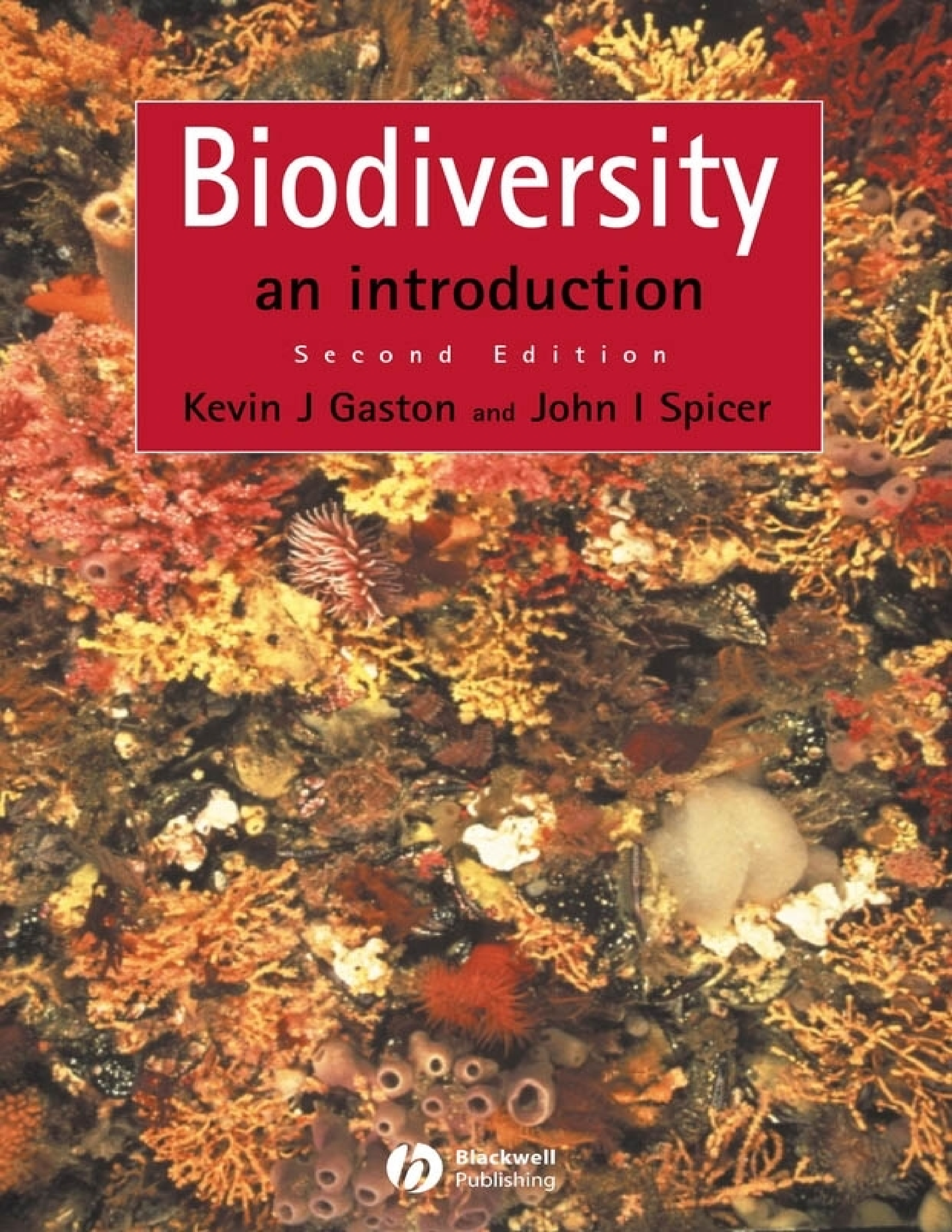

Biodiversity

an introduction

Second Edition

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Blackwell Publishing

SECOND EDITION

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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.
January 2003

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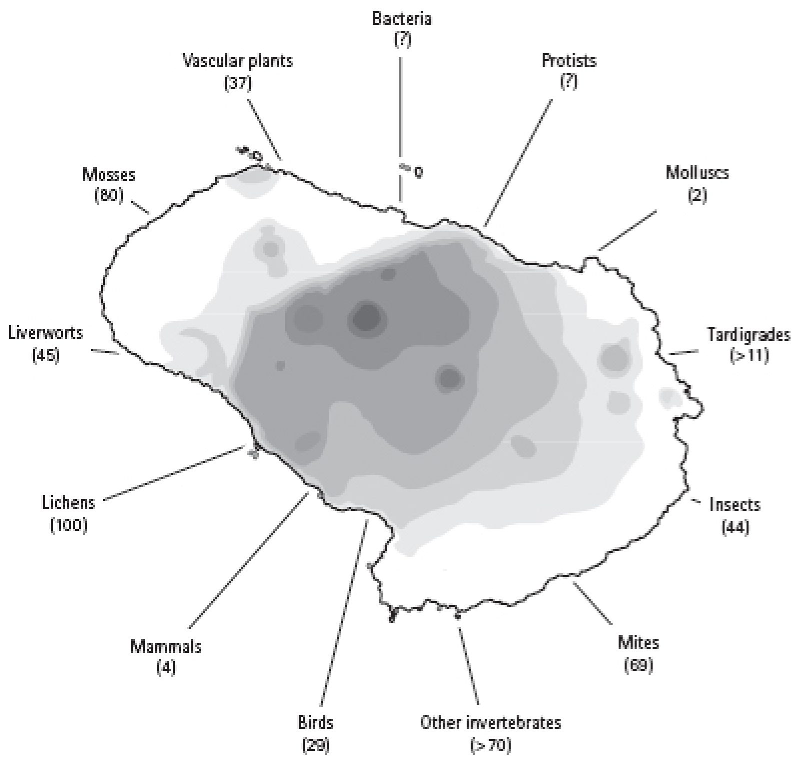
What is biodiversity?

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 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).

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.)



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