An introduction to applied biogeography

Biogeography is about the geographical distribution, both past and present, of plants, animals and other organisms. Ian Spellerberg and John Sawyer bring a modern and new approach to an old subject, writing in a lively and sometimes provocative manner. Throughout, the applications of biogeography in conservation management, economic production, environmental assessment, sustainable use of resources, landscape planning and public health are emphasised . Applications of island biogeography in conservation are critically appraised, analysis of biogeographical data is explained, the concept of wildlife corridors is questioned and the role of humans and their cultures in biogeography is explored. The authors pay warm tributes to important events and people in biogeography and conclude by discussing the future roles for biogeography.

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Foreword

There is an island in Indonesia with a particularly beautiful parrot that lives nowhere else. Local people trap large numbers of the birds for export to bird fanciers around the world and are more than happy to do so because they feel it is a pest. However, there was growing concern that the population was droppping to alarming levels. Conservationists working there conducted surveys of the population size, trapping pressures, breeding biology, and crop damage, thereby determining a way in which the wild population could be harvested at a sustainable rate and crop damage limited. During discussions with officials who would have to monitor and control the rate of harvesting there was only half-hearted preparedness to cooperate. Then they were told that this bird was found nowhere else, and attitudes changed completely. The officials had thought that the parrot was found everywhere, but that they somehow had a monopoly on the supply to those strange people who wanted a pest as a pet. Once those in charge were given a grasp of biogeography their support was won.

Of course, knowledge of biogeography is not in itself going to save the world's biodiversity, but it does at least put into perspective the increasing global concern for the massive decline of populations and loss of species in all ecosystems. It forms the basis of the many and varied exercises to assess conservation priorities around the world, even though the complexities mean that the answers are never precisely the same. This prioritization is essential, since, although there are far more financial resources available now than ever before for global conservation, there are not nearly enough to right every wrong and cure every ill, and decision makers need to allocate funds in as rational a way as possible.

It is over twenty years since Ian Spellerberg taught me biogeography, ecology and behaviour at Southampton University and captured my interest in these fields to the extent that I went off and became wholly engrossed and enmeshed in them. I am thrilled that he, this time together with John Sawyer, has produced another clear and important book which I hope will be used and read widely, and perhaps translated into other languages to touch as many people as possible.

Tony Whitten
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Washington, DC

Preface

Biogeography is the study of the distribution and patterns of distribution of plants, animals and other organisms across the globe, on land, in the sea and in the air. Information from biogeography provides the basis for environmental protection and resource management. It has a very important role to play in managing the world's biological diversity and can be applied in many areas. It can be used to show where species and groups of species are distributed, to provide information which can be used in environmental impact assessments and to provide information to ensure sustainable use and conservation of those biological resources. Biogeography is an interesting and developing subject and is particularly important in providing a basis for understanding the critical relationships between humans and the environment.

In almost any area of natural sciences there are general components, underlying themes and specialist aspects. Biology, for example, is the general name for the study of life but there are many aspects of biology, such as molecular biology, population biology and human biology. Under the general heading of biological sciences we could include genetics, ecology, immunology and biogeography. Similarly, biogeography has a general theme as well as underlying themes and specialist aspects. Underlying themes include historical biogeography, analytical biogeography, ecological biogeography and applied biogeography.

This book is an introduction to applied biogeography. It is an introduction to a subject that underpins human understanding of ecology and it also describes some of the many applications of biogeography in resource management and environmental protection. The text provides structured and analytical ways of looking at the distribution patterns of plants and animals and also the complex patterns of interactions between humans and the environment. We describe patterns of distribution at scales ranging from global to agricultural fields. We also describe research that seeks explanations for those patterns and the processes which maintain them. The patterns may be found on land, sea and in the air and at many spatial scales. The patterns may also change over periods of time (thousands of years, centuries, months or days). One of the challenges of writing this book was to choose the spatial limits for the examples in the text. For example, whereas species patterns of grasses in a whole country would certainly be considered as biogeography, would a study of the distribution pattern of beetles in a woodland also be considered as biogeography? For us the answer was yes.

Chapter 1 includes an introduction to the nature of biogeography and also explains the rationale for the structure of the rest of the book. Biogeography may have had a poor image in the past but we believe that biogeography from an ecological perspective is a challenging science and one which has many applications in a changing world. The most valuable application is provision of the necessary information for sustainable use of some species and conservation of other species.

We commenced researching and writing this book in England and finished it in New Zealand. By chance, both of us had independently moved across the world from a relatively new continental island to an ancient island. That move has helped to enrich our understanding of biogeography. We have used our own experiences of research in ecology and biogeography but have also included a synthesis of some of the most modern aspects of the latter. As well as relying heavily on the results of many recent research programmes, we also pay tribute to many of the historical developments in the discipline and in so doing we put those developments into perspective. We feel that it is important not to interpret historical developments in a modern setting. The work of the earlier biogeographers and actual populations are best understood if we are able to have a glimpse of their time, their culture and their way of life. Although what was thought and known during their time may have been modified and corrected, the same process applies to us today; what we have written will be corrected and modified in the future.

Biogeography has developed largely from descriptive studies, mapping plant and animal distributions, and may therefore appear uninteresting. The biogeographical studies of the 18th century were bold and innovative for their time and, for some of the early biogeographers, it required much courage to make public their discoveries and beliefs. We must ensure that applied biogeography is both rigorous and objective – as a tribute to the early biogeographers. We believe that applied biogeography will continue to play an important role in environmental management and that it will continue to underpin ecological research and conservation well into the 21st century.

Ian Spellerberg and John Sawyer

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This project has spanned two hemispheres in a period of a few years. In that time many people have kindly contributed to the project and consequently made large improvements. We are particularly grateful to all those people and organisations who have kindly allowed us to use material from printed sources. We have endeavoured to contact all persons and organisations for all the copyright material used in this text, and we apologise if we have overlooked any person or any organisation.

Many people have kindly provided information and have found time to read parts of the text. To all those who assisted in this way, we are truly grateful. In particular we would like to acknowledge the help of the following: Ian Abbott, Keith Barber, Andy Barker, Jack Chernin, Jonathan Cowie, Paul Curran, Peter de Lange, Gina Douglas, Richard Duncan, Rowan Emberson, Neil Enright, Dianne Gleeson, Collin Hindmarch, Peter Hopkins, Sandi Irvine, Michael Johnston, John Marsden, John Mitchell, Keith Morrison, Hugh Possingham, Amanda Reid, Alan Saunders, Gillian Sawyer, J. Michael Scott, Phillip Simpson, Kathryn Spellerberg, Bianca Sullivan, Ian Thornton, Geoff Tunnicliffe, Nigel Webb and Tony Whitten.

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1

Biogeography: the nature of the subject, its history and its applications

1.1 Introduction

In 1994, an article in the journal *New Scientist* proclaimed that 'Since biogeography holds the key to the survival of life, it deserves more attention' (Bowman, 1994). That statement is a very fitting opening to this first chapter.

Biogeography is about the geography of plants, animals and other organisms, that is, the study of the geographical distribution of plants, animals and other organisms. Biogeographical research helps us to understand the patterns and processes of distribution and the factors that cause and maintain those patterns and processes. The patterns of distribution that we find today amongst living organisms have been determined by many things, including the following:

Evolution
Physiological and behavioural adaptations
Dispersal mechanisms and levels of dispersal abilities
Competition between species
Ecological succession
Climate change
Sea level changes
Moving continents through a process called plate tectonics
Direct and indirect impact of humans

The distribution and abundance of plants (phytogeography) and animals (zoogeography) have been the two main divisions of biogeography. Both those divisions embrace elements of several disciplines including biology, geography, taxonomy, geology, climatology and ecology. Many biologists, taxonomists, geologists, climatologists and ecologists have interests in various aspects of biogeography and indeed some have particular views as to the precise nature of biogeography. Those differences in views are based partly on differences of scale, be it in time or spatially. For example, a geologist's view might be particularly biased by an interest in evolutionary processes over very long periods of time (millions of years) perhaps in relation to plate tectonics. Geographers might take a special interest in researching the distribution of plants and animals over the last few thousand years, perhaps in relation to the post-glacial periods. An ecologist's view of biogeography might be dominated by those factors which determine and maintain the distribution of plants and animals within certain localities and over much shorter periods of time (perhaps in relation to the reduction and fragmentation of habitats in the last few decades). These different views contribute to the rich and varied nature of biogeographical research and its many important, practical applications. The common theme in all approaches to the study of biogeography is the study of the geographical distribution of groups of plants, animals and other organisms from a spatial or space perspective (that is, over land, in the soil, in water and in the air) and a temporal or time perspective (that is changes in distribution that occur over time). Biogeography provides a valuable link between traditional single disciplines (such as ecology, taxonomy and conservation biology) and a focus for interdisciplinary studies. That is important because many if not all environmental problems facing us today require an interdisciplinary approach (that is an integration of several disciplines, including ecology, geology, economics, policy and sociocultural factors).

Biogeography is more than about mapping the geographical distribution of organisms (present and past) at different spatial scales or merely dividing the land and sea into regions which are based on groups of characteristic organisms. Once a predominantly descriptive discipline, biogeography is now a quantitative science. It has applications in conservation, helping to establish a strategy for the location, extent and management of protected areas. It has applications in trying to achieve sustainable use of living resources and in environmental assessment by helping to ensure the least impact on the natural environment. It has applications in helping to tackle many aspects of environmental change, whether it be modelling the effects of changing weather patterns on agriculture or those of introduced and invasive species on native (indigenous) commercial fish species.

Before we can look in more detail at biogeography we need to know what we are dealing with and thus a brief introduction to the classification of organisms is helpful. We then go on to introduce the subject of biogeography and the history of biogeography. The relation between ecology and biogeography is then discussed and finally we look at some applications of biogeography.

1.2 An introduction to plants, animals and other organisms

There are approximately 1.7 million named species of living oganisms. The total number of living species is of course not known and we can only estimate what the figure might be. Estimates range from about 11 to 30 million or more. What is certain is that human impacts are causing species to become extinct faster than they can be named. Also of concern is our lack of knowledge about the named species. Scientists have intensively investigated only 10 per cent of plant species and a far smaller proportion of animal species (information from the World Commission in Environment and Development 1987 publication *Our Common Future*, Oxford University Press).

There are many terms used to refer to different groups of animals, plants and other kinds of living organism such as fungi, bacteria and viruses. The classification of biota (living organisms) has been reviewed and changed many times as a result of new information. In 1969, R. H. Whittaker of Cornell University suggested five groups of living organisms (Box 1.1). More recently, new taxonomic levels and regrouping of major taxa have been proposed as a result of studies in molecular biology.

Commonly used terms for living organisms include 'wildlife' and more recently the widely misunderstood term 'biological diversity' (often abbreviated to biodiversity). Wildlife is often used only with reference to mammals and birds. In this book it refers to any kind of wild organism (plants, animals, fungi and other groups) and therefore not to domesticated animals or plants.

The term biological diversity is often used in connection with conservation, not because it is fashionable to do so but because of the important concept embodied in its use. Conservation of wildlife conjures up lists of species which are endangered. There is nothing wrong with that but biological diversity draws attention to the need to conserve variety at different levels of biological organisation (from the genetic level to ecosystem levels). Biological diversity is an all-embracing term that means the variety of life at all levels of biological organisation, including 'diversity within species, between species and of ecosystems' (from the 1992 Convention on Biological Diversity). There is biological diversity at different levels of ecological organisation, genetic organisation and taxonomic organisation.

Box 1.1. The diversity of life. Classifications and definitions of biological diversity (see also Table 5.1)

In this five-kingdom system (developed primarily by R. H. Whittaker of Cornell University) living organisms are arranged on the basis of level of biological complexity and mode of nutrition. This is merely a summary of what is a much more detailed classification and it omits many groups within the major taxonomic levels of phylum, class, order, family, genus and species.

The numbers in brackets are the approximate number of named species (numbers are in thousands and are given only where there is good agreement about the number).

Kingdom Monera: Bacteria and blue-green algae.
Kingdom Protista: Primitive fungi, slime moulds, green algae, etc.
Kingdom Fungi: (mode of nutrition by absorption) three main groups of fungi (40).
Kingdom Plantae: (mode of nutrition photosynthesis):
- Division Bryophyta: Mosses and liverworts.
- Division Tracheophyta: This division includes the most complex and advanced plants such as the three classes – ferns, conifers and flowering plants.
  - Class Filicineae: Ferns (10).
  - Class Gymnospermae: Conifers (0.6).
  - Class Angiospermae: Flowering plants (286).
    - Subclass: Monocotyledonae: Grasses, lilies, palms, orchids, etc.
    - Subclass: Dicotyledonae: e.g. Rose Family, . . . Genera in other families such as *Fagus* (northern beech) and *Nothofagus* (Southern beech).

Kingdom Animalia: (mode of nutrition ingestion):
- Phylum Porifera: Sponges (10).
- Phylum Coelenterata: Sea anemones, corals, jellyfish, etc. (10).
- Phylum Platyhelminthes: Flatworms, tapeworms, flukes, etc. (125).
- Phylum Nematoda: Roundworms (30).
- Phylum Mollusca: Shellfish or molluscs, squid, snails, etc. (110).
- Phylum Annelida: Earthworms, leeches, etc. (15).
- Phylum Onychophora: Velvet worms, e.g. the genus *Peripatus.*
- Phylum Arthropoda: Insects (800), spiders (130), crustacens (30), etc.
- Phylum Echinodermata: Starfish, sea urchins, sea lilies, etc. (6).
- Phylum Hemichordata: Acorn worms.

Phylum Chordata: The vertebrates including fish (20), amphibians (2.5), reptiles (6.3), birds (8.5) and mammals (4).

This table indicates the variety of known life in terms of taxonomic diversity. However, this is only one aspect of biological diversity.

Box 1.1 (*cont.*)

The 1992 Convention on Biological Diversity defines Biological diversity 'the variability among living organisms from all sources including, amongst other things, 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'.

Biological Diversity occurs at different levels of organisation (after Angermeier & Karr, 1994):

Taxonomic	Genetic	Ecological
Species	Gene	Population
Genus	Chromosome	Community
Family etc.	Genome	Ecosystems

Plants, animals and other organisms are collectively known as biota or organisms. Aggregations of the same kind of organisms are known as populations, for example trout populations, or oak tree populations. A population of organisms such as trout lives in a habitat; a habitat is usually linked to a population and is the locality or area occupied by the populations. Habitats can be characterised by the physical features, soil conditions, and by the other kinds of organism found in the area. Biological communities are made up of different kinds of populations of organisms; for example a coral reef community consists of coral populations, fish populations, crustaceans, algae and other marine life. Different kinds of community have sometimes been classified on the basis of recognisable mixes or assemblages. Different kinds of woodland or grassland can be recognised by the different composition of the species; for example, we could refer to the mixed-species deciduous woodlands of the temperate climate region.

At a higher level of ecological organisation there are ecosystems. An ecosystem has no boundaries and is characterised by cycles and flows of water, energy, minerals and other elements through both the living components and physical components of the ecosystem. Ecosystems comprise three categories: individual organisms, species etc.; processes such as energy flow or ecological succession; and properties such as fragility and condition.

Biota, living and extinct, have long been classified into different groups; the science of classifying organisms and the study of relationships between those groups is systematics. The science of taxonomy is the oldest of all biological sciences and is about the study and description of the diversity of organisms and how that diversity arose. Living organisms include more than just plants and animals (Box 1.1).

Taxonomic classifications have a hierarchical structure, in which the basic unit is the species (see also Table 5.1). A species is a group of organisms that are recognised as being distinct (in form and reproductively) from other groups. When a species is identified or named, it is typically given a binomial (Latin) name which includes a generic and a specific component. The designation of a binomial name follows an agreed convention and is the same when used within any language. An example of a binomial name is that used for beech trees, of which there are many kinds or species. In northern temperate climate regions, species belong to the genus *Fagus* whereas in southern temperate climate regions there is a different genus, *Nothofagus.* Note the convention of putting the scientific names in italics. There are different species within each of the genera; for example, in the genus *Nothofagus* there are the species *Nothofagus fusca*, *Nothofagus menziesii* and *Nothofagus solandri.*

In much of this book we consider the biogeography of species – the distribution patterns and the reasons for those patterns. This does not mean that biogeography is concerned only with one level of taxonomic organisation, the species. It deals with other levels such as genera and families.

1.3 A history of biogeography

The presence and distribution of plants and animals has been recorded by humans for many thousands of years. Cave drawings of animals could be said to be the beginning of biogeography. The earliest written records and books mention the occurrence, abundance and absence of various plants and animals. Similarly, maps depicting plants, animals, dragons and other creatures have been made for centuries. Until early this century, many of these maps depicted actual organisms rather than indicating their distribution. However, as early as 1697, animals were drawn on an economic map of Hungary and later, in 1845, Heinrich Berghaus's *Physikalischer Atlas* has animal distribution maps (George, 1969). Throughout the 20th century there has been an ever-growing interest in how best to map, survey, record and distribute information about the distribution of plants, animals and natural biological communities. The books listed in Table 1.1 are testament to the varied nature of that mapping, etc. In recent years, the interest in mapping has been greatly facilitated and enhanced by developments in computer and satellite technologies (see Chapter 6).

Biogeography, in the sense of identifying geographical faunal and floral characteristics, probably emerged from early attempts to classify organisms

Table 1.1. *One hundred years of biogeography books*

Charles Darwin's *The Origin of Species* was the first great landmark in books that greatly influenced subsequent writing on biogeography. This table is a list of books or chapters in books (in English or translated into English) published during the 100 years following 1859 and which have been relevant to the advancement of biogeography. This list excludes those publications which specialise on island biogeography (see Section 3.2).

These books represent a history of literature on biogeography which has brought the subject to a wider audience. Underlying these books is a wealth of material from expeditions and research, most of which is published in scientific journals.

1859. *On The Origin of Species by means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*, by C. Darwin. London, John Murray.

1869. *The Malay Archipelago*, by A. R. Wallace. London, Macmillan. (Wallace dedicated this book to Charles Darwin with whom he had shared thoughts about the theories of natural selection.

1876. *The Geographical Distribution of Animals*, by A. R. Wallace. London, Macmillan.

1887. *The Geographical and Geological Distribution of Animals*, by A. Heilprin. London, Kegan Paul, Trench & Co.

1911. *Atlas of Zoogeography*, by J. G. Bartholomew, W. E. Clarke & P. H. Grimshaw. Edinburgh, J. Bartholomew and the Edinburgh Geographical Institute.

1913. *The Wanderings of Animals*, by H. Gadow. London, Cambridge University Press.

1934. *The Life Forms of Plants and Statistical Plant Geography*, by C. Raunkiaer. Oxford, Clarendon Press.

1935. *Zoogeography of the Sea*, by S. Ekman. German edition first published in 1935 and translated into English in 1953. London, Sidgwick and Jackson.

1936. *Plant and Animal Geography*, by M. I. Newbigin. London, Methuen.

1937. *Ecological Animal Geography*, by R. Hesse, W. C. Allee & K. P. Schmidt, New York and London, John Wiley.

1944. *Foundations of Plant Geography*, by S. A. Cain. New York and London, Harper & Bros.

Table 1.1. *(cont.)*

1951. *Zoogeography of the Land and Inland Waters*, by L. de Beaufort. London, Sidgwick & Jackson.
1953. *Zoogeography of the Sea*, by S. Ekman. London, Sidgwick & Jackson (originally published in Germany in 1935).
1953. *Evolution and Geography*, by G. G. Simpson. Eugene, Oregon State System Higher Education.
1954. *The Distribution and Abundance of Animals*, by H. H. Andrewartha & L. C. Birch. Chicago, University of Chicago Press.
1957. *Zoogeography: The Geographical Distribution of Animals*, by P. J. Darlington. New York and London.
1957. *Biogeography: An Ecological Perspective*, by P. M. Dansereau. New York, Ronald Press.
1958. *Panbiogeography or An Introduction Synthesis of Zoogeography, Phytogeography, and Geology; with notes on Evolution, Systematics, Ecology, Anthropology* etc. by L. Croizat. Caracas, published by the Author.

and in the origins of taxonomy and systematics. Georges Louis Leclerc, Comte de Buffon (1707–1788), a wealthy French nobleman had, as early as 1761, observed that the Old World (Europe, Asia and Africa) and the New World (North and South America) had no mammalian species in common. Buffon's work was monumental: 44 large volumes published over a period of 50 years.

The early explorers, the natural history excursions of the 19th century and scientific expeditions of the 20th century, have moulded the study of the geographical distribution of life on land and in the sea. Amongst the notable biogeographers (Fig. 1.1), one stands out as having made a notable contribution and that was the Prussian naturalist and explorer of South America, Alexander, Baron von Humboldt (1769–1859). He was interested in the manner by which plants contributed to the landscape and is sometimes referred to as the father of plant geography.

Early studies (Table 1.1) of plant and animal distributions played a key role in the development of the theory of evolution; for example the observations made by both Charles Darwin (1809–1882) during his passage on the ship *HMS Beagle* (1831–1836) and Alfred Russel Wallace (1823–1913) during his expedition to the Malay archipelago, returning to England in 1862 with a

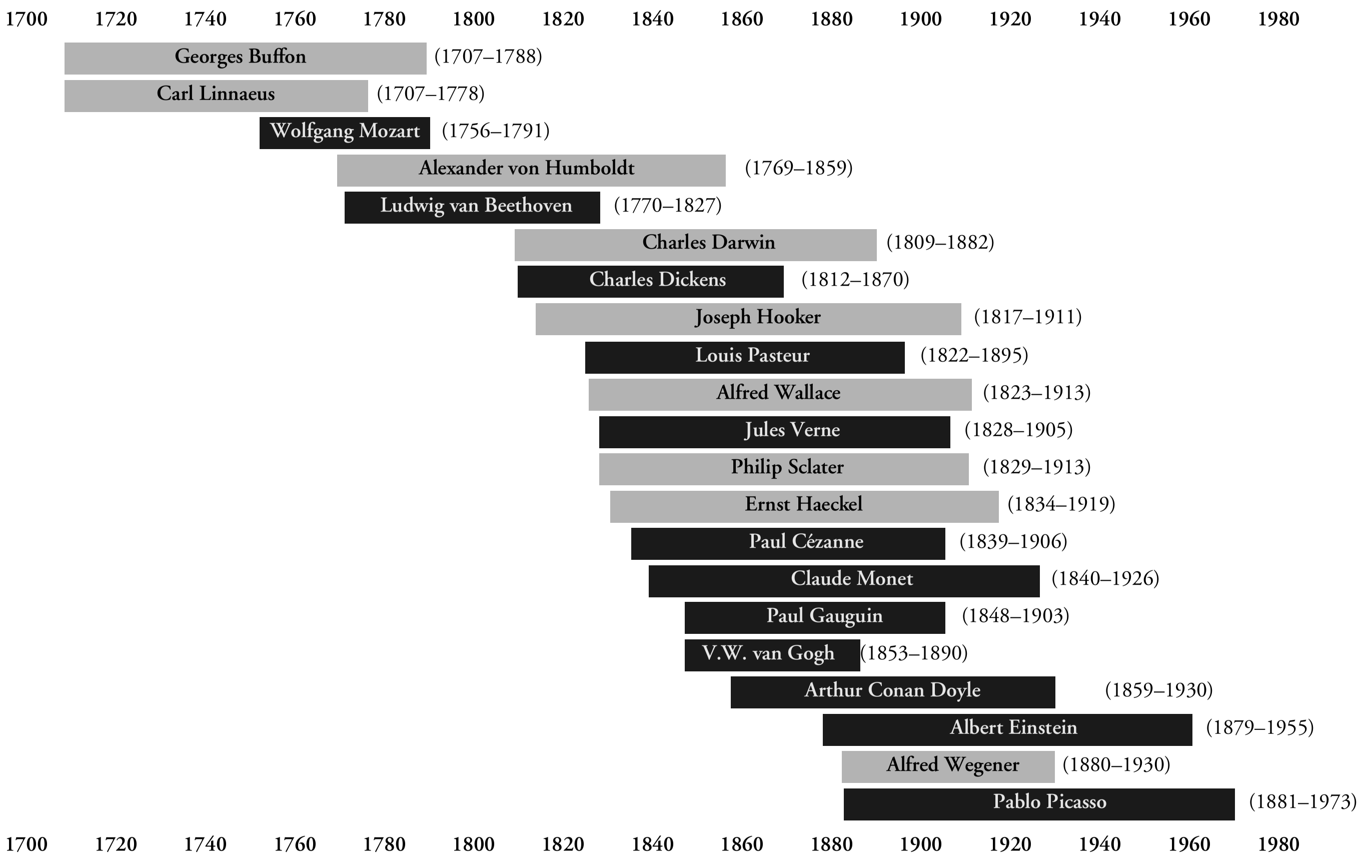

Fig. 1.1. Some notable biogeographers from the 18th and 19th centuries. Names of other famous people are also shown to help to put this chronology into perspective.

Table 1.2. *Texts on biogeography mentioned by Hans Gadow*

The 18th and 19th centuries were rich in biogeographical studies of animals. (References taken from Hans Gadow, 1913, *The Wanderings of Animals*, London, Cambridge University Press).

1707–1788. *Historie Naturelle*, by G. Buffon. 44 volumes published over 50 years during the life of Buffon. (Contains the first general ideas about geographical distribution.)

1777. *Specimen Zoologiae Geographicae Quadrupedum*, by E. A. W. Zimmerman. (The first special treatise on the subject and, according to Gadow, deals in a statistical way with mammals.)

1778. *Philosophia Entomologica*, by J. C. Fabricius. (The first to divide the world into eight regions.)

1803. *Biologie*, by G. R. Treviranus. (This included a chapter on the distribution of the whole animal kingdom.)

1810. *Anatomie und Naturgeschichte der Voegel*, by F. Tiedemann. (Deals with the influence of environment, distribution and migration of birds.)

Text by Latrielle (Date not mentioned). (Proposed that temperature is the main factor in the distribution of animals.)

1822. Text (unknown) by Desmoulins. (Suggested analogous centres of creation – meaning that similar groups of creatures may have arisen independently in different parts of the world.)

1835. Text (not stated) by W. Swainson. (The first book dealing with the geography and classification of the whole animal kingdom.)

1830–1833. *Principles of Geology*, by Charles Lyell. London. Looks at the history of the distribution of animals over time.)

1852. *Physikalischer Atlas: Thiergeographie*, by H. Berghaus. Gotha. (Has the earliest maps dealing with animal distributions.)

1853. Text (not stated) by L. K. Schmarda. (The distribution of the whole animal kingdom. He discusses the possible physical causes and modes of dispersal from original centres of creation and divides the land into 25 'realms'.)

1857. 'On the geographical distribution of the members of the Class Aves'. *Journal of the Proceedings of the Linnean Society, Zoology*, **11**, 130–145, by P. L. Sclater. (He suggests six 'regions' which have been the basis for a classification of biogeographical regions until this day.)

1859. *The Origin of Species*, by Charles Darwin. (A benchmark in biogeographical studies; especially mapping and characterising regions.)

1866. *Geographical Distribution of Mammals*, by A. Murray. (101 coloured distribution maps.)

Table 1.2. (*cont.*)

1868. Text (not stated) by Huxley. (Gives reasons for dividing the world into an Arctogaea or North World and Notogaea or South World.)
1872. Text (not stated) by Alexander Agassiz. (A morphological systematic revision of sea urchins, leading to the suggestion of four realms of the oceans, justified by climatic and other physical conditions.)
1876. *The Geographical Distribution of Animals*, by A. R. Wallace. (The second great landmark.)
1887. *The Geographical and Geological Distribution of Animals*, by A. Heilprin. London, Kegan Paul, Trench & Co. (Caused much discussion when he combined the Nearctic and the Palearctic into a Holarctic region.)
1890. Text (not stated) by W. T. Blanford. (Recognised three main divisions: Australia, South America, and the rest.)

huge number (125 660) of specimens of natural history. Another great contribution to early biogeography came from botanist Joseph Dalton Hooker (1817–1911), who took part in many collecting expeditions and published a classic work entitled *Flora of the British Isles.* He was a friend and confidant of Charles Darwin.

The early part of the 20th century saw the publication of many and varied books on the distribution of plants and animals (Table 1.1). One of these was the delightful publication by Hans Gadow on *The Wanderings of Animals* published by Cambridge University Press in 1913 (Table 1.2). The need for an interdisciplinary approach to biogeography is suggested in his Foreword:

> These outlines of the distribution of animals deal with a rather young branch of science. An attempt has therefore been made to sketch its rapid growth from small beginnings until it has become boundless, because the interpretation of at first seemingly simple facts in the domain of the zoologist, had soon to enlist the help of well-nigh all the other branches of Natural Science.

Many, but not all of these early works were totally descriptive; for example, Hans Gadow mentions Zimmermann's volume (Table 1.2), *Specimen Zoologiae Geographicae Quadrupedum*, which deals in a way with mammals and statistics of mammals. Such works were to be the forerunners of a growing interest in an analytical approach to biogeography.

Biogeography has evolved from geographical studies to specialist studies of regions and of various taxonomic groups. Many countries throughout the world now have their own biogeographical texts. Biogeographical studies have ranged in scale from the biogeography of 'mega-zoos' in the USA (studies for conservation of nature reserves) to biogeography of urban areas. There are specialist marine biogeographical texts and there are specialist taxonomic texts (see references at the end of each chapter).

Patterns and processes over different time scales from geological, through the Pleistocene and Holocene epochs (see Fig. 4.3), to historical times have provided incentives for biogeographers to define different, specialist kinds of biogeography (sometimes causing acrimonious debates about the existence and relevance of such areas of specialist study). One kind is historical biogeography (Box 1.2) and this has been associated largely with attempts to relate geological processes to sequences of the origins, dispersal and extinctions of taxonomic groups. Historical biogeography can be further divided into dispersal and vicariance biogeography. The former is concerned mainly with patterns of dispersal and the latter focuses mainly on the splitting of biota in a region (vicariated) as a result of barriers which inhibit dispersal of the organisms. Vicariance biogeographers are concerned with the general question 'What is the historical relationship among biotas or what is the relationship among areas?' (see for more detail, Andersson, 1996). For example, southern beech (*Nothofagus*) and the invertebrate 'velvet worm' (*Peripatus*) (see Section 4.2) are found in South America, New Zealand and Australia. How could the beech, with its heavy seeds, spread between continents and how could a small terrestrial invertebrate such as *Peripatus* (many of which are inhabitants of rotting logs or forest litter) disperse across continents? Vicariance explanations suggest that these organisms were previously more widespread and that more recently their distribution has become fragmented as a result of barriers, including the break-up of Gondwanaland (see Section 4.4).

Two modern philosophical and methodological approaches to vicariance biogeography have emerged; one is called panbiogeography and the other cladistic biogeography. Panbiogeography was a term first used by the botanist and biogeographer L. Croizat (1958) to refer to a global view of biotic interrelationships (Croizat had spurned Charles Darwin's ideas in favour of a quite novel approach to evolution based on the distribution of organisms). In panbiogeography, phylogenetic relationships between taxa are less important than are spatial and temporal patterns (for an example see Chapter 13 by Craw in Myers & Giller (1988)). Cladistic biogeography contrasts with panbiogeography by being closely associated with phylogeny and taxonomy

Box 1.2. Biogeography and specialist areas of study

Biogeography has many 'schools' or areas of specialist study and it is not a unified science. Consequently there are many 'kinds' of biogeography. The following is a synoptic account of the main kinds of biogeography.

Biogeography:
- Phytogeography: Deals with biogeography of plants.
- Zoogeography: Deals with biogeography of animals.
- Ecological biogeography: Deals mainly with patterns and processes over short time scales and within small spatial scales.
- Historical biogeography: Deals with patterns and processes over evolutionary and geological periods of time.
- Dispersal biogeography: Deals with patterns and processes of dispersal.
- Vicariance biogeography: Deals with splitting biota in a region, based on the barriers which inhibit dispersal.
  - Panbiogeography: Uses both endemic and non-endemic taxa. Based not so much on phylogenetic relationships but on spatial and temporal analysis of distribution patterns.
  - Cladistic biogeography: Cladistics deals with classification of biota based on common ancestry rather than using similarities in form. Thus cladistic biogeography uses phylogeny and relationships between areas (with endemic species) are based on shared, derived taxa.
- Analytical biogeography: Has an integrated approach to patterns and processes of organisms.
- Regional Biogeography. Examples include; *Biogeography and Ecology of the Rain Forests of Eastern Africa* (ed. J. C. Lovett & S. K. Wasser, Cambridge University Press); L. R. Heaney, 1986, 'Biogeography of mammals in Southeast Asia: estimates of rates of colonization, extinction and speciation', *Biological Journal of the Linnean Society*, **29**, 127–165.
- Taxonomic biogeography: The biogeography of various taxa.
- Applied biogeography: The application of biogeography for management and conservation of biota, communities and ecosystems.

(for more detail see Chapter 12 by Humphries *et al.* in Myers & Giller (1988)).

In this small book we have had to be selective with reference to the areas of biogeography discussed. We have chosen not to include any further information in this introductory text on cladistic and vicariance biogeography, despite the current popularity of these subdisciplines.

1.4 Ecology and biogeography

In 1870, the German biologist Ernst Haeckel (1834–1919) first coined the term ‘ecology’ and defined it as ‘the total relations of the animal both to its inorganic and organic environment’. In some ways that encapsulated what ecology is today; the study of the interactions between organisms and their environment; but also including (1) the study of the abundance of organisms in space and time and (2) the processes in biological communities. Early in the 20th century, ecology emerged from natural history and wildlife management as a science. Developments in early ecology occurred simultaneously in both North America and Europe. Landmarks in early animal ecology textbooks included Arthur Pearse’s *Animal Ecology* (published by McGraw-Hill in 1926) and the work of Charles Elton (*Animal Ecology*, published by Sidgwick & Jackson in 1927). Much of the stimulus for the emergence of plant community studies came from the work of Tansley (1935) and Watt (1947) in Britain and from F. E. Clements in North America (*Dynamics of Vegetation*, published by Hafner Press in 1949). The establishment of the British Ecological Society in 1913 and the Ecological Society of America, founded in 1916, provided a professional basis for ecology. Ecology has become a well-known word but sadly the discipline of ecology is not well understood and is even equated with environmentalism and being ‘green’. That is another topic which cannot be discussed here.

As the science of ecology (objective, quantifiable, experimental) began to emerge early this century it was, not surprisingly, going to have close links with biogeography – not surprising because both ecologists and geographers were interested in the patterns of distribution of organisms in space and in time and the processes which determined those patterns. As early as 1924, Richard Hesse in his *Tiergeographie auf Oekologischer Grundlage* wrote about ‘ecological animal geography’ as a young science. When this work was later translated and published in 1937 it made a marked impact on ecological and biogeographical studies in both Europe and North America. Later academics such as the Americans Robert McArthur and Edward Wilson (see Box 3.2) wrote as if there were no real difference between biogeography and ecology. The term ‘ecological biogeography’ has since been widely used.

Although the distribution of organisms and the factors and processes causing those distributions is central to the study of biogeography, ecology is concerned mainly with interactions between organisms and their environment, patterns and processes in ecosystems, as well as with the distribution and abundance. But the study of distribution could also be considered to be a part of the study of abundance; factors affecting distribution will also affect abundance. Studies of distribution and abundance can be undertaken at different levels of organisation, including populations, species and biological communities. Previously, community-based ecological studies were prominent in Europe and North America in the early part of the 20th century. Then in the 1950s came the publication of a particularly important contribution to the scientific study of distribution and abundance. This was a book called *The Distribution and Abundance of Animals* by two Australian biologists, H. G. Andrewartha and L. C. Birch (1954). Rather than studying biological communities, these authors had established a strong statistical and analytical approach to population ecology involving three aspects: (1) physiology and behaviour of animals; (2) physiography, climate, soil and vegetation; (3) numbers of individuals in populations.

Andrewartha & Birch stressed the spatial relations between 'local populations'. Also, in the previous work of early ecologists such as Watt (1947), there was reference to shifting mosaics of populations; that is, species found on naturally occurring patchy and transient habitats. These references to population processes have more recently found their way into the literature dealing with the theory of metapopulations (see Section 7.2.1).

Later, we give examples of how biogeographical information can be analysed (see, for example, Box 7.2). In addition to examples of analysis we also describe some theories and models that have been used in biogeographical studies. But why theories and what is a model? In biogeography, theories (that is, sets of ideas to try to explain or test something) are used to try to understand processes (for example, the processes which determine the number of species on an island). Models are theories that can be tested to some extent and therefore may be used to predict the effects of certain impacts on the natural world (for example, climate change on the distribution of biological communities).

1.5 Applications of biogeography

Biogeography has had a very important role to play in the development of our understanding of biology. For example it was biogeography that was the key to developing the theory of the evolution of life. Today, not only does biogeographical research have important applications in a world of rapidly increasing human population densities and diminishing resources, it has crucial applications for conservation and sustainable use of many levels of biological diversity. If we are to make the best uses of limited resources for conservation we must know much more about the geography and ecology of the many kinds of biological diversity.

Some questions in biogeography may seem rather academic. For example, why are certain species and certain groups of organisms found in certain localities and nowhere else? What has caused these patterns on a world scale? Why is it that for many groups of organisms there are fewer and fewer species in the north and in the south compared to the tropical regions? Why is it that in some regions there are few species but the abundance of some individual species is very high? Answers to these questions help us to understand the processes and interactions that have resulted in present distribution patterns and the mechanism by which they are currently maintained. In turn, that information can be used to help to reduce human impact on the environment and can help us to use the environment in a sustainable manner.

We cannot make good decisions about the conservation of nature if we do not know what is there and where it is. Therefore many questions in biogeography are crucial for conservation. For example, what is the location and distribution of species throughout the world – on land, in the water and in the sea? Where are the highest levels of species richness? Where are the different levels of biological diversity to be found? Where do you find the highest levels of biological diversity? Biogeography has important applications, particularly because of the huge gaps in our knowledge and because of the increasing rate at which so many levels of biological diversity are being damaged and lost (see examples of mapping and gap analysis in Section 2.5).

Conservation of wildlife and habitats is achieved in part by the establishment of various kinds of protected area such as nature reserves on land, in rivers and lakes and in the sea. Where should nature reserves be located and why? How large should they be? How should they be managed? Should protected areas be buffered from perturbations arising from land use activities around the protected areas? Biogeography has played a major role in answering these questions (see Section 7.6).

Biogeography also has a part to play in assessing possible impacts on the environment that might be caused by new developments in land use. Determining the likely effects of major projects on the natural environment (land, water or sea) by way of the formalised procedure of an Environmental Impact Assessment has become a statutory requirement in many countries throughout the world. The probable effects of construction of dams and tidal barrages, for example, have been at the centre of many large investigations. Some years ago there was a proposal to construct a tidal barrage (for electricity generation) in the estuary of the River Severn, between Wales and England in the UK. The distribution of estuarine invertebrates is determined largely by salinity levels. A tidal barrage would change the salinity distribution, which would affect the distribution of estuarine invertebrates. This in turn would affect the distribution of estuarine birds that feed on the invertebrates. The biogeographical and ecological studies of the distributions of organisms and factors determining their distribution in an estuary is an example of the ecological aspect of biogeography and its value in determining impacts arising from habitat modification.

Biogeography is important in developing strategies for biological control of pests. In 1962 a book with the evocative title *Silent Spring* was published. Written by Rachael Carson, this book was a clear statement of her concern about the extensive use of chemicals in agriculture and the possibility that intensive use of herbicides and insecticides could affect organisms other than pest species. Since that time the study of pest control has become more and more integrated endeavouring to combine minimum use of chemicals with maximum use of biological control. Encouraging the presence of predators of insect pests in horticulture and in agriculture is not new. However, manipulating agricultural landscapes to facilitate movements of predators of agricultural pests has become an exciting and important aspect of integrated pest control. This could not have come about without an understanding of the patterns of movements and distribution of the predators (see Section 8.5).

Development of computers, computing and information technology has enabled new applications to occur in biogeography. One of these applications has been in connection with researching the role of tropical forests, deforestation and regenerating forests in the carbon cycle. Every year, about 8.5 gigatonnes of carbon move between the land, the air and the oceans. There has been much recent concern about increases in the levels of atmospheric carbon brought about by the release of carbon when forests are burnt. Increased levels of carbon dioxide have implications for climate change and consequently there has been much research on carbon 'sinks' or the processes which take up atmospheric carbon. Mature tropical forests absorb carbon (photosynthesis) and release it (respiration), resulting in a carbon balance. However, regenerating forests are major sinks of carbon dioxide (CO_2). Knowing where these sinks are, their area and their stage or condition in ecological terms is of great importance in helping to mitigate human impact on the carbon cycle. A highly advanced tool with which to estimate areas of forest at regional and global scales which may be acting as carbon sinks is remote sensing from satellites. One example of this kind of detection has been undertaken by a group of researchers based in the UK but working on tropical forests in Ghana (Foody & Curran, 1994). Data gathered by satellite have been used to characterise tropical forest regeneration and in turn to help to analyse the nature and role of forest regeneration in the carbon cycle.

We live at a time when there are many environmental issues and concerns. One well-known environmental issue is climate change and the implications of any change on agriculture, horticulture and the distribution and abundance of living organisms. Determining the rate of climate change and extent of change depends on the time scale being used. Although there appears to have been an increase in the frequency of extreme weather conditions during the last ten years, some would say that this is variety in nature. Depending on the time scale being used, it could be said that the world climate could be becoming more variable, warmer or cooler. Environmental change occurs not only over different time scales but at different spatial scales. We could consider global changes or regional environmental changes. For example, in New Zealand, river temperatures have been getting slightly lower; at least that is the conclusion after just six years of monitoring river temperatures.

Environmental change has come to dominate much research and even public concern. The implications of climate change on biota are being modelled and researched at many centres by biogeographers and there seems to be no doubt that in the future some aspects of climate change could have severe implications for the way of life of people throughout the world. Climate change could have major impacts on agriculture practices, forestry and fisheries, as well as on the availability of water. These changes could also affect the distributions of wild plants and animals and have implications for the role of protected areas such as nature reserves.

Biogeography provides essential information for the conservation of species (and other taxonomic groups) and for restoration of biological communities. Human actions have 'shaken' and 'stirred' the world's biota (as well as having caused many taxa to become extinct). Consequently there are many parts of the world where the group of taxa does not constitute a natural biological community. In many parks and gardens there are plant species that would not normally occur in those biogeographical areas. The implications of moving species around the world are many. Some introduced species may supplant native species, they may become invasive and they may act as hosts for pests. Human-assembled collections of exotic plants (not native to that area) such as trees and shrubs in a city park or in an urban garden may be attractive visually and may be a living museum of flora. Such collections, however, fail to recognise the rich dynamics and variety of interactions that occur in natural biological communities or plant assemblages. A single exotic (non-native) specimen tree in a park or botanic garden (for example, Fig. 1.2)

Fig. 1.2. A single, isolated 'specimen' tree in a botanic garden.

will interact with other organisms that occur in that area, but in the sense of natural biological communities such a specimen tree is like a single member of an orchestra playing only their part in a Beethoven symphony without the existence of other players and an audience. That single specimen tree is of little significance in terms of biogeography, biological diversity and biological communities. Such a tree may as well be made of plastic for its visual appearance is its only importance.

Biogeography is helping ecological restoration projects throughout the world at many different scales. There are large-scale, country-wide forest restoration projects and there are local initiatives. There seems to be a growing interest in trying to turn around our practice of mixing species around the world. But restoring native species is just the first simple step. Restoring the biological communities with both the species and the interactions between species is a challenge being helped by biogeography and ecology.

Of all the environmental issues facing us today, what is the most serious in terms of the costs and damage incurred? Climate change, pollution, loss of indigenous forests, or fragmentation of habitats? There is a widely held view amongst many ecologists that the most important and most threatening aspect of environmental change is that caused by introduced and invasive organisms. The most damaging of all pests are introduced organisms. The problems of invasive species are likely to become even more severe in the future, with increasing global trade and reduction in trade barriers. There are many, many examples of introduced species which have had dramatic consequences on both ecology and economics. Examples include the klamath weed or St John's wort (*Hypericum perforatum*) from Eurasia and North Africa in the USA, the North American grey squirrel (*Sciurus carolinensis*) in Britain, the Australian brush-tailed possum (*Trichosurus vulpecula*) in New Zealand (see also Section 4.8.3), and the South American cactus *Opuntia* in Australia. Humans have certainly mixed, stirred and changed the distribution of many plant and animals species throughout the world, either deliberately via introductions or by acting as vectors for the transport of organisms. Many species have been introduced to new biogeographical areas and many of those species have become pests. The damage caused by these pests has had very serious economic implications. The costs of control may be extremely high each year. For example, the distribution of the zebra mussel (*Dreissena polymorpha*) from Europe has been extended after being carried in ballasts of ships. The spread of this species in the Great Lakes of North America and cost of subsequent damage now runs into several billion dollars.

Ecologists and biogeographers will have an increasingly important role in identifying possible future invasive species and in mitigation of the effects of current invasive species.

1.6 Last frontiers for human exploration

We find it ironic that so much effort and so many resources are put into the exploration of outer space, at a time when humans are progressively using resources to depletion and when so little is known about the biological diversity of the earth. Why is there all this publicity about ancient life discovered on the planet Mars when there are regions of the Earth where life has yet to be explored? Life at the extremes of environmental conditions are to be found on the Earth. For example, studies of life at great depths in the oceans has hardly begun. Recently, an entire new kingdom of deep sea organisms, the Archaea, has been recognised; although discovered some decades ago, genetic analysis has shown them to be quite unlike any other kind of life (Earle, 1996).

We have been concerned to read of proposals for using deep oceans for disposal of global waste – waste that is inert or rich in metals or even in organic compounds (but not industrial organic compounds). Quite rightly, some proponents of these methods of global waste management have recommended the need for appropriately scaled experiments and further research on the processes that maintain the diversity of benthic assemblages (Angel & Rice, 1996).

The oceans are truly one of the last frontiers for exploration and the challenges of undertaking such exploration are huge. The mechanics of sampling are difficult, little is known about the taxonomy of the biota at great depths, and the low density of some organisms and the cryptic nature of the many creatures make them difficult to locate. Once located and if captured (which is not easy), there are more difficulties because there are no well-developed techniques for ensuring that the material is not damaged during retrieval. The biogeography of the sea, particularly the biogeography of the ocean depths is worthy of much greater attention and can justify much greater support for research than questionable work on the possible existence of life on another planet.

1.7 Structure of the book

While recognising recent and valuable new developments in biogeography, such as cladistic biogeography, this book is concerned mostly with the ecological approach to biogeography. In so doing we look at biogeography at different spatial scales, from global patterns to patterns within biological communities and even individual species distributions and future opportunities to model and predict in the light of environmental change.

The sequence of chapters is based on the following structure: (a) the patterns of distribution, (b) causes of the patterns, (c) data collection and analysis (d) biogeography in practice. Chapters 2 and 3 consider biogeography at different scales, commencing with global patterns and ending with island patterns. Island biogeography deserves a special mention, partly because of the many historical studies of island organisms but also because there are some very real and modern issues to do with the conservation of island fauna and flora.

What has caused the patterns we observe today? There are geological, environmental, evolutionary, biological and human aspects (see Chapter 4). Evolution through long periods of geological history and dispersal of organisms has shaped present distributions of biota but in recent history, human social and cultural aspects have been important. The patterns and types of species distribution pattern (in space and in time) are introduced in Chapter 5.

Throughout this book the emphasis is on the applied aspects of biogeography. It seems logical therefore to consider how biogeographical information is obtained (Chapter 6). What are the field techniques and what role does computer technology have in biogeography?

The process of loss of habitat and subsequent breaking up of habitats into smaller and smaller fragments is a major concern amongst conservation biologists. Chapter 7 looks at the role of biogeography in understanding the ecological aspects of habitat fragmentation and restoration of habitats. A very popular concept has been wildlife corridors; 'What are they?' Do they work?' are two main questions discussed in Chapter 8.

Finally, what of the future? In Chapter 9 we look into the crystal ball of biogeography suggesting ideas for the future. The appendices comprise a glossary of technical terms used in the text and a list of addresses of organizations with biogeographical interests.

1.8 References

At the end of each chapter a small number of references is included either to allow further details to be obtained or as a source of authority for main points.

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