Introduction

Dynamic biogeography concerns the study of biological patterns and processes on broad, geographical scales and time scales. These processes can often be understood from processes operative at finer scales, or even from the properties of the individuals within species. In dynamic biogeography, therefore, it is as if one looks down onto the earth from a great height, and at first distinguishes broad-scale patterns and processes. Only later, on closer inspection and only insofar as they help to explain broad-scale phenomena, can one also identify fine-scale patterns and processes. Dynamic biogeography differs from studies of spatial patterns and processes that concentrate on fine-scale phenomena as seen in the perspective of broad-scale phenomena. This latter approach is distribution ecology, or, by analogy with climatology, synoptic ecology, where one looks in the opposite direction, i.e. from local through geographical to global scales. By presenting these two disciplines, dynamic biogeography and synoptic ecology, in this perspective, they clearly represent two approaches to the same phenomena, namely spatial patterns and processes discernable at different scales of variation.

However, these approaches are not separate or contrasting disciplines, and sharp dividing lines cannot be drawn. Instead, it should be realized that any distinction between biogeography and ecology is simply one of scale over which a phenomenon occurs, together with the direction in which one looks. At the operational scales of ecologists and biogeographers, the subjects merge into one another. The distinction between them is artificial and subjective, and potentially hinders our understanding of important spatial biological phenomena.

Although the immediate aim of dynamic biogeography is to describe and explain spatial patterns and processes of taxa, its ultimate goal is to aid our understanding of evolutionary processes. We must integrate information of a great number of properties of individuals, populations,

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and the species as a whole. Thus, it will sometimes be necessary to collect information about an individual's physiology, anatomy, or morphology, whereas at other times information is required about the spatial distribution of genetic traits, behavioural characteristics, or population dynamic statistics. Biogeography should no longer be subsidiary to taxonomic classification, as it has been for such a long part of its history. Instead, it should develop its own problems, methodology, and models, and collect its own data. Yet it must derive many parameters of its models from those in other biological disciplines. In other words, we must formulate our problems so that biogeography acquires a firm place among other biological disciplines. Looking from the viewpoint of the central issue of biology, namely evolution, distribution ranges and the processes occurring within them should not be considered merely as a taxonomic character, but as the outcome of the interaction of a species' biological properties with each other and with the properties of the environment. Characteristics such as shape, size, structure, location and dynamics of species ranges integrate and reflect all these interactions, and can show their relative importance at a particular moment or through evolutionary time.

We still know little about these characteristics; although many hypotheses have been formulated about them, there are few data to test them directly. Biogeographers are often not particularly interested in doing this type of field work; they often leave it to ecologists. Ecologists, for their part, may feel unable to assist or are disinterested in unravelling a great variety of complex factors, operating on inconveniently broad spatial and temporal scales. They prefer to concentrate their analysis on restricted areas, laboratory experiments, or analytical or simulation models.

The lack of testable hypotheses cannot be explained by a lack of activity within biogeography. On the contrary, recent increase of interest in biogeographical problems indicates the opposite. What are currently needed are sound descriptive data, which at a later stage could be analysed to test hypotheses and theories. Sound and detailed descriptions of size, shape, structure, and location of species ranges are particularly lacking, and descriptions of dynamic aspects of ranges are practically non-existent. One can wonder why already existing data in regional and national atlases of European plants still await critical analysis, particularly since analysis of European pteridophytes by Birks (1976) has given such revealing results. The same can be said about maps of Scandinavian carabid beetles, European butterflies, and birds (cf. Hengeveld and

Hogeweg's (1979) analysis of Dutch carabid beetles in the Netherlands and Europe). It seems that despite the existence of plausible explanatory hypotheses, and despite occasional, detailed information on the regional occurrence of some taxa, biogeographical analysis is still not able to take off. What may be lacking is some formulation of more explicit and testable models on processes operative at the spatial scale of, for example, northwestern Europe. We also need to know more about what data-processing techniques are presently available, how they work, what they can solve, and how their results can be interpreted. This book attempts to supply this information, to develop a model of the structure and dynamics of species ranges, and to show the biological and ecological relevance of such studies.

Discussion of the dynamics of species ranges is an important and integral aspect, not only because it reflects a growing interest in processes as well as in patterns, but also because it is only by understanding processes that patterns can be explained. Species ranges are often not as uniform and static as the solid blots on maps suggest. Population density, for example, varies widely over the range, as well as from year to year. The same holds for other ecological parameters such as aggregation of individuals, habitat preference, and numbers of habitats they occupy. Changes in ecological conditions result in large shifts in local numbers of individuals and possibly in other ecological parameters as well, due to differences in net reproduction or to mass movements of propagules or adult individuals. Rainey (1978) uses the term 'oceanic approach' in the study of insects, comparing mass movements of individuals floating on air currents with those of marine species drifting in ocean currents, thereby covering great distances in a short time.

Looking at species ranges from this point of view not only introduces population dynamics into biogeographical studies, but also incorporates knowledge about species' habitat preferences, geographical and population genetical patterns, and their physiological and anatomical basis into this perspective, as well as anatomical and morphological properties connected with, for example, reproduction and dispersal. We can consider differences or similarities between closely or distantly related species in relation to such properties to explain differences or similarities in geographical distribution or range dynamics. Moreover, we can look at patterns in climatic fluctuation, either over short or long time periods to explain shifts in distribution or changes in range size. The statistical characteristics of ranges, such as size, location, internal structure, and dynamics, are different expressions of the biology of great numbers of

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living individuals considered together, and thus they should be studied as such. When conditions deteriorate, individuals or their descendants will emigrate to other, more favourable locations, resulting either in local shifts in density, or shifts in the entire range. When conditions change over great expanses of the earth, some ranges may expand, whereas others may contract or vanish. The result of continuous changes in environmental conditions at different spatial and temporal scales from fine, temporary, and local scales to broad, long-lasting, and global ones, is a permanent amoeboid creeping of species over the earth, and this in turn results in kaleidoscopic changes in patterns of species ranges relative to each other. The study of this endless movement, described in terms of ever-changing environmental conditions, is the heart of dynamic biogeography.

In attempting to describe the dynamism of species ranges, this book is arranged so that it gradually narrows our interest from the coarsest types of classification to the formulation of a dynamic model of species ranges. This is followed by the model's implications for understanding broad-scale patterns of coincidence shown by many species, as well as for individual species behaviour and future research in biogeography. This whole process, starting from the coarsest classifications and resulting in detailed models is divided into three major steps. The first step, described in Part I, comprises classifications in which no consideration is made of the identity of the taxa or their biological properties. Thus, from the information obtained, it is not possible to infer how the idiosyncrasies of a certain species enable it to fit into particular local habitats within its range, or how it maintains itself there in spite of, or due to, environmental dynamism. This is the field of biogeographical classification where biogeographical units such as kingdoms, regions, or districts are defined. It is the area from which concepts such as biogeographical elements are derived. This is also where much of the recently developed vicariance biogeography belongs, the proponents of which draw inferences from coincident distributions of selected taxa – those with disjunct ranges – in terms of phylogenetic development. These coincidences only emerge from classifications of these taxa. Although statistical testing is often precluded, we should use explicit methodology. This is why discussion of the methodology of biogeographical classification occupies four chapters in Part I.

Part II concentrates on classifications in which the identity of the taxon remains of little or no concern, but where the identity of certain biological properties is important. Here, the aim is to describe and explain con-

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tinuous regional or global trends, or discontinuities in the frequency of one or more biological properties in space. Statistical analysis and its methodology is not emphasized here, although, as in the other two parts, large numbers of taxa that have (or lack) the properties concerned are analysed. Often, trends or differences in location of such patterns are so clear that statistical testing is unnecessary. As in Part I, identification of continuous trends or discontinuities in the distribution of some property serves to identify the ecological or historical factors operative at the spatial scale concerned.

Part III discusses classifications and biological phenomena for which knowledge of both the taxon and its biological properties is required. Statistical analysis of large numbers of unselected species is necessary to evaluate the generality of the patterns. Here, more than before, we are interested in patterns and processes within species ranges, rather than in supra-specific units or trends. Closer and closer looks at biogeographical phenomena result in considering processes on finer scales in time and space. This leads to an evaluation of both dynamic and stochastic aspects within the geographic processes of species maintenance through time. Together with spatially non-uniform distributions of the intensities of many population dynamic processes, these two aspects give insight into the nature of species ranges as dynamic response-surfaces relative to an environment that is heterogeneous and dynamic over all spatio-temporal scales.

By gradually concentrating on finer-scale patterns and processes, we may easily fall victim to reductionism by losing sight of the problems posed initially. Yet, as species respond to a variety of factors on all scales, information about finer-scale processes should not only help us to understand finer-scale patterns, but also to elucidate larger-scale ones. In Part IV, I pick up some of the threads of Part I on concordant patterns and explain them by processes described in Part III. Although this is only a first attempt at integrating multiscale phenomena, I try to indicate the need for their integration. Only by integration of various approaches, aspects, and phenomena can biogeography move from its anecdotal phase and acquire the status of an independent, mature biological discipline.

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Topics

I define dynamic biogeography as the analysis and understanding of spatial biological phenomena in terms of past and present factors and processes. This definition implies five important topics. First, that we know what is meant by biological factors and processes compared with non-biological ones. Second, related to this, we must give biogeography an evolutionary outlook, that is we emphasize the continuous process of adaptation to ever-changing conditions on earth. Evolution is change, not only random change, but change for survival. This can be accomplished in two ways, by genetical adaptation and by spatial adaptation; the latter is of particular concern here. In this context we must be able to distinguish historical components within present-day patterns from ecological ones, consisting of factors and processes operative today. Third, at present, biogeographical methodology is still mainly inductive, which makes it important to adopt explicit, inductive reasoning. This implies that processes studied in dynamic biogeography are essentially statistical and are defined statistically. This means, among other things, that we must decide how far we are concerned only with patterns common to most species, and how much attention should be given to extreme or deviating phenomena. Such extremes can shed light on the interpretation of more general patterns. Another problem is whether we should model null-hypotheses in statistical terms only, or also in biological ones. Fourth, confining our interests to a certain aspect, approach, or process, restricts the possibility of generalizing our results. They may thus give a biased picture of biogeography. Confining our interest is often the only practical way to approach some problem, but we must be aware of the total framework of biogeography to which our results relate. Finally, processes are defined for the spatio-temporal scale at which they occur, as well as by the taxonomic level of the taxa concerned. Looking at phenomena occurring at one particular spatio-temporal scale or taxo-

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nomic level implies using a filter, which prevents us from seeing phenomena at other scales or taxonomic levels.

We shall now discuss these topics in detail.

The biological approach to biogeography

Biogeography is a biological discipline, concerned with the biological phenomena. Yet, it is not always clear in what way we make it a biological discipline that differs, for example, from physical, geological, or mathematical ones. It is usually all too easy to present explanations that neither account for biological properties of the species concerned, nor explain them. For example, a small predator cannot eat a large prey, thus restricting the predator's diet. Such considerations do not lead to biological theories. But the predator's search for particular prey, possibly resulting in the same restricted diet, leads to the biological theory of dietary specialization of species. The problem is then whether the result is a biological theory, or a physical, geological, or mathematical one applied to biological data. If so, we should not speak of biological theories, but rather of physical, geological, or mathematical theories, possibly – but not necessarily – explaining a biological phenomenon. I suggest that biological theories should consider the origin and consequences of biological properties of species or of taxa in general. Two related aspects are relevant – (1) the specificity of biological adaptations and (2) the problem of whether or not general laws can be formulated.

In MacArthur and Wilson's (1967) equilibrium theory of island biogeography species number is related to island size, its distance to a nearby continent or to other islands, its age, and so on. This approach differs from that of Lack (1976) or Carlquist (1974), who both emphasized biological idiosyncrasies of island species and their adaptations to insular life. Similarly, Mueller-Dombois, Bridges and Carson (1981) considered the central issue of which environmental conditions on islands make them differ from continents. If they differ in certain respects, we may ask to what extent are species adapted to particular conditions, namely how do these species fit into them, or even how do they utilize them. Certainly, not all species have identical opportunities to colonize an island or to live on it for some time. Differences in these opportunities depend on the degree to which their specific properties match local conditions. Furthermore, the build-up of species numbers does not simply follow topological rules such as the degree of isolation or size of islands. As shown by Flenley and Richards (1982) for Krakatoa, this build-up follows successional steps of local vegetation development. Species may arrive

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too early, on time, or too late, depending on their biological requirements that do or do not match local conditions. If they arrive on time, they may stay for only a restricted time, depending on the vegetational development. The study of properties that influence why a particular species does or does not occur on an island can thus provide biological insights. However, its biology remains obscure when we just count species numbers, calculate species turnovers, and derive immigration and extinction rates. In those cases, species remain unknown, and their biology seemingly irrelevant. Viewed this way, MacArthur and Wilson's (1967) theory defines some boundary conditions within which biologically relevant processes occur. The study of these processes starts where the equilibrium theory ends.

Their theory was intended to be of general applicability to many different islands. But biological idiosyncrasies of insular species can rarely, if at all, gain a similar, and apparently desired, degree of generality (cf. Kareiva and Odell (1987) for a similar opinion after applying a mechanistic model in an ecological context). This poses another problem: are there general laws in biogeography? Without wanting to go too deeply into scientific philosophy, I suspect that many existing general biological laws, including MacArthur and Wilson's (1967), result from constraints imposed by non-biological laws on biological variation, and that, as a consequence, they are of biological interest only as constraints.

Allometric-growth relationships may be viewed as one of a few, or even the only, general biological law (Peters, 1983), putting constraints on a species' physiology, anatomy, behaviour, and ecology. In my view, mechanical considerations within this context are biologically interesting only in so far as they make understandable different adaptations to the problems imposed by these constraints. Thus, Reynolds (1984) showed that the mucilaginous algae do not conform to the mathematically expected relationship between body size and volume, making them better adapted at remaining in suspension than non-mucilaginous species. To the same end, they can also form colonies, or have irregular shapes. These adaptations, their origin, and their effects make allometric-growth relations biologically interesting, rather than the law itself which results from the general applicability of chemical and physical constraints.

Thus, distinctions made between oceanic islands and continental ones because of their geological history have nothing to do with biology, as it is impossible to predict which species are found on either of them, or what

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adaptations to local conditions these species might have. The same holds for theories based on continental drift, geomorphological properties of islands, general models of species diffusion, or climatic and vegetational classifications in zonal or azonal distribution patterns. In such cases, species are usually assumed to be the same. This is not true, and is contrary to the essence of biology as explaining different forms of life as specific adaptations to environmental conditions. Moreover, suits of traits, together forming multivariate ecological response syndromes, prevent the formulation of general laws. Just as in population genetic breeding systems, we can well distinguish various combinations of traits leading to the same end and forming physiological and demographical systems.

In later chapters I try to explain biogeographical patterns and processes in terms of species properties. To this end I will discuss those techniques that extract information from biogeographical observations for subsequent model building.

The evolutionary approach to biogeography

Viewing biogeography as a biological discipline means not only that we describe geographical patterns and processes, but also that we place them in an evolutionary context. This is not to say that we must try and straitjacket all phenomena or even our approach in this way, as it will often not be necessary to consider evolution or, more particularly, speciation. Essentially, evolutionary change is only a spin-off of adaptation to changeable conditions. The concept of evolution, as used here, is a tool of biogeographical research; it is a means to an end, not an end in itself. We assume that evolution has occurred in order to understand biogeographical patterns and processes. Within a biogeographical context these patterns and processes are not used to explain evolution, as this would shift emphasis away from biogeography to evolutionary biology. Both can be studied in their own right, as shown in later chapters. The time-scale of field investigations is such that evolutionary adaptations can hardly, if ever be observed. If the time-scale chosen is long enough, sampling intensity will usually be too low to give a reliable picture of the patterns and processes operative in the past.

By adopting an evolutionary approach one assumes that every species (1) adapts to conditions in its environment in its own, individualistic way, (2) at present it is adapted just as it has been, since its origin, and (3) its response to environmental conditions becomes less homogeneous throughout its range as the physiological responses of all species resemble

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each other more. We will briefly look at these assumptions in turn.

The first assumption is that species not only adapt in space to changing conditions by shifting, contracting, or expanding their range, or by redistributing individuals within it – that is by purely biogeographical processes – but also by shifts in population genetic content. The result of these two processes together, spatial adaptation and population genetical adaptation, is that species closely relate to their environments. This fit is never perfect, but it will leave scope for further environmental change without necessitating repeated species adaptation. Species with different physiologies and morphologies are usually found side-by-side. Yet, as a consequence of evolutionary changes, all species have their own habitat requirements, due to differences in physiology, morphology, and other properties. These differences make them unique entities. Moreover, species do not respond to changes in their environment as parts of a particular community, but, due to their unique set of biological properties, they behave individualistically. Thus, sometimes species may live side-by-side, at other times they separate, going their own way at their own speed and in different directions (e.g. Davis, 1981*a*; Graham, 1986). We can expect the same individualistic behaviour relative to congeneric species. The occurrence of many such species in a small area, so-called species nests, does not necessarily reflect their area of origin, but simply the degree of similarity in their ecological responses.

The second assumption is that species are adapted to the same environmental conditions that existed when they originated. They have always had the same general habitat requirements, and their life histories and dispersal capacities have always matched, more or less, similar patterns of environmental fluctuation. It thus makes little sense to study geographical patterns and processes as if they were generated or maintained in isolation from the species' environment, rather than reflecting it. Yet the bulk of historical biogeography does not consider the ecological requirements of particular species, the environmental conditions that the species encounter, or possible changes in these conditions. It is only recently that the study of the causation of extinction processes has begun to be considered and the study of environmental factors operative during speciation is in its early development, as is the study of factors that induce species migration. Adopting an evolutionary viewpoint through ecological adaptation is thus a first step in understanding geographical adaptation of species in relation to a continuously changing environment.

Finally, assuming that species adaptation occurs relative to environmental conditions implies that the numbers of individuals are not