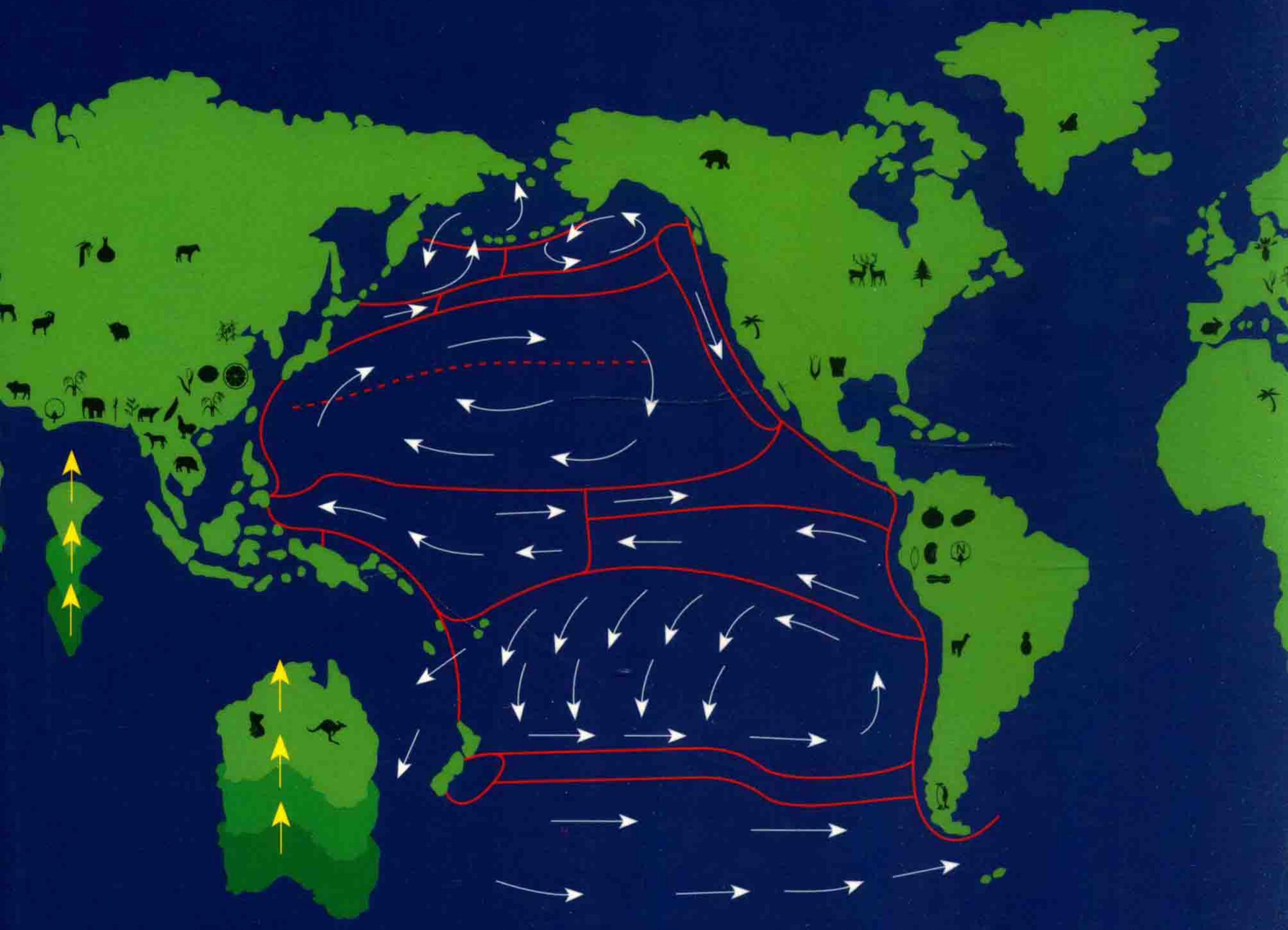
Biogeography

An ecological and evolutionary approach

SIXTH EDITION

C. BARRY COX & PETER D. MOORE



Biogeography

an ecological and evolutionary approach

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Contents

CHAPTER 1: *Introduction to biogeography*

There is one thing that we all have in common; we all share the same planet. For all of us this is home. For this reason, and also because rising human population and declining resources are placing the earth under greater strain, we are now looking to the scientists who study the earth and its living creatures to advise us how best to manage the planet to ensure its future, and with it our own.

Among the sciences involved in this difficult but vital task is biogeography, the study of living things in space and time. Biogeographers seek to answer such basic questions as why are there so many living things? Why are they distributed in the way that they are? Have they always occupied their current distribution patterns? Is the present activity of human beings affecting these patterns and if so, what are the prospects for the future?

One of the most impressive features of the living world is the sheer diversity of organisms it contains, and one of the main problems facing a biogeographer is how to explain this diversity, and also the reasons for the varying patterns of occurrence of different species over the surface of the planet. Why, for example, is there more than one species of seagull? And why do different species of gull have different patterns of distribution, some being widespread and others very local? Why are there so many different types of grass growing in the same field, all apparently doing precisely the same job? Why are there more species of butterfly in Austria than in Norway? It is the task of the biogeographer not only to answer such specific questions, but also to seek general rules that can account for many such observations, and which will provide a general framework of understanding that can subsequently be used for predictions about the consequences of tampering with the natural world.

One of the world's foremost experts on biological diversity, Edward O. Wilson of Harvard University [1], has claimed that the diversity of life on earth was greater at the time of the origin of the human species than it had ever been before in the course of the earth's history. The arrival and cultural development of our species has evidently had, and continues to have, a profound impact on the world's biogeography, modifying species' ranges and bringing some to extinction. From the point of view of biological diversity (the subject of Chapter 2), the evolution of humankind was something of a catastrophe, and it would be quite unrealistic to attempt any synthesis of biogeography without taking the human impact into account. Very few species escape the effects of human activity in some aspect of their ecology and distribution. For this reason our species will play an important role in this book, not only in terms of our influence on other species of plant and animal, but also because we too are one species among many, perhaps as many as 30 million other species, and we obey essentially the same rules as the others. The more we can understand about the Hawaiian goose, the oak tree and the dodo, the more we shall appreciate our own position in the order of things.

Because it faces such wide-ranging questions, biogeography must draw upon an extensive range of other disciplines. Explaining biodiversity, for example, involves the understanding of climate patterns over the face of the earth, and the way in which the productivity of photosynthetic plants differs with climate and latitude. We must also understand what makes particular habitats desirable to animals and plants; why locations of particular soil chemistry, or moisture levels, or temperature range, or spatial structure, should be especially attractive. Hence, climatology, geology, soil science, physiology,

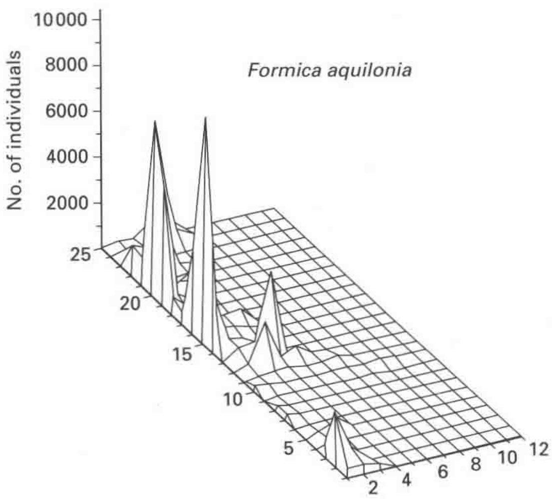

Fig. 1.1 The abundance of two ant species caught in a grid of pitfall traps in the boreal coniferous forest of southern Finland. The numbers on the grid refer to 5-m intervals of trap spacing, so the entire grid is 125 × 60 m, with 300 traps. The two ant species can be seen to exclude one another spatially. Data from Niemela *et al.* [2].

ecology and behavioural sciences must all be invoked to answer such questions.

But the answers to this kind of question are very dependent on the spatial scale at which we approach them. Two species of ant, for example, may share the same continent, even the same area of woodland, but they are unlikely to share the same nest space. When we examine their spatial patterns at a scale of square metres rather than square kilometres, the two species may never be found together. Biogeography concerns itself with all levels of scale, as will be discussed in Chapter 3.

Let us look at an example of the effects of scale at a local level. In a very detailed examination of the small-scale biogeography of an area of boreal coniferous forest in southern Finland, some researchers from the University of Helsinki [2] set a grid of traps, sunk into the ground ('pitfall traps'), in which they gathered those hapless, ground-dwelling insects and invertebrates that happened to stumble into them. In this way they could detect exactly where in their study area these small, rambling creatures were foraging. They laid out a grid measuring 125 m on one axis and 60 m on the other, with traps placed at 5-m intervals, 300 in total. They recorded all the ants and the ground beetles (carabids) that fell into these traps, pooling their records for an entire summer, and some of their results are shown in Figs 1.1 and 1.2.

In Fig. 1.1 we see the pattern of abundance of two ant species that occupy the area. They have very sharp peaks in abundance relating to their nest sites, with *Formica aquilonia* having a number of nest centres and *F. lugubris* having just one main nest. Although the two species are found together when examined at a sample size of hundreds of square metres, they are quite strictly separated when we look in greater detail. Competitive interaction between the colonies is evidently leading to strict spatial segregation.

In Fig. 1.2 we have displayed the results for some of the ground beetles occupying the same area. The first two shown, *Leistus terminatus* (a) and *Cychrus caraboides* (b) have quite similar patterns of distribution. Both are commoner towards the bottom right part of the sample plot, and when we compare their patterns with those of the two ants it is tempting to conclude that they avoid areas where the ants are densest. Such negative relationships between

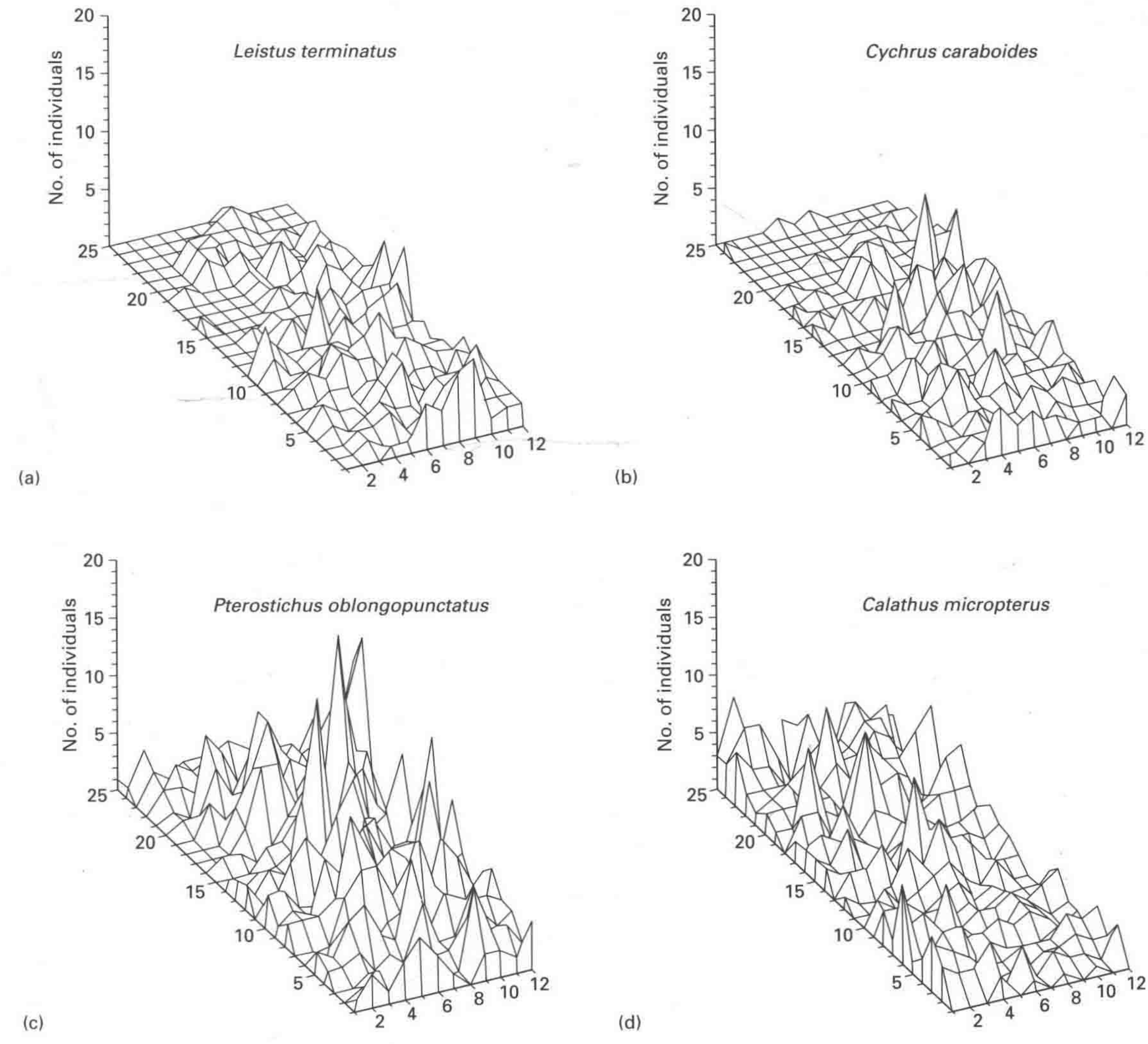

Fig. 1.2 The trap grid shown in Fig. 1.1 but with the records for four species of ground beetle. The species shown in (a), (b) and (c) decline in abundance in the area rich in ants, whereas species (d) is more abundant in the ant regions. It probably preys upon ants. Data from Niemela *et al.* [2].

ground beetles and ants are often the case in nature. The fact that the two species of beetle are found together suggests that they have no such scruples about sharing space with one another, so they probably do not consume one another, nor, in all likelihood, do they compete for food, otherwise one or the other would probably be excluded by the better competitor. *L. terminatus* preys upon tiny animals (the springtails and mites) that feed in leaf litter on decomposing plant material. *C. caraboides*, on the other hand, is a specialist feeder that preys on molluscs—slugs and snails. So the two have quite different food requirements and can cohabit in an area without any negative interactions.

A third beetle, *Pterostichus oblongopunctatus* (c), is more abundant than either of the other two, and also overlaps with them in its range. It is a generalized predator so, although it may well compete with the other two, it has a wider range of food resources to choose from, allowing it to coexist with them. As in the case of the former two species, however, it also seems to avoid the ants. The fourth beetle, *Calathus micropterus* (d), has a rather different pattern. Unlike species a, b and c, it appears to be more abundant at the top end of the sample area. At present it is not known precisely what this species eats, but many of its close relations prey upon ants, so this is the most likely explanation for its abundance in the ant-infested parts of the study area.

This example of a detailed local study of animals reveals how complex the patterns of organisms can be when examined at this scale. This set of data can mainly be explained by feeding relationships, but similar patterns of other organisms often relate to such factors as temperature differences, light microclimates, humidity, etc., or some animals may be active at different times of day (or night), so adding a time dimension to biogeography even at this scale of study.

The interaction between organisms (eating one another, competing with one another for food, etc.) is clearly very important in biogeography, and may determine whether or not different species can be found together in communities (a concept examined further in Chapter 4). These interactions can become so complicated that an alteration in the abundance of one animal or plant can often have very unexpected consequences for the rest of the community, and it is extremely important that ecologists and biogeographers should be aware of these relationships if they are to be capable of predicting the outcome of environmental change, or of the adoption of certain land-use or management practices.

A particularly intricate example of the potential complexity of these interactions has been described by Clive Jones of the Institute of Ecosystem Studies at Millbrook, New York, and his colleagues [3]. They examined the relationship between oak trees, mice, moths, deer, ticks and people in the eastern United States and found a complicated web of interactions.

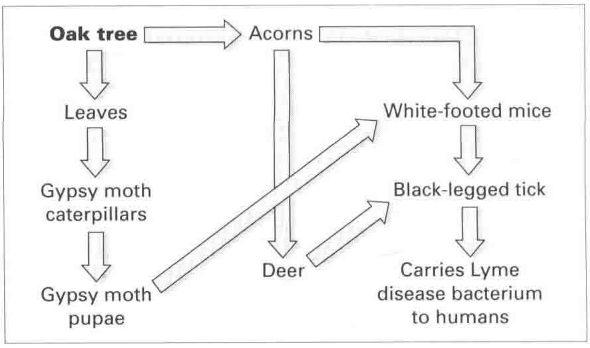

Fig. 1.3 A complex web of interactions relating acorn production by oak trees to mouse and deer abundance and hence the risks of humans contracting Lyme disease from the black-legged tick. Changes in the crop of acorns can affect all other parts of the system.

Oak trees produce a crop of acorns during the autumn ('masting'), but in some years the crop is much bigger than others. Roughly every 2–5 years comes a good 'mast year'. The acorns are eaten by white-footed mice, but mast years also attract deer, which spend 40% of their time in the oak woods in these mast years compared with only 5% in non-mast years. A third consumer of oak is the gypsy moth, whose caterpillars feed on oak leaves and may, in plague years, when its population rises to unusually high levels, defoliate the trees to such an extent that the acorn yield is reduced. Just to add to the complexity, mice eat the soil-dwelling pupae of gypsy moths and can control moth populations in that way (Fig. 1.3).

White-footed mice carry a resident spirochaete bacterium called *Borrelia burgdorferi* and they pass it on to parasitic ticks that initially feed on the mice and then move on to deer, thus spreading the disease. A tick carrying this bacterium may also attach itself to a human wanderer in the woods, who will then contract Lyme disease. The web is given a dynamic element by the occurrence of mast years, because when acorns are abundant mice populations rise, deer spend more time in the woods and the ticks consequently have a particularly successful time. This was demonstrated experimentally by the researchers by artificially supplying extra acorns and then watching the mouse population expand, the deer move into the oak forest, and the ticks proliferate. In a separate experiment, the mice population was artificially reduced by trapping, and the gypsy moth population then rose with the potential to reduce first oak foliage and, subsequently, acorn supply to the system. In the natural situation, tick abundance, and hence risk to human health, is greatest two seasons after a mast year because of the time taken to build up a population of mice. It is therefore possible to predict health risks to wood-walking humans on the basis of an understanding of this complex set of interrelationships within a forest community. This is just one example that has been particularly well studied, but biogeographers need to be aware of the existence of such complexities in the systems they study.

The time factor is also clearly important in biogeography and, like space, it needs to be considered at different scales. Bats and barn swallows hunt flying insects at different times in the diurnal cycle, so they can coexist. Fluctuations in climate from year to year may influence masting in oak trees and plagues in herbivorous insects. Climate changes over centuries may have an impact on the distribution patterns of organisms at a greater spatial scale, and even more so when millenia pass and major climatic cycles are involved. Millenia develop into millions of years, and the process of evolution becomes ever more important in the consideration of biogeographers.

The study of fossils has long made it clear that the diversity of living organisms on earth has not always been the same. New species have arisen and old species have become extinct. Appreciating biodiversity therefore involves understanding the mechanisms by which new species arise, and it is an essential part of the biogeographer's work to study the source of novelty, the means by which new species can be generated. We worry, very reasonably, about the current rate of extinction on the planet. But how fast can we expect new species to evolve to replace them? How fast can species adapt to cope with the modifications which humankind is making to the climate and the living conditions of the world? This aspect of biogeography will be considered in Chapter 5.

We can observe species changing in their form, behaviour and physiology even as conditions change in the present day, and we can see from the fossil record how they have become modified and adjusted to changing conditions in the past. Take the woodrat, for example. There is now strong evidence that this animal has changed in its body size according to climatic conditions in the geologically recent past. There is an observation in biogeography, often referred to as Bergmann's Rule, that animals in warm climates tend to be smaller than their close relatives in cold climates. Large animals, it seems, are more liable to be killed by very high temperature than small ones because of their failure to lose body heat fast enough. Small animals, on the other hand, may radiate too much heat under cold conditions when they cannot afford to do so. In the case of the North American bushy-tailed woodrat, it has proved possible, on the basis of fossil records, to study changes in size over the past 14 000 years. The study, by Felisa Smith of the University of New Mexico and her colleagues [4], does not actually use fossils of the animals themselves, however, but is based on their faecal pellets found in waste heaps, or middens, that the woodrats have deposited at various times in the past.

It is easy to demonstrate experimentally that large woodrats produce large faecal pellets, and a precise relationship has been established between the two, so that we can determine from a population of faeces just how large the woodrats were that produced them. Figure 1.4 shows the results from fossil middens of different ages dated by radiocarbon techniques (see Chapter 10). At 14 000 years ago, the Ice Age was just terminating, and evidence from the middens shows that large faecal pellets were being deposited, presumably by large woodrats. Pellet size falls off to a minimum around 6000 years ago when the climate is thought to have been warmer than at present, and then rises again as the climate cooled. In this way biogeographers can follow microevolutionary developments, in this case in animal size, and can test such hypotheses as

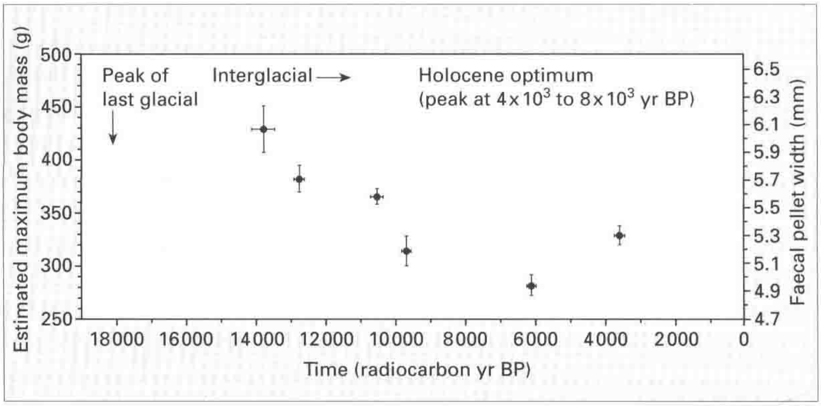

Fig. 1.4 Graph showing the changing size of the woodrat in North America over the past 14 000 years. The body size of the animals has been estimated on the basis of fossil faecal pellets deposited in middens at various times in the past. Data from Smith *et al.* [4] with permission.

Bergmann's Rule. Here the hypothesis seems to hold up well.

The fossil record also enables us to look into the past and observe the changing distribution patterns of organisms during the passage of time. Our current experience of nature represents just one point in a constantly changing mosaic of animals and plants that are responding to an endless sequence of environmental and climatic change. Biogeography therefore can never be a static discipline; it must always be aware of, and take into account, the modifications that organisms are making to their distribution patterns as conditions favour them or render their life more difficult in a particular region. When conditions change too fast to permit genetic adjustment and evolution, populations, species and even whole groups of species may pass into extinction. Extinction is not an exception to the norm in evolutionary terms, it is a regular feature of the constantly changing pattern of life. Novel forms prosper at the expense of old-fashioned, poorly adapted groups, which consequently disappear.

Understanding biogeography must therefore involve the time perspective, not simply encompassing the decades or centuries by which we measure human history, but covering the millions of years, or even hundreds of millions of years, during which whole groups of plants and animals may rise to prominence and progress to extinction. Within this time scale even the continents have not remained static. Convection forces in the earth's mantle have carried land masses over the surface of the globe, resulting in the fragmentation of supercontinents and occasional continental collisions of great violence, and these movements have had significant repercussions in the distribution patterns of plants and animals. Land-mass fragmentation and movement have led to related groups of organisms being widely separated, and collisions have brought together unexpected groups of quite alien origins. Therefore, no account of biogeography can be complete without a consideration of these long-term geological movements. Chapters 6 and 7 provide an overview of these processes and their impact on biogeographical thinking.

Biogeography, then, is concerned with the analysis and explanation of patterns of distribution, and with the understanding of changes in distribution that have taken place in the past and are taking place today. It concerns itself with what units of life, or 'taxa', are found where, and what are the geographical definitions of that 'where': is it North America, or land between 2000 and 5000 m altitude, or land between 17°N and 23°S latitude? Once the pattern has been established, two sets of questions arise. There is the internal question: how is the organism adapted to the conditions of life in this area? This in turn generates the opposite, externally directed questions: why does the organism not exist in adjacent areas, and what are the factors (biological or environmental) that prevent it from doing so? These factors can be thought of as forming a barrier that prevents the further spread of the organism. Islands are a particularly distinct example of such isolation (Chapter 13).

Sometimes the organism's pattern of distribution is discontinuous or 'disjunct', the species being found in several separate areas. Two different explanations may be offered for this. Firstly, the organism may originally have been present in only one area, and been able to cross the intervening barrier regions to colonize the other areas. Alternatively, the barrier may have appeared later, dividing a once-continuous, simple pattern of distribution into separate units. These two explanations are, respectively, termed 'dispersalist' and 'vicariance' (see Chapter 8).

In the case of living organisms, all of these questions can be investigated in detail, examining all aspects of their ecology and adaptations to life and dispersal. These investigations can extend over several decades and analyse, for example, the effects of a series of dry summers that may cause local ecological changes affecting the distribution of individual species over a few thousand square metres. The wide range of phenomena available for analysis under these circumstances has led to this type of biogeographical investigation becoming known as 'ecological biogeography'.

Biogeographical changes that have taken place over the last few centuries are well documented, and their causes are often relatively well understood. They are also restricted to observable, much-studied phenomena, such as climatic change or minor geographical changes in the distribution of land and water. Furthermore, they affected taxa that are comparatively well defined and that can be studied as living organisms. The distributional and climatic data available from cores of lake or deep-sea sediments, or analysis of tree rings, together with radiocarbon dating, have made it possible to extend this ecological biogeography back many thousands of years before the present, which often provides a rich supply of information and explanation for modern distribution patterns of species.

At a slightly greater remove in time, the biogeographical changes of the Ice Ages can be seen as extrapolations of ecological biogeography. They affected entire biota rather than merely individual species, involved changes in the patterns of distribution and biological zonation over several thousand kilometres, and were caused by systematic changes in the earth's orbit or by minor changes in sea levels or currents. Nevertheless, the processes, phenomena and organisms involved are similar in nature to those of today, and the evidence is comparatively abundant.

Understanding even longer-term changes and more ancient patterns of life requires a different approach. These changes took place tens or even hundreds of millions of year, ago, and involved the splitting, moving or fusion of whole continents, raising new mountain chains or causing the appearance or disappearance of major oceans and seas, with accompanying changes in climate. The biota affected were transported over thousands of kilometres and include groups that are now wholly extinct and are therefore not available for ecological study. The data involved in such long-term historical biogeography are therefore restricted and incomplete, and cannot be approached merely as an extrapolation of the methods used to analyse the phenomena of the more recent past. The different types of data, and the methods that have been proposed for analysing them, form the basis of Chapter 8.

The last two million years of the earth's history, the subject of Chapters 9 and 10, have been of particular significance to biogeography for a number of reasons. Within this time period the climate, which has been getting colder for the last 70 million years or so, has become particularly unstable and has entered a series of oscillations in which there is an alternate expansion and contraction of the earth's ice caps. Within these episodes, new ice caps expanded and contracted over the continental land masses of North America and Eurasia. This glacial/interglacial series of cycles has had a particularly important part to play in affecting the current distribution patterns of plants and animals, not only in the direct effect of changing climates, but also in the alterations these have caused to global sea levels. Rising and falling sea level has periodically resulted in the formation and disruption of land bridges linking islands to land masses and even continents to one another, as in the case of eastern Asia and Alaska. Modern distribution patterns of organisms often provide examples of stranded populations and islands from which a particular organism is unexpectedly absent. Since most of the species that now exist have been present for much of the last million years or so, it has proved easier to reconstruct the detailed ecological changes of this ultimate stage in the earth's geological history than has been possible for earlier stages.

One reason why this recent period has a particular interest for the biogeographer is the fact that our own species has evolved and come to prominence within these last two million years or so. The emergence of *Homo sapiens* from the position of a social ape of the savannas to its present position of global dominance has an important message for modern humans. The picture that develops from a biogeographical approach to human development is one of clever manipulation of the environment, deflecting energy from other parts of the natural food webs into the support of one species. This is not unknown in the animal kingdom (some ants herd greenflies and grow fungi in gardens), but in the case of our own species the development of agriculture and, later, industrial processes have created a new set of conditions in the modern world that we find hard to comprehend. It is difficult to grasp that one species has achieved such an impact that it now affects the massive geochemical and climatic processes of the entire planet.

We have also created new barriers for organisms by fragmenting habitats into ever more isolated units. An example of this shrinkage and fragmentation is provided by the rain forests of Madagascar (Fig. 1.5), a habitat that is rich in species that are limited to this particular region (endemic) [5]. This type of development has raised many questions for conservationists, such as how species will cope when reduced to small populations, genetically out of touch with other populations of the same species [6]. Are such populations more liable to extinction?

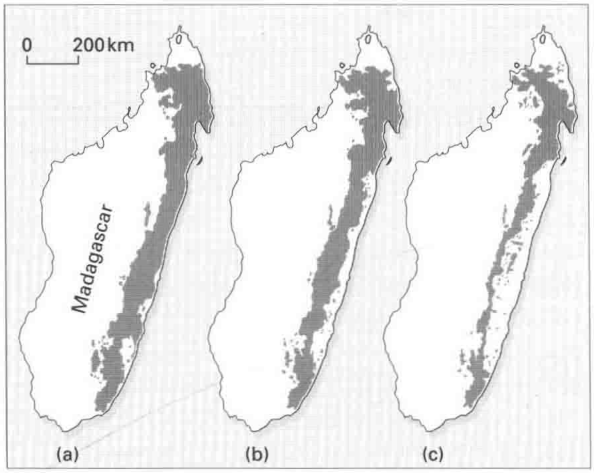

Fig. 1.5 Distribution of rainforest in the island of Madagascar off East Africa. (a) The probable original extent of the forest; (b) the situation in 1950; and (c) in 1985. Data from Green & Sussman [5]. Copyright 1990 by the AAAS.

Will they evolve separately from one another and form new races? How will they respond if the earth's climate changes? Will they be able to migrate to suitable new areas, or will they be stranded in their isolation and simply decline into extinction?

The study of biogeography has particular relevance to some of these problems, because an understanding of the processes and the factors that have influenced the successes and the failures of other species may well assist in the amelioration of our present condition. Biogeography will hopefully develop, in time, into a predictive science, as explained in Chapter 11.

All of the preceding chapters have dealt with different aspects of biogeographical distribution where they are most obvious and have been more thoroughly investigated and understood—on the continental land masses. The oceans have long seemed to be both inexhaustible in their contribution to our food supply, and so vast as to be beyond our powers to change or damage. But it is now clear that our increasing abilities to gather food from the oceans have affected adversely the populations of marine organisms on which we rely to replenish those