BIOGEOGRAPHY

An Ecological and Evolutionary Approach

Ninth Edition

C. Barry Cox | Peter D. Moore | Richard J. Ladle

WILEY Blackwell

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Preface

To interpret the phenomena of biogeography, we need to understand many different areas of science – for example, evolution, taxonomy, ecology, geology, palaeontology and climatology. Although each area makes its own individual contribution, a textbook such as this therefore has to cover a similar scope and must be suitable for students with a variety of different backgrounds. This is particularly necessary today, when the coming-together of molecular methods of demonstrating relationships, and of the cladistic technique of imposing pattern upon the resulting data, is revolutionizing our understanding of biogeography.

Many changes have taken place in the study of biogeography over the 43 years and nine editions that have now passed in the life of this textbook. Back in 1973, the depth of the problem that our species poses for our planet's biota and climate was hardly appreciated, and the 'greenhouse effect' was still mainly a concern for horticulturalists rather than a worry for the whole planet. It was not until the 1980s that the evidence that the Earth's climate is changing, and that this is increasingly the result of human activities, became steadily greater. In interpreting the interaction between the physical world and the living world, and of the human impact on each of these, biogeography clearly has a major role to play in assessing the likely results of climatic change and in suggesting how best to counter them. As climatic change renders old crop areas less fertile, will it be possible to find new areas to replace them – and, if so, where? Or shall we have to find new varieties of plant, adapted to these new conditions – and, if so, where are we likely to find them? The increasing urgency of these questions led to a great increase in the amount of research on biogeography during the 1990s.

But it is not only our foodstuffs that are threatened by climate change; it is the diversity of life that inhabits environments that is shrinking and disappearing. This is not just a concern for the curators of museums and herbaria, for we are also becoming aware of the extent to which we rely on this diversity for new drugs as well as for new food-plants. So we became aware of the need to census this diversity, in order to appreciate where it is greatest and where it is under particular threat. Which habitats are threatened, where, and how should we attempt to preserve them?

Until recently, biologists were unable to document the dates at which new species appeared and diverged from one another. As a result, it was impossible to be sure of the relationship between these biological processes and events such as the separation of units of land by plate tectonics or climatic change. The rise of molecular methods of investigation that provide reliable dates for the times of appearance and divergence of species has given us new confidence in the accuracy of our biogeographical analyses, based on rigorous techniques of analysis of relationships in time and space, using increasingly complex and sophisticated computer algorithms. 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 and of the processes that led to it.

This understanding may have come just in time, for it is clear that it is imperative that we conserve what is left of the natural world of our planet. In this new edition, we welcome the contributions of Richard Ladle, who has not only helped in the revision of some previously existing chapters, but also contributed a new chapter on 'Conservation Biogeography' (Chapter 14). In this chapter he outlines the startling new techniques that are now becoming available for gathering and integrating information on the distribution of species. It is up to the new generations of biogeographers to find ways to use this increasing wealth of data to construct clear arguments that will convince the (sometimes reluctant) politicians and businessmen of the validity of their case. Only then can the vital step of transforming scientific knowledge into potential action take place. We can only hope that this will happen sufficiently soon to save the living world of our planet as we know it today.

After all these years and editions, this is probably the last time that Peter Moore and I will contribute to this book; it has been a long and happy collaboration. We welcome Richard Ladle as the first of a new group of biogeographers who will, we hope, take the book into the future. It is also appropriate now to remember that the first edition was the work, not only of Dr Peter Moore and myself, but also of our colleague Dr Ian Healey, who sadly died before that work was published.

Barry Cox

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As noted earlier, biogeography involves the study of a very great range of data in the fields of both earth sciences and biological sciences, and it is nowadays impossible for any one person to cover all the literature in such a huge area. Our task in trying to identify the significant new references has been greatly aided by many people, but we would like to thank in particular the following:

Professor David Bellwood, School of Marine and Tropical Biology, James Cook University, Queensland, Australia

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Chapter 1

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.

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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