

————— PART II —————

Biogeographic patterns

Introduction

The raw material of biogeography is the distribution of species in space and time. Lists of organisms in different areas must be accumulated before one can proceed to the study of the more intractable problems of how they got there. However, to quote from MacArthur (1972), "To do science is to search for repeated patterns, not simply to accumulate facts." The existence of repeated non-random patterns in species distributions implies the operation of some general causal processes and from an understanding of these one can work towards a reconstruction of the history of life that can explain the present day distribution of species. However, there are serious questions that need to be addressed about the very nature of biogeographical patterns, and there is even ambiguity over the term 'pattern'. An important point raised by several contributors to this book is that success in pattern recognition seems to require that we do not use all the apparently relevant data. Latitudinal diversity gradients (Chapter 3) and species-area relationships (Chapter 4) are examples. How do we decide which data are useful? Any satisfactory explanation of the patterns must encompass both supporting and conflicting data. Rosen (Chapter 2) sets out the philosophical background to these problems with respect to historical patterns in particular, but the ideas are relevant in all areas of biogeography.

PRIMARY PATTERNS

The study of patterns is primarily descriptive and the documentation of patterns is relatively easy. Observations and rigorous quantitative studies are followed by comparisons among features of different natural systems or between natural systems and theoretical models. These can lead to the delineation of species associations in replicated physical environments, along natural environmental gradients or along statistically-derived multifactorial gradients. There may, hopefully, be a relatively limited number of general patterns to be discerned. A major problem in both biogeography and community ecology has been to distinguish determinate patterns from random ones. The patterns may be real but simply a statistical property of the system rather than the end point of the action of some deterministic processes. Were all observed patterns of this random type, there would be no real controlling processes and we

would be unable to understand and predict. Acceptance of some pattern-seeking and theoretical studies over the past two decades has certainly been too enthusiastic and uncritical (May, 1984). In reaction to this, it is now becoming fashionable to test for the existence of patterns of both biogeographic distributions and species compositions of communities against null or neutral hypotheses, or models that involve only stochastic processes to account for the observed pattern. When comparative studies of natural systems yield patterns beyond those in the neutral models, one can be more confident of their existence. Brown (Chapter 3) points out that it is relatively easy to document highly non-random geographic patterns in species richness and there are many problems with the use and derivation of the null models currently employed (Southwood, 1987; and see Chapter 9). Nevertheless, the use of such techniques has been valuable in introducing a degree of rigour to pattern analysis which has hitherto been absent, even though they have been largely confined to the analysis of insular distribution patterns (Brown and Gibson, 1983; Strong *et al.*, 1984b).

Spatial distribution patterns of species are observed and documented on a range of scales. Early naturalists discovered distinctly different assemblages of species around the world, and as data were gathered on these patterns, six major biogeographic realms became recognizable. Each realm was separated by a major physical or climatic barrier to dispersal and there was generally a high degree of taxonomic consistency at the familial and generic levels within regions, but marked differences from one region to another. Although there are now disagreements with respect to the exact boundaries, there is broad agreement on the usefulness of recognizing these regions (Pianka, 1983). Finer scale partitioning of the globe into floristic regions or provinces has been based on the distribution of endemic taxa as discussed in Chapter 5. At an even finer level, distribution patterns can be documented by habitat and finally microhabitat, e.g. plant distributions on soil types (Chapter 5). Such patterns are ultimately the result of physical variation in the environment and the species adaptations to it. The adaptations in turn can lead to recognizable geographical patterns in morphological traits, such as those formulated in Bergmann's, Allen's and Gloger's rules (Lane and Marshall, 1981). Species can themselves impose patterns on other species, e.g. through species interactions (Chapter 9), modification of the habitat through bioturbation, or space occupancy by sessile or colonial species. If, as is believed by many community ecologists, assembly rules govern the structure of most communities, then these could also lead to recognizable patterns of both composition and functioning (see May, 1986 for a recent review) which in turn will affect the distribution of species amongst different communities. Recognition

of such patterns does depend on a stricter framework of definitions for the various levels of species assemblages and for the ecological community itself than has hitherto been the case. Such a framework has recently been proposed by Giller and Gee (1987).

Temporal patterns in the composition of the biota of an area can also be documented, such as patterns of increase in species richness following a major disturbance (Chapter 3) and widespread evolutionary increases in species diversity (Chapter 8). Extinction patterns, such as evolutionary relays (successive, abrupt or gradual replacement of taxa occupying the same adaptive zone) and periodicity of mass extinctions can also be identified (Chapter 8). As mentioned earlier, there is a philosophical problem in defining what constitute historical patterns and Rosen develops the theme of a biogeographical system approach which attempts to identify processes involved in the maintenance, change and origination of species distribution patterns in general, and historical patterns in particular (Chapter 2).

SECONDARY PATTERNS

At a primary level, the patterns outlined above are not of course absolute in the sense that they are only inferred from the collection data of the taxa concerned and from the fact that the distribution of the taxa themselves is not static. This creates its own set of problems and biases (Chapters 8, 11 and 14). At a secondary level, i.e. from the analysis of primary distribution data of many species, the term pattern can be used to describe species richness or nested sets of endemisms over various scales and ultimately the biogeographic realms mentioned above. In Chapter 3, Brown describes the major features of geographic variation in the present day diversity of species and attempts to evaluate the various hypotheses proposed to account for these patterns. Most of the patterns of diversity can be classified as geographic gradients, as the number of species varies relatively continuously with geographic variation in physical features such as latitude, elevation, aridity, salinity and water depth. However, as Brown makes abundantly clear, the natural world is never constant, and any attempt to explain the spatial gradients in diversity must also consider the magnitudes of the most recent disturbances to the system, the time since these events and the dynamics of extinction, colonization and speciation. Brown and Gibson (1983) have pointed out that the history of life has resulted from a series of unique events, so taxa are products of unpredictable histories. Thus both historical events and ecological processes must be part of any complete explanation of patterns of species diversity. In this light, diversity patterns are used in some palaeogeographical reconstruction methodo-

logies (Chapter 14) where interpretation of extant patterns are used to infer historical events from diversity patterns of fossils, e.g. latitudinal patterns can sometimes give distance constraints on hypothesized movement of biotas.

Species diversity patterns are concerned mainly with assemblages of species at a particular point in space, but the distribution of specific taxa provides patterns which also require a causal explanation and can in turn help unravel what has happened in the past. No species of animal or plant is truly cosmopolitan, although some are very widely distributed on a global scale. Such species may be eurytopic with broad local, as well as broad global, distributions, but others may be stenotopic with patchy local distributions within their broad global distributions. Species with restricted ranges are termed endemics, are generally stenotopic with narrow ecological requirements and are often morphologically specialized. Endemics are of two kinds. They may be the result of *in situ* speciation (neoendemics) or may be relicts of species once more widely distributed but which have since become extinct elsewhere (palaeoendemics). Patterns of endemism, like species diversity patterns, are controlled by both historical and ecological processes. In the short term, endemism is largely governed by ecological processes such as food availability, predator-prey interactions and competition, coupled with extant physical factors such as temperature, precipitation and soil type. The primary determinants of endemism are, however, the historical processes of plate tectonics and associated eustatic changes in sea level, and major climatic fluctuations which all isolate or reassort distributions. Clearly, endemism is also a matter of scale and how endemism is explained depends upon the scale applied. If a species is limited in its distribution to two islands, it is endemic to neither but endemic to the two islands together. Endemism can therefore be viewed as a series of nested sets, the final nest incorporating the whole world which has one hundred per cent endemism. We can study endemism at one level in relation to ecophysiological processes and adaptation as reviewed in Chapters 5 and 6. At a historical level however and particularly in the case of the cladistic biogeographic method, in which only endemic taxa provide information (Chapter 12), the historical relationship of geographic areas is determined largely on the basis of shared endemic taxa or sister taxa.

Rarely is the nature of the endemic taxa considered. Are they old taxa gradually becoming extinct through the effects of changing climatic or competitive conditions (palaeoendemics), or new taxa gradually expanding their range (neoendemics)? The biogeographic implications are quite different. Two or more areas, which share taxa endemic to them alone, are generally assumed to be more closely related (more recently

vicariated) to each other than they are to other areas. If the endemic taxa concerned are neoendemics, then the assumption is valid. If the endemics are palaeoendemics, the assumption may not be correct. The taxa may once have been more widely distributed, but through differential extinction may now occur in some, but not all of the areas in which they once occurred. The areas now sharing the endemic taxa will not then necessarily be the most recently vicariated. Insufficient attention has been paid to this problem and progress will be made only through a better understanding of the nature of endemics.

As mentioned above, endemism results from a number of interrelated factors. It has long been recognized that isolation, both temporal (the greater the age of isolation the greater the time for speciation) and spatial (the greater the distance between gene pools the lower the genetic interchange) is important in producing endemics. There is also, as pointed out in Chapter 5, a broad relationship between the number of endemics in an area and the size of the area. This, however, may simply be an expression of the relationship between the number of species in an area and the size of the area (the species–area relationship) which is discussed in Chapter 4. Major (Chapter 5) also notes that endemism generally follows the same latitudinal trend as species richness and indeed may account, to a greater or lesser extent, for the overall global diversity.

TERTIARY PATTERNS

Species–area relationships can be considered as tertiary level patterns, which describe the relationship between secondary level data, i.e. contemporary species richness, and non-biotic data or size of area harbouring the species. As discussed in Chapter 4, the centre of distribution and the spread around the centre are different for each species investigated and one would, in general, expect larger areas to contain more species than smaller ones. But the species–area relationship is not viewed simply as a reflection of these different distribution patterns, *per se*, but as a real result of some higher level, non-random processes that lead to predictable relationships between species number and area and impinge on the structure of ecological communities. The species–area theory has also been used as a link between ecology and geology (plate tectonics and eustasy), in order to provide an insight into historical patterns of species diversity and extinctions (Chapter 8). For example, in the Permian crisis, half the invertebrate families are thought to have become extinct, most noticeably amongst shallow water marine biotas. At this time the continents coalesced into Pangea, thus decreasing the area of continental shelf through a reduc-

tion in the periphery of continents and in sea level (Gould, 1981). The ecological-historical combination is again highlighted and Williamson (Chapter 4) points out that the importance of dispersal, evolution and environmental heterogeneity on the patterns of biogeographic distribution all come together in the species–area effect. The species–area effect is also viewed by Marshall (Chapter 8) as the most important unifying concept in understanding extinction dynamics because it is applicable to and apparent in both living and fossil biotas.

PATTERN-GENERATED HYPOTHESES

Patterns are often explained by reference to inferred processes (constructing logical and realistic scenarios of how patterns and process might be linked – hypothetico-inductive) or by deduction (through the acceptance of an underlying process of a theoretical model as the causal explanation of the pattern – hypothetico-deductive). The problems of these approaches, their relation to model building and testing and the influence of our perception and use of the approaches on our understanding of species distribution patterns is addressed in Chapter 2. Much of the study of biogeographic patterns, especially historical ones, has necessarily been descriptive or narrative and the inherent problems in this scientific approach have been widely discussed. Modelling and hypothetico-deductive approaches are likewise not without their problems, especially when the assumptions take on the role of fact for higher level models without adequate testing and when the patterns derived from the models become transformed into processes. These aspects of modelling are also explored in Chapter 2. To the historical biogeographer, the repetition of similar patterns of distribution by unrelated taxa is highly significant, since it suggests a common process, or processes. The sequence of historical events leading to the observed common pattern may be hypothesized after an examination of the distribution of sister taxa of monophyletic groups, i.e. the areas sharing the most closely related, and hence most recently evolved, taxa, will be the most recently vicariated (separated). The analysis of patterns and the significance of endemism and phylogeny in the reconstruction of historical processes is the subject of Part IV of this volume.

In biogeography, the experimental approach to process derivation is largely limited to island biogeography (Chapter 15) and to the extension of community ecology concepts into an understanding of species distributions on largely local scales (Chapter 9). This can lead to direct testing of the significance of different processes, but we will leave further discussion of this to Part IV of the book.

THE FUTURE

Knowledge of the distributions of most organisms is weak, as is knowledge of the faunas and floras of many regions of the globe. In this respect, current biogeographic hypotheses are built around very incomplete basic data and we are perhaps trying to run before we can walk. Further documentation of distribution patterns is therefore badly needed. At a more inclusive level, patterns of species richness and species-area relationships are relatively well documented, and further documentation of such data is unlikely to add substantially to our understanding of the patterns. On the other hand, identification of incongruent richness and area patterns is likely to be more instructive in that it will aid the development of robust explanations for the more general patterns themselves. Whilst the species richness and species-area phenomena are very important components in a proximate explanation of species distributions, it is doubtful whether any major breakthrough in our understanding of the ultimate (historic) biogeographic processes will result from these research areas.

A better understanding of the nature of endemism is highly desirable, since endemism is seen as fundamental to the testing of several methods of biogeographic reconstruction. Endemism results from a constellation of different factors and different endemics (palaeoendemics, neoendemics) tell us different stories. In the same way that an understanding of the phylogeny of taxa allows us to perceive the sequence of historical processes, so an understanding of the age of endemics will provide greater precision in historical reconstruction. To date, analysis of endemism rarely addresses this temporal aspect.