national product (GNP) of countries of the world in 1986. (From Huston 1994.)

This is particularly so because there is a complex set of interactions between poverty and the environment. First, the majority of biodiversity tends to occur towards low latitudes, and there is also a decline in the wealth of nations (as measured by per capita gross national product, GNP) towards low latitudes (Fig. 6.4), which means that the majority of biodiversity occurs in those nations that have the least resources with which to conduct conservation and sustainable use. Second, damage to ecosystems often impacts most directly on the poor, who suffer the effects of polluted environments, the loss of productive lands, the collapse of fisheries, and the loss of traditional sources of food, fodder, fuel and fibre when forests are cut down (Lean 1998). The poor do not have the financial resources with which to acquire the resources that they need (food, water, etc.) from elsewhere; the large ecological footprint (Section 4.3) of the rich reduces their vulnerability to local environmental degradation. Third, as a consequence, the relative impacts of factors affecting biodiversity are not the same in poorer and richer countries (Fig. 6.5).

6.6 *Ex-situ* conservation

Conservation actions have traditionally been divided into *in-situ* and *ex-situ*, and having dealt with the former in Article 8, the Convention moves on to the latter in Article 9.

Each Contracting Party shall, as far as possible and as appropriate, and predominantly for the purpose of complementing in-situ *measures:*
(a) Adopt measures for the ex-situ *conservation of components of biological diversity, preferably in the country of origin of such components;*
(b) Establish and maintain facilities for ex-situ *conservation of and research on plants, animals and micro-organisms, preferably in the country of origin of genetic resources;*



(a)

	Genes and populations	Species	Communities	Ecosystems
Habitat loss	■	■	▨	▨
Habitat fragmentation	■	■	■	□
Overexploitation	■	■	▨	□
Exotic species	■	■	■	■
Pollution	▨	▨	▨	■
Climate change	▨	▨	▨	▨

(b)

	Genes and populations	Species	Communities	Ecosystems
Habitat loss	▨	▨	▨	▨
Habitat fragmentation	■	■	▨	□
Overexploitation	□	□	□	□
Exotic species	■	■	■	■
Pollution	■	■	▨	■
Climate change	■	▨	■	■

Fig. 6.5 Relative impacts of factors affecting terrestrial biodiversity in: (a) poor; and (b) rich countries. Shading indicates intensity of impact, from black (highest) to light grey (lowest). (From Soulé 1991.)

(c) Adopt measures for the recovery and rehabilitation of threatened species and for their reintroduction into their natural habitats under appropriate conditions;
(d) Regulate and manage collection of biological resources from natural habitats for ex-situ *conservation purposes so as not to threaten ecosystems and* in-situ *populations of species, except where special temporary* ex-situ *measures are required under subparagraph (c) above; and*
(e) Cooperate in providing financial and other support for ex-situ *conservation outlined in subparagraphs (a) to (d) above and in the establishment and maintenance of* ex-situ *conservation facilities in developing countries.*

Ex-situ conservation measures may include seed banks, sperm and ova banks, culture collections (e.g. of plant tissues), artificial propagation of plants and captive breeding of animals. In a growing number of instances, more individuals of given species are held in such facilities than occur in the wild. The relative costs and benefits of *ex-situ* conservation have been much debated (e.g. Tudge 1992; Rahbek 1993; Hurka 1994; Balmford et al. 1995, 1996; Frankel et al. 1995). This is particularly true with regard to large-bodied vertebrates (such as primates, big cats and cetaceans). Key issues here include the ethics of keeping individuals in captivity, whether the resources so used could practically be deployed in other ways (e.g. for *in-situ* conservation), the short- and long-term viability of both captive and wild populations, the relationship between the two (including the use and efficacy of reintroductions of species into areas in which they have become extinct, and to bolster declining natural populations), and other potential benefits of captive populations (e.g. in education of urban human populations). Whatever one's position on these matters, *ex-situ* activities should play only a very secondary role to *in-situ* conservation, as implied by the opening statement of this Article.

6.7 Sustainable use of components of biological diversity

The sustainable use of biological diversity is one of the objectives of the Convention (Article 1). Article 10 embodies the obligations for attaining this goal.

Each Contracting Party shall, as far as possible and as appropriate:
(a) Integrate consideration of the conservation and sustainable use of biological resources into national decision-making;
(b) Adopt measures relating to the use of biological resources to avoid or minimize adverse impacts on biological diversity;
(c) Protect and encourage customary use of biological resources in accordance with traditional cultural practices that are compatible with conservation or sustainable use requirements;
(d) Support local populations to develop and implement remedial action in degraded areas where biological diversity has been reduced; and
(e) Encourage cooperation between its governmental authorities and its private sector in developing methods for sustainable uses of biological resources.

To live sustainably, the human population must do so within the biosphere's regenerative capacity, drawing on its natural capital without depleting the capital stock. Evidence suggests that since the 1980s, human exploitation of the Earth's biological productivity may well have exceeded this capacity, such that the ecological footprint (Section 4.3) of the global population in 1999 was 1.2 times that of the entire Earth (Wackernagel et al. 2002). Issues of sustainability thus extend far beyond the frequent media focus on trade in particular commodities of high economic value, such as wood from mahoganies, horn from rhinoceros, body parts from tigers and ivory from elephants. Put simply, most present use of biodiversity is not sustainable (management approaches have often focussed on maximizing short-term yield and economic gain rather than long-term sustainability).

A major difficulty lies in controlling the level of use. Even where use may be reasonably sustainable at low levels, it may significantly impact at higher levels. This highlights the potential tradeoffs between levels of use, the spatial extent of that use (to obtain the same resource, low levels of use have to be spread over greater areas), and the impacts of use. Such considerations span the extraction of products from natural tropical forests to the planting of genetically modified crops.

In essence, the Convention proposes that sustainable use is to be attained by its integration into national planning. How this can most effectively be done is a complex issue, with debate particularly centred on the most appropriate approach to trade (free-market, highly regulated, etc.).

Sustainable use requires the support of local peoples, and the protection and encouragement of customary use is one way in which to achieve this. However, it is important to distinguish those traditional uses that are compatible with conservation and sustainable use from those that are not. For example, the widespread belief that 'primitive' peoples have no appreciable adverse impact on their environment is, expressed in such a generic fashion, simply a myth (Section 5.2.1; Milberg & Tyrberg 1993). Even when not based on distortions of history, appeals to traditional uses often reflect situations in which human densities were far lower and there was no commercial exploitation (van Schaik & Rijksen 2002).

6.8 Incentive measures

Biodiversity loss is driven in major part by economic forces. Article 11 is an attempt to harness these same forces to its conservation and sustainability.

> *Each Contracting Party shall, as far as possible and as appropriate, adopt economically and socially sound measures that act as incentives for the conservation and sustainable use of components of biological diversity.*

Put simply, the obligation is to adopt measures that encourage conservation and sustainable use (Glowka et al. 1994). In contrast, as exemplified by perverse subsidies, the converse is often the case.

The interactions between society and the environment are complex, requiring careful analysis to determine the full consequences of particular actions. A causal framework for examining these interactions adopted by the European Environment Agency is DPSIR (Fig. 6.6), which provides a useful basis for working through such complexities.

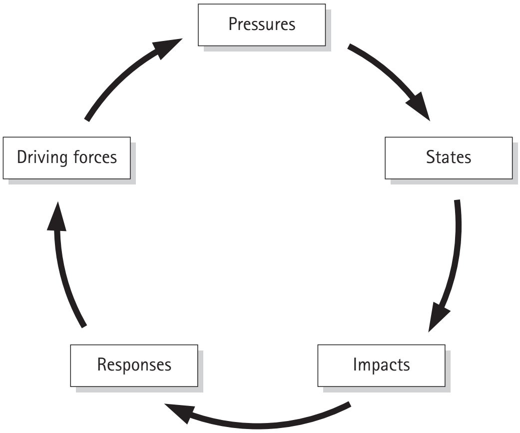


Fig. 6.6 The DPSIR model adopted by the European Environment Agency.

6.9 Responses to the Convention

As has already been mentioned (Section 6.3), a number of Parties to the Convention have produced Biodiversity Strategies and Action Plans. This is, however, a rather easy step in responding to its contents, albeit one which may attract significant media attention. Implementing the changes required to conserve biodiversity effectively and to exploit it in a sustainable fashion is much more difficult, and typically unpalatable to politicians with short-term goals (like re-election and personal financial gain). A number of nations have made small steps in the right direction, but substantial moves are largely wanting.

The obvious way forward, employed by other treaties and agreements, is to establish and agree targets for each party to achieve in fulfilment of the Convention, and protocols for reporting progress so that this can be rigorously assessed. Unfortunately, such an approach has yet to be adopted, despite several Conferences of the Parties (CoPs) and summit meetings; at the time of writing, the most recent summit, the World Summit on Sustainable Development, was held in Johannesburg in 2002. Until significant progress is made in achieving the principles laid down in the Convention, whether by ensuring its application or by some other mechanism (individual nations could make much progress unilaterally), then biodiversity will continue to decline as a consequence of human activities. Whether ultimately this will threaten the existence of humanity is less significant than whether it will threaten the kind of existence people would like to enjoy. For us, it is already doing so.

6.10 Summary

1 The Convention on Biological Diversity is one of the main global attempts to set an agenda for maintaining biodiversity and provides a useful framework for considering these issues.

2 The main objectives of the Convention are the conservation of biological diversity, the sustainable use of its components, and the fair and equitable sharing of the benefits arising from the utilization of genetic resources.

3 The conservation and sustainable use of biodiversity will not emerge fortuitously in each nation, but will require the establishment of explicit mechanisms.

4 In order to know whether strategies, programmes and plans for conservation and sustainable use are appropriate and are working effectively, it will be necessary to gather suitable information.

5 Conservation of biodiversity will require a network of protected areas for *in-situ* protection, measures for its conservation in the wider landscape, and perhaps also the use of *ex-situ* measures.

6 Sustainable use will only be attained by its integration into national planning, to minimize the adverse impacts of use on biodiversity.

7 Whilst there have been moves in the direction of the changes embodied in the Convention, as yet these are wholly inadequate.

Further reading

The Convention on Biological Diversity

Glowka, L., Burhenne-Guilmin, F., Synge, H., McNeely, J.A. & Gündling, L. (1994) *A Guide to the Convention on Biological Diversity*. IUCN, Gland & Cambridge. (*A detailed guide to the Convention on Biological Diversity*.)

Johnson, S.P. (1993) *The Earth Summit: The United Nations Conference on Environment and Development (UNCED)*. Graham & Trotman, London. (*Rio – the official autobiography*.)

McConnell, F. (1996) *The Biodiversity Convention: A Negotiating History*. Kluwer Law International, London. (*A fascinating account of negotiating the Convention by the head of the UK delegation*.)

The Convention on Biological Diversity and all of the material associated with it is accessible at http://www.biodiv.org/.

Conserving and sustainably exploiting biodiversity

Adams, W.M. (1997) *Future Nature. A Vision for Conservation*. Earthscan, London. (*A readable and thought-provoking 'history' of conservation in the UK*.)

Barthlott, W. & Winiger, W. (eds.) (1998) *Biodiversity: A Challenge for Development Research and Policy*. Springer-Verlag, Berlin. (*Another multi-authored, multidisciplinary symposium proceedings, predictably eclectic but with some nice chapters*.)

Byron, H. (2000) *Biodiversity Impact. A Good Practice Guide for Road Schemes*. RSPB, WWF-UK, English Nature and the Wildlife Trusts, Sandy. (*Goes from background theory – what is biodiversity – through to literally where the rubber hits the road*.)

Davidson, E.A. (2000) *You Can't Eat GNP: Economics as if Ecology Mattered*. Perseus Publishing, Cambridge, MA. (*Argues that traditional economic techniques don't work when you're talking about real things such as trees and rubbish*.)

Entwistle, A. & Dunstone, N. (2000) *Priorities for Conservation of Mammalian Diversity. Has the Panda Had its Day?* Cambridge University Press, Cambridge. (*Reviews of recent academic advances and how they can be applied practically*.)

Forey, P.L., Humphries, C.J. & Vane-Wright, R.I. (eds.) (1994) *Systematics and Conservation Evaluation*. Clarendon Press, Oxford. (*An important treatise on methodology, mostly still state of the art*.)

Guruswamy, L.D. & McNeely, J.A. (eds.) (1998) *Protection of Global Biodiversity*. Duke University Press, Durham & London. (*Interdisciplinary approach to formulating policies aimed at protecting biodiversity*.)

Holdgate, M. (1999) *The Green Web: A Union for World Conservation*. Earthscan, London. (*Written by a former director general of IUCN, this book shows how far the conservation movement has come in the last half century*.)

Juniper, T. (2002) *Spix's Macaw: The Race to Save the World's Rarest Bird*. Fourth Estate, London. (*An account of the realities of trying to conserve a magnificent animal, and 'the lethal cocktail of egos, jealousy, law-breaking, suspicion, politicking and greed that has all but wiped them out'*.)

MacDonald, M. (1998) *Agendas for Sustainability: Environment and Development into the Twenty-first Century*. Routledge, London. (*Very practical suggestions for devising global environmental and development agendas*.)

McNeely, J.A., Miller, K.R., Reid, W.V., Mittermeier, R.A. & Werner, T.B. (1990) *Conserving the World's Biological Diversity*. IUCN, Gland; WRI, CI, WWF-US and the World Bank, Washington, DC. (*Authoritative book that champions the view that we 'need to recognise the reasons for the existence of species and ecosystems may be more subtle and inscrutable than simply supporting the economic desires of the current generation of consumers'*.)

Miller, K., Allegretti, M.H., Johnson, N. & Jonsson, B. (1995) Measures for conservation of biodiversity and sustainable use of its components. In: *Global Biodiversity Assessment* (ed. V.H. Heywood), pp. 915–1061. Cambridge University Press, Cambridge. (*More of a book than a chapter, seven lead authors and 39 contributors put together a practical, considered framework for protecting, restoring and managing biodiversity*.)

Milner-Gulland, E.J. & Mace, R. (1998) *Conservation of Biological Resources*. Blackwell Science, Oxford. (*Written by an anthropologist and a biologist, with 10 case studies by invited contributors – that should give you some insight into the book's approach*.)

Moffat, I., Hanley, N. & Wilson, M.D. (2001) *Measuring and Modelling Sustainable Development*. Parthenon Publishing, Lancaster. (*Uses Scotland as a model system – so can't be bad*.)

Norris, K. & Pain, D.J. (eds.) (2002) *Conserving Bird Biodiversity*. Cambridge University Press, Cambridge. (*Not just a book about birds*.)

Oates, J.F. (1999) *Myth and Reality in the Rain Forest: How Conservation Strategies are Failing in West Africa*. University of California Press, Berkeley, CA. (*A clear demonstration that integrated conservation and development projects have failed as a method of maintaining biodiversity in protected areas*.)

Stein, B.A., Kutner, L.S. & Adams, J.S. (2000) *The Precious Heritage. The Status of Biodiversity in the United States*. Oxford University Press, New York. (*With a foreword by E.O. Wilson this is a readable account of the state of biodiversity in the USA*.)

Sutherland, W.J. (2000) *The Conservation Handbook: Research, Management and Policy*. Blackwell Science, Oxford. (*A practical and yet optimistic mixture of information and advice*.)

Swanson, T. (1997) *Global Action for Biodiversity*. Earthscan, London. (*A discussion of the elements of the Convention on Biological Diversity that can only be achieved if there is international agreement, written by an innovative environmental economist*.)

Terborgh, J. (1999) *Requiem for Nature*. Island Press, Washington, DC. (*An account of the realities of trying to conserve tropical forests, and the hard choices that have to be made.*)

Terborgh, J., van Schaik, C., Davenport, L. & Rao, M. (eds.) (2002) *Making Parks Work: Strategies for Preserving Tropical Nature*. Island Press, Washington, DC. (*An account of how and where protected areas work, and what should be done when they don't.*)

Victor, D.G. (2001) *The Collapse of the Kyoto Protocol and the Struggle to Slow Global Warming*. Princeton University Press, Princeton, NJ. (*Makes a strong case that without political action which is both strategic and global, there is no chance of tackling climate change.*)

WRI/IUCN/UNEP (1992) *Global Biodiversity Strategy: Guidelines for Action to Save, Study, and Use Earth's Biotic Wealth Sustainably and Equitably*. World Resources Institute, Washington, DC, World Conservation Union, Gland and United Nations Environment Programme, Nairobi.

Conservation biology

Caughley, G. & Gunn, A. (1996) *Conservation Biology in Theory and Practice*. Blackwell Science, Oxford. (*A great book.*)

Frankham, R., Ballou, J.D. & Briscoe, D.A. (2002) *Introduction to Conservation Genetics*. Cambridge University Press, Cambridge. (*Excellent undergraduate text that covers a lot of ground.*)

Gibbs, J.P., Hunter, M.L. & Sterling, E.J. (1998) *Problem-solving in Conservation Biology and Wildlife Management: Exercises for Class, Field and Laboratory*. Blackwell Science, Oxford. (*Written primarily with a North American audience in mind, this is still a valuable book for an international one, containing 27 practical exercises for use in teaching final-year undergraduates conservation biology.*)

Hunter, M.L. Jr (2002) *Fundamentals of Conservation Biology*, 2nd edn. Blackwell Science, Oxford. (*A well-organized, and wide-ranging, introduction to this subject.*)

Meffe, G.K. & Carroll, C.R. (1997) *Principles of Conservation Biology*, 2nd edn. Sinauer Associates, Sunderland, MA. (*Addresses the major issues in conservation biology, with many helpful examples.*)

Primack, R.B. (2002) *Essentials of Conservation Biology*, 3rd edn. Sinauer Associates, Sunderland, MA. (*A well-organized, and wide-ranging, introduction to this subject.*)

Pullin, A.S. (2002) *Conservation Biology*. Cambridge University Press, Cambridge. (*Simple and clear undergraduate text, but avoids economic and political issues.*)

Spellerberg, I.F. (ed.) (1996) *Conservation Biology*. Longman, Harlow. (*A useful set of reviews of many of the major issues.*)

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This concise introductory text provides a complete overview of biodiversity – what it is, how it arose, its distribution, why it is important, human impact upon it, and what should be done to maintain it.

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Kevin J. Gaston is Professor of Biodiversity and Conservation at the University of Sheffield. He has broad research interests in the fields of biodiversity, macroecology and conservation biology.

John I. Spicer is a Reader in Marine Biology at the University of Plymouth. His research interests range from the ecophysiology of marine animals through to the functional biodiversity of marine systems.

Cover illustration shows most of a 0.25m² quadrat from a vertical marine rock wall habitat at 13m depth off the west coast of the Cape Peninsula, South Africa. © Jon D. Witman.

Cover design Baseline Arts Ltd

Printed in the United Kingdom

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ISBN 1-4051-1857-1

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