The History of Biogeography

This introductory chapter begins with an explanation of why the study of the history of a subject is important, and highlights some of the important lessons that students may gain from it. This is followed by a review of the ways in which each of the areas of research in biogeography developed from its foundation to today.

Lessons from the Past

One of the best reasons for studying history is to learn from it; otherwise, it becomes merely a catalogue of achievement. So, for example, it is often valuable to think about why and when a particular advance was made. Was it the result of personal courage in confronting the current orthodoxy of religion or science? Was it the result of the mere accumulation of data, or was it allowed by the development of new techniques in the field of research, or in a neighbouring field, or by a new intellectual permissiveness? But the study of history also gives us the opportunity to learn other lessons – and the first of these is humility. We must be wary, when considering the ideas of earlier workers, not to fall into the trap of arrogantly dismissing them as in some way inferior to ourselves, simply because they did not perceive the 'truths' that we now see so clearly. In studying their ideas and suggestions, one soon realizes that their intellect was no less penetrating than those that we can see at work today. However, compared to the scientists of today, they were handicapped by lack of knowledge and by living in a world in which, explicitly or implicitly, it was difficult or impossible to ask some questions.

Firstly, less was known and understood. When Isaac Newton, who originated the theory of gravitational attraction, wrote that he had 'stood on the shoulders of giants', he was acknowledging that in his own work he was building upon that of generations of earlier thinkers, and was taking their ideas and perceptions as the foundations of his own. So, the further we go back in time, the more we see intellects that had to start afresh, with a page that was either blank or contained little in the way of earlier ideas or syntheses.

Secondly, we must be very aware that, for every generation, the range of theories that might be suggested was (and is!) limited by what contemporary society or science views as permissible or respectable. Attitudes towards the ideas of evolution (see Chapter 6) and continental drift (this chapter) are good examples of such inhibitions in the 19th and 20th centuries. The history of scientific debate is rarely, if ever, one of dispassionate, unemotional evaluation of new ideas, particularly if they conflict with one's own. Scientists, like all men and women, are the product of their upbringing and experience, affected by their political and religious beliefs (or disbeliefs), by their position in society, by their own previous judgments and publicly expressed opinions and by their ambitions – just as 'there's no business like show business', there's no interest like self-interest! Very good examples of this, discussed further in this chapter, are the use of the concept of evolution by the rising middle-class scientists of England as a weapon against the 19th-century establishment and, at the individual level, the history of Leon Croizat.

In our survey of the history of biogeography, we shall therefore see people who, like most of us, grew up accepting the intellectual and religious ideas current in their time, but who also had the curiosity to ask questions of the world of nature around them. Sometimes the only answers that they could find contradicted or challenged the current ideas, and it was only natural then to seek ways to circumvent the problem. Could these ideas be reinterpreted to avoid the problem, was there any way, any loophole, to avoid a complete and direct challenge and rejection of what everyone else seemed to accept?

So, to begin with, the reactions of any scientist confronted with results or ideas that conflict with current dogma are either to reject them ('Something must have gone wrong with his methods, or with my methods') or to view them as an exception ('Well, that's interesting, but it's not mainstream'). Sometimes, however, these difficulties and 'exceptions' start to become too numerous or varied, or they begin to arise from so many different parts of science as to suggest that something must be wrong. The scientist may then realize that the only way around it is to start again, starting from a completely different set of assumptions, and to see where that leads. Such a course is not easy, for it involves the tearing-up of everything that one has previously assumed and completely reworking the data. And, of course, the older you get, the more difficult it is to do so, for you have spent a longer time using the older ideas and publishing research that explicitly or implicitly accepts them. That is why, all too often, older workers take the lead in rejecting new ideas, for they see them as attacking their own status as senior, respected figures. Sometimes these workers also refuse to accept and use new approaches long after these have been thoroughly validated and widely used by their younger colleagues (see attitudes towards plate tectonic theory in Chapter 5). Another problem is that the debate can become polarized, with the supporters of two contrasting ideas being concerned merely to try to prove that the opponents' ideas are false, badly constructed and untrue (see dispersal vs. vicariance, discussed later in this chapter, and punctuated vs. gradual evolution, discussed in Chapter 6). Neither side then stops to consider whether it is perhaps possible that both of the apparently conflicting ideas are true, and that the debate should

instead be about when, under what circumstances and to what extent one idea is valid, and when the other is instead the more important. Also, too often, scientists have rejected the suggestions of another worker, not because the suggestions were in themselves unacceptable, but because the scientists rejected *other* opinions of that same author (e.g. Cuvier vs. Lamarck on evolution; see further in this chapter).

All of this is particularly true of biogeography, for it provides the additional difficulty of being placed at the meeting point of two quite different parts of science – biological sciences and earth sciences. This has had two interesting results. The first is that, from time to time, lack of progress in one area has held back the other. For example, the assumption of stable, unchanging geography made it impossible to understand past patterns of distribution. Nonetheless, it was a reasonable assumption until the acceptance of **plate tectonics** (continental drift) provided a vista of past geographies that had gradually changed through time. But it is also interesting to note that this major change in the basic approaches of earth sciences came in two stages.

To begin with, the problem was clearly posed and a possible solution was given. This was in 1912, when the German meteorologist Alfred Wegener (see later in this chapter) pointed out that many patterns in both geological and biological phenomena did not conform to modern geography, but that these difficulties disappeared if it was assumed that the continents had once lain adjacent to one another and had gradually separated by a process that he called **continental drift**. This explanation did not convince the majority of workers in either field, largely because of the lack of any known mechanism that could cause continents to move horizontally or to fragment. The fact that Wegener himself was not a geologist but an atmosphere physicist did not help him to persuade others of the plausibility of his views, for it was only too easy for geologists (who, of course, 'knew best') to dismiss him as a meddling amateur. Most biologists, faced with the uncertainties of the fossil record, did not care to take on the assembled geologists.

The second stage came only in the 1960s, when geological data from the structure of the seafloor and from the magnetized particles found in rocks (see Chapter 5) not only provided unequivocal

evidence for continental movements, but also suggested a mechanism for them. Only then did geologists accept this new view of world history (known as plate tectonics; see Chapter 5), and only then could biogeographers confidently use the resulting coherent and consistent series of palaeogeographical maps to explain the changing patterns of life on the moving continents. Such a theory, based on a great variety of independent lines of evidence, is known as a **paradigm**, and the theory of plate tectonics is the central paradigm of the earth sciences.

The moral of this story is, perhaps, that it is both understandable and reasonable for workers in one field (here, biologists) to wait until specialists in another field (here, geology) have been convinced by new ideas before they feel confident in using them to solve their own problems. This, in turn, leads to the second topic that results from the position of biogeography between biology and geology. That is the temptation for workers in one field, frustrated by lack of progress in some aspect of their own work, to accept, uncritically and without proper understanding, new ideas in the other field that seem to provide a solution [1]. One must be particularly wary of new theories that are directed at explaining merely one difficulty in the currently accepted interpretations. This is because such suggestions sometimes simultaneously destroy the rest of the framework, without satisfactorily explaining the vast majority of the phenomena that were covered by that framework. For example, in the second half of the 20th century, some geologists suggested that the Earth had expanded, or that there had once been a separate 'Pacifica' continent between Asia and North America. Some biological biogeographers welcomed these ideas as the solution to some detailed problems of the distribution of terrestrial vertebrates, even though they were not supported by geological data and had not been accepted by geologists.

All of this has important lessons for us today, for it would be naive to believe that the assumptions and methods used in biogeography today are in some way the final and 'correct' ones that will never be rejected or modified. Similarly, every student should realize that those who teach science today have, of course, been trained to accept the current picture of the subject and may find it difficult to accept changes in its methodology. The price that we pay for gaining experience with age is an increasing conviction of the correctness of our own methods and assumptions! (On the other hand, it is interesting to note that whereas in the physical sciences major new discoveries are usually made by intuitive leaps early in the scientist's career, those in the biological sciences are more often made only later, after the accumulation of data and knowledge.) It is also worth noting that erroneous assumptions are far more dangerous than false reasoning because the assumptions are usually unstated, and therefore far more difficult to identify and correct. So, the past with its false assumptions and erroneous theories is merely a distant mirror of today, warning us in our turn not to be too sure of our current ideas. Sometimes the limitations and problems of a new technique only become apparent gradually, some time after it has been introduced.

But, of course, those of us who carry out research and publish our ideas in books such as this also have a responsibility to use their experience and judgment in trying to choose between conflicting ideas, showing which we prefer and why. For example, in this book the author who wrote this chapter (Barry Cox) has criticized the methodology of a school of (mainly) New Zealand panbiogeographers (see later in this chapter). But, of course, he could be wrong, and interested students should read around the subject and come to their own conclusions. After all, the purpose of learning a subject at this level is for students to develop their own critical faculties, not merely to acquire attitudes and opinions. Even over the past 50 years, we have seen attitudes to a new idea, the Theory of Island Biogeography, change quite considerably (see later in this chapter, and Chapter 7). How many of the explanations and assumptions in this book will still seem valid in 50 years' time? But that is also one of the pleasures of being part of science, and of having to try continually to adapt to new ideas, rather than merely being part of some ancient monolith of long-accepted 'truths'.

Ecological versus Historical Biogeography, and Plants versus Animals

The most fundamental split in biogeography is that between the ecological and historical aspects of the subject. **Ecological biogeography** is

concerned with the following types of questions. Why is a species confined to its present range in space? What enables it to live where it does, and what prevents it from expanding into other areas? What roles do soil, climate, latitude, topography and interactions with other organisms play in limiting its distribution? How do we account for the replacement of one species by another as one moves up a mountain or seashore, or from one environment to another? Why are there more species in the tropics than in cooler environments? Why are there more endemic species in environment X than in environment Y? What controls the diversity of organisms that is found in any particular region? Ecological biogeography is, therefore, concerned with short-term periods of time, at a smaller scale; with local, within-habitat or intracontinental questions; and primarily with species or subspecies of living animals or plants. (Subspecies, species, genus (plural: genera), family, order and phylum (plural: phyla) are progressively larger units of biological classification. Each is known as a **taxon** (plural: taxa).)

Historical biogeography, on the other hand, is concerned with different questions. How did the taxon come to be confined to its present range in space? When did that pattern of distribution come to have its present boundaries, and how have geological or climatic events shaped that distribution? What are the species' closest relatives, and where are they found? What is the history of the group, and where did earlier members of the group live? Why are the animals and plants of large, isolated regions, such as Australia or Madagascar, so distinctive? Why are some closely related species confined to the same region, but in other cases they are widely separated? Historical biogeography is, therefore, concerned with long-term, evolutionary periods of time; with larger, often sometimes global areas; and often with taxa above the level of the species and with taxa that may now be extinct.

Because of the different nature of plants and of animals, the ways in which their ecological and historical biogeography have been investigated and understood have differed in the two groups. Plants are static, and their form and growth are therefore much more closely conditioned by their environmental, ecological conditions than are those of animals. It is also far easier to collect and preserve plants than animals, and to note the conditions of

soil and climate in which they live. But the fossil remains of plants are less common than those of animals, and they are also far more difficult to interpret, for several reasons. There are many more flowering plants than there are mammals – some 450 living families and 17 000 genera of plant, compared with 150 living families and 1250 genera of mammal. Furthermore, although the leaves, wood, seeds, fruit and pollen grains of flowering plants may be preserved, they are rarely found so closely associated that one can be sure which leaf belongs with which type of pollen grain, and so on. Finally, the taxonomy of flowering plants is based on the characteristics of their flowers, which are only rarely preserved. In contrast, the fossil bones of mammals are often associated as complete skeletons, which are easy to allocate to their correct family, and which provide a detailed record of the evolution and dispersal of these families within and between the continents through geological time.

For all these reasons, the biogeography of the more distant past was, until recently, largely the preserve of zoologists, whereas plant scientists were far more concerned with ecological biogeography – although studies of fossil pollen from the Ice Ages and postglacial times, which are easy to allocate to existing species, have been fundamental in interpreting the history and ecology of this most recent past (see Chapter 12).

In following the history of biogeography, it would be easy merely to follow a path through time, recounting who discovered what and when. But it is more instructive instead to take each thread of the components of biogeography in turn, to follow the different contributions to its understanding, and on the way to note the lessons to be learned from how the scientists reacted to the problems and ideas of their time.

Biogeography and Creation

Biogeography, as a part of Western science, began in the mid-18th century. At that time, most people accepted the statements in the Bible as the literal truth, that the Earth and all living things that we see today had been created in a single series of events. It was also thought that these events had taken place only a few thousands of

years before, and it was believed that God's actions had always been perfect. It followed that the animals and plants that had been created were perfect, and had not changed (evolved) or become extinct, and that the world itself had always been as we see it today. The history of biogeography between then and the middle of the 20th century is the story of how that limited vision was gradually replaced by the realization that both the living world and the planet that it inhabits are continually changing, driven by two great processes – the biological process of evolution and the geological process of plate tectonics.

So, when the Swedish naturalist Linnaeus in 1735 started to name and describe the animals and plants of the world, he assumed that each belonged to an unchanging species, which had been created by God. But he soon found that there were species whose characteristics were not as constant and unchanging as he had expected. That might puzzle him, but he could only accept it. But there was a further problem, for, according to the Bible, the whole world had once been covered by the waters of the Great Flood. All the animals and plants that we see today must therefore have spread over the world from the point where Noah's Ark had landed, thought to be Mount Ararat in eastern Turkey. Linnaeus ingeniously suggested that the different environments to be found at different altitudes, from tundra to desert, had been colonized in turn by different animals and plants from the Ark as the floodwaters receded, progressively uncovering lower and lower levels of land. Linnaeus recorded in what type of environment each species was found, and so began what we now call ecological biogeography. He also recorded whereabouts in the world each species is found, but he did not synthesize these observations into any account of faunal or floral assemblages of the different continents or regions.

The first person to realize that similar environments, found in different regions of the world, contained different groupings of organisms was the French naturalist Georges Buffon; this important insight has come to be known as **Buffon's Law**. In various editions of his multivolume *Histoire Naturelle* [2], published from 1761 onward, he identified a number of features of world biogeography and suggested possible explanations. He noted that many of the mammals of North America, such as bears, deer, squirrels, hedgehogs and moles, were found also in Eurasia, and he pointed out that they could only have travelled between the two continents, via Alaska, when climates were much warmer than today. He accepted that some animals, such as the mammoths, had become extinct. Buffon also realized that most of the mammals of South America are quite different from those of Africa, even though they live in similar tropical environments. Accepting that all were originally created in the Old World, he suggested that the two continents were at one time adjacent and that the different mammals then sought out whichever area they found most congenial. Only later did the ocean separate the two continents and the two now-different faunas, whereas some other differences might have been due to the action of the climate. Buffon also used the fossil record to reconstruct a history of life that clearly had extended over at least tens of thousands of years. Only the last part had witnessed the presence of human beings, and included earlier periods within which tropical life had covered areas that are now temperate or even subarctic.

Buffon strongly felt that one had to be guided by study of the facts, and this conviction drove him to accept that geography, climate and even the nature of the species were not fixed, but changeable, and to suggest that continents might move laterally and seas encroach upon them. That was a truly courageous and visionary deduction to make in the late 18th century. So Buffon recognized, commented upon and attempted to explain many phenomena that other, later workers either ignored or merely recorded without comment. His observations on the differences between the mammals of the two regions were soon extended to land birds, reptiles, insects and plants.

The Distribution of Life Today

As 18th-century explorers and naturalists revealed more and more of the world, they also extended the horizons of biogeography itself, discovering a greater diversity of organisms. For example, in his second voyage around the world in 1772–1775, the British navigator Captain James Cook took the British botanist Joseph Banks and the German Johann Reinhold Forster, together with his son

Georg Forster, who collected thousands of species of plants, many of them new to science. Forster found that Buffon's Law applied to plants as well as to animals, and also applied to any region of the world that was separated from others by barriers of geography or climate [3]. He also realized that there are what we now call gradients of diversity (see Chapter 4), there being more plant species closer to the equator and progressively fewer as one moves towards the poles, and he made the first observations of island biogeography.

The concepts of ecological biogeography, botanical regions and island biogeography had, then, all been recognized by the end of the 18th century. But it was still generally accepted that there could be little or no change in the nature of each species, or in the pattern of the geography of the world. The early naturalists therefore still struggled to explain how all these different floras had come into existence, widely scattered over the Earth's surface. Perhaps the most plausible explanation was that of the German botanist Karl Willdenow, who in 1792 suggested that, although there had been only one act of creation, it had taken place simultaneously in many places. In each area, the local flora had been able to survive the Flood by retreating to the mountains, from which it was able later to spread downward to recolonize its own part of the world as the floodwaters receded. His book also included a chapter on the history of plants, and he noted that plants' growth habits were related to the conditions of their environment.

Despite the work of these two earlier botanists, the German Alexander von Humboldt is usually recognized as the founder of plant geography, perhaps because he was a far wealthier and more flamboyant figure. But Forster and Willdenow not only preceded Humboldt but also greatly influenced his life. It was Georg Forster who inspired Humboldt to become an explorer, and the slightly older Willdenow introduced him to botany and became his lifelong friend. Humboldt became famous for his 1799–1804 expedition to South America, during which he climbed to over 5800 m (19 000 feet) on the volcano Chimborazo – a world height record that he held for 30 years. He noticed that the plant life on the mountain showed a zonation according to altitude, much like the latitudinal variation that Forster had described. Plants at lower levels are of the tropical type, those of intermediate levels are of the temperate type, and finally arctic types of plant are found at the highest levels. (Humboldt used the term *association* to describe the assemblages of plants that characterized each of these life zones; today, they are more commonly referred to as *formations* or *biomes*; see Chapter 3.) Humboldt believed that the world was divided into a number of natural regions, each with its own distinctive assemblage of animals and plants. He was also the first to insist that biological observations had to include detailed, accurate and precisely recorded data. He published a thorough account of his botanical observations in 1805, as part of a 30-volume series recording his findings in the New World [4].

Another early plant biogeographer was Augustin de Candolle of Geneva who, in 1805 together with Lamarck, published a map showing France divided into five floristic regions with different ecological conditions. Candolle later went on to study the dispersal of plants by water, wind or the actions of animals, pointing out that this would lead to the plants spreading until they encountered barriers of sea, desert or mountains. He was also the first to realize that another limiting factor was the presence of other plants that competed with them. The result of these processes would be the appearance of regions that, even though they might contain a variety of climatic zones and ecological environments, were distinct from one another because they contained plants that were restricted to that area, for which he coined the word **endemic** (see Chapter 2). The distinctions between these regions were thus partly dependent on their histories. Candolle went on to define 20 such regions, of which 18 were continents or parts of continents, and two were island groups [5]. He also noted that some plants had apparently worldwide distributions, that species pairs are to be found in Europe and North America and that some taxa are found in both the north and the south temperate regions (what we now call **bipolar distributions**). Finally, he realized that other plants have strangely 'disjunct' distributions (see Chapter 2) in locations that are widely separated from one another, such as the Proteas of southern Africa and Australia/Tasmania. Candolle also commented on Forster's contributions to island biogeography.

All in all, Candolle made a massive and varied intellectual contribution to the botany of the early

19th century. However, he did not provide any world maps to illustrate these concepts, and most of the maps that botanists published in the later 19th century, and even in the 20th century, continued to be primarily 'vegetation maps' – maps of the relationships of vegetation to temperature and climate. So, even though the Danish botanist Joakim Schouw was the first to classify the world's flora and show the results on maps [6], these were mainly the distribution maps of particular groups of plants, rather than maps of regional floras. Grisebach's more detailed, coloured map of 1866 was similarly a vegetation map. So all of these maps were primarily concerned with ecological biogeography, rather than with systematic studies of the distribution of organisms, which would have demanded an historical explanation. But then, it was only after biologists had become convinced of the reality of evolution that they could start to integrate into their thinking the consequences of a fourth dimension – time.

Evolution – a Flawed and Dangerous Idea!

During the late 18th century, much of the leading work on biological and geological subjects had been carried out in areas of Europe that we now call Germany, but the French Revolution of 1789 led to a flowering of French science. To some extent, this was because the power of the Church, with its conservative influence on the generation and acceptance of new ideas, had been decisively broken. But the new government also carried out a complete reorganization of French science, liberally supported by the state and centred on the new National Museum of Natural History, which became a powerhouse of ideas and debate in Europe. One of those employed in this new museum was Jean-Baptiste Lamarck. As an older worker, he had been brought up to believe that there was some underlying pattern and structure to every aspect of the physical and biological world – a mind-set common among many 18th-century inquirers into the phenomena of nature. It should therefore be possible to recognize a 'scale of beings' in which different groups of organisms could be allocated to 'lower' or 'higher' places according to the level of 'perfection' of their organization – with, of course,

human beings at the apex of the resulting structure! In 1802, Lamarck suggested that the 'lower' organisms might also be found earlier in time and that they might gradually change into the 'higher' forms, due to an 'inherent tendency of life to improve itself' [7]. So there was no need to suggest that fossil organisms were in reality extinct, for it was possible that they had evolved into different and perhaps still-living descendants.

All of this was strenuously opposed by one of the new, young appointees in the museum, the great Georges Cuvier, who founded the science of comparative anatomy. Cuvier used this new branch of science to prove that such great fossil mammals as the mammoths of Europe and North America and the giant ground sloth of South America, as well as many others, belonged to quite different species from those of today and were extinct [8]. But, he believed, his detailed anatomical studies showed that even these creatures had been thoroughly and stably adapted to their environment. Their extinction must therefore have been due to a sudden catastrophic change in their environment. So, to Cuvier, Lamarck's theory of continual transformation was deeply unacceptable, for its suggestion that organisms were flexible and changeable challenged his own conviction that they were, on the contrary, irrevocably adapted to their existing environment. Cuvier was therefore opposed to Lamarck's views because they cast doubt on his belief in extinction (which was, perhaps, understandable). But this unfortunately also led him to reject the whole idea of evolution that Lamarck had championed – so throwing out the baby of evolution with the bathwater of extinction.

It is always very convenient if, in an argument, your opponent's views are championed by someone else of lesser ability. Lamarck's ideas were supported by another worker in the museum, Geoffroy St Hilaire. Over the years 1818–1828, Geoffroy suggested evolutionary homologies and links between such widely different animals as fish and cephalopods (octopus, squid, etc.) [9], but his ideas were ridiculed by other zoologists. Similarly, his supposed evolutionary sequences of fossils placed them in an order that was contradicted by the sequence of the rocks in which they were found. So it was easy for Cuvier to make a devastating attack on Geoffroy, and this had the effect of also discrediting Lamarck and the whole idea of evolution. In England, the

case for evolution was further damaged in 1844, when the Scottish journalist Robert Chambers published a book, *Vestiges of the Natural History of Creation*, which contained astonishingly ignorant ideas. Chambers suggested, for example, that the bony armour of early fossil fishes was comparable to the external skeleton of arthropods (lobsters, crabs, insects, etc.) and that the fish might therefore have evolved from them. The progressively more detailed fossil record that was by then being revealed also gave no hint or indication that the major groups of organisms, traced back in time, converged towards a common, ancient ancestor. The fact that such people as Geoffroy and Chambers supported the idea of evolution unfortunately gave the impression that it was associated with the lunatic fringe of science. And, by now, Lamarck's explanation of evolution as due to an 'inherent tendency' seemed dreadfully old-fashioned.

When the geologist Robert Jameson translated Cuvier's ideas into English in 1813, he added notes suggesting that the most recent of Cuvier's continent-wide catastrophes could be interpreted as the biblical Flood. But Cuvier himself, and other scientists working in post-revolutionary France, accepted that science and religion should not interfere in each other's affairs. Matters were very different in England. There, the Church of England had become closely integrated into the power structure of a still-hierarchical Establishment, and entry to the universities (and so to the professions) was barred to non-Protestants. So both the authorities of the state (monarchy, aristocracy and wealthy landowners) and those of the Church (bishops and comfortable clergy) felt themselves threatened by the new-model social order of France, which they saw as encouraging a rising tide of atheism, republicanism and revolution. For, in the first half of the 19th century, English society was undergoing fundamental changes, fuelled by unemployment resulting from the end of the Napoleonic Wars and by the Industrial Revolution, which was driving people from the land and into overcrowded cities. In this conflict, the new ideas of evolution became a weapon that the rising middle class used in their attempts to gain entry to the universities and access to the professions and financial security. In response, to defend their own positions, the establishment portrayed evolution as atheistic, or even heretical.

Enter Darwin – and Wallace

So, in the early 19th century, evolution was seen as a slightly disreputable idea that also had links with a dangerously anarchic approach to the structure of society. It is therefore not surprising that the young Charles Darwin was cautious, secretive and reluctant to publish his ideas when he began to suspect that the problems he found in trying to interpret the patterns of life could only be explained by invoking evolution. He was the son of a fairly wealthy country doctor, whose father had been an atheist who believed in evolution – so the family was not exactly mainstream. As a student at Cambridge, Darwin had become interested in geology and natural history, and in 1831 he was invited to join the crew of a government ship, *HMS Beagle*, to act as a companion to the captain and also as a naturalist for what became a 6-year voyage to survey the coasts of South America [10]. Several experiences during this long voyage led him to wonder whether the idea of evolution might not, after all, contain some truth.

On the Galápagos Islands in the Pacific Ocean, isolated from South America by 960 km of sea, Darwin noticed that the mockingbirds on three islands were different from one another, suggesting that they had independently become different varieties on each island. He was also told that the giant tortoises of the different islands had differently shaped shells. Darwin also noticed great flocks of finches, with a variety of sizes of beaks, but they all fed together, and he couldn't make up his mind whether there were any different varieties. (Only later, when Darwin's collections were studied back in England by the ornithologist John Gould, was it realized that there were 13 different species of finch in the islands.) All of this suggested that species were not, perhaps, quite as unchanging as was then assumed. Equally disturbing were the fossils that Darwin had found in South America. The sloth, armadillo and guanaco (the wild ancestor of the domesticated llama) were represented by fossils that were larger than the living forms, but were clearly very similar to them. Again, the idea that the living species were descended from the fossil species that had existed in the same part of the world was a straightforward explanation, but one that contradicted the view that each species was a fixed, unchanging product of creation and had no blood relationship with any other species.

As explained, Darwin was not the first to suggest that organisms were related to one another by evolution; the British worker Alfred Russel Wallace was thinking along exactly the same lines. (In fact, Wallace was the first to realize and publish the significant fact that closely related species were often also found close to one another geographically, with the clear implication that the two were linked by an evolutionary process.) In the end, it was the receipt of a letter from Wallace, then working in the East Indies, that stimulated Darwin to finalize and publish his ideas after many years of agonizing over its possible hostile reception by the vociferously antievolutionary sections of British society. (It is interesting to note that, in the case of both workers, it was observation of the patterns of distribution of individual species of animals, i.e. their biogeography, that led them to consider the possibility of evolution.) Their great discovery was to deduce the driving mechanism of evolution – natural selection.

Any pair of animals or plants produces far more offspring than would be needed simply to replace that pair. There must, therefore, be competition for survival among the offspring. Furthermore, these offspring are not identical to one another, but vary slightly in their characteristics. Inevitably, some of these variations will prove to be better suited to the mode of life of the organism than others. The offspring that have these favourable characteristics will then have a natural advantage in the competition of life and will tend to survive at the expense of their less fortunate relatives. By their survival, and eventual mating, this process of natural selection will lead to the persistence of these favourable characteristics into the next generation. (More detail on how this takes place is given in Chapter 6.)

The idea of natural selection was announced by short papers from both Darwin and Wallace, read at a meeting of the Linnean Society of London on 30 June 1858; and Darwin quickly went on to publish his great book the next year [11]. There can be no doubt that Darwin has to share with Wallace the credit for identifying natural selection as the mechanism of evolution and identifying the patterns of biogeography as evidence for evolution. However, the lion's share of the credit for the almost immediate acceptance of the reality of evolution has to be given to Darwin and his book *On the Origin of Species*. For Darwin had spent the 40 years after his return from the voyage of the *Beagle* in detailed research on many other areas of biology that provided evidence for evolution (see Box 6.3), and published this research in 19 books and hundreds of scientific papers. The essentials of this work were given in his great book (which sold out immediately on publication and had to be reprinted twice in its first year) and were far more convincing in their variety and detail than the short papers read to the Linnean Society.

Darwin's theory of natural selection was extremely logical and persuasive. His studies on the ways in which animal breeders had been able to modify the anatomical and behavioural characteristics of dogs and pigeons provided a neat parallel to what he believed had happened in nature over long periods of time, and were even more convincing. But, said his critics, all these different breeds of dog or pigeon were still able to breed with one another, which did not support Darwin's suggestion that this was the way in which new species could appear. Nor could Darwin provide any explanation of precisely how the different characteristics were controlled and passed from generation to generation. In fact, the outlines of the ways in which all this took place had been discovered by the Austrian monk Gregor Mendel in 1866, but his work remained unnoticed until the beginning of the next century. So, our modern science of genetics was still a closed book. Also, Darwin did not understand the nature of species. It was generally assumed at that time that each species was innately stable and resisted innovation – which would have impeded the action of natural selection in trying to alter its characteristics. In fact, we now know that the continual appearance of changed characters or 'mutations' (see Chapter 6) would quickly alter the nature of any species, and it is only the continual action of natural selection in weeding out most of these that gives the species the appearance of unchanging stability.

Another problem for Darwin was that most people believed that the Earth was only a few thousand years old. This was partly because some theologians considered that passages in the Bible could be interpreted as indicating that it had only been created some 8000 years ago – and, perhaps more fundamentally, also because few people could even imagine the enormous periods of time that were in fact required for evolution to take place. However, the British geologist Charles Lyell argued that many lines of evidence suggested that the Earth must be

many millions of years old [12]. These included the evidence that sea levels had changed greatly over time, the presence of marine fossils at high levels in the mountains, the presence of tropical deposits such as coals or desert sandstones in what are now temperate regions and, even more dramatically, the time required to raise such great mountain chains as the Himalayas, Rockies or Andes. But this argument was weakened by the work of the physicist J.J. Thompson who, basing his work on calculations on estimates of the rate of cooling of the Earth from an original molten state, eventually concluded that it was less than 10 000 years old. He was unaware, of course, of the fact that much of the Earth's continuing warmth comes from radioactivity, for this was only discovered in the 20th century, leading to the eventual realization that the Earth is several billion years old. So, like any scientist, Darwin was a child of his time, unaware of future discoveries that might have explained his difficulties.

Despite these difficulties, the concept of evolution, and of natural selection as its mechanism, was very quickly accepted and is now a part of the basic philosophy of biological science. Just as the theory of plate tectonics is the central paradigm of the earth sciences (see Chapter 5), so the theory of evolution by natural selection is the central paradigm of the biological sciences. Biogeography provides a striking example of the concordance of the implications of these two paradigms. For example, the dates that plate tectonics theory indicates for the different islands in the Hawaiian chain are similar to those that evolutionary studies indicate for their animals and plants. The way in which biogeography provides interlocking support for these two paradigms is overwhelming evidence for the correctness of each and gives it a unique position in the natural sciences.

World Maps: Biogeographical Regions of Plants and Animals

Thanks to Darwin and Wallace, then, the process that was responsible for the living world's reactions to changes in the physical world was at last understood and accepted. Its mechanism (genetics) was yet to be identified, and it would take another century before the mechanisms of the geological process responsible for those changes were discovered. Nevertheless, it was now clear that some of the differences between the floras and faunas of the separate continents might have resulted from their having had separate evolutionary histories. The German botanist Adolf Engler (1879) was the first to make a world map (Figure 1.1) showing the limits
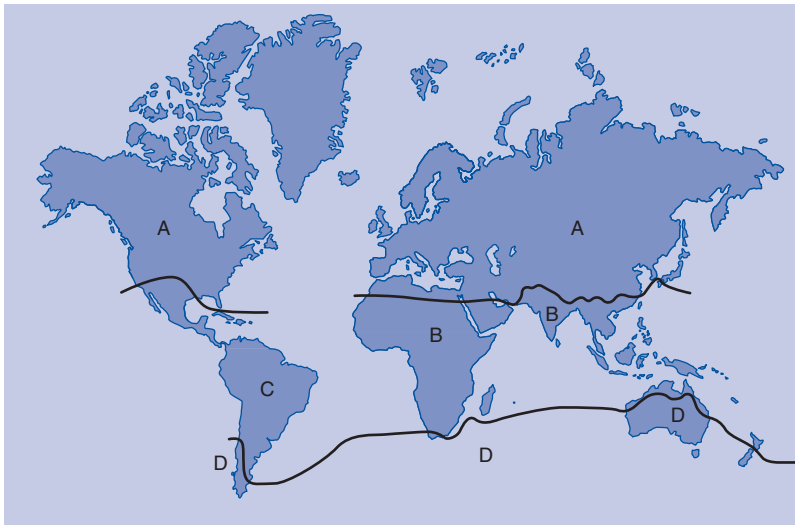

Figure 1.1 The world's botanic realms according to Engler [13]. A, The Northern Extratropical Realm; B, the Palaeotropical Realm, stretching from Africa to the East Indies; C, the South American Realm; and D, the Old Ocean Realm, stretching from coastal Chile via southernmost Africa, and the islands of the South Atlantic and Indian oceans, to Australia and part of New Zealand.

of distribution of distinct regional floras [13] – although his map also shows the different types of vegetation in each of his major areas. He identified four major floral regions, or 'realms', in the world, and attempted to trace the history of each of these back into what we now call the Miocene Epoch of the Tertiary Period, about 25 million years ago (see Figure 5.5). He also noted some of the plant families or genera that are characteristic or dominant in each realm. He had also read the work of the British botanist Joseph Hooker (discussed further in this chapter), who had found many similarities between the floras of the continents and islands of the Southern Hemisphere, and had suggested that these might be explained partly by the dispersal of floating seeds. This led Engler to distinguish what he called an *Old Ocean Realm*. Apart from comparatively minor modifications [14–16], the system of plant regions accepted today (Figure 1.2a) is very similar to that of Engler – although no one has yet
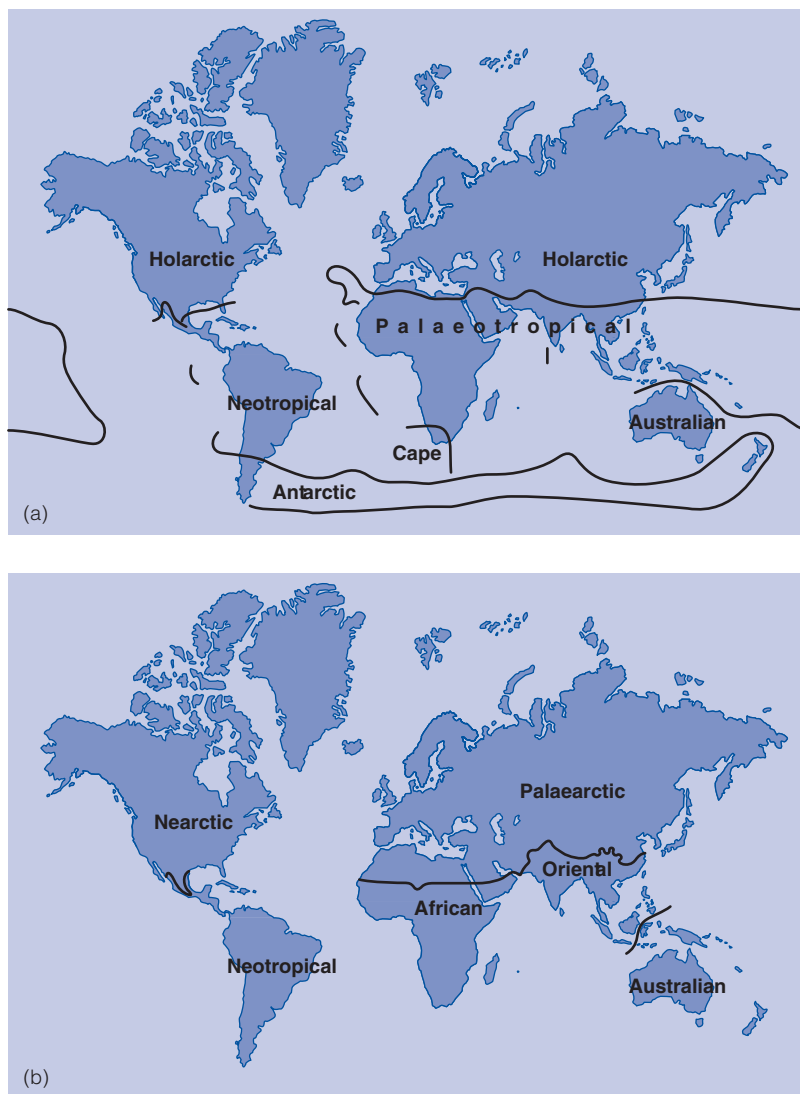

Figure 1.2 (a) Floral kingdoms, according to Good [15] and Takhtajan [16]. (b) Zoogeographical regions, according to Sclater [20] and Wallace [22]. From Cox [17]. (Reproduced with permission of John Wiley & Sons.)

provided any systematic comparison and contrast of the composition of the floras of these different realms [17]. He was also surprisingly perceptive in realizing that, scattered over the islands and lands of the southernmost part of the world, lay the remains of a single flora, which he called the *Ancient Ocean Flora*. (It was over 80 years before acceptance of the movement and splitting of continents at last explained this very surprising pattern of distribution.)

Zoogeography, too, had been developing from the early 19th century onward, but with a different emphasis. Because such dominant groups as the birds and mammals are warm-blooded, they are largely insulated from the surrounding environmental conditions and are often found in a great variety of environments. So, unlike the plants, they do not show a close correlation to local ecology. Even such early zoogeographers as Prichard in 1826 [18] and Swainson in 1835 [19] were therefore free to concern themselves with distribution at the world level, and they recognized six regions that corresponded with the continents. This was first formalized in 1858 by the British ornithologist Philip Sclater [20], who based his system on the distribution of the most successful group of birds, the passerines or 'songbirds', because he thought that they were less adept than other birds at spreading from place to place. He believed that all species had been created within the area in which they are found today, so that comparison of the different local bird faunas might identify where the centres of creation might have been. (He even thought that these might reveal where the different races of human being had been created.) As was normal in those days, he gave classical names to the six continental areas that he identified but, even though he listed or described the areas included in each region, he gave no maps to illustrate his views.

Alfred Wallace made his living by collecting bird skins, butterflies and beetles in the East Indies, and selling them to naturalists. (He had already made extensive collections in the Amazon rainforest.) These travels and collections had led him to become, like Darwin, interested in their patterns of distribution. He immediately accepted Sclater's scheme, including his names for the regions, and expanded it to include the distribution of mammals and other vertebrates (Figure 1.2b). Because of the pattern of barriers of ocean, desert and mountain between the zoogeographical regions, the only area where there is a significant overlap between the faunas of adjacent regions is precisely where Wallace was working: in the East Indies chain of islands between Asia and Australia. Wallace became fascinated by the unexpectedly abrupt north–south demarcation line that separated the more western islands, which had an overwhelmingly Oriental fauna, from those to the east that were, equally overwhelmingly, Australian. His map and the 'Line' that has been named after him have been largely accepted by zoogeographers ever since (cf. Figure 11.9).

Although he should always be remembered as the joint discoverer of natural selection, in many ways Wallace's greater claim to fame is as a profound thinker and contributor to the fundamentals of zoogeography. His books *The Malay Archipelago*, *The Geographical Distribution of Animals* and *Island Life* [21–23] were read by many people and were very influential. Wallace identified or commented on many aspects of biogeography that still occupy us today. These include the effects of climate (especially the most recent changes), extinctions, dispersal, competition, predation and adaptive radiation; the need to be knowledgeable about past faunas, fossils and stratigraphy, as well as about those of today; many aspects of island biogeography (see further in this chapter); and the possibility that the distributions of organisms might indicate past migrations over still-existing or even now-vanished land connections. He and Buffon were truly the giants in the development of zoogeography.

Getting around the World

The final acceptance of evolution gave a new importance to biogeography and posed new problems, which persisted over the century that elapsed before the mechanics of its geological counterpart, continental drift or plate tectonics, were revealed. If Darwin (and Wallace) were correct, new species arose in a particular place and dispersed from there over the pattern of geography that we see today, except where this had become modified by comparatively minor changes in climate or sea level. This concept of **dispersalism** therefore assumed that, where a taxon or two

related taxa are found on either side of a barrier to their spread, this is because they had been able to cross that barrier after it formed.

But this was inadequate to explain many of the facts of world biogeography, especially some that were revealed by the rapidly expanding knowledge of patterns of distribution in the past. One might be able to invoke floating islands of vegetation, mud on the feet of birds or violent winds to explain dispersal between islands or otherwise isolated locations today. But even Darwin's old friend, the botanist Joseph Hooker, who had travelled and collected widely in the Southern Hemisphere continents and islands, found these explanations quite unconvincing. Hooker became one of a group who instead believed that the many similarities between the plants and animals of the separate southern continents, and of India, could only be explained by their having once been connected. This could have been by narrow land bridges, or by wider tracts of dry land across the present South Atlantic and Indian Oceans, that had later become submerged. But even by the end of the 19th century, this had been dismissed as a fanciful explanation for which there was no geological evidence.

The past, too, was providing more and more examples of puzzling patterns of distribution. For example, 300 million years ago, the plant *Glossopteris* existed in Africa, Australia, Antarctica, southern South America and, most surprisingly of all, India (Figure 1.3). A linkage between all these areas at that time was also suggested by the fact that all of them contained deposits of coal and traces of a major glaciation, contemporary in all those continents. Such facts, together with similarities in the outline of the Atlantic coasts of the Americas, Europe and Africa, and comparison of the detailed stratigraphy of the rocks along these coastlines, were what led the German meteorologist Alfred Wegener to present his theory of continental drift in 1912 [24]. Wegener suggested that all of today's continents had originally been part of a single supercontinent, **Pangaea** (Figure 1.4). But, as noted at the beginning of this chapter, in the absence of any known mechanism that might split and move whole continents, his suggestions were not accepted by either geologists or biologists. Biogeographers were instead driven back on progressively more desperate defences of dispersal as the only possible explanation of the patterns of distribution.

This was particularly true of what the botanist Leon Croizat called the New York School of Zoogeographers, a group of vertebrate zoologists founded by Walter Matthew. In his 1924 paper 'Climate and Evolution' [25], Matthew suggested

Figure 1.3 Distribution of the *Glossopteris* flora (shaded area).
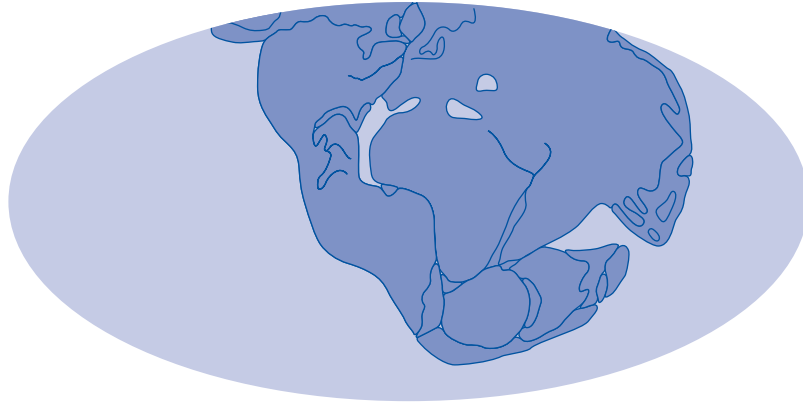
Figure 1.4 How today's landmasses were originally linked together to form a single supercontinent, Pangaea, according to Wegener. (Compare this with Figure 10.1 to see the modern, plate tectonic reconstruction of Pangaea.)

that all the patterns of mammal distribution could be explained if the different groups had originated in the challenging environments of the Northern Hemisphere. From there, they had dispersed across the intermittently open Bering land bridge between Asia and North America, and southward to the various continents of the Southern Hemisphere. Probably the most influential later member of the New York School was George Simpson, who not only wrote many papers on mammalian palaeontology and biogeography [26], but also several important books on evolutionary theory. He had no doubt that the patterns of distribution of mammals could be explained perfectly well without invoking continental drift. (This was largely true, for the radiations of the families of living mammals took place well after the fragmentation of Pangaea; only the presence of marsupials, but not placentals, in Australia provided an obvious problem.) Together with such other workers as the herpetologist Karl Schmidt, George Myers (who worked on freshwater fishes) and the zoogeographer Philip Darlington (who in 1957 wrote a major and influential textbook on zoogeography [27]), they provided a powerful and united body of opinion that was wholly opposed to the idea of continental drift and equally fervently supportive of the idea of dispersal.

Some idea of the lengths to which these workers were driven in trying to explain the facts of distribution is shown by Darlington's statement, in discussing the distribution of *Glossopteris*: 'The plants may have been dispersed partly by wind,

and, since they were frequently associated with glaciation, they may have been carried by floating ice, too. I do not pretend to know how they really did disperse, but their distribution is not good evidence of continuity of land' [28, p. 193]. Surely, one might think, this distribution, scattered across continents separated by thousands of miles of ocean (Figure 1.3), *was* evidence of continuity of land, but Darlington gave no reason why he thought that it was not *good* evidence.

It is not surprising that such attitudes provoked opposition, and this surfaced most strongly in the person of Leon Croizat. Born in Italy in 1894, Croizat was overwhelmed by the effects of fascism, World War I (1914–1918) and the Great Depression. After spending periods as an artist in New York and Paris, he became a botanist, at first in New York and eventually in Venezuela, where he lived from 1947 until his death in 1982. Croizat rightly felt that the dispersalists were going to extremes in their refusal to countenance any other explanation for the patterns of distribution that one could see in the world today, such as the widely disjunct distributions of many taxa, especially in the Pacific and Indian oceans. He amassed a vast array of distributional data, representing each biogeographical pattern as a line, or **track**, connecting its known areas of distribution. He found that the tracks of many taxa, belonging to a wide variety of organisms, could be combined to form a **generalized track** that connected different regions of the world. These generalized tracks (Figure 1.5) did not conform to
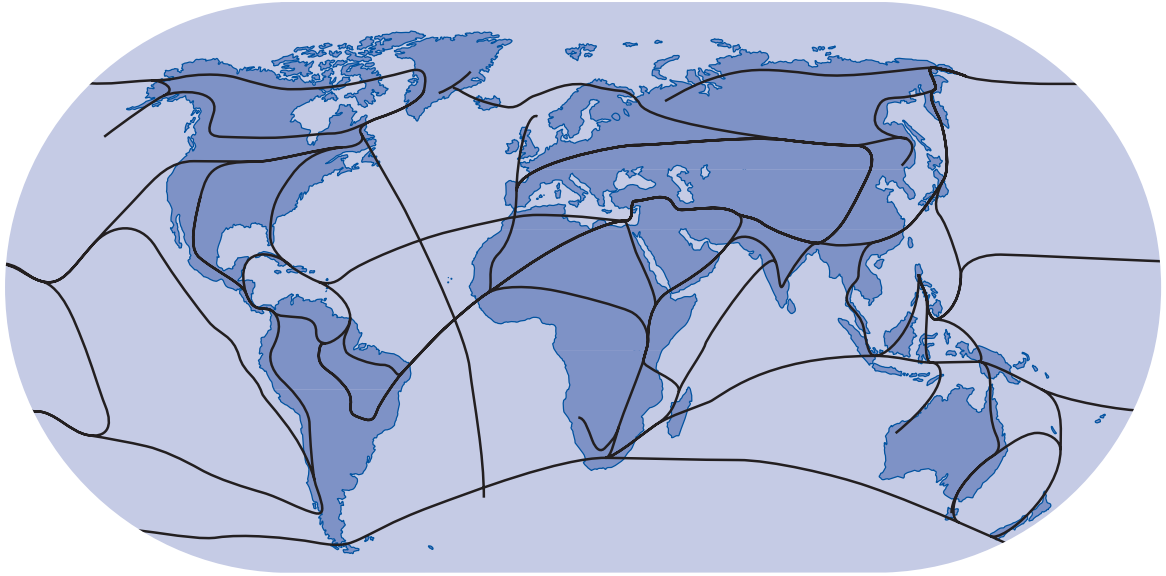
Figure 1.5 Croizat studied the distribution patterns of many unrelated taxa, and for each he drew lines or 'tracks' on the map linking the areas in which they are found. In many cases, these lines were similar enough in position to be combined as 'generalized tracks', shown here.

what might have been expected if these organisms had evolved in a limited area and had dispersed from there over the modern pattern of geography, as other biologists then believed. Croizat felt that it would be surprising if any single taxon had managed by chance to cross the intervening gaps, and incredible that a considerable variety, with different ecologies and methods of distribution, should have been able to do so. His method, which he called **panbiogeography**, argued that all of the areas connected by one of these tracks had originally formed a single, continuous area that was inhabited by the groups concerned. This theory therefore rejected both the concept of origin in a limited area and that of dispersal between subsidiary locations within that area. However, having rejected the facile use of dispersal as an explanation of each and every example of a trans-barrier pattern of distribution, Croizat then went to the other extreme and completely rejected dispersal in any shape or form – although, confusingly, he used the word 'dispersal' in a different sense, as describing the pattern of distribution of a taxon.

Instead, Croizat believed that the organisms had *always* occupied the areas where we now see them, together with the intervening areas, and that they had colonized all these areas by slow spread over continuous land. So, the flora of such isolated island chains as the Hawaiian Islands, or the scattered patterns of distribution of plants along the Pacific margins of North and South America, had arisen because land had once linked all these areas, or because islands containing the plants had moved to fuse with the mainland. Croizat believed that any barriers, such as mountains or oceans, that exist today within the pattern of distribution of the taxa had appeared *after* that pattern had come into existence, so that these taxa had never needed to cross them – a concept that came to be known as **vicariance**. To this extent, Croizat's theorizing anticipated the way in which plate tectonics would provide a geological contribution to the spread of organisms.

Croizat published his ideas in the 1950s and 1960s, his major presentation being his 1958 book *Panbiogeography* [29] – but little attention was paid to his work. This was partly because of the dominance of the New York School, with its acceptance of dispersalism, but also because of several weaknesses in Croizat's own work. He concentrated on the patterns of distribution of living organisms, was scornful of the significance of the fossil record

and paid little attention to the effects of changes in geography or climate. In addition, because the idea of the stability of modern geography seemed to have successfully weathered Wegener's heresies, Croizat's theories of the movement of islands or of massive extensions of land into the Pacific and Atlantic cast him into that same mould – of passionate amateurs. And, even after the theory of plate tectonics had become well documented and widely accepted, Croizat refused to accept it and never integrated it into his methodology. He also became increasingly embittered by the way in which his work was largely ignored.

Ironically, the recognition of some of Croizat's perceptions and methods began in New York, where there arose a new generation of biogeographers who had not been brought up under the influence of the old New York School. For Croizat was correct, and ahead of his time, in believing that in many cases speciation had taken place *after* a barrier had emerged within an existing area of distribution of a taxon. But, unfortunately, the pendulum now swung to the opposite extreme – instead of 'Dispersal explains everything', their attitude was 'Vicariance explains everything', and dispersal is merely random noise in the system. Even more unfortunately, Croizat's supporters also inherited his confrontational approach, and the argument between the supporters of dispersal and the supporters of vicariance became increasingly bitter. (One problem that underlay this whole argument may have been that the available evidence was, in the majority of cases, inadequate for anyone to be able to prove whether dispersal or vicariance had been the cause. Although biogeographers were only too aware of this, they were nevertheless desperate to find some method, whether or not it was perfect, to explain the patterns of life that so intrigued them. Quite often, those who shout the loudest are those who are least secure of their case, and are trying to silence their own doubts as well as those of their opponents!)

Perhaps the most enthusiastic of Croizat's supporters was a group of biogeographers, most of whom worked in New Zealand, where the origins of the fauna and flora provide particularly difficult problems. These panbiogeographers accepted his generalized tracks running across the ocean basins, referring to them as **ocean baselines** (Figure 1.6), and viewed them as more useful and important than the conventional system of continental zoogeographical and plant geographical regions. Their methodology also considered the area where a taxon is most diverse in numbers, genotypes or morphology as the centre from which the track for that particular taxon had radiated – a dangerous assumption. The author of this chapter (Barry Cox) has reviewed the history and development of the New Zealand school of panbiogeographers [30], one of whom (John Grehan) responded to these criticisms [31]. More recently, the Mexican biogeographer Juan Morrone has written a defence of the concept of track analysis [32].

The long and bitter argument about dispersal versus vicariance only ended with the appearance of new molecular techniques of establishing the patterns of relationship of organisms and the time that has elapsed since the origin of each lineage. This now allows us to compare the timing of biological events and of the geological or climatic events that might have been associated with them. The result has been, rather ironically, to show the prevalence of dispersal to an extent far greater than the most optimistic dreams of the dispersalists!

The Origins of Modern Historical Biogeography

A century after Darwin had published his theory, acceptance of his ideas had revolutionized approaches to nearly every aspect of the biological sciences. These ideas had implicitly suggested that the contents of each biogeographical unit might have changed and diversified through time, and discoveries of the fossil record had in many cases documented these changes. But as long as the Earth's geography was assumed to have been stable, problems remained in the explanation of at least some of the patterns of disjunct distribution. Some of these could be explained by patterns of extinction. For example, the presence of fossil camelids and tapirs in North America and Asia showed that the disjunct distribution of these groups today, in South America and South-East Asia, did not have to be explained by some theory of the rafting of early members of these groups across the Pacific. However, the patterns of distribution shown by the ancient *Glossopteris* flora, or by the Antarctic Floral Kingdom today, still provided a major puzzle. How
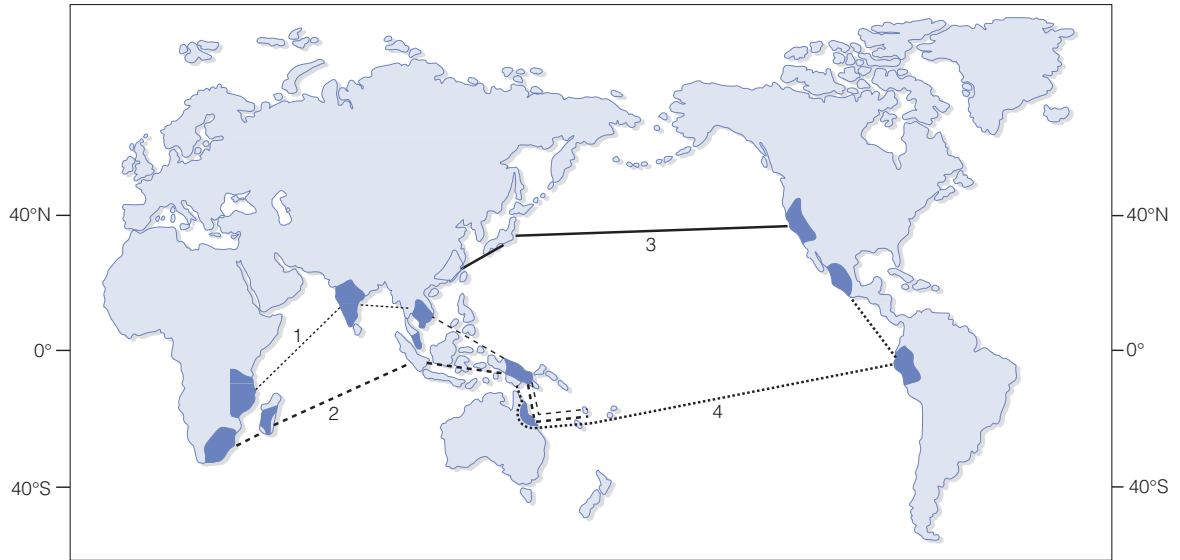
Figure 1.6 Craw's panbiogeographical method. The tracks link areas (dark blue) where related taxa are found. Tracks 1 and 2 are examples of an Indian Ocean baseline, and tracks 3 and 4 similarly are examples of a Pacific Ocean baseline. Adapted from Craw [58].

could organisms have dispersed across oceans to reach these scattered locations? As already mentioned, Wegener's theory of continental drift had provided an explanation to this conundrum early in the 20th century, but he had been unable to suggest any convincing mechanism that might have caused the movement and splitting of huge masses of land. As a result, his theory had been rejected by most geologists, and most biogeographers had reluctantly felt obliged to follow their lead. It was only in the 1960s that strong new evidence of the mechanism for Wegener's theory, now renamed *plate tectonics*, led to the acceptance of the reality of this phenomenon (see Chapter 5). It was only now that geologists were able to provide a series of palaeogeographic maps that showed, from the Silurian Period onward, the changing patterns of association of the various tectonic plates [33].

Until now, biogeographers had tried to analyse the biogeography of the past according to the different geological periods – the life of the Carboniferous, Permian and so on. But, as the new maps showed, there were major changes in the patterns of land and ocean within these periods of geological time. There would therefore have been corresponding changes in the likely biogeographical patterns, dooming to failure any attempt to detect a single

pattern of biogeography for the time in question. However, the new maps also made it possible to identify stretches of time (*not* corresponding to the geological periods) within which the geographical patterns had remained constant. As the British biogeographer Barry Cox realized [34], these maps therefore provided the potential basis for appropriate biogeographical analysis, if to them one added the patterns of the shallow 'epicontinental' seas that lie on the edges of the continental plates – for these, too, are biological barriers. All that a palaeobiogeographer then had to do was to summate the faunas and floras from every locality within each of the resulting palaeocontinents. For the first time, the results made perfect sense, with elements of these faunas and floras showing clear evidence of endemicity (see Chapter 10) (Figure 1.7).

The theory of plate tectonics was soon accepted by nearly all biogeographers, but, perhaps unsurprisingly, some of the older ones held out against it. For example, Philip Darlington [28] rejected the idea of a general union of southern continents into a single supercontinent. He felt that such a geography would not have provided enough adjacent water for the development of the ice sheets that appeared to have covered it about 300 million years ago.
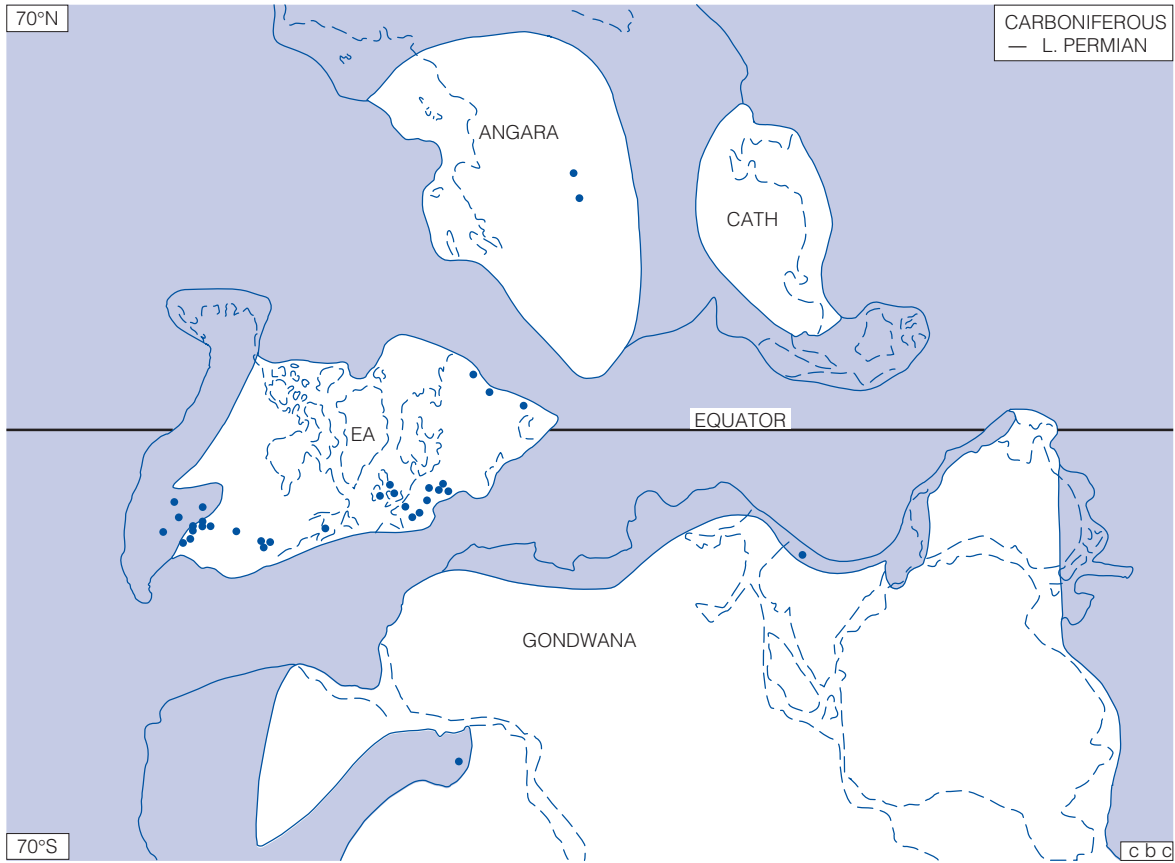
Figure 1.7 Palaeogeographical map of the Carboniferous–Lower Permian period of time, as reconstructed in 1973. The seas and oceans are tinted blue. The small dark blue circles show the positions of all the localities containing early terrestrial vertebrates. The one indicated in northern South America was later shown to belong to a later period of time, whereas those in northern India and in Siberia are doubtful fragments. The map thus strongly suggests that the earliest land vertebrates evolved in Euramerica. The four different floras recognized by palaeobotanists (the Angaran, Cathaysian (CATH), Euramerican (EA) and Gondwana floras) are also found to have lived on different palaeocontinents. This explains the previously puzzling fact that the *Glossopteris* flora, found in Gondwana, is found scattered over five of today's continents. From Cox [34]. (Reproduced with permission of John Wiley & Sons.)

At long last, biogeographers could build up a coherent, increasingly detailed set of pictures of the geography of the world over many millions of years. Now they could start to analyse the changing patterns of distribution of living organisms over that period of time and discover the historical roots of the patterns of biogeography that are seen in the world today. The results of this are reviewed in Chapters 10 and 11. But some biogeographers were particularly interested in the more recent past – partly because it encapsulated the origin and spread of our own species. However, this period of time demanded quite different techniques of investigation, for it included the Ice Ages, with their major, oscillating effects on climate and sea level. In the end, it was found that the most reliable evidence of the general patterns of change in climate could be deduced from oxygen isotope studies of the fossil skeletons of plant microfossils in cores of the sediments in the deep ocean floors. The American Cesare Emiliani was the first, in 1958, to provide reliable temperature curves for the past

700 000 years. But in order to relate these general changes to more local climatic changes on land, biologists had to turn to fossil pollen, a technique pioneered by the Swedish worker Gunnar Erdtmann and the British worker Harry Godwin in the 1930s [35]. The pollen of different species of plant is often easily recognizable and is well preserved in sediments found in peats and lake deposits, so that study of these shows clearly how the vegetation of the area has gradually changed. The results of all of these studies, and their implications for the origins of our own species and of civilization, are dealt with in Chapters 12 and 13.

Biogeographers now had the tools with which, they thought, it should be possible to construct satisfying correlations between the patterns of geography and climate, on the one hand, and of life, on the other hand. But at first this was still disappointingly difficult to achieve, because different taxonomists had different opinions as to the taxonomy (and, therefore, the pattern of evolution) of the organisms involved. Two innovations have transformed this biological problem. The first, known as cladistics (see Chapter 8), provided a rigorous methodology for analysing the patterns of evolutionary relationship between the different members of a group. Still, as long as the characters used in this evaluation were morphological ones, the problems remained, for such characteristics can show convergent or parallel evolution, or may be dependent on one another for functional or developmental reasons. This problem has now been reduced by the development of molecular systematics, which uses more abstract and fundamental characteristics of the organisms, which lie in the detailed molecular make-up of their DNA and proteins (see Chapter 6). This not only provides more confidence in the accuracy of our reconstructions of the patterns of evolutionary divergence of the group under study, but also indicates the times at which the different branching events took place. This in turn allows us to make an informed decision as to whether a particular event was due to vicariance or dispersal (in those cases where the two explanations involve different periods of time).

These two advances have permitted major improvements in our methods of establishing biological relationships and are revolutionizing our understanding of biogeography at all levels (see Chapter 8).

The Development of Ecological Biogeography

As we have seen, ecological biogeography began with the simple observations of men such as Linnaeus, who recorded in what type of environment each plant was found, whereas Forster recognized latitudinal gradients of diversity, later matched by Humboldt's altitudinal gradients, and Candolle pointed out the importance of competition in limiting the distribution of plants. But the full development of this field of inquiry came much later, mainly in the 20th century, for it depended on the rise of modern science with its techniques of experimental, physiological studies. Unlike that of historical biogeography, its history was not complicated by the need to counter the attitudes of antagonistic philosophies or religion, nor by having to wait until data from another field, such as the earth sciences, could be understood. The development of ecological biogeography was, however, strongly dependent on the increasing application of chemical and physical concepts and techniques to the understanding of plant and animal function, and hence distribution. The birth of the science of genetics in the 20th century, leading ultimately to the development of molecular genetics, also expanded the horizons of ecological biogeography.

It was, of course, obvious to the earliest botanists that the distribution of plants was closely linked to climate. In trying to structure the results of this relationship, they could focus either on the demands of the environment on the physiology of the plants, or on the type of vegetation that resulted. Candolle, in 1855, was the first to contribute to this field of inquiry, recognizing three physiologically different types of plant that resulted from their adaptations to different levels of heat and moisture. He called these **megatherms**, **mesotherms** and **microtherms**, which, respectively, required high, moderate and low levels of heat and moisture, and **hekistotherms**, which live in the polar regions. Later, he added **xerophytes**, which can tolerate low levels of moisture.

Botanists soon also started to analyse the effects of the geology of the area in which the plants lived, and the interacting role of climate and of the plants themselves in breaking down the native rocks and converting them into soils of different characteristics.

The American botanist E.W. Hilgard showed, in 1860, how climate and plant life combined to gradually break down the native rock into smaller fragments and provide an increasing component of soil as a product of the biological activity; and the Russian V.V. Dokuchaev analysed the mineralogical and physical attributes of the soils that resulted from the breakdown of different types of rock.

The alternative focus, on the type of vegetation that resulted from the action of the climate, had begun with Engler's map (see Figure 1.1), which had shown the limits of various types of vegetation; but he had used a confusing system of classification. The first clear and simple system of categorizing the different types of vegetation was produced by the German botanists Hermann Wagner and Emil von Sydow in 1888 [36]. Their system was amazingly advanced for its time, for it recognized nine of the 10 categories that are still commonly used, such as tundra, desert, grassland, conifer forest and rainforest; only the Mediterranean type of scrubland was not identified. The many maps and systems produced by various workers since then have contributed different details and variations in emphasis, but have added little to Wagner and Sydow's basic system, although various terms have been coined to describe its elements. The earliest of these, introduced by Clements and Shelford in 1916, were **plant formation** or, with the addition of its animals, a **biome**. Tansley in 1935 [37] added the climatic and soil aspects of the complex, calling it an **ecosystem**, which became the basic unit of ecology. *Biome* has remained the usual term for classification at the macroscale level, but it is used in a variety of ways. If the main emphasis is on vegetation structure, ecophysiology and climate, then biomes can be seen to be the reactions of the living world to these conditions, and the 'same' biome can be found in different continents. If, instead, the emphasis is on the taxonomic or phylogenetic aspect of its plant components, then the biomes become regional, as in Takhtajan's 'floristic regions' [16]. On the whole, the word *biome* is best used in the former, nontaxonomic sense.

Living Together

The rise of ecology as a scientific discipline during the early part of the 20th century led to new approaches to biogeographical studies. Ecophysiology, the study of the ecological implications of plant and animal physiology, played an important role in these developments. The German botanist and plant physiologist Julius von Sachs had injected a strong physiological approach into the debates concerning adaptation to the environment that were prominent at the end of the 19th century [38]. Environmental stresses were seen as limiting factors in plant distribution patterns, and the morphology, anatomy and physiology of plants often reflected their capacity to cope with these stresses. Known as **plant form**, these features were recognized as a more effective way of defining the formations and biomes than any taxonomic or evolutionary system of classification. It was from this line of thinking that the Danish botanist Christen Raunkiaer developed his proposal of **life forms** of plants, based on their means of survival from one growing season to the next (see Chapter 3). A plant's growing points, he argued, are the most sensitive to environmental stress during an unfavourable period (be it cold or dry), and the position in which those growing points are held therefore provides an indication of the degree of stress to which it is exposed. He classified plants according to the height of their growing points above ground (or below ground). Plants growing in the unstressed conditions of the wet tropics could develop forms with their buds high above ground, whereas those in the polar regions or in deserts survived only if their buds were close to the ground or, in the case of the dry lands, below the surface. Annuals were a special case, as they survived an unfavourable period as dormant seeds.

The life form concept has been highly influential in plant geographical studies and generally fits well with observed facts. Plant formations, or biomes, are indeed characterized by the proportions of the different life forms of plants present – what Raunkiaer described in 1934 as the 'biological spectrum' of the vegetation. There are other important adaptations, however, apart from those associated with growing points of plants, or their means of surviving from one year to the next. Evergreen and **deciduous** leaf characters (deciduous plants shed their leaves during a cold or dry season of the year), rooting characteristics, drought and flooding physiology and symbiotic nitrogen fixation are all important aspects of coping with environmental stresses that are unrelated to bud positions.

In the latter part of the 20th century, the concept of **plant functional types** emerged, incorporating and moving beyond that of life forms. It is an approach that actually can be traced back over 2000 years to the work of the Greek botanist Theophrastus around 300 BC, but its use in recent times has drawn strongly upon the idea of **guilds**, a concept borrowed from animal ecology [39]. A guild is a group of animals, not necessarily related taxonomically, which all make use of the same resource or overlap significantly in their environmental requirements. It is a concept that has been used in a rather varied manner, sometimes being applied to organisms that respond in the same way when disturbed or have a particular management system applied. In one respect, all green plants are part of a single guild in that they all obtain energy directly from the sun, but with respect to other resources, such as water, nutrient elements, pollinators, seed dispersal vectors and so on, plants have different ways of coping with their environments. They can thus be classified as different functional types. The concept owes much to the work of Philip Grime, who developed the idea that plants have a range of survival strategies available to them [40]. It is an approach that is proving useful in studies such as those examining the nature of stability and resilience in communities, and is also being used in predicting the outcome of global change on vegetation.

The use of the word **community** has itself generated much debate in ecological biogeography. (Communities and ecosystems are examined in more detail in Chapter 4.) We observe organisms mixed together in groups, or assemblages, whose relative stability suggests that the different species are in an equilibrium, tolerating or perhaps even encouraged by the presence of others – perhaps because the different species may coevolve and adapt to the presence of those others. The American plant ecologist Frederic Clements was the first to suggest, in the early 20th century, that such integrated communities resemble individual organisms in their degree of internal organization, and may similarly behave as units in their patterns of distribution. The community concept was very convenient for biogeographers, as it facilitated the precise classification of vegetation, which is needed for it to be mapped effectively. But the voices of many ecologists were raised against it.

Henry Gleason formally set out the alternative approach in his Individualistic Hypothesis, stating that each species was distributed according to its own ecological requirements, and what we regard as a community is really little more than a chance assemblage of species with compatible ecological tolerances.

Emphasis on the concept of community led to the development of a distinct branch of plant geography, **phytosociology**, in which the plant communities are classified and may be arranged in a hierarchy – which is undoubtedly convenient, but may be unrealistic. Highly detailed systems of plant community classification have been established by using the techniques of phytosociology, pioneered by the botanist J. Braun-Blanquet [41]. The classification of vegetation, rather like the classification of organisms, is based on the idea that relatively sharp lines can be drawn around each defined unit. Field ecologists, however, soon recognized that in the case of vegetation there is usually gradual change from one type to another, leading to gradients along a continuum. Only where there are abrupt changes in the environment does one find sharp boundaries in vegetation. Recent developments in classification have therefore been based on the idea of defined reference points between which there may be a whole range of intermediates. Classification is necessary for the purpose of mapping, but in a situation of continuous variation, any system has to be considered relatively fluid.

Vegetation varies not only in space but also in time, adding to the complexity involved in classification. Increasing amounts of data from fossil pollen grains in lake and peat sediments have shown quite clearly that the distribution patterns of different plant species change quite independently of one another during periods of climatic change. What we currently regard as a community will change in its composition as the environment changes, and assemblages of the past will never be fully repeated. The community, therefore, is a convenient but artificial concept. Changes in assemblages of plants and animals are constantly taking place, and these sometimes follow a predictable pattern. The American botanist Henry Cowles, working in the Chicago region, showed that vegetation develops over the course of time, passing through several different assemblages of plants to

finally reach what came to be known as the **climax vegetation** of the region, governed mainly by climate. This climax he regarded as both predictable and stable [42].

The linked concepts of **succession** and **climax**, first developed by Henry Cowles, also have been questioned over the last 100 years. Ecosystems certainly develop over time, and we can make some generalizations about this (see Chapter 4). But it is difficult to show that this somehow involves a predictable process, ending in a predetermined climax that is governed by climatic factors. The climax itself is never static but is in a constant state of change, so the idea of equilibrium has to be more dynamic than Cowles' original concept. An alternative approach is that of *chaos theory*, a concept which assumes that the outcome of a process is highly dependent on the initial conditions. If that is true, the development and outcome of successions may be determined by relatively minor differences in such original conditions as the availability of organisms and soil and weather conditions. So, although climate may in very general terms determine the end point (i.e. the biome) of succession, its detailed composition and nature will be affected by many other factors, including chance.

The ecosystem concept was one of the most influential ideas to emerge from ecological studies in the 20th century, and it has proved extremely useful in biogeographical studies. One of its most valuable features is that it can be applied at any scale, from a rock pool on the shore to the entire Earth. The concept owes much to the work of Raymond Lindemann, who in 1942 put forward a formal account of energy flow in nature. The idea was expanded by the work of American ecologists Howard and Eugene Odum, and named by the British botanist Arthur Tansley. It allows any selected portion of nature to be viewed as an entity, within which energy flows and elements cycle. The concept has recently proved especially valuable when applied on a large scale, where the global circulation of elements can be studied, and the relationships between human and natural processes can be identified. In the early 1960s, the first landscape-scale ecosystem was subjected to monitoring and manipulative management at Hubbard Brook, a forested mountainside in New Hampshire [43]. The budgets of chemical elements were examined in the undisturbed ecosystem, and again following deforestation, thus establishing an experimental approach to the study of large-scale ecosystems.

Ecophysiology, which examines how plants and animals vary in their physiological processes in response to the environment, also developed in new directions in the 20th century. Subtle differences between plants in their photosynthetic systems may provide some species with the capacity to survive in stressful environments. Similarly, animals vary in their capacities to cope with abiotic stresses, such as cold or high altitude, and in their tolerance to human-produced toxins. Thus, the explanation for the presence of a particular species in a given locality (one of the main questions underlying biogeography) may relate closely to the physiological capacity of the species to cope with local environmental stress. This area of research is now entering a new phase as it seeks to understand physiological processes at a molecular level. Molecular biology holds clues to many biogeographical problems and will undoubtedly increasingly be used to advance biogeographical science. Its value in determining taxonomic relationships is casting a new light on many controversial areas of historical biogeography, and its applications in physiological ecology will allow us to increase our understanding of the current distribution patterns of species and of their environmental limitations.

Advances in physiological research, together with ecological and behavioural studies, will help biogeographers to understand more fully the environmental requirements and the niches of organisms within ecosystems. The concept of the niche is complex, broadly being the role played by an organism in its particular setting. A very large number of variables contributes to the niche, including physical factors, chemical factors, food requirements, predation and parasitism, and competition from similar organisms. The concept of the niche was first devised by G.E. Hutchinson in the 1950s and has established itself as a valuable contribution to ecology and biogeography. Perhaps it is best viewed as a kind of conceptual envelope that has many dimensions relating to each requirement of an organism. An organism cannot survive outside these limits, so a full knowledge of those limits could be used to predict its theoretical geographical range [44]. Such knowledge, however, demands the accumulation of very large databases and very

complex analyses, and both are becoming increasingly available to researchers as a result of the development of fast and powerful computers.

The application of niche theory in ecological biogeography places emphasis on the environmental factors that control the survival of a species in an area, but it does not really take into account the availability of a species and its dispersal capacity. An alternative approach has been developed called the **neutral theory of biodiversity**, which is based on the idea that the assemblage of species in a site is entirely a matter of chance [45]. The neutral theory claims that the arrival of a species is a stochastic process and that the best predictive models are based on this concept of chance dispersal. Certainly, the part played by chance needs to be taken into account when trying to explain the composition of communities.

Computers were first applied to problems in ecology and biogeography in the 1960s, and their use has expanded to the point where almost all such studies make use of them. Complex statistics, such as multivariate analyses, as used in niche research and community analysis, are vital analytical tools and can be performed rapidly and routinely on computers small enough to be carried in the field. Global positioning systems, using satellites to establish the precise location of an observer on the ground, have also revolutionized the mapping of distribution patterns in remote areas. Technological advances in the last half century must, therefore, be regarded as major steps forward in the history of ecological biogeography.

All of the above avenues of inquiry, using increasingly sophisticated methods of experimentation and analysis, are now used in modern research on ecological biogeography, as explained in Chapters 2, 3 and 4. They are also now used in trying to cope with the problems and questions that arise from humanity's use, and abuse, of an increasingly crowded planet, as explained in Chapter 14.

Marine Biogeography

As explained at the beginning of Chapter 9, the biogeography of the oceans is similar to that of the continents because it is concerned with the biota of vast areas of the surface of the globe. But it is also very different because of the nature of the environment and of the organisms that it contains. We ourselves are terrestrial and air breathing, so the oceans are a far more challenging environment for us to study and census, and they also contain little in the way of obvious demarcations between biogeographical regions or zones. As a result, marine biogeography has been relatively slow to develop, and we still have a great deal to learn about it.

Although earlier naturalists had published limited studies on the faunas of particular regions, the first worldwide survey, based on the distribution of corals and crustaceans, was that of the American scientist James Dana, who later became an eminent geologist. His brief paper, published in 1853, divided the surface waters of the globe into several different zones based on their mean minimum temperature. Three years later, the British zoologist Edward Forbes [46] published the first comprehensive work, recognizing five depth zones and 25 faunal provinces along the coasts of the continents. He was the first to recognize the enormous Indo-Pacific faunal region; stated that the coastal faunas varied according to the nature of the coast, seabed, local currents and depth; and placed the 25 faunal provinces in nine latitudinal belts. Forbes also later published a little volume on the natural history of European seas which made important contributions to marine zoogeography and ecology.

In 1880, the British zoologist Albert Günther published a book on fishes in which he recognized 10 different regions in the distribution of shore fishes, and the German Arnold Ortmann published a similar work based on the distribution of crustaceans such as crabs and lobsters. However, the great landmark in early studies of marine zoogeography was the 1911 *Atlas of Zoogeography* [47] assembled by three British zoologists (John Bartholomew, William Clark and Pery Grimshaw). Their 30 maps of the distributions of fishes were based on the patterns of distribution of 27 families. An influential review and synthesis of all the relevant literature was carried out by the Swedish worker Sven Ekman; it was published initially in German in 1935, followed by an English translation in 1953 [48]. This divided the faunas of the shallow seafloors into seven (mainly climatic) areas, and included the recognition of the unity of the faunas of the Indian and West Pacific oceans, as well as the unity of the faunas of the East Pacific and Atlantic oceans. Ekman suggested

that the Panama barrier must formerly have been absent, and that the island-free East Pacific acted as a barrier to the dispersal of organisms; and he commented on the phenomenon of 'bipolarity', where a species is found on either side of the equatorial regions, but not within them.

Ekman's work was extended by the American marine zoologist Jack Briggs in 1974. In his book, *Marine Zoogeography* [49], Briggs used the patterns of endemicity of coastal faunas to identify locations where there appears to be a zone of unusually rapid faunal change, and then used this to distinguish 23 zoogeographical regions. Out in the oceans themselves, our knowledge of the distribution of plankton was greatly increased thanks to the work of the Dutch oceanographer Siebrecht van der Spoel and his co-workers. Their *Comparative Atlas of Zooplankton* [50] included over 130 maps of examples of different types of distribution, categorizing these and the different types of seawaters, the physical properties of the waters and diagrams of the relationships between the faunas of the different oceans.

The greatest of the more recent advances in our knowledge of marine biogeography have come partly from our increasing ability to explore the depths of the sea but also, surprisingly, from our ability to establish sensing and recording satellites in space. Our now-possible journeys into the deepest part of the oceans led to the discovery in 1977 of what is probably the last of the ecosystems of the world to be found, as well as perhaps the weirdest – the strange hydrothermal vent faunas. But, far more importantly, space satellites such as Nimbus have enabled scientists to monitor and record the changing patterns of planktonic life in the oceans continually and comprehensively. This has allowed the British marine biologist Alan Longhurst to propose a system of biomes and provinces within the oceans [51]. These provide for the first time a framework for their regional ecology that integrates their physical features with our increasing knowledge of the annual periodicity in the life, movements and reproduction of the plankton. We shall have great need of such studies in our efforts to comprehend and manage the life of the oceans, which we are increasingly affecting, and we also need it increasingly to feed the rapidly growing population of our planet.

Island Biogeography

As mentioned in this chapter, Georg Forster was the first biologist to remark on some of the particular features of island biogeography; he noted that island floras contain fewer species than the mainland, but that the number of species varies according to the size and ecological diversity of the island. Another early contributor was Candolle, who pointed out that the age, climate and degree of isolation of an island, and whether or not it was volcanic, would also affect the diversity of its flora. Nevertheless, the sheer variety and volume of the works on island biogeography published by Alfred Wallace mark him as the real founder of studies on this subject. His travels around the islands of the East Indies led him to make many profound observations on the reasons for their differing faunas and floras. He realized that the origins of the islands would affect the nature of their biota (i.e. their faunas and floras). Those of islands that had once been a part of a neighbouring continent were likely to contain most of the elements of the fauna and flora that they had inherited from the mainland. In contrast, islands that had arisen independently, as volcanic or coral-atoll islands, would only have organisms that had been able to cross the intervening stretch of sea. Wallace also pointed out that their distance from the mainland, or from one another, would affect the diversity of their biota. Finally, he realized that the diversity of islands made them good natural experiments, in each of which the processes of colonization, extinction and evolution had taken place independently, and so provided abundant material for comparative studies. These fundamental perceptions, as well as the sheer number of his books and research papers, leave no doubt that Alfred Wallace was the father of island biogeography.

But in Wallace's day, and for nearly a century afterward, island biogeography remained the preserve of the naturalist. There were so many islands whose biota needed to be described, for they are fertile breeding grounds for evolutionary innovation. Hundreds of papers were published on the plants of this group of islands, on the animals of that group of islands, or on the distribution of animals or plants over the islands of this or that part of the world. But each group of organisms or plants

was treated as unique, with its own special history. Relatively few studies contained any attempts to be analytical and to identify underlying phenomena or processes that might explain some of this myriad diversity. An exception was Philip Darlington's observation in 1943 that larger islands contain a greater number of individuals, and a greater diversity of species, than smaller islands, the species diversity increasing by a factor of 10 for every doubling of island area.

Although science always tries to provide a unifying theory that can integrate a mass of data, it can only produce such an analysis once it has developed the tools to do so. It may be significant that such an integrated, synthetic approach to island biogeography only appeared after sophisticated mathematical techniques had been used to analyse biological phenomena in the new field of population genetics. The ground-breaking little paperback book, *The Theory of Island Biogeography* [52], published in 1967, was written by two American biologists: the mathematical ecologist Robert MacArthur and the taxonomist–biogeographer Edward Wilson. Other workers, such as the Swedish worker Olof Arrhenius in 1921, and the Americans Eugene Munroe in 1948 and Frank Preston in 1962, had noted the relationship between the area of an island and the number of species that it contains. But MacArthur and Wilson's book was on a quite different level, for it was a sustained (181 pages of text) exploration not only of the basic concepts but also of the ecological evidence and implications of the theory. The book put forward two main suggestions: that the changing, and interrelated, rates of colonization and immigration would eventually lead to an equilibrium between these two processes, and that there is a strong nonlinear correlation between the area of the island and the number of species it contains. The arguments for these ideas were mathematical, with detailed equations and graphs, and the results were very persuasive. Here, at last, it seemed as though biologists would be able to move beyond the raw data to understand the relationships between the simple biological processes. Even more importantly, in a world increasingly worried about the effects of human activity, the concept of an equilibrium of numbers promised to allow predictions as to what would happen under given circumstances, and so to optimize designs for conservation areas.

Over the years that followed the publication of *The Theory of Island Biogeography*, many papers were written that interpreted individual biota in terms of the theory. These papers were in turn taken as providing such a wide measure of support for the theory that it became almost uncritically accepted as a basic truth. In turn, therefore, results that did not conform to expectations based on the theory were re-examined in search of procedural or logical faults, or for unusual phenomena that might explain the 'anomalous' result. Sometimes they were simply ignored, rather than being seen to cast doubts on the applicability or universality of the theory. Unfortunately, this is far from unique as an example of the way in which new theories can come to so dominate the scientific field that critical evaluation, and even the concept that it may hold some of the truth but not necessarily all of it, is forgotten. This can happen especially either when the field in question has been seen as extremely difficult to interpret, as in the case of this theory, or when the field has been dominated previously by another, equally dominant and intolerant concept, as in the case of the confrontation between the dispersalist and vicariance schools of biogeography.

The story of the rise of the theory and of the later mounting wave of criticism has been told in the fascinating book *The Song of the Dodo – Island Biogeography in an Age of Extinction*, by the American science writer David Quammen (see the Further Reading list at the end of this chapter). It now seems clear that the theory cannot predict equilibrium levels for the biota of any island and that it is valid only in relating island area to biotic diversity. But MacArthur and Wilson nevertheless revolutionized the study of island biogeography, for they led the way in introducing mathematical techniques, and in providing a standard format for analysis and comparison. As we shall see in this volume, the ecology of island faunas and floras is far more fragile than that of the continents. We therefore greatly need to understand them, for, as a result of their number, diversity and role as natural laboratories for evolutionary change, they contain a high proportion of the biotic diversity that we now desperately need to conserve. For example, although New Guinea contributes only 3% of the world's land area, it contains some 10% of its species of terrestrial organism.

Biogeography Today

As explained in this chapter, the first aspect of biogeography to be recognized by scientists, during the 18th century, was its ecological component. Inevitably, its historical component could become recognized as a field of research only after the scientific community accepted the reality of evolution itself in the middle of the 19th century. Until quite recently, these two approaches to biogeography remained largely independent of one another. Ecologists began with the study of living species or subspecies, and with the factors that control, or alter, their patterns of distribution today. But if they attempted to extend their conclusions into the past, they soon ran into difficulties. This was because they were working at a scale of detail, both in geographical terms and in taxonomic terms, that could not be perceived in the historical record. Only in the study of the comparatively recent past, such as the Ice Ages, could the biogeographer be confident of the ecological preferences of the organisms under study, because they were closely related to those alive today. Only for that period of time was the fossil record sufficiently detailed for the palaeontologist to be confident of the nature and taxonomic level of the changes that were taking place. And only for that period of time were the records of changes in the environment sufficiently detailed, in both time and space, for it to be possible to make plausible correlations between the environmental changes and any biogeographical changes. For the more distant past, it was not possible to establish precisely when any evolutionary changes had taken place, and therefore it was impossible to correlate these to any ecological changes that might have occurred at that time.

The lack of integration between historical biogeography and ecological biogeography continued until the 1990s, when it was rapidly transformed by developments in two areas of study. The development of techniques of analysis of the details of the molecular structure of their genes provided an enormous quantity of data on the molecular characteristics of the organisms (see Chapter 6), showing precisely how they differed from one another. At the same time, as it became easier and cheaper to obtain this data, the number of organisms whose molecular characteristics had been analysed rapidly increased. So great was the quantity of data that it would have been impossible to make any sense of it, had it not been for the parallel development of techniques of computer analysis. This, together with the use of cladistics, made it possible to work out the patterns of relationship between the different members of a group. But, even more importantly for biogeographers, these techniques made it possible to show precisely when two different lineages had diverged from one another. Now, for the first time, biogeographers could start to correlate the patterns of evolutionary divergence of the organisms and the patterns of change in the environment, over the timescales with which historical biogeographers worked. These advances have also made it possible to discover when related groups that live in different biomes diverged from one another. This in turn allows us to start to work out the history of the assemblage of the different components of the biomes – again, permitting an important linkage between historical and ecological biogeography (see Chapter 8). It now seems likely that the combination of cladistics and molecular analysis will allow us to solve many of the current problems in biogeography. So, today, the old distinction between the two approaches has largely disappeared. At last, it seems that biogeographical research is revealing, with increasing scope and detail, a single, consistent story of the history of the biogeography of the world today.

Ecological biogeography has also raised its level of research from the mainly local to larger scales of analysis, and is developing rapidly both in its establishment of a firm theoretical base and in its practical application to current global problems. In 1995, James H. Brown of the University of New Mexico proposed a new type of research programme, which he termed **macroecology** [53], dealing with ecological questions that demanded large-scale analysis. Range changes in response to climate change, patterns of diversity and analysis of ecological complexity all lend themselves to statistical and mathematical analysis on a larger scale than normally used by experimental ecologists. This is not a new discipline, but a fresh approach to old problems, and one that is increasingly appropriate in days of rapid global change.

During the latter part of the 20th century, it was progressively recognized that the human impact on the landscape was virtually ubiquitous. Throughout the world, landscapes have been so

modified that they effectively can be considered *cultural landscapes*, a term that became increasingly used from the 1940s onward [54]. An entirely new discipline of **landscape ecology** appeared, pioneered by Richard Forman of Harvard University [55]. One of the main emphases of the study on the ecology of cultural landscapes was the predominance of fragmentation, as reflected in the title of Forman's classic book, *Land Mosaics*. Landscape ecology needed to examine the ecological consequences of habitat fragmentation on animal and

plant populations (Figure 1.8), and so this discipline began to develop in a new direction, leading to the concept of **metapopulations**. A metapopulation consists of a series of separated subpopulations between which genetic exchange may be limited. Clearly, this is an important area of research in the study of gene flow in populations, and hence in the process of evolution. Not just populations but whole communities are fragmented as a result of human agricultural and industrial activities, so one can conceive of metacommunities of organisms
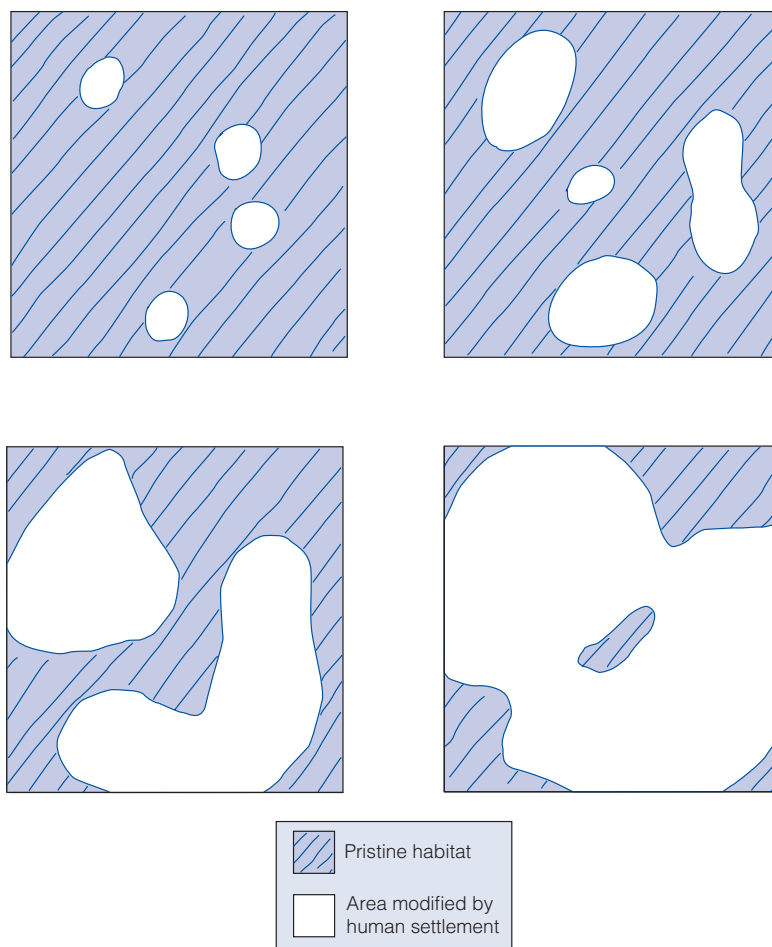

Pristine habitat

Area modified by human settlement

Figure 1.8 The impact of human settlement and disturbance on a natural habitat is progressive, leading to an increasing degree of fragmentation of the original habitat into isolated units. For some species, especially those animals that are of limited mobility and those plants that have limited seed dispersal, this can result in reduced gene flow. Genetic impoverishment can lead to an increased risk of local extinction, and the loss of such a species is not always compensated for by reinvasion.

that can be highly complex in their spatial dynamics [56]. This is precisely the type of problem one can assign to the area of macroecology.

One of the problems presented by habitat fragmentation and the development of metapopulations is the increased danger of genetic isolation and impoverishment, leading to possible extinction. Biogeographical studies thus come into contact with the discipline of wildlife conservation [57]. Many aspects of biogeographical research have a direct bearing on conservation, from the study of biogeochemical cycles and the monitoring of changing ranges of species in response to climate change, to the recording of the spread of invasive organisms and their impact on native populations. Thus, a growing body of work can be classified under the heading of **conservation biogeography** (see Chapter 14).

Biogeography today can be divided into three major areas. The first, and perhaps best understood, is that of the great continental areas, whose varied biota are continually changing as they evolve, compete and spread to new areas or become extinct.

This knowledge is helping us to confront, understand and cope with our need to conserve these biota. Secondly although there is an equally pressing need to conserve the faunas of the oceans, we are still in the process of even making an inventory of these faunas. We are now increasing our understanding of the oceans' basic patterns of biogeography and, especially, the nature of the environmental stimuli in an aquatic environment to which its animal life responds by evolutionary change. Thirdly, the enormous diversity of islands, each with a unique biota and history, provides a huge series of natural laboratories for our efforts to understand the processes of evolutionary change and the interactions between organisms in a developing ecosystem.

Biogeography today is thus developing both in its theoretical aspects and in its practical application to modern environmental problems. The remaining chapters of this book review our knowledge and techniques of analysis in biogeography today and identify those areas in which important new developments seem likely to take place.

Summary

1 Examining the history of biogeography helps us to understand the nature of the subject today and how biogeographers carry out their work within the current framework of the theories and assumptions of science and society.

2 The early biogeographers were inevitably preoccupied with the immense task of documenting the distributions of animals and plants on the surface of the planet, and trying to establish how these vary according to latitude, altitude and climate.

3 Increasing knowledge of the fossil record showed how the world's faunas and floras had undergone great changes, which could only have taken place over long periods of time. It was difficult to reconcile this with the doctrines of the Church that life on Earth was a comparatively recent creation and that species were unchanging. By providing a plausible explanation of how and why these changes might have taken place, Darwin's idea of evolution by natural selection was a major step in getting the general public to accept this very different view of the world's history.

4 However, as long as it was assumed that landmasses had always been stable in their positions, it was still very difficult to understand the patterns of life in the past, and biologists were driven to

sometimes bizarre theories to explain these. It was only in the 1960s that the discovery of plate tectonics provided the key to understanding how the Earth's geography, as well as its living cargo, had varied through time.

5 Finally, two advances have transformed the whole field of research into the history of organisms and of their patterns of distribution. The first was the conception and acceptance of cladistic taxonomy. This gave biologists a rigorous system for establishing patterns of relationship that could then be used as a framework onto which patterns of distribution could be applied. Secondly, the use of molecular methods has provided biologists, for the first time, with reliable procedures for the analysis of relationships and the dating of divergences between lineages.

6 Meanwhile, ecological biogeographers were establishing a framework for the description of the varied types of vegetation, and were progressively coming to understand how climate affects the form of plants and how, together with the local geology and soil, it also affects the development and succession of plant communities.

7 Because of the alien nature of its environment, the study of marine biogeography is far more difficult

than that of the land. The general outlines of the distribution of shallow-sea marine faunas were documented in the 18th and early 19th centuries, along with the recognition of faunal zones controlled by latitude and depth. But the huge extent of the open oceans made it difficult to understand the dynamics of the annual changes in their faunas and floras until the recent introduction of satellite-based mapping and modern techniques of marine exploration. Even today, we have much to learn about the organisms of the oceans and about the processes that underlie their biogeography.

8 Islands, too, posed problems for the biogeographer because each is a unique natural 'experiment' in the evolution of floras and faunas. The radical concepts of *The Theory of Island Biogeography*, published by MacArthur and Wilson in 1963, introduced a major attempt to provide a framework for understanding this bewildering mass of data. The subsequent history of attitudes towards the theory, from initial almost uncritical acceptance through subsequent criticism and evaluation, provides a fascinating study of science at work today.

9 The introduction of molecular methods of analysis of the genetic basis of the taxonomy of living organisms, and their application to a large and increasing number of species, together with the development of powerful methods of computer analysis of the resulting mass of data have allowed us to extend our application and understanding of ecological biogeography into the past, blurring the old distinction between ecological and historical biogeography.

10 Biogeography today can be divided into three major areas of research which differ fundamentally in the nature of their environment and of the problems under investigation. These three are continental biogeography, marine biogeography and island biogeography.

Further Reading

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