FUNDAMENTALS OF BIOGEOGRAPHY

Second Edition

Richard John Huggett

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FUNDAMENTALS OF BIOGEOGRAPHY

Second Edition

Fundamentals of Biogeography presents an accessible, engaging, and comprehensive introduction to biogeography, explaining the ecology, geography, history, and conservation of animals and plants. Starting with an outline of how species arise, disperse, diversify, and become extinct, the book examines how environmental factors (climate, substrate, topography, and disturbance) influence animals and plants; investigates how populations grow, interact, and survive, and how communities form and change; and explores the connections between biogeography and conservation.

The second edition has been extensively revised and expanded throughout to cover new topics and revisit themes from the first edition in more depth. Illustrated throughout with informative diagrams and attractive photographs, and including guides to further reading, chapter summaries, and an extensive glossary of key terms, *Fundamentals of Biogeography* clearly explains key concepts in the history, geography, and ecology of life systems. In doing so, it tackles some of the most topical and controversial environmental and ethical concerns, including species overexploitation, the impacts of global warming, habitat fragmentation, biodiversity loss, and ecosystem restoration.

Fundamentals of Biogeography presents an appealing introduction for students and all those interested in gaining a deeper understanding of key topics and debates within the fields of biogeography, ecology, and the environment. Revealing how life has been and is adapting to its biological and physical surroundings, Huggett stresses the role of ecological, historical, and human factors in fashioning animal and plant distributions, and explores how biogeography can inform conservation practice.

Richard John Huggett is a Reader in Geography at the University of Manchester.

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FUNDAMENTALS OF BIOGEOGRAPHY

Second Edition

Richard John Huggett

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for my family

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SERIES EDITOR'S PREFACE

We are presently living in a time of unparalleled change and when concern for the environment has never been greater. Global warming and climate change, possible rising sea-levels, deforestation, desertification, and widespread soil erosion are just some of the issues of current concern. Although it is the role of human activity in such issues that is of most concern, this activity affects the operation of the natural processes that occur within the physical environment. Most of these processes and their effects are taught and researched within the academic discipline of physical geography. A knowledge and understanding of physical geography, and all it entails, is vitally important.

It is the aim of this *Fundamentals of Physical Geography Series* to provide, in five volumes, the fundamental nature of the physical processes that act on or just above the surface of the earth. The volumes in the series are *Climatology*, *Geomorphology*, *Biogeography*, *Hydrology*, and *Soils*. The topics are treated in sufficient breadth and depth to provide the coverage expected in a *Fundamentals* series. Each volume leads into the topic by outlining the approach adopted. This is important because there may be several ways of approaching individual topics. Although each volume is complete in itself, there are many explicit and implicit references to the topics covered in the other volumes. Thus, the five volumes together provide a comprehensive insight into the totality that is Physical Geography.

The flexibility provided by separate volumes has been designed to meet the demand created by the variety of courses currently operating in higher education institutions. The advent of modular courses has meant that physical geography is now rarely taught, in its entirety, in an 'all-embracing' course but is generally split into its main components. This is also the case with many Advanced Level syllabuses. Thus students and teachers are being increasingly frustrated by the lack of suitable books and are having to recommend texts of which only a small part might be relevant to their needs. Such texts also tend to lack the detail required. It is the aim of this series to provide individual volumes of sufficient breadth and depth to fulfil new demands. The volumes should also be of use to sixth form teachers where modular syllabuses are becoming common.

The volumes have been written by higher education teachers with a wealth of experience in all aspects of the topics they cover and a proven ability in presenting information in a lively and interesting way. Each volume provides a comprehensive coverage of the subject matter using clear text divided into easily accessible sections and subsections. Tables, figures, and photographs are used where

appropriate as well as boxed case studies and summary notes. References to important previous studies and results are included but are used sparingly to avoid overloading the text. Suggestions for further reading are also provided. The main target readership is introductory level undergraduate students of physical geography or environmental science, but there will be much of interest to students from other disciplines and it is also hoped that sixth form teachers will be able to use the information that is provided in each volume.

John Gerrard

AUTHOR'S PREFACE TO THE SECOND EDITION

The first edition of *Fundamentals of Biogeography* was published in 1998. Since that time, the subject has moved on, with some interesting developments. Other textbooks have appeared. *Biogeography: An Ecological and Evolutionary Approach* (2000) by Cox and Moore is now in its sixth edition and it has been joined by Brown and Lomolino's *Biogeography*, second edition (1998), and MacDonald's *Biogeography: Introduction to Space, Time and Life* (2003). After having read these books and having taught the material in *Fundamentals of Biogeography* for several years, I felt that some rearrangement, especially in the early chapters and in the final chapter would be beneficial. The key changes are the division of the book into four parts: Introducing Biogeography, Ecological Biogeography, Historical Biogeography, and Conservation Biogeography.

Part I consists of four chapters dealing with the nature of biogeography, basic biogeographical processes, and distributions. A chapter on speciation, diversification, and extinction is new.

Part II is long. It starts with a chapter on habitats, environments, and niches. Four chapters follow that cover environmental factors: climate, substrate, topography, and disturbance. This expansion allows a much fuller treatment of this material than in the first edition. The remaining chapters in this part examine populations, interacting populations, communities (including a new section on the theory of island biogeography), and community change.

Part III tackles the history of organisms. Three chapters consider dispersal and diversification in the distant past (a largely new chapter), vicariance in the distant past, and past community change (with much new material).

Part IV explores the application of biogeography to conservation issues, focusing on conserving species and populations, and conserving communities and ecosystems. These two chapters replace the final chapter in the first edition and are sharply focused on conservation biogeography.

The effect of these major changes, plus some updating of examples and ideas, should be to give the book an even tighter, more logical, and better-balanced structure, and to offer students better value for money.

Once again, I should like to thank many people who have made the completion of this book possible: Nick Scarle for revising many of the first edition diagrams and drawing the many new ones; Andrew Mould for having the good sense to realize that the book needed a refreshing overhaul and

expansion; Chris Fastie, Rob Whittaker, Stephen Sarre, Karen A. Poiani, and Pat Morris for letting me re-use their photographs; and Francisco L. Pérez, Stefan Porembksi, and Cam Stevens for supplying me with fresh ones; Clive Agnew and other colleagues in the School of Geography at Manchester University for lending their support for writing a textbook in a research-driven climate; Derek Davenport for endless discussions on all manner of things; and, as always, my wife and family for letting me spend so much time in front of the PC.

Richard John Huggett
Poynton
December 2003

AUTHOR'S PREFACE TO THE FIRST EDITION

Biogeography means different things to different people. To biologists, it is traditionally the history and geography of animals (zoogeography) and plants (phytogeography). This, historical biogeography, explores the long-term evolution of life and the influence of continental drift, global climatic change, and other large-scale environmental factors. Its origins lie in seventeenth-century attempts to explain how the world was restocked by animals disembarking from Noah's ark. Its modern foundations were laid by Charles Darwin and Alfred Russel Wallace in the second half of the nineteenth century. The science of ecology, which studies communities and ecosystems, emerged as an independent study in the late nineteenth century. An ecological element then crept into traditional biogeography. It led to analytical and ecological biogeography. Analytical biogeography considers where organisms live today and how they disperse. Ecological biogeography looks at the relations between life and the environmental complex. It used to consider mainly present-day conditions, but has edged backwards into the Holocene and Pleistocene.

Physical geographers have a keen interest in biogeography. Indeed, some are specialist teachers in that field. Biogeography courses have been popular for many decades. They have no common focus, their content varying enormously according to the particular interests of the teacher. However, many courses show a preference for analytical and ecological biogeography, and many include human impacts as a major element. Biogeography is also becoming an important element in the growing number of degree programmes in environmental science. Biogeography courses in geography and environmental science departments are supported by a good range of fine textbooks. Popular works include *Biogeography: Natural and Cultural* (Simmons 1979), *Basic Biogeography* (Pears 1985), *Biogeography: A Study of Plants in the Ecosphere* (Tivy 1992), and *Biogeography: An Ecological and Evolutionary Approach* (Cox and Moore 1993), the last being in its fifth edition with a sixth in preparation.

As there is no dearth of excellent textbooks, why is it necessary to write a new one? There are at least four good reasons for doing so. First, all the popular texts, though they have been reissued as new editions, have a 1970s air about them. It is a long time since a basic biogeography text appeared that took a fresh, up-to-date, and geographically focused look at the subject. Second, human interaction with plants and animals is now a central theme in geography, in environmental science, and in environmental biology. Existing textbooks tackle this topic, but there is much more to be said

about application of biogeographical and ecological ideas in ecosystem management. Third, novel ideas in ecology are guiding research in biogeography. It is difficult to read articles on ecological biogeography without meeting metapopulations, heterogeneous landscapes, and complexity. None of these topics is tackled in existing textbooks. They are difficult topics to study from research publications because they contain formidable theoretical aspects. Nevertheless, it is very important that students should be familiar with the basic ideas behind them. First- and second-year undergraduates can handle them if they are presented in an informative and interesting way that avoids excessive mathematical formalism. Fourth, environmentalism in its glorious variety has mushroomed into a vast interdisciplinary juggernaut. It impinges on biogeography to such an extent that it would be inexcusably remiss not to let it feature in a substantial way. It is a facet of biogeography that geography students find fascinating. Without doubt, a biogeography textbook for the next millennium should include discussion of environmental and ethical concerns about such pressing issues as species exploitation, environmental degradation, and biodiversity. However, biogeography is a vast subject and all textbook writers adopt a somewhat individualistic viewpoint. This book is no exception. It stresses the role of ecological, geographical, historical, and human factors in fashioning animal and plant distributions.

I should like to thank many people who have made the completion of this book possible. Nick Scarle patiently drew all the diagrams. Sarah Lloyd at Routledge bravely took yet another Huggett book on board. Several people kindly provided me with photographs. Rob Whittaker and Chris Fastie read and improved the section on vegetation succession. Michael Bradford and other colleagues in the Geography Department at Manchester University did not interrupt my sabbatical semester too frequently. Derek Davenport again discussed all manner of ideas with me. And, as always, my wife and family lent their willing support.

Richard John Huggett
Poynton
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PART I INTRODUCING BIOGEOGRAPHY

WHAT IS BIOGEOGRAPHY?

Biogeographers study the geography, ecology, and evolution of living things. This chapter covers:

- ecology – environmental constraints on living
- history and geography – time and space constraints on living

Biogeographers address a misleadingly simple question: why do organisms live where they do? Why does the speckled rangeland grasshopper live only in short-grass prairie and forest or brushland clearings containing small patches of bare ground? Why does the ring ouzel live in Norway, Sweden, the British Isles, and mountainous parts of central Europe, Turkey, and southwest Asia, but not in the intervening regions? Why do tapirs live only in South America and southeast Asia? Why do the nestor parrots – the kea and the kaka – live only in New Zealand?

Two groups of reasons are given in answer to such questions as these – ecological reasons and historical-cum-geographical reasons.

ECOLOGY

Ecological explanations for the **distribution** of organisms involve several interrelated ideas. First is the idea of *populations*, which is the subject of *analytical biogeography*. Each species has a characteristic life history, reproduction rate, **behaviour**, means of dispersion, and so on. These traits affect a population's response to the environment in which it lives. The second idea concerns this biological response to the **environment** and is the subject of *ecological biogeography*. A population responds to its physical surroundings (**abiotic** environment) and its living surroundings (**biotic** environment). Factors in the abiotic environment include such physical factors as temperature, light, **soil**, geology, topography, fire, water, and air currents; and such chemical factors as oxygen levels, salt concentrations, the presence of toxins,

and acidity. Factors in the biotic environment include competing species, parasites, diseases, predators, and humans. In short, each species can tolerate a range of environmental factors. It can only live where these factors lie within its tolerance limits.

The speckled rangeland grasshopper

This insect (*Arphia conspersa*) ranges from Alaska and northern Canada to northern Mexico, and from California to the Great Plains. It lives at less than 1,000 m elevation in the northern part of its range and up to 4,000 m in the southern part. Within this extensive latitudinal and altitudinal range, its distribution pattern is very patchy, owing to its decided preference for very specific habitats (e.g. Schennum and Willey 1979). It requires short-grass prairie, or forest and brushland openings, peppered with small pockets of bare ground. Narrow-leaved grasses provide the grasshopper's food source. It needs the bare patches to perform its courtship rituals. Dense forest, tall grass **meadows**, or dry scrubland fail to meet these ecological and behavioural needs. Roadside meadows and old logged areas are suitable and subject to slow **colonization**. Moderately grazed pastures are also suitable and support large populations.

Even within suitable habitat, the grasshopper's low vagility (the ease with which it can spread) limits its distribution. This poor ability to spread is the result of complex social behaviour, rather than an inability to fly well. Females are rather sedentary, at least in mountain areas, while males make mainly short, spontaneous flights within a limited area. The two sexes together form tightly knit population clusters within areas of suitable habitat. Visual and acoustic communication displays hold the cluster together.

Ring ouzel

A mix of ecology and history may explain the biogeography of most species. The ring ouzel or 'mountain blackbird', which goes by the undignified scientific name of *Turdus torquatus* (Box 1.1), lives in the cool temperate climatic zone, and in the alpine equivalent to the cool temperate zone on mountains (Figure 1.1). It likes cold climates. During the last **ice age**, the heart of its range was probably the Alps and Balkans. From here, it spread outwards into much of Europe, which was then colder than now. With climatic warming during the last 10,000 years, the ring ouzel has left much of its former range, surviving only in places that are still relatively cold because of their high latitude or altitude. Even though it likes cold conditions, most ring ouzels migrate to less severe climates during winter. The north European populations move to the Mediterranean while the alpine populations move to lower altitudes.

HISTORY

Historical-cum-geographical explanations for the distribution of organisms involve two basic ideas, both of which are the subject of *historical biogeography*. The first idea concerns *centres-of-origin* and **dispersal** from one place to another. It argues that species originate in a particular place and then spread to other parts of the globe, if they should be able and willing to do so. The second idea considers the importance of geological and climatic changes splitting a single population into two or more isolated groups. This idea is known as **vicariance** biogeography. The following case studies illustrate these two basic biogeographical processes.

Tapirs

The tapirs are close relatives of the horses and rhinoceroses. They form a family – the Tapiridae. There are four living species, one of which dwells in southeast Asia and three in central and South America (Plate 1.1). Their present distribution is thus broken and poses a problem

Box 1.1

WHAT'S IN A NAME? CLASSIFYING ORGANISMS

Everyone knows that living things come in a glorious diversity of shapes and sizes. It is apparent even to a casual observer that organisms appear to fall into groups according to the similarities between them. No one is likely to mistake a bird for a beetle, or a daisy for a hippopotamus. Zoologists and botanists classify organisms according to the similarities and differences between them. Currently, five great kingdoms are recognized – prokaryotae (monera), protoctista, plantae, fungi, and animalia. These chief subdivisions of the kingdoms are phyla. Each phylum represents a basic body plan that is quite distinct from other body plans. This is why it is fairly easy, with a little practice, to identify the phylum to which an unidentified organism belongs. Amazingly, new phyla are still being discovered (e.g. Funch and Kristensen 1995).

Organisms are classified hierarchically. Individuals are grouped into species, species into genera, genera into families, and so forth. Each species, genus, family, and higher-order formal group of organisms is called a **taxon** (plural **taxa**). Each level in the hierarchy is a taxonomic category. The following list shows the classification of the ring ouzel:

Kingdom:	Animalia (animals)
Phylum:	Chordata (chordates)
Subphylum:	Vertebrata (vertebrates)
Class:	Aves (birds)
Subclass:	Neornithes ('new birds')
Superorder:	Carinatae (typical flying birds)
Order:	Passeriformes (perching birds)
Suborder:	Oscines (song birds)
Family:	Muscicapidae (thrush family)
Subfamily:	Turdinae (thrushes, robins, and chats)
Genus:	*Turdus*
Species:	*Turdus torquatus*

Animal family names always end in -idae, and subfamilies in -inae. Dropping the initial capital letter and using -ids as an ending, as in felids for members of the cat family, gives them less formal names. Plant family names end in -aceae or -ae. The genus (plural genera) is the first term of a binomial: genus plus species, as in *Turdus torquatus*. It is always capitalized and in italics. The species is the second term of a binomial. It is not capitalized in animal species, and is not normally capitalized in plant species, but is always italicized in both cases. The specific name signifies either the person who first described it, as in *Muntiacus reevesi*, Reeve's muntjac deer, or else some distinguishing feature of the species, as in *Calluna vulgaris*, the common (= vulgar) heather. If subspecies are recognized, they are denoted by the third term of a trinomial. For example, the common jay in western Europe is *Garrulus glandarius glandarius*, which would usually be shortened to *Garrulus g. glandarius*. The Japanese subspecies is *Garrulus glandarius japonicus*. In formal scientific writing, the author or authority of the name is indicated. So, the badger's full scientific name is *Meles meles* L., the L. indicating that Carolus Linnaeus (1707–78) first described the species. The brown hare's formal name is *Lepus europaeus* Pallas, which shows that Peter Simon Pallas first described it (in 1778). In this book, the authorities will be omitted because they confer a stuffy feel. After its first appearance in each chapter, the species name is abbreviated by reducing the generic term to a single capital letter. Thus, *Meles meles* becomes *M. meles*.

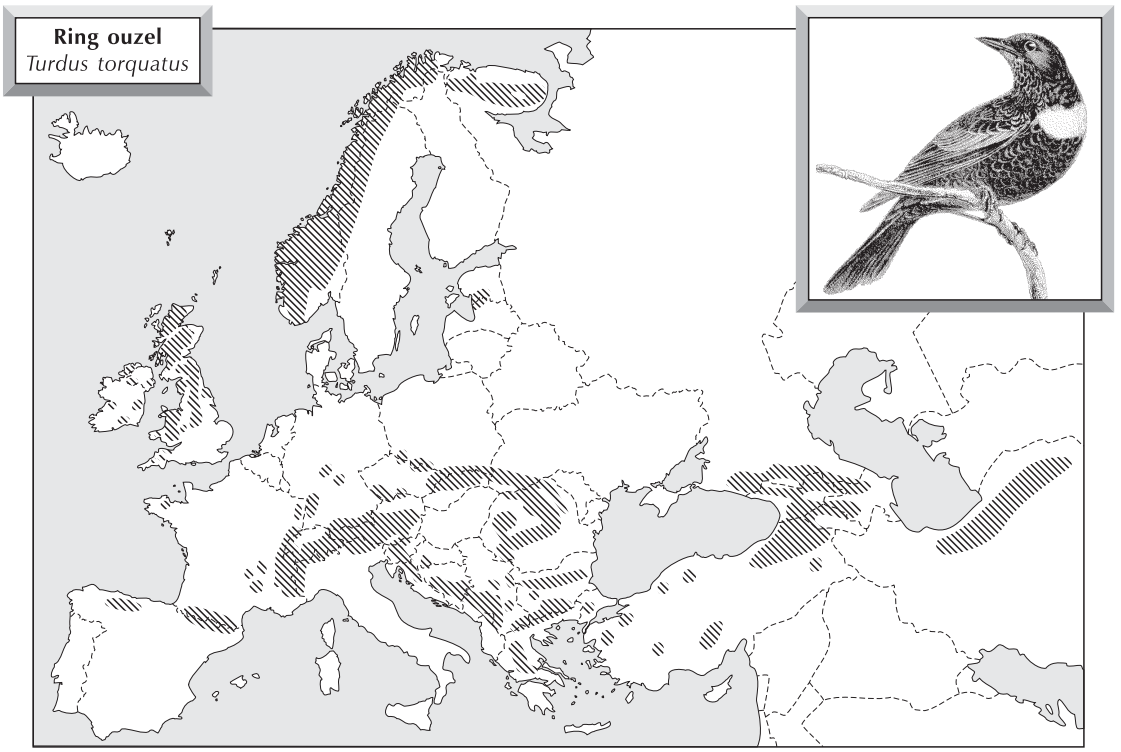


Figure 1.1 The breeding distribution of the ring ouzel (*T. torquatus*).
Sources: Map adapted from Cramp (1988); picture from Saunders (1889)

for biogeographers. How do such closely related species come to live in geographically distant parts of the world? Finds of fossil tapirs help to answer this puzzle. Members of the tapir family were once far more widely distributed than at present (Figure 1.2). They lived in North America and Eurasia. The oldest fossils come from Europe. A logical conclusion is that the tapirs evolved in Europe, which was their centre-of-origin, and then dispersed east and west. The tapirs that went northeast reached North America and South America. The tapirs that chose a southeasterly **dispersal route** moved into southeast Asia. Subsequently, probably owing to climatic change, the tapirs in North America and the Eurasian homeland went extinct. The survivors at the tropical edges of the distribution spawned the present species. This explanation is plausible, but it is not watertight – it is always possible that somebody will dig up even older tapir remains from somewhere else. The incompleteness of the fossil record dogs historical biogeographers and dictates that they can never be fully confident about any hypothesis.

Nestor parrots

The nestor parrots (Nestorinae) are endemic to New Zealand. There are two species – the kaka (*Nestor meridionalis*) and the kea (*N. notabilis*) (Plate 1.2). They are closely related and are probably descended from a 'proto-kaka' that reached

Plate 1.1 Central American or Baird's tapir (*Tapirus bairdi*), Belize.
Photograph by Pat Morris.

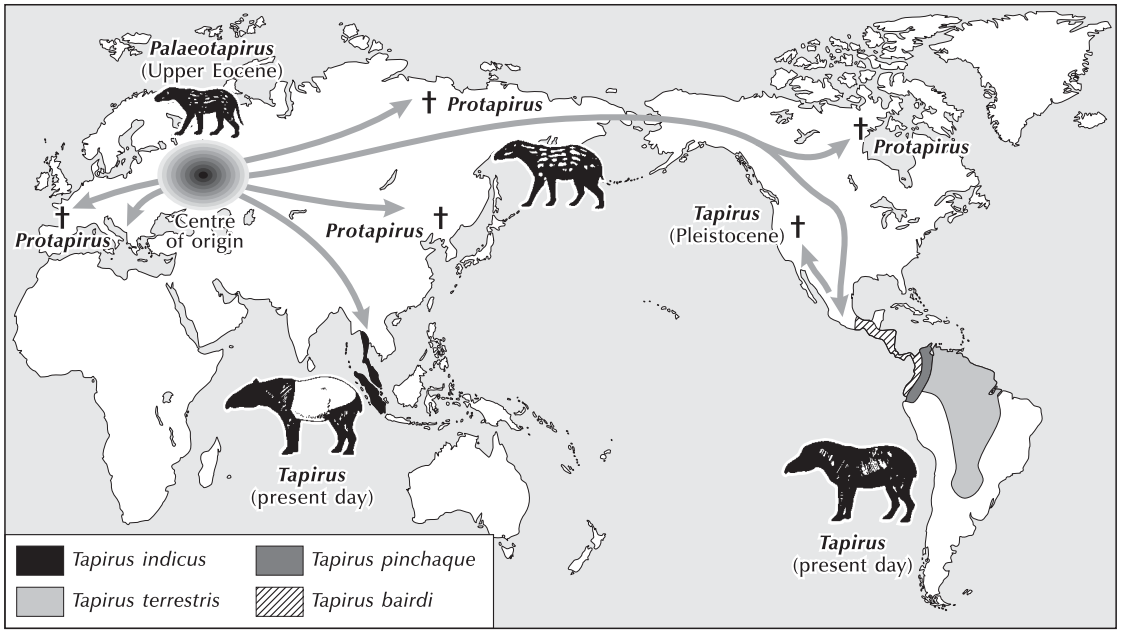


Figure 1.2 Tapirs: their origin, spread, and present distribution.
Source: Adapted from Rodríguez de la Fuente (1975)

(a)

(b)

Plate 1.2 Nestor parrots. (a) Kaka (*N. meridionalis*). (b) Kea (*N. notabilis*).
Photographs by Pat Morris.

New Zealand during the **Tertiary period** (see Appendix). Then, New Zealand was a single, forest-covered island. The proto-kaka became adapted to forest life. Late in the Tertiary period, the northern and southern parts of New Zealand split. North Island remained forested and the proto-kakas there continued to survive as forest parrots, feeding exclusively on vegetable matter and nesting in tree hollows. They eventually evolved into the modern kakas.

South Island gradually lost its forests because mountains grew and climate changed. The proto-kakas living on South Island adjusted to these changes by becoming 'mountain parrots', depending on alpine shrubs, insects, and even **carrion** for food. They forsook trees as breeding sites and turned to rock fissures. The changes in the South Island proto-kakas were so far-reaching that they became a new species – the kea. After the **Ice Age**, climatic amelioration promoted some reforestation of South Island. The kakas dispersed across the Cook Strait and colonized South Island. Interaction between North and South Island kaka populations is difficult across the 26 km of ocean. In consequence, the South Island kakas have become a subspecies. The kaka and the kea are now incapable of interbreeding and they continue to live side by side on South Island. The kea has never colonized North Island, probably because there is little suitable habitat there. The biogeography of the nestor parrots thus involves **adaptation** to changing environmental conditions, dispersal, and vicariance events.

SUMMARY

Ecology (including behaviour), history, and geography determine the distribution of organisms. Most species distributions result from a combination of all these factors, but biogeographers tend to specialize in ecological aspects (ecological biogeography) or historical aspects (historical biogeography). Ecological biogeographers are interested in the effects of environmental factors in constraining species ranges, and in the role of

past environmental changes in shaping species ranges. Some historical biogeographers are interested in finding centres-of-origin and dispersal routes of various groups of organism; others prefer to interpret biogeographical history through vicariance (range-splitting) events.

ESSAY QUESTIONS

1 What is ecological biogeography?

2 What is historical biogeography?

FURTHER READING

Brown, J. H. and Lomolino, M. V. (1998) *Biogeography*, 2nd edn. Sunderland, MA: Sinauer Associates.

An excellent text covering virtually all aspects of biogeography in rich detail.

Cox, C. B. and Moore, P. D. (2000) *Biogeography: An Ecological and Evolutionary Approach*, 6th edn. Oxford: Blackwell.

Already a classic. A deservedly popular textbook.

George, W. (1962) *Animal Geography*. London: Heinemann.

Written before the revival of continental drift, but worth a look.

MacDonald, G. (2003) *Biogeography: Introduction to Space, Time and Life*. New York: John Wiley & Sons.

An excellent, up-to-date textbook with lots of examples.

Pears, N. (1985) *Basic Biogeography*, 2nd edn. Harlow: Longman.

A good, if dated, text on ecological biogeography.

Tivy, J. (1992) *Biogeography: A Study of Plants in the Ecosphere*, 3rd edn. Edinburgh: Oliver & Boyd.

An enjoyable introductory textbook with a chapter on historical biogeography.

2 BIOGEOGRAPHICAL PROCESSES I

SPECIATION, DIVERSIFICATION, AND EXTINCTION

Species appear, flourish, and disappear. This chapter covers:

- How new species arise
- How species diversify
- Why species become extinct

GENETIC INFORMATION: THE BASIS OF EVOLUTIONARY CHANGE

New species arise through the process of **speciation**. The nature of speciation and its causes are fiercely debated. A key element is a store of genetic information that is mutable. The debate largely focuses on the relative importance of the various sources of change; for example, is geographical isolation the primary driving force or is it ecological differentiation? This section will examine these causes of change, having first outlined the nature of stores of genetic material.

Genes, genomes, and gene pools

Genetic information provides a blueprint, so to speak, for making an organism. The **genome** is the total genetic information stored in an organism (or **organelle** or cell). Genetic information is stored in **chromosomes** within cells. In prokaryotes (bacteria and cyanobacteria), deoxyribonucleic acid (DNA) forms a coiled structure called a nucleoid. In eukaryotes (all other organisms), chromosomes are made of DNA and protein. The *karyotype* is the number, size, and shape of the chromosomes in a somatic cell arranged in a standard manner. The human karyotype has 46 chromosomes.

DNA is found in mitochondria as well as in cell nuclei. Mitochondrial DNA (mtDNA) is a closed, circular molecule. (Mitochondria are vitally important organelles that are the site of cell respiration and produce energy-rich molecules of adenosine triphosphate (ATP).) As a rule, specific genes in mtDNA are present in all taxa, be they toad, tortoise, titmouse, or tiger. Because change within mtDNA occurs about five to ten times faster than in nuclear DNA, mtDNA 'records'

recent demographic events: in short, it is a repository of phylogenetic history. Techniques of molecular biology allow this 'history' to be unlocked and have enabled a new branch of biogeography – **phylogeography** – to emerge (e.g. Avise 2000), though the role of this subject in biogeography is debated (see Ebach *et al*. 2002; Ebach and Humphries 2003).

A **gene** is a specific piece of genetic information – a unit of inheritance passed from generation to generation by the gametes (eggs and spermatozoa). It consists of a length of DNA at a particular site or **locus** on a chromosome. Some genes have alternative forms or **alleles** at the same locus, which differ in one or more bases. For instance, in humans, two alleles exist at a locus controlling eye colour: one allele determines blue eyes and the other brown eyes. Multiple alleles may occur at some loci, though there are seldom more than ten. Species with at least two discrete genetic variants are *polymorphic species* and display **polymorphism**. Alleles of one gene may be identical or may differ at the same loci in a genotype. Where two alleles received from both parents are identical, the condition is **homozygous** and the individual is a *homozygote*; where they differ, the condition is **heterozygous** and the individual a *heterozygote*. Dominant alleles affect the phenotype in a heterozygote and a homozygote, whereas only in a homozygote do recessive alleles affect the phenotype. In a randomly mating population, the average homozygosity is a measure of gene identity and the average heterozygosity is a measure of gene diversity.

The **genotype** is the genetic make-up of an individual, the sum of all its genes. It contrasts with its **phenotype**, which is its form, physiology, and way of life; in other words, the sum of its characteristics. The phenotype of an organism changes throughout its life, but its genotype remains the same, except for occasional **mutations**. The genotype determines the range of phenotypes that may develop, and the environment determines the actual phenotypes that do develop. For example, in California, USA, populations of Hansen's cinquefoil (*Potentilla glandulosa hanseni*) living at different altitudes have the same genotype but different phenotypes.

A *gene pool* is the totality of the genes or genotypes of all individuals within a 'reproductive community' at a given time. A reproductive community is a community comprising individuals that reproduce sexually (as opposed to asexually) and mate with each other. A *panmictic population*, in which matings occur at random, is the smallest reproductive community. A **deme** is a local population of interbreeding individuals (although it could also be a population of individuals that reproduce asexually).

A **species** is the most inclusive reproductive community. Before the 1990s, it was a mainstay of evolutionary theory that the genetic discontinuities between species are absolute because *isolating mechanisms* prevent sexually reproducing organisms of different species from interbreeding. Many biologists now question this view and call into doubt the reality of species as fully isolated entities (e.g. Mallet 2001; Wu 2001). They see speciation as a process in which groups of organisms gradually become genealogically distinct, rather than a discontinuity that affects all genes at once. This means that boundaries between species are fuzzier than was once thought. In addition, some biologists now feel that total reproductive isolation is not the best definition of a species, a view bolstered, for example, by studies revealing the transfer of genes between closely related fruit fly (*Drosophila*) species (Wu 2001).

Some species display considerable geographical variability in form and possess distinct geographical **races** and ecological races, which are often designated as subspecies. *Geographical races* either live side by side and may grade into each other, or else live separately (that is, have a disjunct distribution). An example is the human species that has marked geographical racial variations – Amerindian, Polynesian, Asiatic, European, African, and so on. *Ecological races* have different genotypes and phenotypes, are interfertile with numerous intergrades in zones of contact, and

live together (have sympatric distributions). Species bearing geographical and ecological races are *polytypic* (contain several types). Polytypism is the variability between populations or groups and is often expressed as several races or subspecies. It is not the same as polymorphism, which is the variability within populations. However, polymorphisms may furnish a store of genetic raw material from which polytypisms evolve.

Changing genes

Evolution occurs in populations, not in individuals. It requires changes in DNA, which may arise from processes of gene mutation and chromosomal change. Potential changes in a gene pool arise from several processes: mutation (which creates new alleles and alters chromosomes), genetic drift, gene flow, natural selection, and geographical variation.

Mutation

Mutations are changes in hereditary materials. As a rule, information encoded in a DNA sequence reproduces dependably during replication. Occasionally, 'errors' occur so that the nucleotide sequence in parent and daughter DNA molecules differ. *Gene* (or *point*) *mutation* involves the altering of the DNA sequence of a gene and the passing of the new nucleotide sequence to the offspring. *Chromosome mutation* (or *aberration*) involves the changing of the number of chromosomes, or the number or arrangement of genes in a chromosome (Table 2.1).

Genetic drift

Chance changes in the frequency of alleles, occurring as interbreeding populations exchange genetic material, produces *genetic drift*. Normally, genetic drift is a weak force of genetic change with very little effect on a large population. It may have a significant effect in small populations produced by a few individuals colonizing a new habitat (founder populations), by remnants of a population becoming marooned in refugia, by population crashes causing **bottlenecks** (sudden reductions in genetic diversity), and by metapopulation patches (p. 171) with limited inter-patch

Table 2.1 A classification of chromosome mutations

Change in	*Mechanism*	*Description*
Number of genes	Deficiency or deletion	Chromosome loses a segment of DNA containing one or more genes
	Duplication	A DNA segment of one or more genes occurs twice or more in a set of chromosomes
Location of genes	Inversion	Location of a block of genes inverted within a chromosome
	Translocation	Location of a block of genes changes in a chromosome
Number of chromosomes	Fusion	Two non-homologous chromosomes fuse into one
	Fission	A chromosome splits into two
	Aneuploidy	One or more chromosomes of the normal set is either missing or present in excess
	Haploidy and polyploidy	The number of sets of chromosomes is other than two. Most organisms are diploid (have two sets of chromosomes in their somatic cells (but one set in their gametic cells). Some organisms are normally haploid, that is, have one set of chromosomes. Organisms with more than two sets of chromosomes are polyploid, a condition common in many species in some groups of plants

Source: Based on discussion in Dobzhansky *et al.* (1977, 57–8)

gene flow. Genetic drift is possible in large populations where a few individuals monopolize breeding. An example is red deer stags that run harems.

Gene flow

This is the movement of genetic information between different parts of an interbreeding population. High gene flow keeps the gene pool 'well stirred'; low gene flow may lead to genetic divergence in different parts of the population.

Natural selection

According to the latest thinking of some biologists, **natural selection** is a primary driving force of speciation and may be more potent than allopatry (the geographical isolation of populations). The argument is that divergent natural selection, which fine-tunes phenotypes to local environments, may outweigh gene flow, leading to further divergence, and so forth, until speciation is accomplished (Dieckmann and Doebeli 1999; Via 2001).

Selection tests the genetic foundation of individuals, acting directly on the phenotype and indirectly on the genotype. It may be directional, stabilizing, or disruptive (Figure 2.1).

Directional or *progressive selection* drives a unidirectional change in the genetic composition of a population, favouring individuals with advantageous characteristics bestowed by a gene or set of genes (Figure 2.1a). It may occur when a population adapts to a new environment, or when the environment changes and a population tracks the

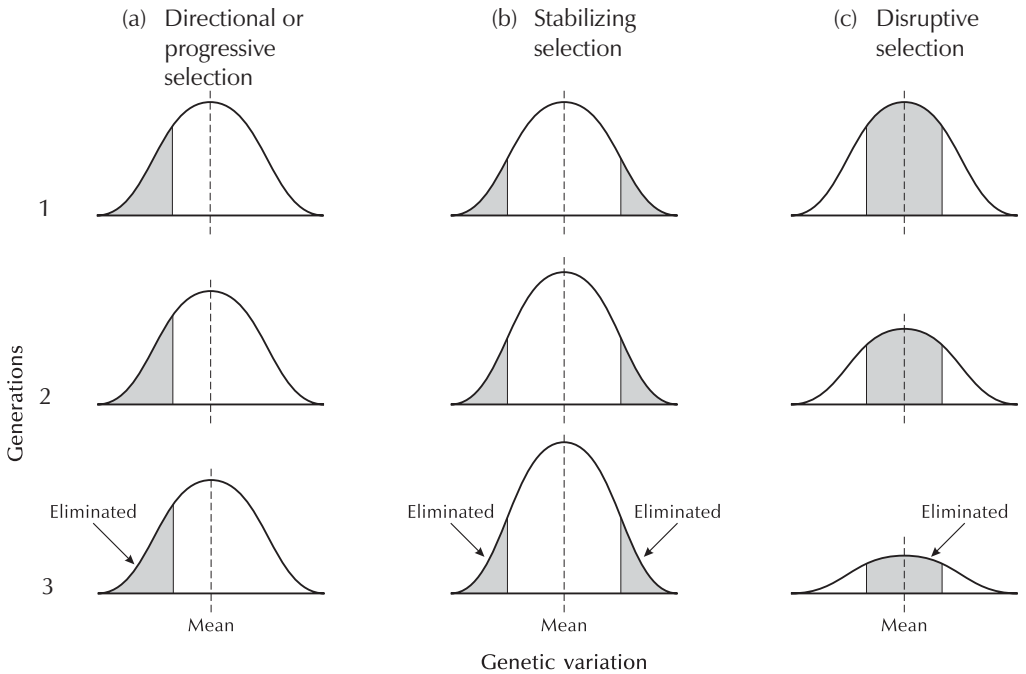


Figure 2.1 Directional, stabilizing, and disruptive selection.
Source: After Grant (1977)

changes. The response of the melanic (dark) form of the peppered moth (*Biston betularia*) when confronted with industrial soot illustrates the first case (Box 2.1). Anita Malhotra and Roger S. Thorpe (1991) believed that they demonstrated selection in action by manipulating natural populations of the Dominican lizard (*Anolis oculatus*). They translocated several ecotypes (a race adapted to local ecological conditions) of the lizard into large experimental enclosures, and monitored them over two months. The rate of survival and non-survival depended on the degree of similarity between the ecological conditions of the enclosure site and the original habitat. The changes in size of the white-tailed deer (*Odocoileus virginianus*) during the Holocene epoch, which appear to track environmental changes, exemplify the second type of directional selection (Purdue 1989).

Stabilizing selection occurs when a population is well adapted to a stable environment. In this case, selection weeds out the ill-adapted combinations of alleles and fixes those of intermediate character (Figure 2.1b). Stabilizing selection is omnipresent and probably the most common mode of selection. The peppered moth's response to industrial pollution illustrated directional selection; but the moth population also displays stabilizing selection. Before industrialization altered the moth's environment, stabilizing selection winnowed out the rare melanic mutants, a situation that probably prevailed for centuries.

Disruptive or *diversifying selection* favours the extreme types in a polymorphic population and eliminates the intermediate types, so encouraging polymorphism (Figure 2.1c). Disruptive selection under experimental conditions occurs in the common fruit fly (*Drosophila melanogaster*) (e.g. Thoday 1972). In nature, at least three situations may promote disruptive selection (Grant 1977, 98–9). The first situation is where well-differentiated polymorphs have a strong selective advantage over poorly differentiated polymorphic types, as in sexually dimorphic species, where males and females that possess distinct secondary sexual characters have a better chance of mating and reproduction than intermediate types (intersexes, homosexuals, and so on). The second situation is where a polymorphic population occupies a heterogeneous habitat. The polymorphic types could be specialized for different subniches in the habitat. This may occur in the sulphur butterfly (*Colias eurytheme*), the females of which species are

Box 2.1

NATURAL SELECTION IN ACTION: INDUSTRIAL MELANISM IN THE PEPPERED MOTH

The peppered moth (*B. betularia*) in Britain is a small, drab moth with three colour phases – whitish, brownish mottled, and dark (almost black) – that exist in British populations. In Victorian insect collections, the lighter and mottled types predominate. In the late nineteenth century, the rare dark phase began to make more appearances, until by the 1920s the species was nearly all black. H. Bernard Kettlewell and his colleagues correlated the change in predominate colour to the industrialization of the Manchester area (e.g. Kettlewell 1973, 131–51). Soot and sulphur discharged from mills and factories blackened tree trunks and killed mottled tree lichens. The lighter and mottled moths stood out clearly on the trunks and were easy pickings for predatory birds, while the darker moths became hard to see. By 1986, a study of 1,825 moths collected throughout Great Britain showed that the area dominated by the black moths is steadily shrinking towards the north-east corner of the country.

polymorphic for wing colour, with one gene controlling orange and white forms. At several localities in California, the white form has an activity peak in the morning and late afternoon, and the orange form has a peak of activity around midday, indicating that the polymorphic types have different temperature and humidity preferences. The third situation occurs when a plant population crosses two different ecological zones. Under these circumstances, different adaptive characteristics may arise in the two halves of the population and persist despite interbreeding. This appears to be the case for whitebark pine (*Pinus albicaulis*), a high-montane species living at and just above the **treeline** in the Californian Sierra Nevada (Clausen 1965). On the mountain slopes up to the timberline, the population grows as erect trees; above the timberline, it grows as a low, horizontal, elfinwood form. The arboreal and elfinwood populations are contiguous and cross-pollinated by wind, as witnessed by the presence of some intermediate individuals.

Geographical and ecological variation

The phenotypes and genotypes of many species display geographical and ecological variations. Two types of geographical variation arise: continuous geographical variation and disjunct geographical variation. Large and continuous populations, such as the human population and populations of many forest trees and plains grasses, have polymorphic local populations within them with characteristic balances of polymorphic types fashioned by gene flow and various kinds of selection. In moving through such a population, the frequencies of the polymorphic type shift little by little. The allele frequencies for human blood groups exhibit this pattern.

Many species adapt to conditions in their local environment, and especially to gradual geographical changes in climate across continents. Such adaptation is often expressed in the phenotype as a measurable change in size, colour, or some other trait. The gradation of form along a climatic gradient is called a *cline* (Huxley 1942). Clines result from local populations developing tolerances to local conditions, including climate, through the process of natural selection (see Saloman 2002). Commonly observed clines of pigmentation, body size, and so on have generated a set of biogeographical rules (Box 2.2). Morphological clines may evolve very swiftly. In 1852, the house sparrow (*Passer domesticus*) was introduced into the eastern USA from England. Fifty years later it had already developed geographical variation in size and colour. Today it is smallest along the central Californian coast and southeast Mexico, and is largest on the Mexican Plateau, the Rocky Mountains, and the northern Great Plains. The clines in house sparrows that have evolved in North America resemble the clines found in Europe (Johnston and Selander 1971). The American robin (*Turdus migratorius*) displays similar geographical variation in size and shape to the house sparrow (Aldrich and James 1991): it is small in the southeastern USA and along the central Californian coast, and large in the Rocky Mountains and associated high plains. The European wild rabbit (*Oryctolagus cuniculus*), introduced in eastern Australia a little over a century ago, already displays clinal variation in skeletal morphology. The rapidity of clinal evolution revealed by these, and other, examples has been reproduced using genetic models of populations that show, even in the presence of gene flow, that clines can develop within a few generations (Endler 1977).

Disjunct geographical races evolve where a population is discontinuous, comprising a set of island-like, spatially separate subpopulations. For instance, fineflower gilia (*Gilia leptantha*) lives in openings of montane pine forests in southern California. The forests occur at middle and high elevations on mountain ranges separated by many miles of unforested lowlands. In consequence, the plant has a disjunct geographical distribution and four disjunct geographical races (Grant 1977, 166).

Box 2.2

BIOGEOGRAPHICAL RULES

Most biogeographical rules were established during the nineteenth century when it was observed that the form of many warm-blooded animal species varies in a regular way with climate.

Gloger's rule

Proposed by Constantin Wilhelm Lambert Gloger in 1833, this rule states that races of birds and mammals in warmer regions are more darkly coloured than races in colder or drier regions. Or, to put it another way, birds and mammals tend to have darker feathers and fur in areas of higher humidity. This is recognized as a valid generalization about clines of **melanism**. A credible explanation for it is that animals in warmer, more humid regions require more pigmentation to protect them from the light. Gloger's rule was first observed in birds, but was later seen to apply to mammals such as wolves, foxes, tigers, and hares. It has also been observed in beetles, flies, and butterflies. Given that colour variation shows a concordance of pattern in birds that have vastly different competitors, diets, histories, and levels of gene flow, some common physiological adaptation seems likely.

Bergmann's rule or the size rule

Established by Carl Bergmann in 1847, this rule states that species of birds and mammals living in cold climates are larger than their **congeners** that inhabit warm climates. It applies to a wide range of birds and mammals. Bergmann believed many species conform to the rule because big animals have a thermal advantage over small ones in cold climates: as an object increases in size, its surface area becomes relatively smaller (increasing by the square) than its volume (increasing by the cube).

Examples of Bergmann's rule, and exceptions to it, abound. In central Europe, the larger mammals, including the red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), brown bear (*Ursus arctos*), fox (*Vulpes vulpes*), wolf (*Canis lupus*), and wild boar (*Sus scrofa*), increase in size towards the northeast and decrease in size towards the southwest. In Asia, larger tigers (*Panthera tigris*) tend to occur at higher latitudes. Species that decline to obey Bergmann's rule include the capercaillie (*Tetrao urogallus*), which is smaller in Siberia than in Germany. Also, many widespread Eurasian and North American bird species are largest in the highlands of the semi-arid tropics (Iran, the Atlas Mountains, and the Mexican Highlands), and not in the coldest part of their range. The geographical variation of size in some vertebrate and invertebrate poikilotherms ('cold-blooded') species conforms to Bergmann's rule (e.g. Lindsey 1966).

The explanation of Bergmann's rule is the subject of much argument, but climate does appear to play a leading role (see Yom-Tov 1993). This is borne out by Frances C. James's (1970) study of bird size and various climatic measures sensitive to both temperature and moisture (wet-bulb temperature, vapour pressure, and absolute humidity) in the eastern USA. She found that wing length, a good surrogate of body size, increased in size northwards and westwards from Florida in the following species: the hairy woodpecker (*Dendrocopos villosus*), downy woodpecker (*D. pubescens*), blue jay (*Cyanocitta cristata*), Carolina chickadee (*Parus carolinensis*), white-breasted nuthatch (*Sitta carolinensis*), and eastern meadowlark (*Sturnella magna*). In all

cases, there was a tendency for larger (or longer-winged) birds to extend southwards in the Appalachian Mountains, and for smaller (or shorter-winged) birds to extend northwards in the Mississippi River valley. In the downy woodpecker, female white-breasted nuthatches, and female blue jays, relatively longer-winged birds tended to extend southwards into the interior highlands of Arkansas, and relatively shorter-winged birds to extend northwards into other river valleys. These subtle relations between clinal size variation and topographic features indicated that the link between the two phenomena might involve precise adaptations to very minor climatic gradients. The variation in wing length in these bird species correlated most highly with those variables, such as wet-bulb temperature, which register the combined effects of temperature and humidity. This suggested that size variation depends on moisture levels as well as temperature. James reasoned that a relationship with wet-bulb temperature and with absolute humidity in ecologically different species strongly suggests that a common physiological adaptation is involved. Absolute humidity nearly determines an animal's ability to lose heat: any animal with constant design will be able to unload heat more easily if it has a higher ratio of respiratory surface to body size. This new twist to Bergmann's rule bolsters some aspects of Bergmann's original interpretation about thermal budgets. Climate tends to be cooler, and therefore drier, at high altitudes and latitudes. This accounts for the fact that many clines of increasing size parallel increasing altitude and latitude. Additionally, size tends to increase in arid regions irrespective of altitude and latitude, and widespread species tend to be largest in areas that are high, cool, and dry. James concluded that, if the remarkably consistent pattern of clinal size variation in breeding populations of North American birds represents an adaptive response, then 'Bergmann's original rationale of thermal economy, reinterpreted in terms of temperature and moisture rather than temperature alone, still stands as a parsimonious explanation' (James 1991, 698).

An observed body-mass decline in several resident bird species in Israel since 1950 presents an interesting demonstration of Bergmann's rule in operation (Figure 2.2). Yoram Yom-Tov (2001) found that the body mass of the yellow-vented bulbul (*Pycnonotus xanthopygos*), house sparrow (*Passer domesticus*), Sardinian warbler (*Sylvia melanocephala*), and graceful prinia (*Prinia gracilis*) showed significant declines during the second half of the twentieth century. Minimum summer temperatures in Israel rose by an average of 0.26ºC per decade over the same period.

Allen's rule or the proportional rule

Joel A. Allen's (1877) rule extends Bergmann's rule to include protruding parts of the body, such as necks, legs, tails, ears, and bills. Allen found that protruding parts in wolves, foxes, hares, and wild cats are shorter in cooler regions. Like large body-size, short protruding parts help to reduce the surface area and so conserve heat in a cold climate. The jackrabbit (subgenus *Macrotolagus*), which lives in the southwestern USA, has ears one third its body length; in the common jackrabbit (*Lagus campestris*), which ranges from Kansas to Canada, the ears are the same length as the head. Another observation conforming to Allen's rule is that such mammals as bats, which have a large surface area for their body mass, are found chiefly in the tropics. Allen's rule has been observed in poikilotherms as well as homeotherms.

Guthrie's or Geist's rule

This is a modern biogeographical rule based on the observation that the seasonal amount of food

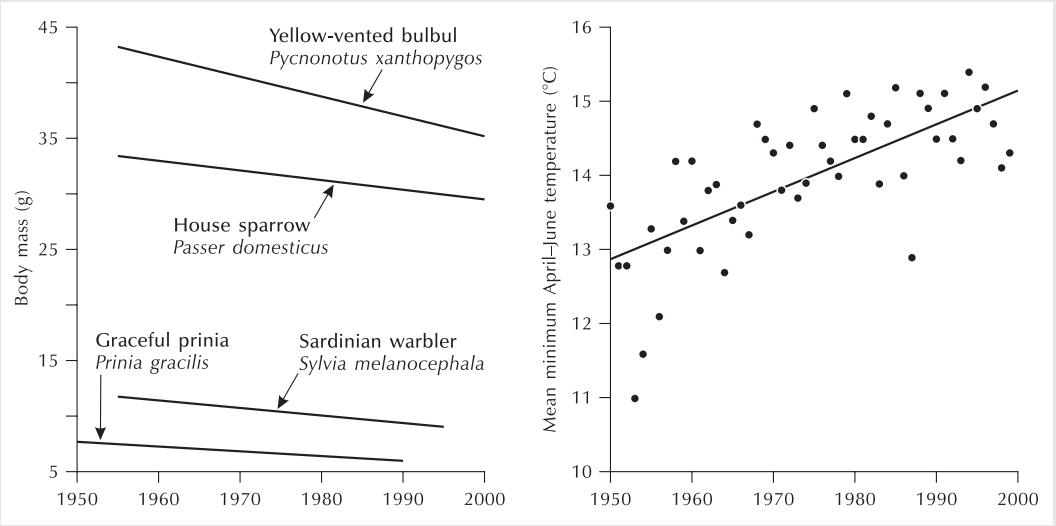


Figure 2.2 Body-mass decline in several resident bird species in Israel since 1950.
Source: Adapted from Yom-Tov (2001)

available influences body size in large mammals. Proposed by R. Dale Guthrie (1984) and Valerius Geist (1987), the basis of this rule is that animals in areas of high seasonal food abundance can achieve a greater proportion of their potential annual growth and therefore develop bigger bodies.

Differentiation into ecological races provides a third kind of intraspecies variation pattern. Many forms of ecological race include altitudinal races in montane species, host races in insects, and seasonal races in organisms with demarcated breeding systems.

SPECIES BIRTH: SPECIATION

Processes of speciation

Speciation is the production of new species. It demands mechanisms for bringing new species into existence and mechanisms for maintaining them and building them into cohesive units of interbreeding individuals that maintain some degree of isolation and individuality. There is a threshold at which *microevolution* (evolution through adaptation within species) becomes *macroevolution* (evolution of species and higher taxa). Once this threshold is traversed, evolutionary processes act to uphold the species' integrity and fine-tune the new species to its niche: gene flow may smother variation; unusual genotypes may be less fertile, or may be eliminated by the environment, or may be looked over by would-be mates. Various mechanisms may thrust a population through the *speciation threshold*, each being associated with a different model of speciation: allopatric speciation, peripatric speciation,

stasipatric speciation, and sympatric speciation (Figure 2.3). Evolutionary biologists argue over the effectiveness of each type of speciation (e.g. Losos and Glor 2003).

Allopatric speciation

Geographical isolation reduces or stops gene flow, severing genetic connections between once interbreeding members of a continuous population. If isolated for long enough, the two daughter populations will probably evolve into different species. This mechanism is the basis of the classic model of **allopatric** ('other place' or geographically separate) **speciation**, as propounded by Ernst Mayr (1942) who called it *geographical speciation* and saw geographical subdivision as its driving force. Mayr recognized three kinds of allopatric speciation: strict allopatry without a population bottleneck; strict allopatry with a population bottleneck; and extinction of intermediate populations in a chain of races:

1 *Strict allopatry without a population bottleneck* occurs in three stages. First, the original population extends its range into new and unoccupied territory. Second, a geographical barrier, such as a mountain range, forms and splits the population into two; and genetic modification affects the separate populations to the extent that if they come back into contact, genetic isolating mechanisms will prevent their reproducing. The model includes cases where species extend their range by traversing an existing barrier, as when birds cross the sea to colonize an island.

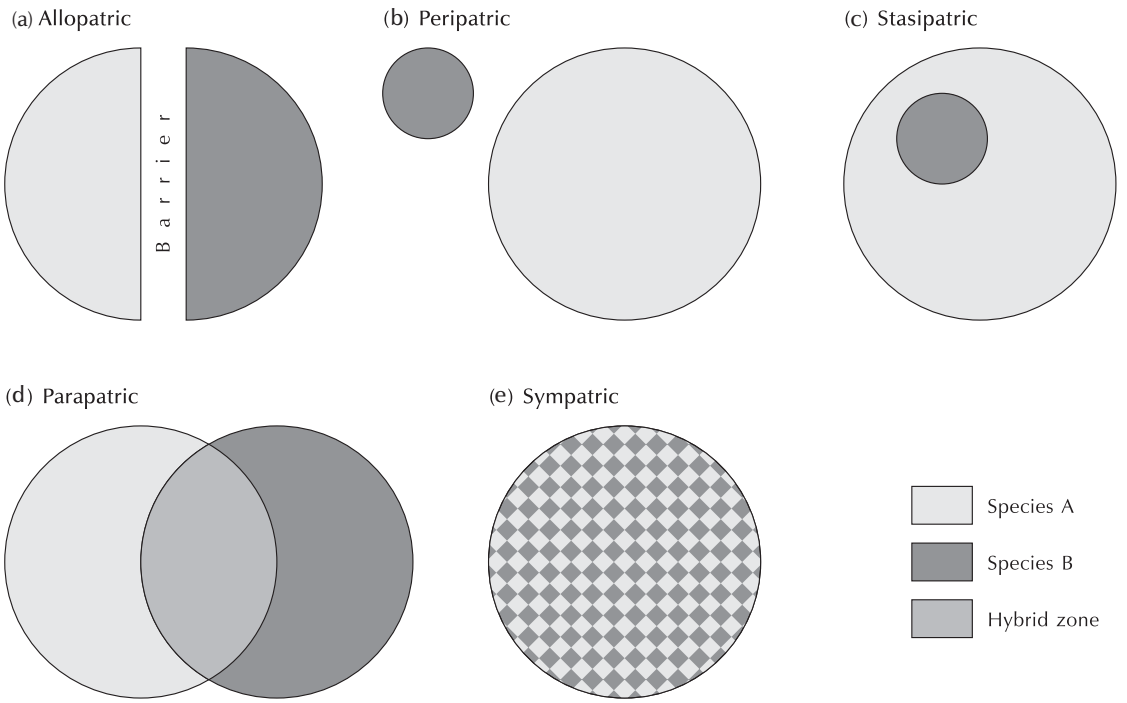


Figure 2.3 Types of speciation: allopatric speciation, peripatric speciation, stasipatric speciation, parapatric, and sympatric speciation.

2 In *strict allopatry with a population bottleneck*, a small band of founder individuals (or even a single gravid female) colonizes a new area. Mayr argued that the founding population would carry but a small sample of the alleles present in the parent population, and the colony would have to squeeze though a genetic bottleneck; he called this the *founder effect*. However, from the 1970s onwards, it became apparent that the bottleneck might not be as tight as originally supposed, even with just a few founding intervals (White 1978, 109). Some 10 to 100 founding colonists may carry a substantial portion of the alleles present in the parent population. Even a single gravid female colonist, providing she is heterozygous at 10–15 per cent of her gene loci and providing an equally heterozygous male (largely of different alleles) fertilized her, could carry a considerable amount of **genetic variability**. Admittedly, a newly founded colony will initially be more homozygous and less polymorphic than the parent population. If the colony should survive, gene mutation should restore the level of polymorphism, probably with new alleles with new allele frequencies.
3 Two species of European gull – the herring gull (*Larus argentatus*) and the lesser black-backed gull (*L. fuscus*) – exemplify the extinction of intermediate populations in a *chain of species* (Figure 2.4). These species are the terminal members of a chain of *Larus* subspecies encircling the north temperate region. Members of the chain change gradually but the end members occur sympatrically in northwest Europe without **hybridization**.

Vicariance events and dispersal-cum-founder events may drive allopatric speciation (Figure 2.5). Two species of North American pines illustrate vicariance speciation. Western North American lodgepole pine (*Pinus contorta*) and eastern North American jack pine (*P. banksiana*) evolved from a common ancestral population that the advancing Laurentide Ice Sheet split asunder some 500,000 years ago. The colonization of the Galápagos **archipelago** from South America by an ancestor of the present giant tortoises (*Geochelone* spp.), probably something like its nearest living relative the Chaco tortoise (*G. chilensis*), is an example of a dispersal and founder event. The giant tortoises are all the same species on the Galápagos – *G. elephantopus* – but there are 11 living subspecies and 4 extinct subspecies. Five subspecies occur on Isabela and the rest occur on different islands.

Once populations are isolated and become differentiated, they may then stay isolated and never come into contact again. In this case, it may take a long time for reproductive isolation to occur and it is difficult to know when the two populations are different species. If contact is re-established, perhaps because the barrier disappears, then three things may happen: (1) the populations may not interbreed, or fail to produce fertile offspring, reproductive isolation is complete, and speciation has occurred. This happened with the kaka and kea in New Zealand. (2) The two populations may hybridize, but the hybrids may be less fit than the offspring of the within-populations matings. *Reinforcement* is the process that selects within-population matings, and *isolating mechanisms* are traits that evolve to augment reproductive isolation. (3) The two populations may interbreed comprehensively, producing fertile fit hybrids, so that the populations merge and the differentiation is diluted, and eventually disappears.

Peripatric speciation

This is a subset of allopatric speciation. **Peripatric speciation** occurs in populations on the edge (perimeter) of a species range that become isolated and evolve divergently to create new species. A small founding population is often involved. An excellent example of this is the paradise kingfishers (*Tanysiptera*) of New Guinea (Mayr 1942). The main species, the common paradise kingfisher (*T. galatea galatea*), lives on the

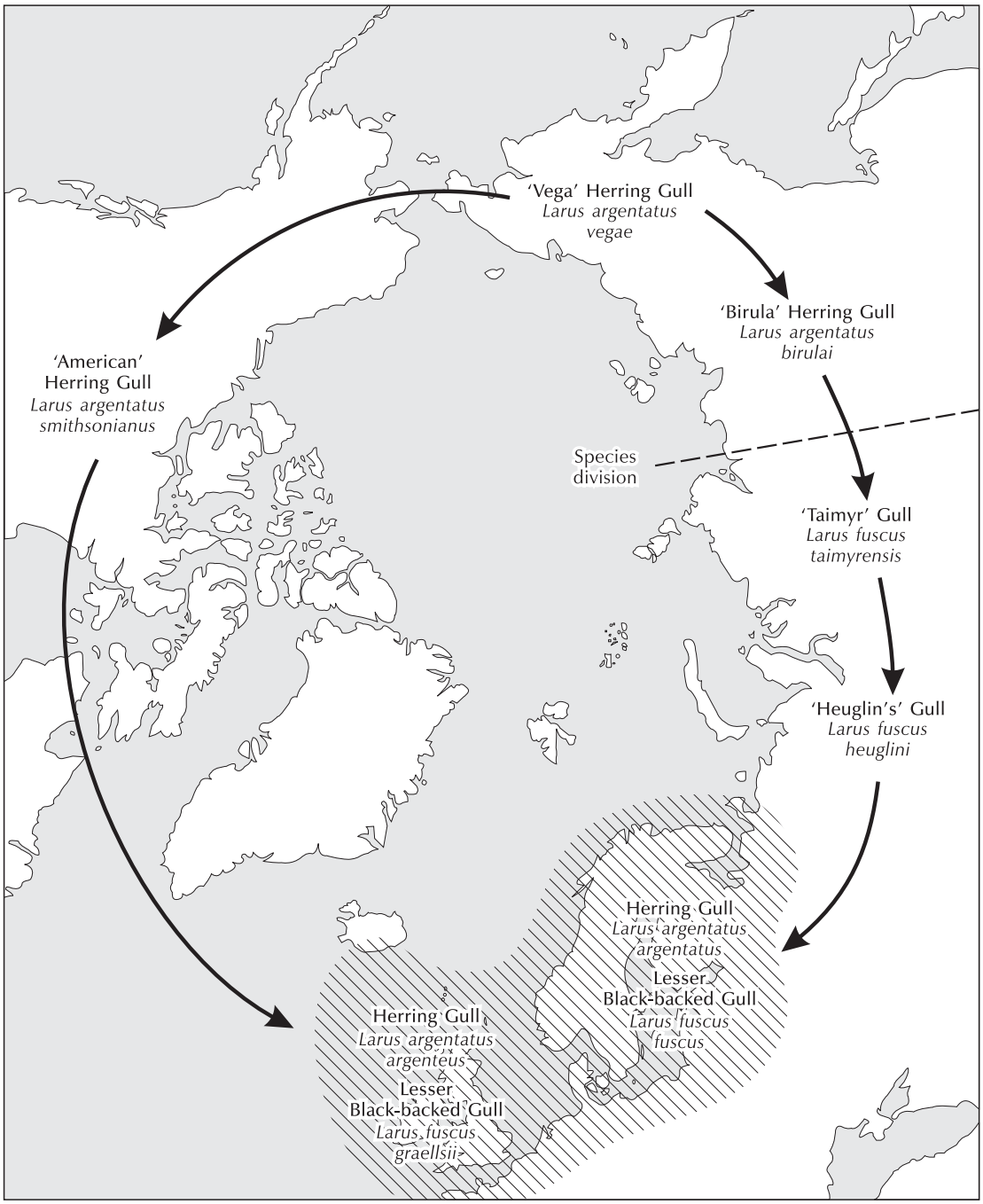


Figure 2.4 Chain or ring of species of gull around the North Pole. Change between subspecies is gradual but the two end members live sympatrically in northwest Europe.

main island. The surrounding coastal areas and islands house a legion of morphologically distinct races of the paradise kingfishers (Figure 2.6).

Parapatric speciation

Parapatric (abutting) **speciation** is the outcome of divergent evolution in two populations living geographically next to each other. The divergence occurs because local adaptations create genetic gradients or clines. Once established, a cline may reduce gene flow, especially if the species is a poor disperser, and selection tends to weed out hybrids and increasingly pure types that wander and find themselves at the wrong end of the cline. A true hybrid zone may develop, which in some cases, once reproductive isolation is effective, will disappear to leave two adjacent species. An example is the main species of the house mouse in Europe (Hunt and Selander 1973). A zone of hybridization separates the light-bellied eastern house mouse (*Mus musculus*) of eastern Europe and the

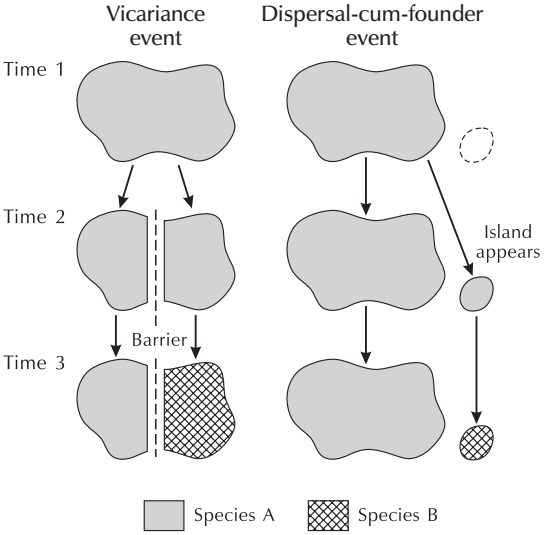


Figure 2.5 The chief drivers of allopatric speciation: vicariance events and dispersal-cum-founder events.
Source: Adapted from Brown and Lomolino (1998)

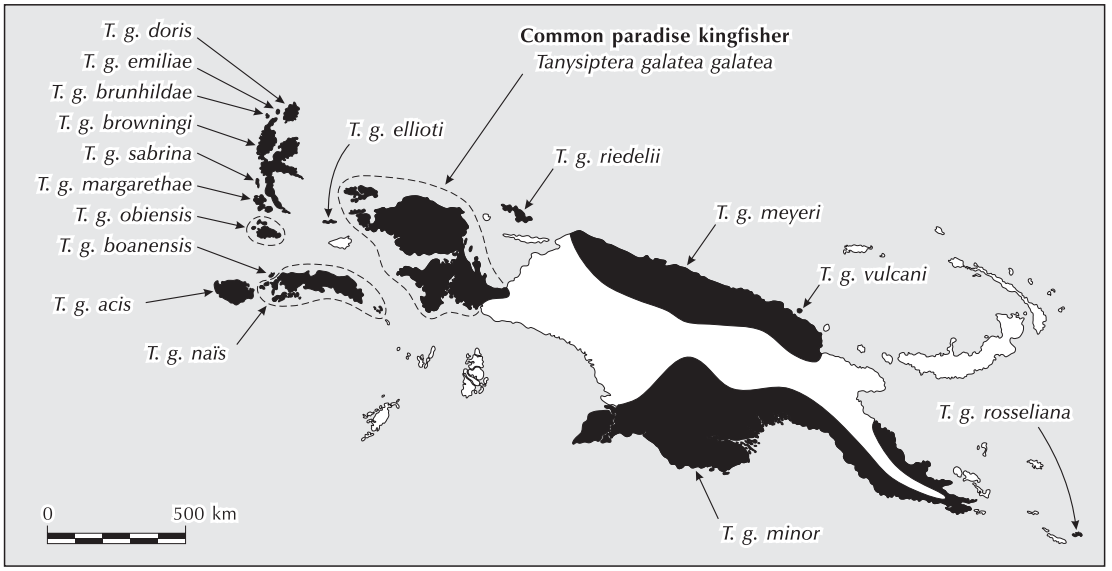


Figure 2.6 Races of paradise kingfishers (*Tanysiptera*) on New Guinea and surrounding islands.
Source: Partly adapted from Mayr (1942)

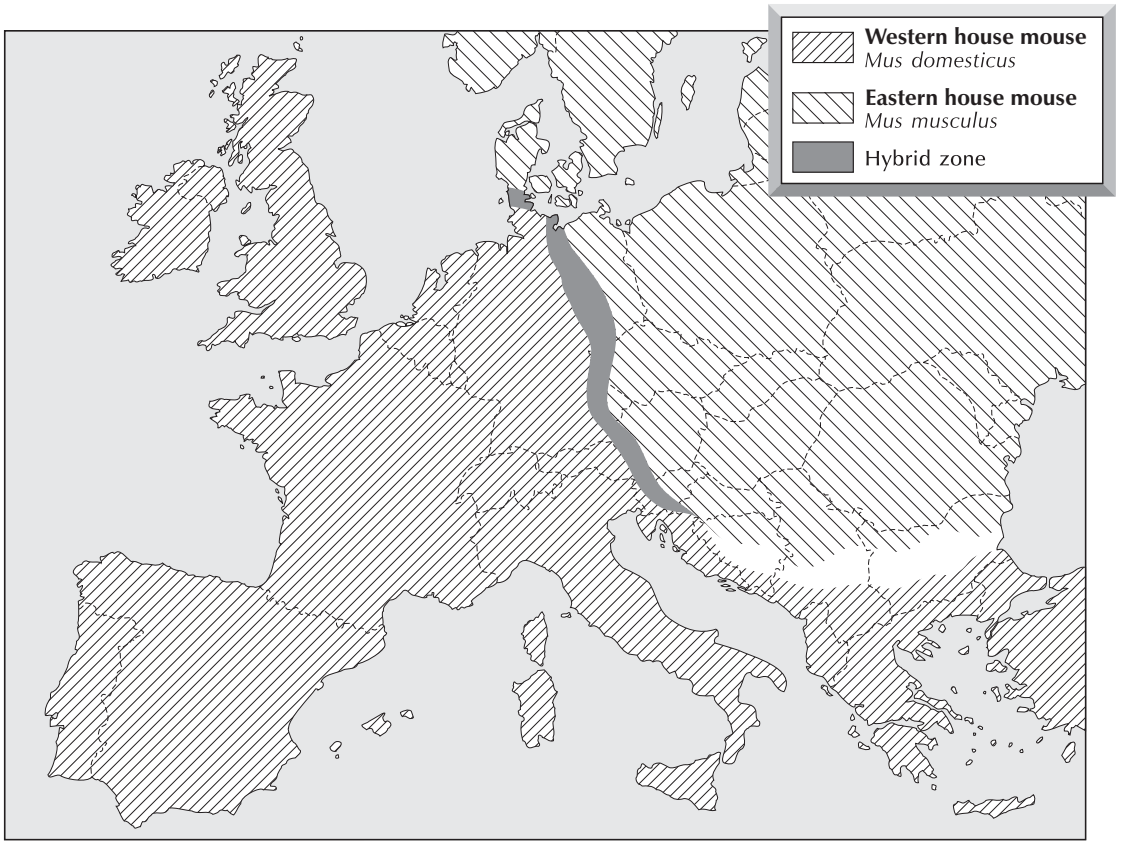


Figure 2.7 The distribution of the light-bellied eastern house mouse (*M. musculus*) of eastern Europe and the dark-bellied western house mouse (*M. domesticus*) of western Europe (which some authorities treat as a subspecies of *M. musculus*) and the zone of hybridization between them.

Source: Adapted from distribution maps in Mitchell-Jones *et al.* (1999)

dark-bellied western house mouse (*M. domesticus*) of western Europe (Figure 2.7).

Sympatric speciation

Sympatric speciation occurs within a single geographical area and the new species overlap – there is no spatial separation of the parent population. Separate genotypes evolve and persist while in contact with each other. Once deemed rather uncommon, new studies suggest that parapatric and sympatric speciation may be a potent process of evolution (e.g. Via 2001).

Several processes appear to contribute to sympatric speciation (p. 14). Disruptive selection favours extreme phenotypes and eliminates intermediate ones. Once established, natural selection encourages reproductive isolation through *habitat selection* or *positive assertive mating* (different phenotypes choose to mate with their own kind). Habitat selection in insects may have favoured sympatric speciation and account for much of the large diversity of that group. *Competitive selection*, a variant of disruptive selection, favours phenotypes within a species that avoid intense competition and clears out intermediate types.

Two irises that grow in the southern USA appear to result from sympatric speciation. The giant blue iris (*Iris giganticaerulea*) grows in damp meadows, while its close relative, the copper iris (*I. fulva*), grows in drier riverbanks. The two species hybridize, but the hybrids are not as successful in growing on either the dry or very wet sites as the pure forms and usually perish. So, the inability of hybrids to survive restricts the gene flow between the two species.

Stasipatric speciation

Stasipatric speciation occurs within a species range owing to chromosomal changes. Chromosomal changes occur through: (1) a change in chromosome numbers, or (2) a rearrangement of genetic material on a chromosome (an inversion) or a transferral of some genetic material to another chromosome (a translocation). *Polyploidy* doubles or more the normal chromosome component, and **polyploids** are often larger and more productive than their progenitors. Polyploidy is rare in animals but appears to be a major source of sympatric speciation in plants: 43 per cent of dicotyledon species and 58 per cent of monocotyledon species are polyploids. Stasipatric speciation seems to have occurred in some western house mouse (*M. domesticus*) populations (see p. 22). In Europe, the normal karyotype for the species contains 20 sets of chromosomes. Specimens with 13 sets of chromosomes were first discovered in southeast Switzerland in the Valle di Poschiavo. At first, these were classed as a new species and designated *M. poschiavinus*, the tobacco mouse. Later, specimens from other alpine areas of Switzerland and Italy (as well as from northern Africa and South America) also had non-standard karyotypes. Surprisingly, all the populations showed no morphological or genetic differences other than differences in their karyotypes and all belonged to *M. domesticus*.

Subterranean mole rats of the *Spalax ehrenbergi* complex living in Israel provide an outstanding example of a species' overall adaptive response to climate (Nevo 1986). These mole rat populations comprise four morphologically identical incipient chromosomal species (with **diploid** chromosome numbers 2n = 52, 54, 58, and 60). The four chromosomal species appear to be evolving and undergoing ecological separation in different climatic regions: the cool and humid Galilee Mountains (2n = 52), the cool and drier Golan Heights (2n = 54), the warm and humid central Mediterranean part of Israel (2n = 58), and the warm and dry area of Samaria, Judea, and the northern Negev (2n = 60). All the species are adapted to a subterranean ecotype: they are little cylinders with short limbs and no external tail, ears, or eyes. Their size varies according to heat load, presumably so that there is only a small risk of overheating under different climates: large individuals live in the Golan Heights; smaller ones in the northern Negev. The colour of the mole rats' pelage ranges from dark on the heavier black and red soils in the north, to light on the lighter soils in the south. The smaller body size and paler pelage colour associated mainly with 2n = 60 helps to mitigate against the heavy heat load in the hot steppe regions approaching the Negev desert. The mole rats show several adaptations at the physiological level. **Basal metabolic rates** decrease progressively towards the desert. This minimizes water expenditure and the chances of overheating. More generally, the combined physiological variation in basal metabolic rates, non-shivering heat generation, body-temperature regulation, and heart and respiratory rates, appears to be adaptive at both the mesoclimatic and microclimatic levels, and both between and within species, so contributing to the optimal use of energy. Ecologically, territory size correlates negatively, and population numbers correlate positively, with productivity and resource availability. Behaviourally, activity patterns and habitat selection appear to optimize energy balance, and differential swimming ability appears to overcome winter flooding, all paralleling the climatic origins of the different species. In

summary, the incipient species are reproductively isolated to varying degrees, representing different adaptive systems that can be viewed genetically, physiologically, ecologically, and behaviourally. All are adapted to climate, defined by humidity and temperature regimes, and ecological speciation is correlated with the southward increase in aridity stress.

Lineages and clades

Several terms pertain to the study of species in the past (Figure 2.8). A *lineage* is single line of descent. One speaks of the human lineage and the reptilian lineage. **Extinction** is the termination of a lineage and marks the end of the line – a lineage that failed to survive to the present. Extinction is the eventual fate of all species, as discussed later in this chapter. In the fossil record, *speciation* is the branching of lineages. In other words, it marks the point where a single line of descent splits into two lines that diverge from their common ancestor. It occurs when a part of a population becomes reproductively isolated from the remaining populations of the established species by any of the mechanisms mentioned in the previous section. It is well nigh impossible to reconstruct the isolating mechanisms involved in fossil populations, although evidence may sometimes exist for geographical isolation.

Fossil assemblages traced through time reveal clades. A **clade** is a cluster of lineages produced by repeated branching (speciation) from a single lineage. The branching process that generates clades is *cladogenesis*. The clade Elephantinae comprises two extinct genera – *Primelephas* and *Mammuthus* – and two living genera – *Elephas* (modern Asian elephants) and *Loxodonta* (modern African elephants). Evidence from mtDNA suggests that *Elephas*, *Loxondonta*, and *Mammuthus* started to differentiate in the Late **Miocene epoch** around 5.6–7.0 million years ago. This supports fossil

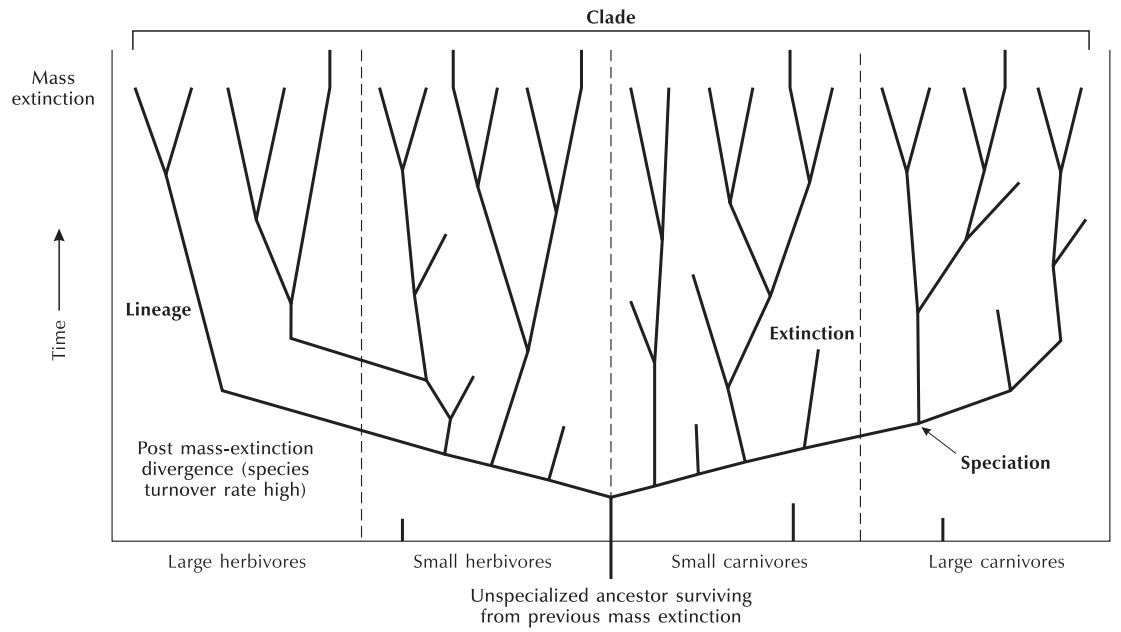


Figure 2.8 Lineage, speciation, extinction, and clade explained.

finds since 1980: the oldest known *Loxodonta* specimen comes from Baringo, Kenya, and Nkondo-Kaiso, Uganda, between 7.3 and 5.4 million years ago; and the oldest known *Elephas* comes from Lothagam, Kenya, about 6–7 million years ago (Tassy and Debruyne 2001).

Evolution

The fossil record permits the inference of evolutionary changes in organisms. Evolution that generates new species to create a clade or a group of clades is *cladogenesis* or *phylogenetic evolution*. Phylogeny is the origin of the branches and the 'trees of life' and encompasses the relationships between all groups of organisms as seen in the genealogical links between ancestors and descendants.

Phylogenetic evolution requires an answer to a difficult question – how do species relate to each other? *Cladistics* is a method of biological classification that attempts to find phylogenetic relationships by constructing branching diagrams based on shared derived characters (synapomorphies). Willi Henning (1966), a German entomologist, laid down its basic principles. Henning defined relationships using branching diagrams, which he saw as evolutionary trees. He contended that only shared derived characters (*synapomorphies*) betray a close common ancestry, and shared primitive characters (*symplesiomorphies*), inherited from a remote common ancestor, are irrelevant or misleading when seeking phylogenetic relationships. In addition, he recognized characters unique to any one group (*autapomorphies*). To illustrate these ideas, consider Figure 2.9, which represents the phylogenetic relationships of the New World monkeys. The vertical bars show synapomorphies. For instance, bimanual locomotion is a derived character shared by the woolly monkey, woolly spider monkey, and spider monkey. The three shades of circles show autapomorphies, that is, characters unique to a group. Nocturnality is an autapomorphy of the owl monkey, and tool use an autapomorphy of the capuchin.

Hennig set his ideas in an evolutionary framework – his branching diagrams are *evolutionary trees* with an implicit time dimension and with forks marking the splitting of ancestral species. The diagram of the New World monkey relationships (Figure 2.9) may be seen in this way. However, it is possible to look at branching diagrams in a more general way that has no evolutionary connotations. They can be seen as *cladograms* with no timescale and the nodes simply imply shared characters (synapomorphies). The differences between evolutionary trees and cladograms may appear minor, but they are hugely important (Patterson 1982). A cladogram is a summary the pattern of character distributions among taxa, in which the nodes are shared characters and the lines are immaterial, the relationships being expressible as a Venn diagram (Figure 2.10). An evolutionary tree is a summary of pattern plus a summary of the historical process of descent with modification (evolution) that created the pattern of characters, in which the nodes are real (if not also identifiable) ancestors, the forks are speciation events, and the lines are lineages of descent by modification.

Phylogenetic evolution contrasts with *phyletic evolution* (*anagenesis*, *chronospeciation*), in which an established species slowly changes into another species within the same lineage. The new species produced in this way go by a variety of names: *chronospecies*, *palaeospecies*, and *evolutionary species*. The recognition of chronospecies is arbitrary and subjective: it is assumed that, in Europe, *Mammuthus primigenius* evolved by phyletic evolution from *M. armeniacus*, which evolved by phyletic evolution from *M. meridionalis*, but it is somewhat arbitrary where the dividing lines between the chronospecies are placed. When a chronospecies changes into a new form, *pseudoextinction* (sometimes called *phyletic extinction*) occurs. Thus *M. meridionalis* became pseudoextinct when it evolved into *M. armeniacus*.

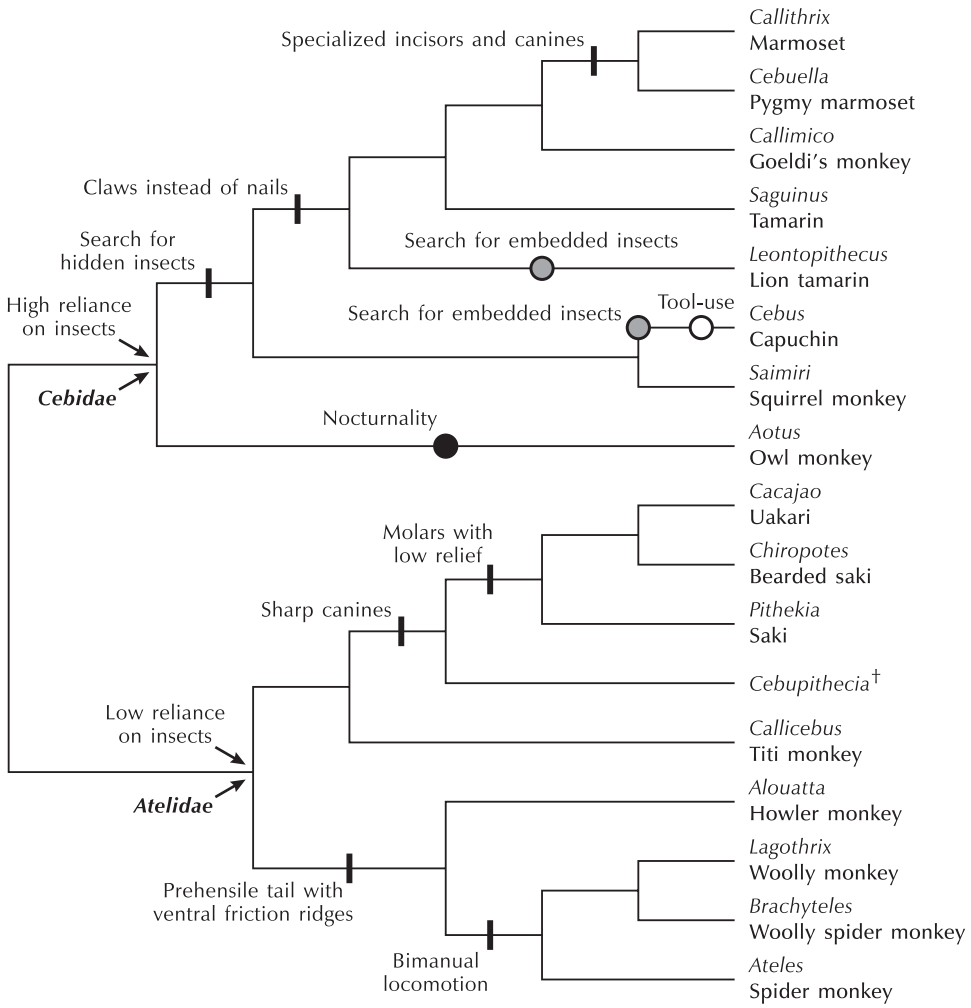
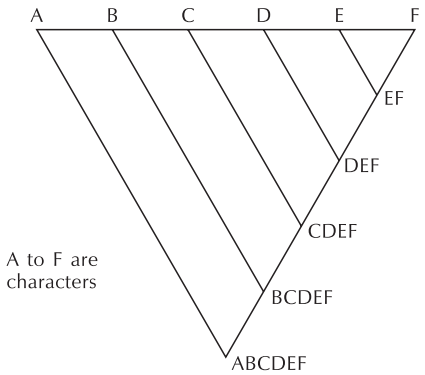


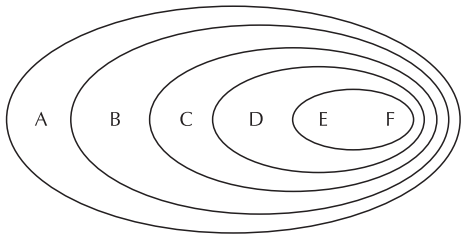
Figure 2.9 Phylogenetic relationships in the New World monkeys.
Source: Adapted from Horovitz and Meyer (1997)
† extinct

Evolution works through adaptation, a process in which natural selection shapes a character for current use. Occasionally, a *key innovation* is thrown up that permits species to exploit a lifestyle novel to that taxon or, sometimes, new to any form of life. Such key innovations may help to trigger **adaptive radiation** (see p. 29). Innovations may be brand new or they can be exaptations. *Exaptations* are characters acquired from ancestors that are co-opted for a new use. An example is the blue-tailed gliding lizard (*Holaspis guentheri*) from tropical Africa that has a flattened head, which allows it to hunt and hide in narrow crevices beneath bark. The flattened head also allows it to glide from tree to tree. The head flattening was originally an

(a) Cladogram



(b) Venn diagram



(c) Written form

(A (B (C (D (E F)))))

Figure 2.10 Relationships between hypothetical species expressed as (a) a cladogram, (b) a Venn diagram, and (c) in written form. All species share characters A to F.

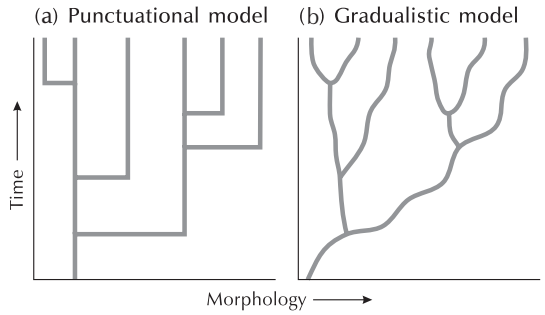


Figure 2.11 Punctuational and gradualistic macroevolution.

adaptation to crevice use and was later co-opted for gliding (an exaptation) (Arnold 1994).

A big debate surrounds the question of evolutionary patterns shown by clades and groups of clades. Two extreme cases arise: (1) all evolution is concentrated in speciation (the branching of lineages) and (2) all evolution takes place within lineages (Figure 2.11). The first case leads to the *punctuational model* of evolution, with most major evolutionary transitions occurring at speciation events. The second cases give rise to the *gradualistic model* of evolution, with most evolution occurring as phyletic change and rapid divergent speciation playing a minor role.

SPECIES GROWTH: DIVERSIFICATION

Ecological diversification

This is the fate of nearly all newly formed species. Species are similar to each other after a speciation event, but are likely to diverge when exposed to different environments with different selective pressures. The biogeographical equivalent of the competitive exclusion principle (p. 192) states that species within similar niches have non-overlapping geographical distributions, whereas species that coexist in the same area and habitat tend to use significantly different resources. A striking example of this is *sibling* or *cryptic species* that are genetically distinct but very close in ecology and morphology. Sibling species commonly display abutting, but non-overlapping (parapatric) **geographical ranges**, numerous examples coming from animals and plants. Several species of pocket gophers (of the genera *Thomomys* and *Geomys*) have ranges that come into contact in North America but do not overlap. Where species ranges do overlap, then there are normally big differences in resource use achieved through slight differences in niches (seen in form, physiology, and behaviour) that evolve through character displacement (p. 198).

Adaptive radiation

Adaptive radiation is the diversification of species to fill a wide variety of ecological niches, or the 'rise of a diversity of ecological roles and attendant adaptations in different species within a lineage' (Givnish and Sytsma 1997, xiii). It is one the most important processes bridging ecology and evolution. It occurs when a single ancestor species diverges, through recurring speciation, to create many kinds of descendant species that become or remain sympatric. These species tend to diverge to avoid interspecific competition. Even when allopatric species are generated, some divergence still occurs as the allopatric species adapt to different environments.

Examples of adaptive radiation are legion. Darwin's finches (Geospizinae) on the Galápagos Islands are a famous example (Figure 2.12). A single ancestor, possibly the blue-black grassquit

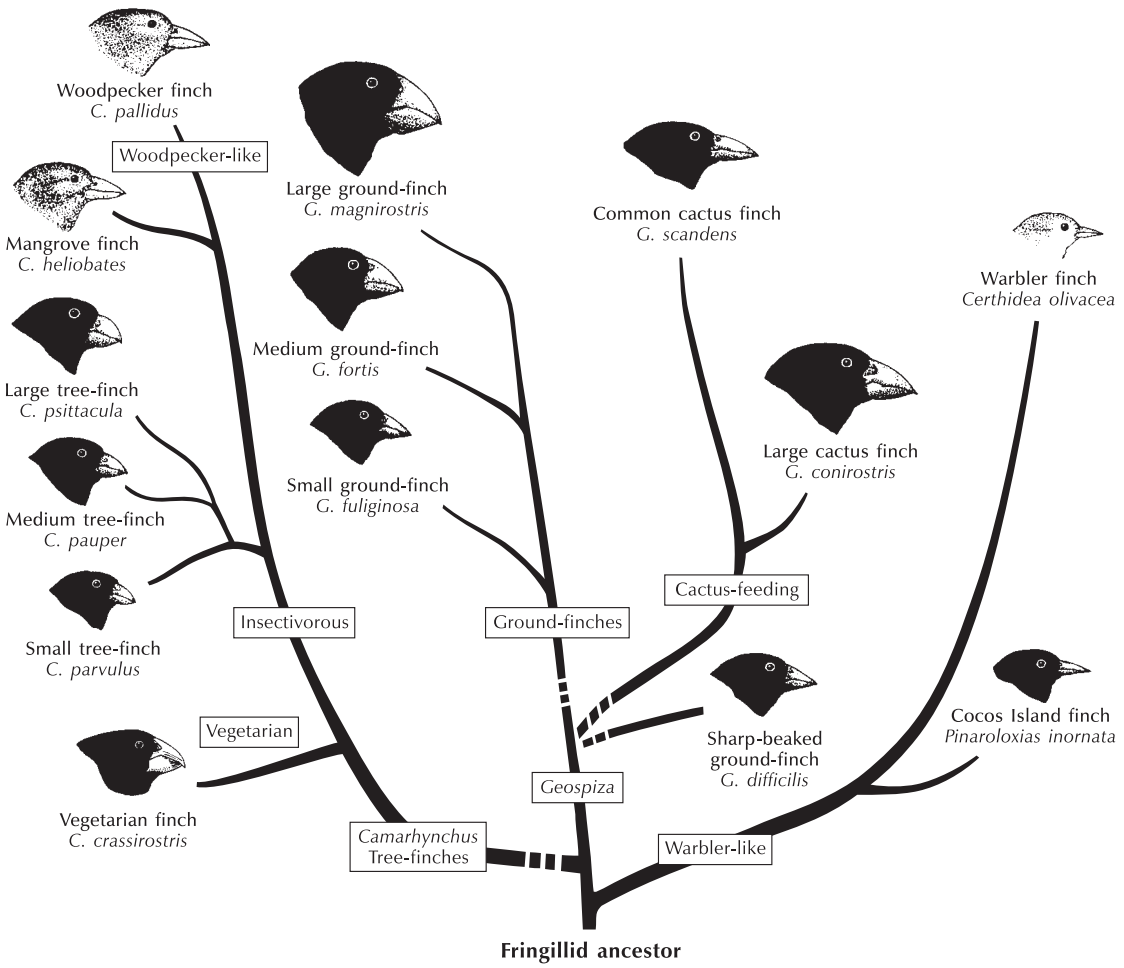


Figure 2.12 Adaptive radiation seen as beak size and shape in Darwin's finches.
Sources: Adapted from Grant (1986) and Lack (1947)