# Biodiversity: An Introduction

## SECOND EDITION

### Kevin J. Gaston

Professor of Biodiversity and Conservation

Department of Animal & Plant Sciences

University of Sheffield

and

## John I. Spicer

Reader in Marine Biology and Physiological Ecology School of Biological Sciences University of Plymouth



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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.

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- Table 2.4: Table 3.1-2 from Hawksworth, D.L. & Kalin-Arroyo, M.T. (1995) Magnitude and distribution of biodiversity. In: Global Biodiversity Assessment (ed. V.H. Heywood), pp. 107-199. Cambridge University Press, Cambridge. Reprinted by permission of Cambridge University Press.
- Table 3.1: Table 7-1 from Reaka-Kudia, M.L. (1997) The global biodiversity of coral reefs: a comparison with rain forests. In: Biodiversity II: Understanding & Protecting our Biological Resources (eds. M.L. Reaka-Kudia, D.E. Wilson & E.O. Wilson), pp. 83-108. Joseph Henry, Washington, DC. Reprinted with permission from Biodiversity II © 1996 by the National Academy of Sciences, courtesy of the National Academies Press, Washington, DC.

- Table 4.1: Table 1.1 from Lovelock, J. (1989) *The Ages of Gaia: A Biography of our Living Earth.*Oxford University Press, Oxford. Reprinted by permission of Oxford University Press.
- Table 5.2: Table 2 from Hannah, L., Carr, J.L. & Lankerani, A. (1995) Human disturbance and natural habitat: a biome level analysis of a global data set. *Biodiversity and Conservation* 4, 128–155. With kind permission of Kluwer Academic Publishers.
- Table 5.4: Excerpted from A Plague of Rats and Rubbervines: The Growing Threat of Species

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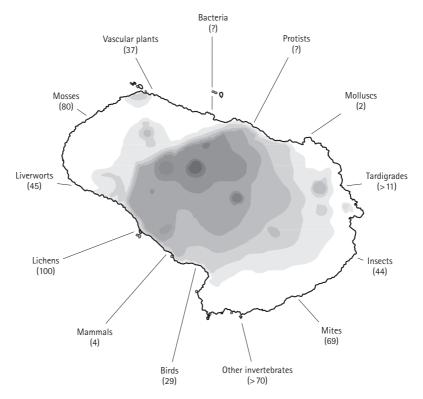
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# 1 What is biodiversity?

#### 1.1 Marion Island

The biotas of a few sites around the world have received disproportionate attention from biologists. One such is Marion Island, the larger of the two islands that make up the Prince Edward archipelago. Small (c. 290 km<sup>2</sup>) 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  $30 \times 30$  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).