CHAPTER 2

Biodiversity

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Biological diversity or biodiversity (the latter term is simply a contraction of the former) is *the variety of life*, in all of its many manifestations. It is a broad unifying concept, encompassing all forms, levels and combinations of natural variation, at all levels of biological organization (Gaston and Spicer 2004). A rather longer and more formal definition is given in the international Convention on Biological Diversity (CBD; the definition is provided in Article 2), which 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". Whichever definition is preferred, one can, for example, speak equally of the biodiversity of some given area or volume (be it large or small) of the land or sea, of the biodiversity of a continent or an ocean basin, or of the biodiversity of the entire Earth. Likewise, one can speak of biodiversity at present, at a given time or period in the past or in the future, or over the entire history of life on Earth.

The scale of the variety of life is difficult, and perhaps impossible, for any of us truly to visualize or comprehend. In this chapter I first attempt to give some sense of the magnitude of biodiversity by distinguishing between different key elements and what is known about their variation. Second, I consider how the variety of life has changed through time, and third and finally how it varies in space. In short, the chapter will, inevitably in highly summarized form, address the three key issues of how much biodiversity there is, how it arose, and where it can be found.

2.1 How much biodiversity is there?

Some understanding of what the variety of life comprises can be obtained by distinguishing between different key elements. These are the basic building blocks of biodiversity. For convenience, they can be divided into three groups: genetic diversity, organismal diversity, and ecological diversity (Table 2.1). Within each, the elements are organized in nested hierarchies, with those higher order elements comprising lower order

Table 2.1 Elements of biodiversity (focusing on those levels that are most commonly used). Modified from Heywood and Baste (1995).

Ecological diversity		Organismal diversity
Biogeographic realms		Domains or Kingdoms
Biomes		Phyla
Provinces		Families
Ecoregions		Genera
Ecosystems		Species
Habitats	**Genetic diversity**	Subspecies
Populations	Populations	Populations
	Individuals	Individuals
	Chromosomes	
	Genes	
	Nucleotides	

ones. The three groups are intimately linked and share some elements in common.

2.1.1 Genetic diversity

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. This is the raw material on which evolutionary processes act. Perhaps the most basic measure of genetic diversity is genome size—the amount of DNA (Deoxyribonucleic acid) in one copy of a species' chromosomes (also called the C-value). This can vary enormously, with published eukaryote genome sizes ranging between 0.0023 pg (picograms) in the parasitic microsporidium *Encephalitozoon intestinalis* and 1400 pg in the free-living amoeba *Chaos chaos* (Gregory 2008). These translate into estimates of 2.2 million and 1369 billion base pairs (the nucleotides on opposing DNA strands), respectively. Thus, even at this level the scale of biodiversity is daunting. Cell size tends to increase with genome size. Humans have a genome size of 3.5 pg (3.4 billion base pairs).

Much of genome size comprises non-coding DNA, and there is usually no correlation between genome size and the number of genes coded. The genomes of more than 180 species have been completely sequenced and it is estimated that, for example, there are around 1750 genes for the bacteria *Haemophilus influenzae* and 3200 for *Escherichia coli*, 6000 for the yeast *Saccharomyces cerevisiae*, 19 000 for the nematode *Caenorhabditis elegans*, 13 500 for the fruit fly *Drosophila melanogaster*, and ~25 000 for the plant *Arabidopsis thaliana*, the mouse *Mus musculus*, brown rat *Rattus norvegicus* and human *Homo sapiens*. There is strong conservatism of some genes across much of the diversity of life. The differences in genetic composition of species give us indications of their relatedness, and thus important information as to how the history and variety of life developed.

Genes are packaged into chromosomes. The number of chromosomes per somatic cell thus far observed varies between 2 for the jumper ant *Myrmecia pilosula* and 1260 for the adders-tongue fern *Ophioglossum reticulatum*. The ant species reproduces by haplodiploidy, in which fertilized eggs (diploid) develop into females and unfertilized eggs (haploid) become males, hence the latter have the minimal achievable single chromosome in their cells (Gould 1991). Humans have 46 chromosomes (22 pairs of autosomes, and one pair of sex chromosomes).

Within a species, genetic diversity is commonly measured in terms of allelic diversity (average number of alleles per locus), gene diversity (heterozygosity across loci), or nucleotide differences. Large populations tend to have more genetic diversity than small ones, more stable populations more than those that wildly fluctuate, and populations at the center of a species' geographic range often have more genetic diversity than those at the periphery. Such variation can have a variety of population-level influences, including on productivity/biomass, fitness components, behavior, and responses to disturbance, as well as influences on species diversity and ecosystem processes (Hughes *et al.* 2008).

2.1.2 Organismal diversity

Organismal diversity encompasses the full taxonomic hierarchy and its components, from individuals upwards to populations, subspecies and species, genera, families, phyla, and beyond to kingdoms and domains. Measures of organismal diversity thus include some of the most familiar expressions of biodiversity, such as the numbers of species (i.e. species richness). Others should be better studied and more routinely employed than they have been thus far.

Starting at the lowest level of organismal diversity, little is known about how many individual organisms there are at any one time, although this is arguably an important measure of the quantity and variety of life (given that, even if sometimes only in small ways, most individuals differ from one another). Nonetheless, the numbers must be extraordinary. The global number of prokaryotes has been estimated to be 4–6×10^{30} cells—many million times more than there are stars in the visible universe (Copley 2002)—with a production rate of 1.7×10^{30} cells per annum (Whitman *et al.* 1998). The numbers of protists is estimated at 10^4–10^7 individuals per m^2 (Finlay 2004).

Impoverished habitats have been estimated to have 10^5 individual nematodes per m^2, and more productive habitats 10^6–10^7 per m^2, possibly with an upper limit of 10^8 per m^2; 10^{19} has been suggested as a conservative estimate of the global number of individuals of free-living nematodes (Lambshead 2004). By contrast, it has been estimated that globally there may be less than 10^{11} breeding birds at any one time, fewer than 17 for every person on the planet (Gaston *et al.* 2003).

Individual organisms can be grouped into relatively independent populations of a species on the basis of limited gene flow and some level of genetic differentiation (as well as on ecological criteria). The population is a particularly important element of biodiversity. First, it provides an important link between the different groups of elements of biodiversity (Table 2.1). Second, it is the scale at which it is perhaps most sensible to consider linkages between biodiversity and the provision of ecosystem services (supporting services—e.g. nutrient cycling, soil formation, primary production; provisioning services—e.g. food, freshwater, timber and fiber, fuel; regulating services—e.g. climate regulation, flood regulation, disease regulation, water purification; cultural services—e.g. aesthetic, spiritual, educational, recreational; MEA 2005). Estimates of the density of such populations and the average geographic range sizes of species suggest a total of about 220 distinct populations per eukaryote species (Hughes *et al.* 1997). Multiplying this by a range of estimates of the extant numbers of species, gives a global total of 1.1 to 6.6 x 10^9 populations (Hughes *et al.* 1997), one or fewer for every person on the planet. The accuracy of this figure is essentially unknown, with major uncertainties at each step of the calculation, but the ease with which populations can be eradicated (e.g. through habitat destruction) suggests that the total is being eroded at a rapid rate.

People have long pondered one of the important contributors to the calculation of the total number of populations, namely how many different species of organisms there might be. Greatest uncertainty continues to surround the richness of prokaryotes, and in consequence they are often ignored in global totals of species numbers. This is in part variously because of difficulties in ap-

plying standard species concepts, in culturing the vast majority of these organisms and thereby applying classical identification techniques, and by the vast numbers of individuals. Indeed, depending on the approach taken, the numbers of prokaryotic species estimated to occur even in very small areas can vary by a few orders of magnitude (Curtis *et al.* 2002; Ward 2002). The rate of reassociation of denatured (i.e. single stranded) DNA has revealed that in pristine soils and sediments with high organic content samples of 30 to 100 cm^3 correspond to c. 3000 to 11 000 different genomes, and may contain 10^4 different prokaryotic species of equivalent abundances (Torsvik *et al.* 2002). Samples from the intestinal microbial flora of just three adult humans contained representatives of 395 bacterial operational taxonomic units (groups without formal designation of taxonomic rank, but thought here to be roughly equivalent to species), of which 244 were previously unknown, and 80% were from species that have not been cultured (Eckburg *et al.* 2005). Likewise, samples from leaves were estimated to harbor at least 95 to 671 bacterial species from each of nine tropical tree species, with only 0.5% common to all the tree species, and almost all of the bacterial species being undescribed (Lambais *et al.* 2006). On the basis of such findings, global prokaryote diversity has been argued to comprise possibly millions of species, and some have suggested it may be many orders of magnitude more than that (Fuhrman and Campbell 1998; Dykhuizen 1998; Torsvik *et al.* 2002; Venter *et al.* 2004).

Although much more certainty surrounds estimates of the numbers of eukaryotic than prokaryotic species, this is true only in a relative and not an absolute sense. Numbers of eukaryotic species are still poorly understood. A wide variety of approaches have been employed to estimate the global numbers in large taxonomic groups and, by summation of these estimates, how many extant species there are overall. These approaches include extrapolations based on counting species, canvassing taxonomic experts, temporal patterns of species description, proportions of undescribed species in samples, well-studied areas, well-studied groups, species-abundance distributions, species-body size

distributions, and trophic relations (Gaston 2008). One recent summary for eukaryotes gives lower and upper estimates of 3.5 and 108 million species, respectively, and a working figure of around 8 million species (Table 2.2). Based on current information the two extremes seem rather unlikely, but the working figure at least seems tenable. However, major uncertainties surround global numbers of eukaryotic species in particular environments which have been poorly sampled (e.g. deep sea, soils, tropical forest canopies), in higher taxa which are extremely species rich or with species which are very difficult to discriminate (e.g. nematodes, arthropods), and in particular functional groups which are less readily studied (e.g. parasites). A wide array of techniques is now being employed to gain access to some of the environments that have been less well explored, including rope climbing techniques, aerial walkways, cranes and balloons for tropical forest canopies, and remotely operated vehicles, bottom landers, submarines, sonar, and video for the deep ocean. Molecular and better imaging techniques are also improving species discrimination. Perhaps most significantly, however, it seems highly probable that the majority of species are parasites, and yet few people tend to think about biodiversity from this viewpoint.

How many of the total numbers of species have been taxonomically described remains surprisingly uncertain, in the continued absence of a single unified, complete and maintained database of valid formal names. However, probably about 2 million extant species are regarded as being known to science (MEA 2005). Importantly, this total hides two kinds of error. First, there are instances in which the same species is known under more than one name (synonymy). This is more frequent amongst widespread species, which may show marked geographic variation in morphology, and may be described anew repeatedly in different regions. Second, one name may actually encompass multiple species (homonymy). This typically occurs because these species are very closely related, and look very similar (cryptic species), and molecular analyses may be required to recognize or confirm their differences. Levels of as yet unresolved synonymy are undoubtedly high in many taxonomic groups. Indeed, the actual levels have proven to be a key issue in, for example, attempts to estimate the global species richness of plants, with the highly variable synonymy rate amongst the few groups that have been well studied in this regard making difficult the assessment of the overall level of synonymy across all the known species. Equally, however, it is apparent that cryptic species abound, with, for example, one species of neotropical skipper butterfly recently having been shown actually to be a complex of ten species (Hebert *et al.* 2004).

New species are being described at a rate of about 13 000 per annum (Hawksworth and

Table 2.2 Estimates (in thousands), by different taxonomic groups, of the overall global numbers of extant eukaryote species. Modified from Hawksworth and Kalin-Arroyo (1995) and May (2000).

	Overall species			
	High	**Low**	**Working figure**	**Accuracy of working figure**
'Protozoa'	200	60	100	very poor
'Algae'	1000	150	300	very poor
Plants	500	300	320	good
Fungi	2700	200	1500	moderate
Nematodes	1000	100	500	very poor
Arthropods	101 200	2375	4650	moderate
Molluscs	200	100	120	moderate
Chordates	55	50	50	good
Others	800	200	250	moderate
Totals	107 655	3535	7790	very poor

Kalin-Arroyo 1995), or about 36 species on the average day. Given even the lower estimates of overall species numbers this means that there is little immediate prospect of greatly reducing the numbers that remain unknown to science. This is particularly problematic because the described species are a highly biased sample of the extant biota rather than the random one that might enable more ready extrapolation of its properties to all extant species. On average, described species tend to be larger bodied, more abundant and more widespread, and disproportionately from temperate regions. Nonetheless, new species continue to be discovered in even otherwise relatively well-known taxonomic groups. New extant fish species are described at the rate of about 130–160 each year (Berra 1997), amphibian species at about 95 each year (from data in Frost 2004), bird species at about 6–7 each year (Van Rootselaar 1999, 2002), and terrestrial mammals at 25–30 each year (Ceballos and Ehrlich 2009). Recently discovered mammals include marsupials, whales and dolphins, a sloth, an elephant, primates, rodents, bats and ungulates.

Given the high proportion of species that have yet to be discovered, it seems highly likely that there are entire major taxonomic groups of organisms still to be found. That is, new examples of higher level elements of organismal diversity. This is supported by recent discoveries of possible new phyla (e.g. Nanoarchaeota), new orders (e.g. Mantophasmatodea), new families (e.g. Aspidytidae) and new subfamilies (e.g. Martialinae). Discoveries at the highest taxonomic levels have particularly served to highlight the much greater phyletic diversity of microorganisms compared with macroorganisms. Under one classification 60% of living phyla consist entirely or largely of unicellular species (Cavalier-Smith 2004). Again, this perspective on the variety of life is not well reflected in much of the literature on biodiversity.

2.1.3 Ecological diversity

The third group of elements of biodiversity encompasses the scales of ecological differences from populations, through habitats, to ecosys-

tems, ecoregions, provinces, and on up to biomes and biogeographic realms (Table 2.1). This is an important dimension to biodiversity not readily captured by genetic or organismal diversity, and in many ways is that which is most immediately apparent to us, giving the structure of the natural and semi-natural world in which we live. However, ecological diversity is arguably also the least satisfactory of the groups of elements of biodiversity. There are two reasons. First, whilst these elements clearly constitute useful ways of breaking up continua of phenomena, 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. In consequence, numerous schemes have been developed for distinguishing between many elements of ecological diversity, often with wide variation in the numbers of entities recognized for a given element. Second, some of the elements of ecological diversity clearly have both abiotic and biotic components (e.g. ecosystems, ecoregions, biomes), and yet biodiversity is defined as the variety of *life*.

Much recent interest has focused particularly on delineating ecoregions and biomes, principally for the purposes of spatial conservation planning (see Chapter 11), and there has thus been a growing sense of standardization of the schemes used. Ecoregions are large areal units containing geographically distinct species assemblages and experiencing geographically distinct environmental conditions. Careful mapping schemes have identified 867 terrestrial ecoregions (Figure 2.1 and Plate 1; Olson *et al.* 2001), 426 freshwater ecoregions (Abell *et al.* 2008), and 232 marine coastal & shelf area ecoregions (Spalding *et al.* 2007). Ecoregions can in turn be grouped into biomes, global-scale biogeographic regions distinguished by unique collections of species assemblages and ecosystems. Olson *et al.* (2001) distinguish 14 terrestrial biomes, some of which at least will be very familiar wherever in the world one resides (tropical & subtropical moist broadleaf forests;

Figure 2.1 The terrestrial ecoregions. Reprinted from Olson *et al.* (2001).

tropical & subtropical dry broadleaf forests; tropical & subtropical coniferous forests; temperate broadleaf & mixed forests; temperate coniferous forests; boreal forest/taiga; tropical & subtropical grasslands, savannas & shrublands; temperate grasslands, savannas & shrublands; flooded grasslands & savannas; montane grasslands & shrublands; tundra; Mediterranean forests, woodlands & scrub; deserts & xeric shrublands; mangroves).

At a yet coarser spatial resolution, terrestrial and aquatic systems can be divided into biogeographic realms. Terrestrially, eight such realms are typically recognized, Australasia, Antarctic, Afrotropic, Indo-Malaya, Nearctic, Neotropic, Oceania and Palearctic (Olson *et al.* 2001). Marine coastal & shelf areas have been divided into 12 realms (Arctic, Temperate North Atlantic, Temperate Northern Pacific, Tropical Atlantic, Western Indo-Pacific, Central Indo-Pacific, Eastern Indo-Pacific, Tropical Eastern Pacific, Temperate South America, Temperate Southern Africa, Temperate Australasia, and Southern Ocean; Spalding *et al.* 2007). There is no strictly equivalent scheme for the pelagic open ocean, although one has divided the oceans into four primary units (Polar, Westerlies, Trades and Coastal boundary), which are then subdivided, on the basis principally of biogeochemical features, into a further 12 biomes (Antarctic Polar, Antarctic Westerly Winds, Atlantic Coastal, Atlantic Polar, Atlantic Trade Wind, Atlantic Westerly Winds, Indian Ocean Coastal, Indian Ocean Trade Wind, Pacific Coastal, Pacific Polar, Pacific Trade Wind, Pacific Westerly Winds), and then into a finer 51 units (Longhurst 1998).

2.1.4 Measuring biodiversity

Given the multiple dimensions and the complexity of the variety of life, it should be obvious that there can be no single measure of biodiversity (see Chapter 16). Analyses and discussions of biodiversity have almost invariably to be framed in terms of particular elements or groups of elements, although this may not always be apparent from the terminology being employed (the term 'biodiversity' is used widely and without explicit qualification to refer to only some subset of the variety of life). Moreover, they have to be framed in terms either of "number" or of "heterogeneity" measures of biodiversity, with the former disregarding the degrees of difference between the

occurrences of an element of biodiversity and the latter explicitly incorporating such differences. For example, organismal diversity could be expressed in terms of species richness, which is a number measure, or using an index of diversity that incorporates differences in the abundances of the species, which is a heterogeneity measure. The two approaches constitute different responses to the question of whether biodiversity is similar or different in an assemblage in which a small proportion of the species comprise most of the individuals, and therefore would predominantly be obtained in a small sample of individuals, or in an assemblage of the same total number of species in which abundances are more evenly distributed, and thus more species would occur in a small sample of individuals (Purvis and Hector 2000). The distinction between number and heterogeneity measures is also captured in answers to questions that reflect taxonomic heterogeneity, for example whether the above-mentioned group of 10 skipper butterflies is as biodiverse as a group of five skipper species and five swallowtail species (e.g. Hendrickson and Ehrlich 1971).

In practice, biodiversity tends most commonly to be expressed in terms of number measures of organismal diversity, often the numbers of a given taxonomic level, and particularly the numbers of species. This is in large part a pragmatic choice. Organismal diversity is better documented and often more readily estimated than is genetic diversity, and more finely and consistently resolved than much of ecological diversity. Organismal diversity, however, is problematic inasmuch as the majority of it remains unknown (and thus studies have to be based on subsets), and precisely how naturally and well many taxonomic groups are themselves delimited remains in dispute. Perhaps most importantly it also remains but one, and arguably a quite narrow, perspective on biodiversity.

Whilst accepting the limitations of measuring biodiversity principally in terms of organismal diversity, the following sections on temporal and spatial variation in biodiversity will follow this course, focusing in many cases on species richness.

2.2 How has biodiversity changed through time?

The Earth is estimated to have formed, by the accretion through large and violent impacts of numerous bodies, approximately 4.5 billion years ago (Ga). Traditionally, habitable worlds are considered to be those on which liquid water is stable at the surface. On Earth, both the atmosphere and the oceans may well have started to form as the planet itself did so. Certainly, life is thought to have originated on Earth quite early in its history, probably after about 3.8–4.0 Ga, when impacts from large bodies from space are likely to have declined or ceased. It may have originated in a shallow marine pool, experiencing intense radiation, or possibly in the environment of a deeper water hydrothermal vent. Because of the subsequent recrystallisation and deformation of the oldest sediments on Earth, evidence for early life must be found in its metabolic interaction with the environment. The earliest, and highly controversial, evidence of life, from such indirect geochemical data, is from more than 3.83 billion years ago (Dauphas et al. 2004). Relatively unambiguous fossil evidence of life dates to 2.7 Ga (López-García et al. 2006). Either way, life has thus been present throughout much of the Earth's existence. Although inevitably attention tends to fall on more immediate concerns, it is perhaps worth occasionally recalling this deep heritage in the face of the conservation challenges of today. For much of this time, however, life comprised Precambrian chemosynthetic and photosynthetic prokaryotes, with oxygen-producing cyanobacteria being particularly important (Labandeira 2005). Indeed, the evolution of oxygenic photosynthesis, followed by oxygen becoming a major component of the atmosphere, brought about a dramatic transformation of the environment on Earth. Geochemical data has been argued to suggest that oxygenic photosynthesis evolved before 3.7 Ga (Rosing and Frei 2004), although others have proposed that it could not have arisen before c.2.9 Ga (Kopp et al. 2005).

These cyanobacteria were initially responsible for the accumulation of atmospheric oxygen. This in turn enabled the emergence of aerobically

metabolizing eukaryotes. At an early stage, eukaryotes incorporated within their structure aerobically metabolizing bacteria, giving rise to eukaryotic cells with mitochondria; all anaerobically metabolizing eukaryotes that have been studied in detail have thus far been found to have had aerobic ancestors, making it highly likely that the ancestral eukaryote was aerobic (Cavalier-Smith 2004). This was a fundamentally important event, leading to heterotrophic microorganisms and sexual means of reproduction. Such endosymbiosis occurred serially, by simpler and more complex routes, enabling eukaryotes to diversify in a variety of ways. Thus, the inclusion of photosynthesizing cyanobacteria into a eukaryote cell that already contained a mitochondrion gave rise to eukaryotic cells with plastids and capable of photosynthesis. This event alone would lead to dramatic alterations in the Earth's ecosystems.

Precisely when eukaryotes originated, when they diversified, and how congruent was the diversification of different groups remains unclear, with analyses giving a very wide range of dates (Simpson and Roger 2004). The uncertainty, which is particularly acute when attempting to understand evolutionary events in deep time, results principally from the inadequacy of the fossil record (which, because of the low probabilities of fossilization and fossil recovery, will always tend to underestimate the ages of taxa) and the difficulties of correctly calibrating molecular clocks so as to use the information embodied in genetic sequences to date these events. Nonetheless, there is increasing convergence on the idea that most known eukaryotes can be placed in one of five or six major clades—Unikonts (Opisthokonts and Amoebozoa), Plantae, Chromalveolates, Rhizaria and Excavata (Keeling *et al.* 2005; Roger and Hug 2006).

Focusing on the last 600 million years, attention shifts somewhat from the timing of key diversification events (which becomes less controversial) to how diversity *per se* has changed through time (which becomes more measurable). Arguably the critical issue is how well the known fossil record reflects the actual patterns of change that took place and how this record can best be analyzed to address its associated biases to determine those actual patterns. The best fossil data are for marine invertebrates and it was long thought that these principally demonstrated a dramatic rise in diversity, albeit punctuated by significant periods of stasis and mass extinction events. However, analyses based on standardized sampling have markedly altered this picture (Figure 2.2). They identify the key features of change in the numbers of genera (widely assumed to correlate with species richness) as comprising: (i) a rise in richness from the Cambrian through to the mid-Devonian (∼525–400 million years ago, Ma); (ii) a large extinction in the mid-Devonian with no clear recovery until the Permian (∼400–300 Ma); (iii) a large extinction in the late-Permian and again in the late-Triassic (∼250–200 Ma); and (iv) a rise in richness through the late-Triassic to the present (∼200–0 Ma; Alroy *et al.* 2008).

Whatever the detailed pattern of change in diversity through time, most of the species that have ever existed are extinct. Across a variety of groups (both terrestrial and marine), the best present estimate based on fossil evidence is that the average species has had a lifespan (from its appearance in the fossil record until the time it disappeared) of perhaps around 1–10 Myr (McKinney 1997; May 2000). However, the variability both within and between groups is very marked, making estimation of what is the overall average difficult. The longest-lived species that is well documented is a bryozoan that persisted from the early Cretaceous to the present, a period of approximately 85 million years (May 2000). If the fossil record spans 600 million years, total species numbers were to have been roughly constant over this period, and the average life span of individual species were 1–10 million years, then at any specific instant the extant species would have represented 0.2–2% of those that have ever lived (May 2000). If this were true of the present time then, if the number of extant eukaryote species numbers 8 million, 400 million might once have existed.

The frequency distribution of the numbers of time periods with different levels of extinction is markedly right-skewed, with most periods having relatively low levels of extinction and a
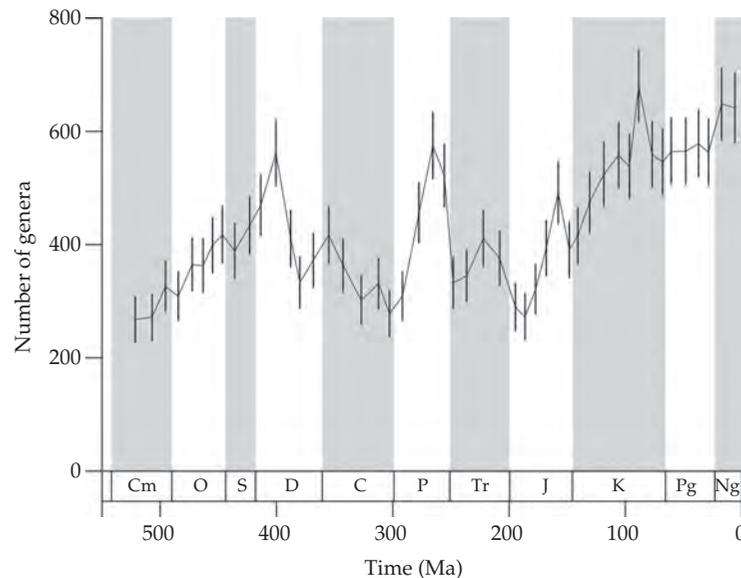
Figure 2.2 Changes in generic richness of marine invertebrates over the last 600 million years based on a sampling-standardized analysis of the fossil record. Ma, million years ago. Reprinted from Alroy *et al.* (2008) with permission from AAAS (American Association for the Advancement of Science).

minority having very high levels (Raup 1994). The latter are the periods of mass extinction when 75–95% of species that were extant are estimated to have become extinct. Their significance lies not, however, in the overall numbers of extinctions for which they account (over the last 500 Myr this has been rather small), but in the hugely disruptive effect they have had on the development of biodiversity. Clearly neither terrestrial nor marine biotas are infinitely resilient to environmental stresses. Rather, when pushed beyond their limits they can experience dramatic collapses in genetic, organismal and ecological diversity (Erwin 2008). This is highly significant given the intensity and range of pressures that have been exerted on biodiversity by humankind, and which have drastically reshaped the natural world over a sufficiently long period in respect to available data that we have rather little concept of what a truly natural system should look like (Jackson 2008). Recovery from past mass extinction events has invariably taken place. But, whilst this may have been rapid in geological terms, it has nonetheless taken of the order of a few mil-

lion years (Erwin 1998), and the resultant assemblages have invariably had a markedly different composition from those that preceded a mass extinction, with groups which were previously highly successful in terms of species richness being lost entirely or persisting at reduced numbers.

2.3 Where is biodiversity?

Just as biodiversity has varied markedly through time, so it also varies across space. Indeed, one can think of it as forming a richly textured land and seascape, with peaks (hotspots) and troughs (coldspots), and extensive plains in between (Figure 2.3 and Plate 2, and 2.4 and Plate 3; Gaston 2000). Even locally, and just for particular groups, the numbers of species can be impressive, with for example c.900 species of fungal fruiting bodies recorded from 13 plots totaling just 14.7 ha (hectare) near Vienna, Austria (Straatsma and Krisai-Greilhuber 2003), 173 species of lichens on a single tree in Papua New Guinea (Aptroot
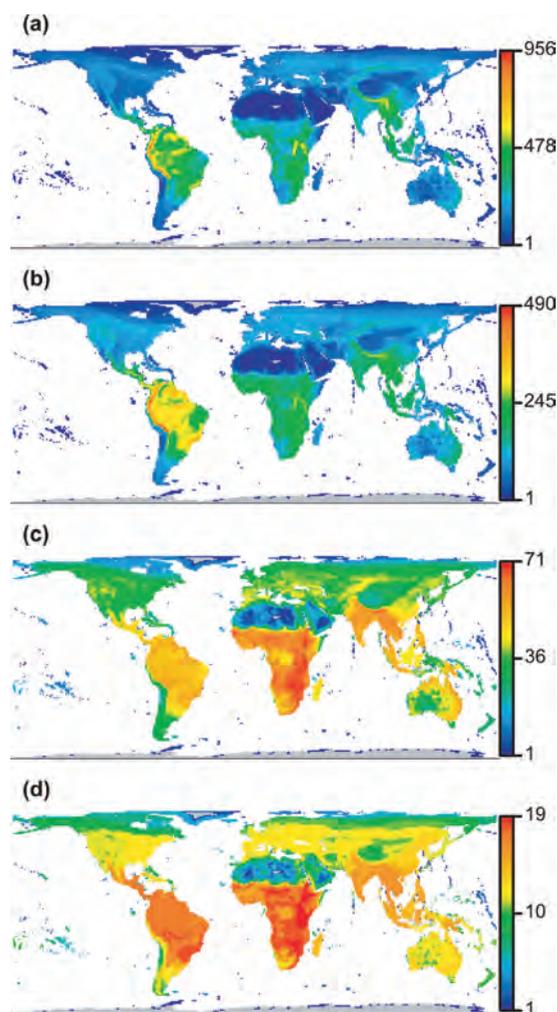
Figure 2.3 Global richness patterns for birds of (a) species, (b) genera, (c) families, and (d) orders. Reprinted from Thomas *et al.* (2008).

1997), 814 species of trees from a 50 ha study plot in Peninsular Malaysia (Manokaran *et al.* 1992), 850 species of invertebrates estimated to occur at a sandy beach site in the North Sea (Armonies and Reise 2000), 245 resident species of birds recorded holding territories on a 97 ha plot in Peru (Terborgh *et al.* 1990), and >200 species of mammals occurring at some sites in the Amazonian rain forest (Voss and Emmons 1996).

Although it remains the case that for no even moderately sized area do we have a comprehen-sive inventory of all of the species that are present (microorganisms typically remain insufficiently documented even in otherwise well studied areas), knowledge of the basic patterns has been developing rapidly. Although long constrained to data on higher vertebrates, the breadth of or-ganisms for which information is available has been growing, with much recent work particular-ly attempting to determine whether microorgan-isms show the same geographic patterns as do other groups.
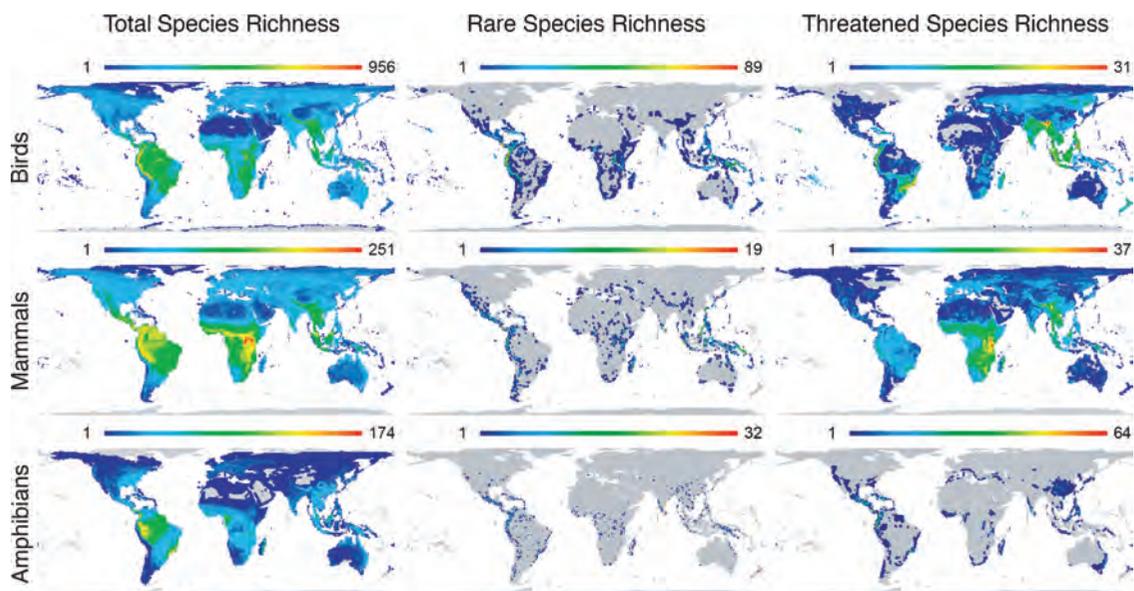
Figure 2.4 Global species richness patterns of birds, mammals, and amphibians, for total, rare (those in the lower quartile of range size for each group) and threatened (according to the IUCN criteria) species. Reprinted from Grenyer *et al.* (2006).

2.3.1 Land and water

The oceans cover ~340.1 million km^2 (67%), the land ~170.3 million km^2 (33%), and freshwaters (lakes and rivers) ~1.5 million km^2 (0.3%; with another 16 million km^2 under ice and permanent snow, and 2.6 million km^2 as wetlands, soil water and permafrost) of the Earth's surface. It would therefore seem reasonable to predict that the oceans would be most biodiverse, followed by the land and then freshwaters. In terms of numbers of higher taxa, there is indeed some evidence that marine systems are especially diverse. For example, of the 96 phyla recognized by Margulis and Schwartz (1998), about 69 have marine representatives, 55 have terrestrial ones, and 60 have freshwater representatives. However, of the species described to date only about 15% are marine and 6% are freshwater. The fact that life began in the sea seems likely to have played an important role in explaining why there are larger numbers of higher taxa in marine systems than in terrestrial ones. The heterogeneity and fragmentation of the land masses (particularly that associated with the breakup of the "supercontinent" of Gondwana from ~180 Ma) is important in explaining why there are more species in terrestrial systems than in marine ones. Finally, the extreme fragmentation and isolation of freshwater bodies seems key to why these are so diverse for their area.

2.3.2 Biogeographic realms and ecoregions

Of the terrestrial realms, the Neotropics is generally regarded as overall being the most biodiverse, followed by the Afrotropics and Indo-Malaya, although the precise ranking of these tropical regions depends on the way in which organismal diversity is measured. For example, for species the richest realm is the Neotropics for amphibians, reptiles, birds and mammals, but for families it is the Afrotropics for amphibians and mammals, the Neotropics for reptiles, and the Indo-Malayan for birds (MEA 2005). In parts, these differences reflect variation in the histories of the realms (especially mountain uplift and climate changes) and the interaction with the emergence and spread of the groups, albeit perhaps

Table 2.3 The five most species rich terrestrial ecoregions for each of four vertebrate groups. AT – Afrotropic, IM – Indo-Malaya, NA – Nearctic, and NT–Neotropic. Data from Olson *et al.* (2001).

	Amphibians	Reptiles	Birds	Mammals
1	Northwestern Andean montane forests (NT)	Peten-Veracruz moist forests (NT)	Northern Indochina subtropical forests (IM)	Sierra Madre de Oaxaca pine-oak forests (NT)
2	Eastern Cordillera real montane forests (NT)	Southwest Amazon moist forests (NT)	Southwest Amazon moist forests (NT)	Northern Indochina subtropical forests (IM)
3	Napo moist forests (NT)	Napo moist forests (NT)	Albertine Rift montane forests (AT)	Sierra Madre Oriental pine-oak forests (NA)
4	Southwest Amazon moist forests (NT)	Southern Pacific dry forests (NT)	Central Zambezian Miombo woodlands (AT)	Southwest Amazon moist forests (NT)
5	Choco-Darien moist forests (NT)	Central American pine-oak forests (NT)	Northern Acacia-Commiphora bushlands & thickets (AT)	Central Zambezian Miombo woodlands (AT)

complicated by issues of geographic consistency in the definition of higher taxonomic groupings.

The Western Indo-Pacific and Central Indo-Pacific realms have been argued to be a center for the evolutionary radiation of many groups, and are thought to be perhaps the global hotspot of marine species richness and endemism (Briggs 1999; Roberts *et al.* 2002). With a shelf area of 6 570 000 km^2, which is considered to be a significant influence, it has more than 6000 species of molluscs, 800 species of echinoderms, 500 species of hermatypic (reef forming) corals, and 4000 species of fish (Briggs 1999).

At the scale of terrestrial ecoregions, the most speciose for amphibians and reptiles are in the Neotropics, for birds in Indo-Malaya, Neotropics and Afrotropics, and for mammals in the Neotropics, Indo-Malaya, Nearctic, and Afrotropics (Table 2.3). Amongst the freshwater ecoregions, those with globally high richness of freshwater fish include the Brahmaputra, Ganges, and Yangtze basins in Asia, and large portions of the Mekong, Chao Phraya, and Sitang and Irrawaddy; the lower Guinea in Africa; and the Paraná and Orinoco in South America (Abell *et al.* 2008).

2.3.3 Latitude

Perhaps the best known of all spatial patterns in biodiversity is the general increase in species richness (and some other elements of organismal diversity) towards lower (tropical) latitudes. Several features of this gradient are of note: (i) it is exhibited in marine, terrestrial and freshwaters, and by virtually all major taxonomic groups, including microbes, plants, invertebrates and vertebrates (Hillebrand 2004; Fuhrman *et al.* 2008); (ii) it is typically manifest whether biodiversity is determined at local sites, across large regions, or across entire latitudinal bands; (iii) it has been a persistent feature of much of the history of life on Earth (Crane and Lidgard 1989; Alroy *et al.* 2008); (iv) the peak of diversity is seldom at the equator itself, but seems often to be displaced somewhat further north (often at ∼20–30°N); (v) it is commonly, though far from universally, asymmetrical about the equator, increasing rapidly from northern regions to the equator and declining slowly from the equator to southern regions; and (vi) it varies markedly in steepness for different major taxonomic groups with, for example, butterflies being more tropical than birds.

Although it attracts much attention in its own right, it is important to see the latitudinal pattern in species richness as a component of broader spatial patterns of richness. As such, the mechanisms that give rise to it are also those that give rise to those broader patterns. Ultimately, higher species richness has to be generated by some combination of greater levels of speciation (a cradle of

diversity), lower levels of extinction (a museum of diversity) or greater net movements of geographic ranges. It is likely that their relative importance in giving rise to latitudinal gradients varies with taxon and region. This said, greater levels of speciation at low latitudes and range expansion of lineages from lower to higher latitudes seem to be particularly important (Jablonski *et al.* 2006; Martin *et al.* 2007). More proximally, key constraints on speciation and extinction rates and range movements are thought to be levels of: (i) productive energy, which influence the numbers of individuals that can be supported, thereby limiting the numbers of species that can be maintained in viable populations; (ii) ambient energy, which influences mutation rates and thus speciation rates; (iii) climatic variation, which on ecological time scales influences the breadth of physiological tolerances and dispersal abilities and thus the potential for population divergence and speciation, and on evolutionary time scales influences extinctions (e.g. through glacial cycles) and recolonizations; and (iv) topographic variation, which enhances the likelihood of population isolation and thus speciation (Gaston 2000; Evans *et al.* 2005; Clarke and Gaston 2006; Davies *et al.* 2007).

2.3.4 Altitude and Depth

Variations in depth in marine systems and altitude in terrestrial ones are small relative to the areal coverage of these systems. The oceans average c.3.8 km in depth but reach down to 10.9 km (Challenger Deep), and land averages 0.84 km in elevation and reaches up to 8.85 km (Mt. Everest). Nonetheless, there are profound changes in organismal diversity both with depth and altitude. This is in large part because of the environmental differences (but also the effects of area and isolation), with some of those changes in depth or altitude of a few hundred meters being similar to those experienced over latitudinal distances of several hundred kilometers (e.g. temperature).

In both terrestrial and marine (pelagic and benthic) systems, species richness across a wide variety of taxonomic groups has been found progressively to decrease with distance from sea level (above or below) and to show a pronounced hump-shaped pattern in which it first increases and then declines (Angel 1994; Rahbek 1995; Bryant *et al.* 2008). The latter pattern tends to become more apparent when the effects of variation in area have been accounted for, and is probably the more general, although in either case richness tends to be lowest at the most extreme elevations or depths.

Microbial assemblages can be found at considerable depths (in some instances up to a few kilometers) below the terrestrial land surface and the seafloor, often exhibiting unusual metabolic capabilities (White *et al.* 1998; D'Hondt *et al.* 2004). Knowledge of these assemblages remains, however, extremely poor, given the physical challenges of sampling and of doing so without contamination from other sources.

2.4 In conclusion

Understanding of the nature and scale of biodiversity, of how it has changed through time, and of how it varies spatially has developed immeasurably in recent decades. Improvements in the levels of interest, the resources invested and the application of technology have all helped. Indeed, it seems likely that the basic principles are in the main well established. However, much remains to be learnt. The obstacles are fourfold. First, the sheer magnitude and complexity of biodiversity constitute a huge challenge to addressing perhaps the majority of questions that are posed about it, and one that is unlikely to be resolved in the near future. Second, the biases of the fossil record and the apparent variability in rates of molecular evolution continue to thwart a better understanding of the history of biodiversity. Third, knowledge of the spatial patterning of biodiversity is limited by the relative paucity of quantitative sampling of biodiversity over much of the planet. Finally, the levels and patterns of biodiversity are being profoundly altered by human activities (see Box 2.1 and Chapter 10).

Box 2.1 Invaluable biodiversity inventories
Navjot S. Sodhi

This chapter defines biodiversity. Due to massive loss of native habitats around the globe (Chapter 4), biodiversity is rapidly being eroded (Chapter 10). Therefore, it is critical to understand which species will survive human onslaught and which will not. We also need to comprehend the composition of new communities that arise after the loss or disturbance of native habitats. Such a determination needs a "peek" into the past. That is, which species were present before the habitat was disturbed. Perhaps naturalists in the 19th and early 20th centuries did not realize that they were doing a great service to future conservation biologists by publishing species inventories. These historic inventories are treasure troves—they can be used as baselines for current (and future) species loss and turnover assessments.

Singapore represents a worst-case scenario in tropical deforestation. This island (540 km^2) has lost over 95% of its primary forests since 1819. Comparing historic and modern inventories, Brook *et al.* (2003) could determine losses in vascular plants, freshwater decapod crustaceans, phasmids, butterflies, freshwater fish, amphibians, reptiles, birds, and mammals. They found that overall, 28% of original species were lost in Singapore, probably due to deforestation. Extinctions were higher (34–43%) in butterflies, freshwater fish, birds, and mammals. Due to low endemism in Singapore, all of these extinctions likely represented population than species extinctions (see Box 10.1). Using extinction data from Singapore, Brook *et al.* (2003) also projected that if the current levels of deforestation in Southeast Asia continue, between 13–42% of regional populations could be lost by 2100. Half of these extinctions could represent global species losses.

Fragments are becoming a prevalent feature in most landscapes around the globe (Chapter 5). Very little is known about whether fragments can sustain forest biodiversity over the long-term. Using an old species inventory, Sodhi *et al.* (2005) studied the avifaunal change over 100 years (1898–1998) in a four hectare patch of rain forest in Singapore (Singapore Botanic Gardens). Over this period, many forest species (e.g. green broadbill (*Calyptomena viridis*); Box 2.1 Figure) were lost, and replaced with introduced species such as the house crow (*Corvus splendens*). By 1998, 20% of individuals observed belonged to introduced species, with more native species expected to be extirpated from the site in the future through competition and predation. This study shows that small fragments decline in their value for forest birds over time.

Box 2.1 Figure Green broadbill. Photograph by Haw Chuan Lim.

continues

Box 2.1 (Continued)

The old species inventories not only help in understanding species losses but also help determine the characteristics of species that are vulnerable to habitat perturbations. Koh *et al.* (2004) compared ecological traits (e.g. body size) between extinct and extant butterflies in Singapore. They found that butterflies species restricted to forests and those which had high larval host plant specificity were particularly vulnerable to extirpation. In a similar study, but on angiosperms, Sodhi *et al.* (2008) found that plant species susceptible to habitat disturbance possessed traits such as dependence on forests and pollination by mammals. These trait comparison studies may assist in understanding underlying mechanisms that make species vulnerable to extinction and in preemptive identification of species at risk from extinction.

The above highlights the value of species inventories. I urge scientists and amateurs to make species lists every time they visit a site. Data such as species numbers should also be included in these as such can be used to determine the effect of abundance on species persistence. All these checklists should be placed on the web for wide dissemination. Remember, like antiques, species inventories become more valuable with time.

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Summary

• Biodiversity is the variety of life in all of its many manifestations.

• This variety can usefully be thought of in terms of three hierarchical sets of elements, which capture different facets: genetic diversity, organismal diversity, and ecological diversity.

• There is by definition no single measure of biodiversity, although two different kinds of measures (number and heterogeneity) can be distinguished.

• Pragmatically, and rather restrictively, biodiversity tends in the main to be measured in terms of number measures of organismal diversity, and especially species richness.

• Biodiversity has been present for much of the history of the Earth, but the levels have changed dramatically and have proven challenging to document reliably.

• Biodiversity is variably distributed across the Earth, although some marked spatial gradients seem common to numerous higher taxonomic groups.

• The obstacles to an improved understanding of biodiversity are: (i) its sheer magnitude and complexity; (ii) the biases of the fossil record and the apparent variability in rates of molecular evolution; (iii) the relative paucity of quantitative sampling over much of the planet; and (iv) that levels and patterns of biodiversity are being profoundly altered by human activities.

Suggested reading

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Relevant website

- Convention on Biological Diversity: http://www.cbd.int/

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