

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 km²) 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

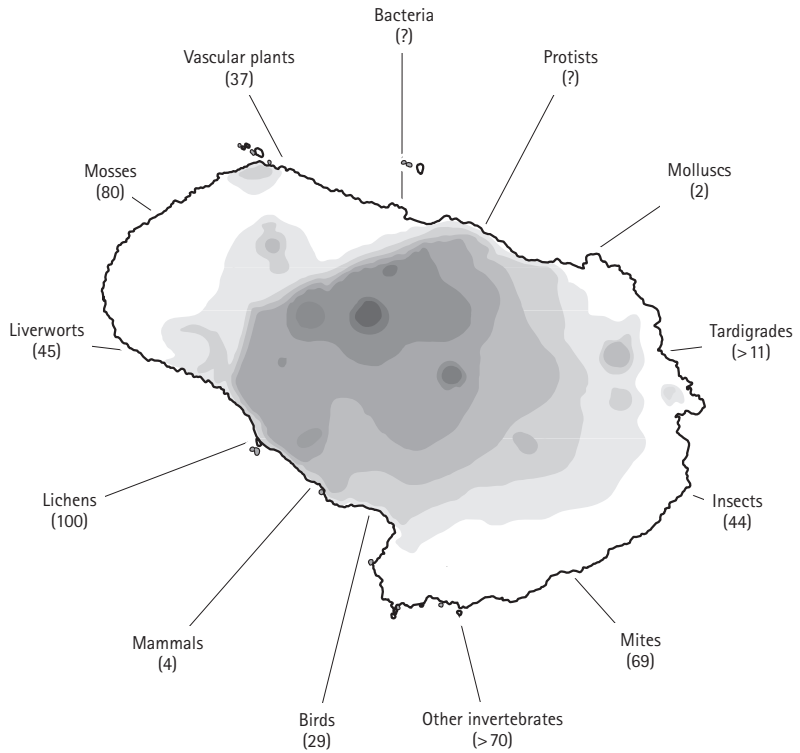


Fig. 1.1 The breeding species of sub-Antarctic Marion Island, one of the two remote Prince Edward Islands. Grey scales indicate variation in elevation. (Data from a variety of sources, including Gremmen 1981; Hänel & Chown 1999; Gaston et al. 2001; Øvstedal & Gremmen 2001; S.L. Chown pers. comm.)

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		Organismal diversity
Biomes		Domains or Kingdoms
Bioregions		Phyla
Landscapes		Families
Ecosystems		Genera
Habitats		Species
Niches	Genetic diversity	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).

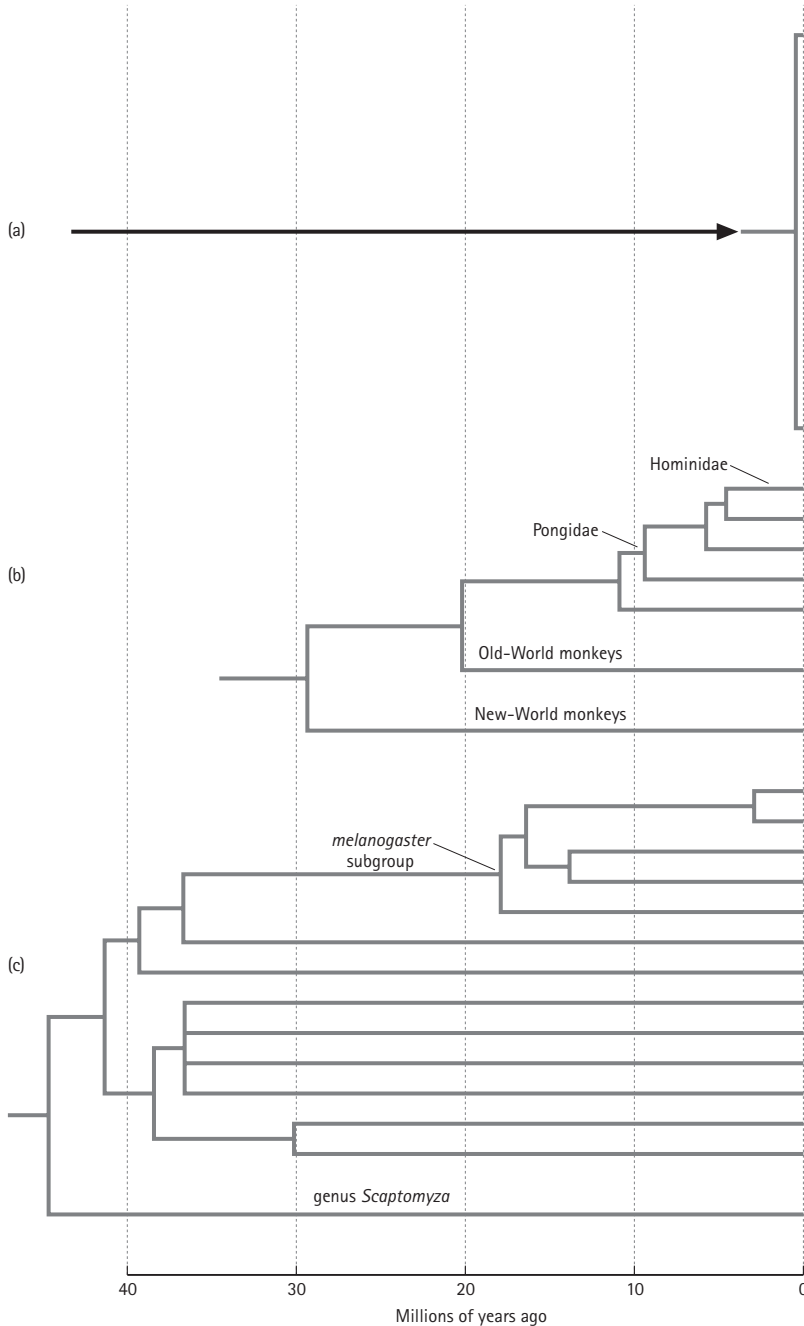


Fig. 1.2 Examples of disparities of taxonomic assignments in classifications of representatives of: (a) cichlid fish in Lake Victoria (14 species in nine genera); (b) anthropoid primates (seven species of several families); and (c) the genus *Drosophila* (13 species). (From Avise & Johns 1999.)

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

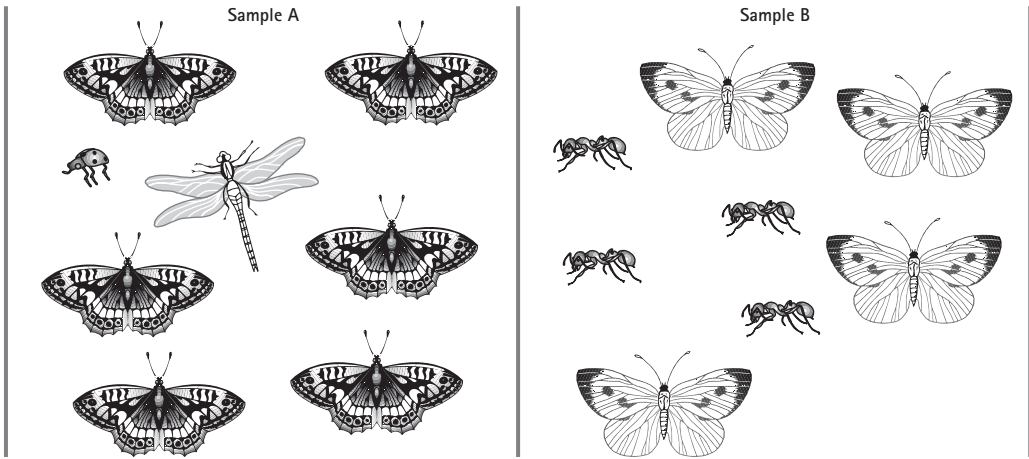


Fig. 1.3 Two samples of insects from different locations, illustrating two of the many different measures of biodiversity: species richness and species evenness. Sample A could be described as being the more diverse as it contains three species to sample B's two. However, in sample B there is less chance 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.

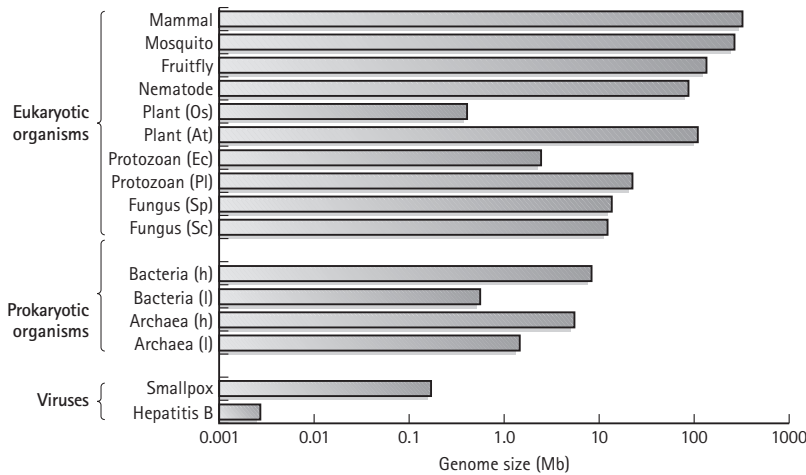


Fig. 1.4 Genome size for a range of organisms and viruses for which there are complete sequences (data derived from Genome Monitoring Table at <http://www2.ebi.ac.uk/genomes/mot> and Genomes online database at <http://wit.integratedgenomics.com/GOLD>). Abbreviations: l, lowest value for the grouping; 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.

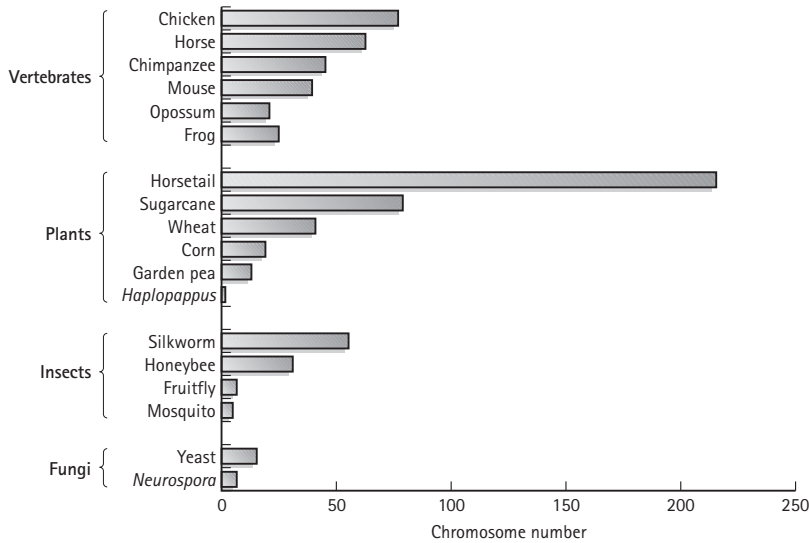


Fig. 1.5 Chromosome number for a range of organisms. (Data from various sources.)

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.

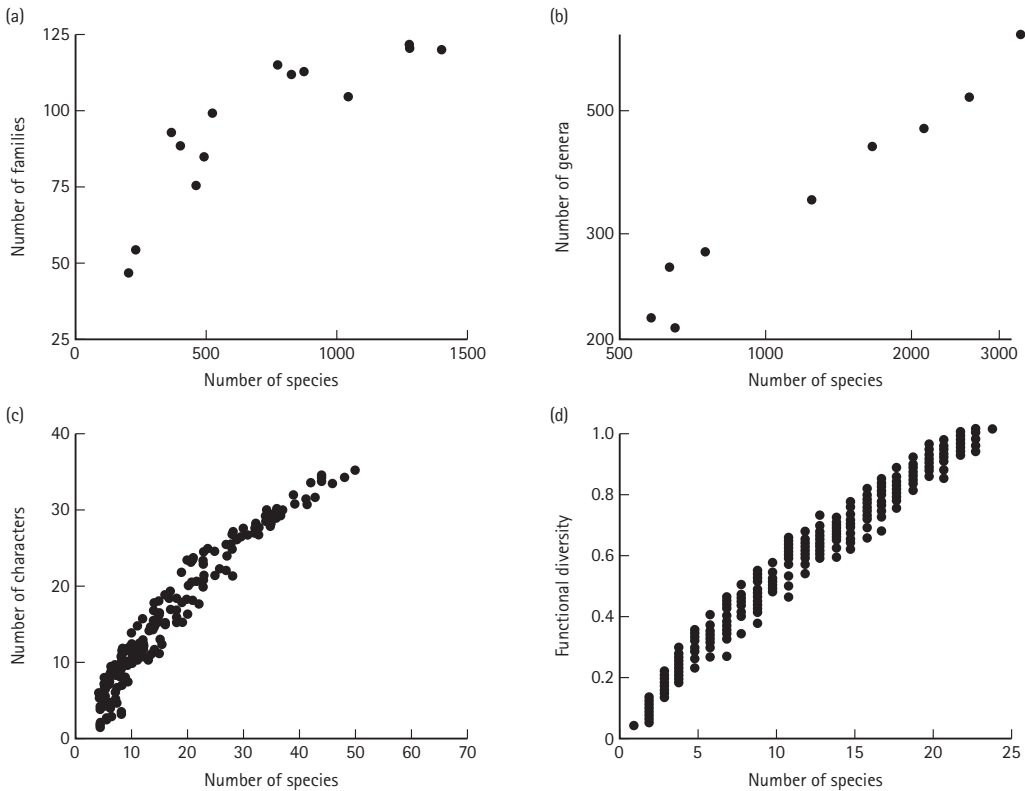


Fig. 1.6 Relationships between species richness and: (a) family richness for eastern Pacific benthic molluscs in different latitudinal bands; (b) generic richness for macromycete fungi for areas of the UK; (c) character richness for bumblebees among 611,000 km² grid cells; and (d) functional diversity (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!)
- Huston, M.A. (1994) *Biological Diversity: The Coexistence of Species on Changing Landscapes*. Cambridge University Press, Cambridge. (A very ecological perspective on biodiversity.)
- Jeffries, M.J. (1997) *Biodiversity and Conservation*. Routledge, London. (A gentle introduction to these topics.)
- Karp, A., Ingram, D.S. & Isaac, P.G. (eds.) (1997) *Molecular Tools for Screening Biodiversity*. Kluwer Academic, Dordrecht. (Comprehensive description and evaluation of a range of molecular techniques for use in addressing different questions concerning diversity.)
- Levin, S.A. (ed.) (2001) *Encyclopedia of Biodiversity*, Vols. 1–5. Academic Press, San Diego, CA. (A fantastic resource, covering the length and breadth of the field.)
- Perlman, D.L. & Adelson, G. (1997) *Biodiversity: Exploring Values and Priorities in Conservation*. Blackwell Science, Oxford. (Basic text on the concepts and their implications.)
- Reaka-Kudla, M.L., Wilson, D.E. & Wilson, E.O. (eds.) (1997) *Biodiversity II: Understanding and Protecting our Biological Resources*. Joseph Henry Press, Washington, DC. (The sequel to Wilson & Peter (1988).)
- Solbrig, O.T. (ed.) (1991) *From Genes to Ecosystems: A Research Agenda for Biodiversity*. The International Union of Biological Sciences (IUBS), Paris. (Identifies some of the major issues to be addressed in the study of biodiversity.)
- Wilson, E.O. (1992) *The Diversity of Life*. Penguin Books, London. (A popular, wide-ranging, and very readable account by perhaps the most influential proponent of biodiversity.)
- 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.)
- Wilson, E.O. & Peter, F.M. (eds.) (1988) *BioDiversity*. National Academy Press, Washington, DC. (Where it all began? The 'milestone' volume that drew attention to the importance of biodiversity.)
- World Conservation Monitoring Centre (1992) *Global Biodiversity: Status of the Earth's Living Resources*. Chapman & Hall, London. (A useful collation of essays and data.)
- 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.)

World Conservation Monitoring Centre, Groombridge, B. & Jenkins, M.D. (2000) *Global Biodiversity: Earth's Living Resources in the 21st Century*. World Conservation Press, Cambridge. (*The first edition of Groombridge & Jenkins.*)

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.