BIOGEOGRAPHY

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Summary

Biogeography is a natural science that deals with the study of the earth's plant and animal distribution patterns in geographical space, both in terms of the present day and also in the context of their evolution and development over time. It has deep historical roots in the identification of the spatial relationships of organisms, while its fundamental principles embody those of the theory of evolution and the ecosystem concept. The most significant theorists of biogeography in the past have been Carl Linnaeus, Alexander von Humboldt and Charles Darwin, while more recently the work of, for example, Robert MacArthur and Edward Wilson has proved instrumental in developing thinking as to how organisms achieve and maintain their ranges. Over longer, geological, time scales, the key principles of biogeography include the influence of changing global geography, especially through continental drift, on biological distributions. In the context of the present day and more recent past, climate and climatic change are regarded as the most significant factors determining the distributions of organisms. Biogeography is applicable to a wide range of practical environmental problems. In particular, the discipline has made important advances in understanding issues such as the establishment and management of conservation areas, the prediction of the impact of global climate change on organisms, and on the

management of plant animal communities, including humans, as integral components of ecosystems.

1. Introduction: defining the indefinable

Biogeography is an interdisciplinary natural science with a complex, even cryptic identity that defies definition. In essence, it is the science of the distribution of living organisms and the factors that underlie this distribution. Such a one-line descriptor does no justice, however, to the range of approaches and concepts that constitute contemporary biogeography. Not only is biogeography concerned with spatial patterns in the contemporary sense, but also there is a strong evolutionary component and a concern with changes over time. It is a discipline that leans heavily on several other scientific fields of enquiry, such as ecology, systematics, the environmental sciences, the various branches of physical geography and even, in an applied context, aspects of the social sciences.

As the very word *biogeography* is an amalgamation of two roots, *viz:* biology, broadly dealing with organisms, and geography, broadly based on the description and analysis of distributions, the science has at least two conceptual and philosophical roots. Those approaching biogeography from within the biological sciences study spatial biological phenomena, sometimes from a historical perspective. Such a science considers questions such as: 'where is a particular species (or other taxonomic group) distributed?' 'how did this species achieve this distribution pattern?' and 'what factors determine this pattern?'. The answers are frequently, though by no means exclusively, spatial in nature and may be illustrated in the form of maps, at various scales and for a range of different time periods. Geographical considerations of biogeography tend to adopt a wider range of contexts. For example, geographers consider the analysis of the multiple functional roles of the many components of the biosphere to be biogeography. Geographers are also more concerned with applied aspects of the discipline, for example the impact of people on biodiversity. Finally, geographers tend to restrict their consideration of temporal factors in biogeography to what can be thought of as *ecological time*, i.e. relatively short periods of change over decades up to millennia, whereas the more biologically-minded frequently consider long-term evolutionary changes over periods encompassing deeper geological time.

Ecology and biogeography are closely related, interdependent and are easily confused because of the overlap regarding subject matter. There are, nevertheless, some distinctions that can be drawn and it is helpful to note these. While biogeography is concerned with distributional patterns and their explanations, including those with a historical element, ecology is more concerned with factors controlling abundance in the present day or recent past. While biogeography deals with a range of taxonomic groups, from species to phyla, ecology is more generally focused on the species level and developed through a consideration of interactions between individuals within a population and between populations of different species within a community and their environmental relations. Scale is also a defining feature, since ecologists tend to study the relatively small geographical scale encompassing distribution of populations and communities, while biographers may cast their distributional nets wider and account for distribution at regional, continental and even global scales.

There is, therefore, no single, holistic, view of biogeography and the angle of approach, which may differ fundamentally depending on which of the two roots, biology or geography, is the basis for analysis, and can be highly individual, even eclectic. A glance at the contents pages of any recent issue of the *Journal of Biogeography*, confirms that this science is as diverse as the organisms that form the basis of its subject matter. Examples of these various approaches are explored below.

2. History of biogeography

In a sense biogeography is as old as the human species itself, for in their quest for survival our earliest ancestors must have asked and answered questions such as 'where can we find the plants and animals that we need for food?' and even 'where do dangerous animals live and what can we do to make them go away?'. Both of these questions are legitimately biogeographical, although of course there was no formal science and scientific method in the Neanderthal days. Exploring the later, formally documented, history of the discipline is hampered both by the large number of different approaches and by the simple historical expedient that the use of the term biogeography is itself is a relatively recent phenomenon. Arguably, the various distinctive approaches have developed their own histories, but in line with most other reviews of the development of biogeography, it is convenient to rationalise these into a more manageable number of major themes. Although expanded upon and further developed below, we can recognize two main sub-fields in biogeography, *viz:* a) spatial and historical biogeography and b) ecological biogeography and their respective histories, to a certain extent intertwined in more recent years, are considered here separately.

2.1 Development of the spatial tradition

Without doubt, this is the oldest field of inquiry in biogeography, since fundamental information on the distribution of plants and animals has been a requirement for human survival since the dawn of our existence. The question as to the first formal publication dealing with these matters is more elusive. Chi Han's flora of southern China, published in the fourth century A.D., is possibly the earliest example of a tradition that is still practised, i.e. the formal inventorisation of the plant (or animal) species occurring within a defined geographical area. Such a treatise is an attempt to answer the question 'where?' in regard to distribution of organisms, but a more interesting challenge is to address the questions 'why?' and 'how?'. For this more analytical approach we had to wait more than a millennium.

Carl Linnaeus (1707-1778) was a Swedish botanist whose prolific output was highlighted by the publication of his *Systema Naturae* in 1735. In this short work (it runs to only seven folio leaves), he outlined a classification of the plant kingdom, much of which has subsequently been rejected. At the core of the work, however, lies the binary nomenclature of genus and species still in use and of considerable significance to biogeography. Linnaeus also recognised the biogeographical constrasts between one geographical region and another and sought explanations for these differences.

Alexander von Humboldt (1769-1859) has been called the father of physical geography and, indeed, of phytogeography. There is much of substance to the published work

emanating from his research expeditions, in particular to South America, influencing modern thinking about the natural world. His best-known work is *The Cosmos* (1848-49) and this certainly helped to popularise science at the time, but it was his expedition to South and Central America with a French botanical colleague, Aimé Bonpland, that established a benchmark for biogeographical observation and reporting. Humboldt and Bonpland spent five years, from 1799 to 1804, in Central and South America and covered almost 10,000 km on foot, horseback and in canoes. In addition to a truly enormous collection of previously undescribed plant specimens, they made supporting observations of precise geographical locality and of meteorological conditions. The work was eventually published between 1805 and 1834 as a 23 volume series entitled: *Voyage de Humboldt et Bonpland aux régions équinoxiales du nouveau continent, fait en 1799-1804* and which included an *Essai sur la geographie des plantes*.

Arguably the greatest contribution, not only to biogeography, but to natural science as a whole, dates to the 19th Century and probably also owes its existence to a lengthy expedition voyage which, in part at least, focused on South America. The British Royal Naval ship *HMS Beagle* had on board a naturalist called Charles Darwin, whose 1859 first edition of *On the Origin of Species by Natural Selection* eventuated a massive, if at first controversial, leap forward in our understanding of how organisms evolve in time and space. It is now known that other scientists, in particular Alfred Russel Wallace (1823-1913), had thought along similar lines; indeed Darwin and Wallace presented their concepts jointly to the Linnean Society in London in 1858. It is conventionally Darwin, however, who is credited with formalising the twin ideas of natural selection and decent with modification that underpin so much of contemporary thought in biogeography. Wallace's own two volume *The Geographical Distribution of Animals* (1876) was also influential and it espouses many of the fundamental principles of modern zoogeography, for example the evidence for former land connections in the common presence of organisms not adapted for long distance dispersal.

Arising out of the search for an explanation as to the factors underlying distribution patterns of organisms came the recognition that historical factors play an important role. In the eighteenth century, natural scientists were preoccupied with finding room for the newly described organisms on the biblical Ark but soon, especially under the influence of the British geologist Charles Lyell (1797-1875), biogeography developed a sense of change through time. The early twentieth century saw many important developments, such as the 'age and area' hypothesis of J.C. Willis in which he hypothesises that the older the species the greater the geographical area it should occupy. Around this time, too, Alfred L. Wegener (1880-1930) was publishing the first four editions of his book *Die entstehung der Kontinente und Ozeane* including the English edition entitled *The Origin of Continents and Oceans*. Most natural scientists, however, remained sceptical as to the veracity of the central idea in this work – that of continental drift. In the early 1960s, geophysicists discovered a mechanism, plate tectonics, that could explain the movement of continental landmasses and the 'revolution' in the earth sciences was underway. Biogeography did not escape the ramifications of this essentially geophysical theory, for it is clear that mobile land masses act as rafts for plant and animal species, reordering the distribution patterns in the process. Out of this rose the concept of vicarianism, in which speciation primarily occurs in response to the development of barriers to dispersal imposed by, among other processes, continental

drift. This elegant model is now accepted as working in concert with long-distance dispersal to explain global biogeographical patterns, but for a while in the 1970's proponents of vicariance, led by the Venezuelan Leon Croizat, waged a virtual crusade against the establishment view. The *bête noire* of the vicarianists was Darwin himself. No longer alive to defend theories based on the primacy of dispersal and, in any event, evolved without knowledge of plate tectonics, Darwin's defence was taken up vehemently by others, in particular Ernst Mayr and GG Simpson. The modern view is that both dispersal and vicariance are viable, indeed necessary, mechanisms with which to explain biogeographical patterns.

2.2 Ecological biogeography

The spatial tradition in biogeography views distributions from the point of view of taxonomy and defines patterns on the basis of, for example, species or higher order taxonomic group. There is no concern with relationships at the organism, population or community level and, although the fundamental influence of the physical environment in determining the presence or absence of particular groups is recognised, the principal determinants are seen as geological and evolutionary history. Nevertheless, many biogeographers take a less long-term view of distributions and work with time only insofar as it operates at the individual, population and community level, i.e. ecological as opposed to evolutionary time. It is here that the sciences of ecology and biogeography overlap and integrate to a greater degree.

Ernst Haeckel is documented as the first scientist to formally apply the term *ecology*, in his 1876 *History of Creation*, in respect of the science dealing with relationships of organisms to their surroundings. The identification of ecological units, organisational elements akin to the taxonomic units of the systematist, underlies subsequent development in ecology, together with documentation and measurement of the processes that maintain these units. By far the most influential of these various units recognised was the *plant community*. Prominent proponents of the idea included the American, Frederic Clements, and the Englishman, Arthur Tansley. An important concept emerging from their work, and that of others in the first part of the twentieth century, was the idea that ecological communities operated through a complex series of interactions and that such interactions are dynamic over time. Thus was born the family of theories around the ideas succession and climax. Tansley is best known for his 1935 coining of the term *ecosystem* to embody the set of organisms, their interrelationships and the environment in which they prevail. To this day it remains the fundamental unit of the science of ecology and has been adopted by many geographers as a convenient tool by which to interpret the biological part of physical geography. A significant inclusion here is the consideration of humans as an integral component of the ecosystem, a key concept in the establishment of the more applied focus for biogeography that characterises many contemporary approaches.

Biogeographers have long fostered an interest in the biota of islands – Darwin and Wallace for example formulated many of their ideas based on the study of plants and animals on island archipelagos. In 1967, two American biologists, Robert MacArthur and Edward Wilson formulated a general theory of island biogeography that was almost intoxicatingly simple. Equilibrium theory has not survived the rigours of scientific

testing completely intact but the search for a unifying set of explanations for the fate of populations in isolated islands, be they truly oceanic or 'habitat', has led to other developments in biogeography. Among the most important is the emphasis on small populations of species threatened with extinction.

Concern with the past is not the exclusive preserve of those who follow the spatial tradition of biogeography. It was accepted even during the nineteenth century, due to the efforts of the likes of Louis Agassiz, that the earth's environment had changed over time. Some of the most remarkable shifts in environmental conditions appear to have occurred during the last two million years or so, the Quaternary period, when the great ice sheets of the northern hemisphere in particular, expanded and contracted in response to fluctuating climate. It became obvious that plant and animal communities had been markedly impacted by such changes. Through the development of various so-called palaeoecological techniques, in particular pollen analysis, it became possible to reconstruct the biogeographies of the past with increasing degrees of certainty. Pioneers of this approach included the Cambridge botanist Harry Godwin and the Swede, Lennart von Post and this theme in biogeography is now very popular indeed. Tracking the changes in distributions over the later Quaternary may also play a vital role in the development of more accurate predictions as to the role of climate changes in future biogeographies.

3. The major approaches to biogeography

The major approaches to the discipline are classified broadly into those rooted in the spatial tradition and those associated with a more ecological theme, as shown in the schematic representation of Figure 1. Although there are obvious connections and inter-dependencies between many of the themes represented on the schematic, it is convenience to discuss the various elements separately. The applied nature of biogeography is illustrated in the three shaded boxes at the base of Figure 1; these elements are discussed subsequently.

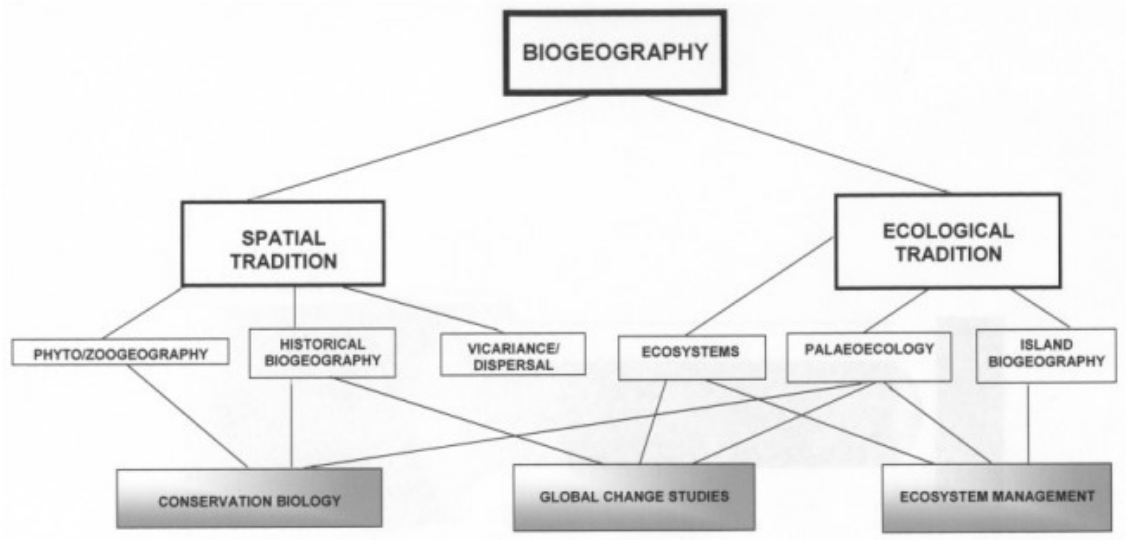

Figure 1: Themes in biogeography as discussed in the text. The fundamental division is broadly between the spatial and ecological traditions of the discipline.

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Biographical Sketch

Mike Meadows was born in Liverpool, United Kingdom, in 1955. He attended St Mary's College, Crosby before completing a first class BSc Honours degree in Geography and Biological Sciences at the University of Sussex. He went on to do his PhD in the Department of Geography at Cambridge University under the supervision of AT Grove, the topic of his thesis being: 'Past and Present Environments of the Nyika Plateau, Malawi'. In 1983, Mike Meadows moved to South Africa to take up a lectureship at Rhodes University in Grahamstown and three years later transferred to the University of Cape Town, where he is now Associate Professor and Head of the Department of Environmental and Geographical Science. His research, published in more than seventy refereed articles, is mainly in Quaternary palaeoecology of southern Africa and, increasingly, in the interdisciplinary field of land degradation and desertification. Mike Meadows is editor of *The South African Geographical Journal*, President Elect of the Society of South African Geographers and Secretary of the Commonwealth Geographical Bureau.