

## Alternative Hypotheses in Biogeography: Introduction and Synopsis of the Symposium<sup>1</sup>

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**SYNOPSIS.** Biogeography has had a long history, but only recently has it started to be more than a descriptive subject. Models have been developed which help to explain patterns of geographical distributions of animals and plants. Examples include dispersal, vicariance, and ecological determinism. The dispersal model proposes that present-day distributions were caused by long distance dispersal among disjunct localities. The vicariance model proposes that the distributions resulted from the fragmentation of formerly continuous distributions with accompanying speciation. Ecological determinism proposes that whatever the historical changes in distribution (dispersal or vicariance), present-day ecological factors are the major determinant of distributions. We too often see in the literature large bodies of data analyzed with respect to only one of these competing models. I organized the symposium to bring together what I thought were particularly interesting examples of each approach. It is obvious from the papers that there are multiple explanations for most species distributions, and that some effort should be made to integrate them.

Biogeography has had a long history, but only recently has it started to be more than a descriptive subject. Models have been developed which help to explain and sometimes predict patterns of geographical distributions of animals and plants. Examples include dispersal, vicariance, and ecological determinism. Presumably as a result of the newness of the quantitative techniques and ideas in many of the models, we too often see in the literature large bodies of data analyzed with respect to only one of several competing hypotheses. Too often a model is chosen apparently because it is familiar, and explanations have often been those of plausibility rather than a comparison of alternative hypotheses. Even those interested in testing hypotheses rarely consider alternative hypotheses or even testing other predictions of their favorite model if the first test is successful. Biogeography has become divided into "schools" which largely ignore one-another. As a first step towards a new synthesis, I organized this symposium on Alternative Hypotheses in Biogeography.

The contributions represent what I think are particularly interesting examples of each approach to biogeography.

Biogeography attempts to explain the distribution of species. There are three classes of phenomena which affect which species and how many are found in a particular area: ecology, dispersal ability, and patterns of speciation. The species in a particular place can be there because their ecology permits them to survive, because they dispersed there from elsewhere, or because they speciated there. These classes of phenomena correspond roughly to the three main schools of biogeography: ecological determinism, dispersal, and vicariance biogeography.

Ecology determines which species can actually survive in a particular place. Physiological limits, presence of competitors, or merely microhabitat requirements can limit the number of species in a given locality (Andrewartha and Birch, 1954; MacArthur, 1972; Krebs, 1972; May, 1976). These factors operate continuously, and may wholly or partially obliterate historical factors. Ecological factors act on a short time scale, so their patterns can change with geological and climatic changes. Ecological biogeography tends to assume that all species can disperse to the location of interest, and that speciation does not occur. This is simply a matter of the short

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time scale of interest to ecologists, as compared to historical biogeographers (Udvardy, 1969).

Classical historical biogeography assumes that species originated in particular areas and dispersed from those centers of origin. The distribution of species in a particular place is dependent upon which species happened to disperse there (Ekman, 1953; Darlington, 1957; Simpson, 1965; Briggs, 1974*a, b*; Pielou, 1979). Even though the probability of crossing a barrier may be very low, given enough time some species will cross it. Dispersal biogeography is primarily concerned with identifying the centers of origin and is not concerned with ecology except insofar as it limits the establishment of dispersing organisms (for example, Carlquist, 1965). It is also not concerned with the process of speciation; it assumes that speciation is a rare event.

Island biogeography combines ecological and dispersal ideas, along with some statistical notions. It seeks to predict the numbers and kinds of species found in islands or isolated patches of habitats on the basis of probabilities of immigration and extinction. These rates and their relationships to species numbers vary in predictable ways with island size, distance from the source of dispersing species, and the dispersabilities of the species concerned (MacArthur and Wilson, 1967; MacArthur, 1972; Diamond and May, 1976). Unlike classical historical biogeography, it is less concerned with unique events and more concerned with the effects of many uncommon events. In addition, unlike dispersal biogeography, it yields specific testable predictions.

Vicariance biogeography ignores ecology, downgrades the importance of dispersal, and concentrates on the effects of speciation on the distributions of organisms. It is therefore exclusively concerned with the effects of history, and in particular the effects of geological changes which cause species to split, allowing the character distributions of the split populations to diverge. The basic idea is that: (1) A given species spreads over a large continuous area or range. (2) The range fragments

owing to geological or climatic changes. A range split is called a vicariant event (Udvardy, 1969). (3) The allopatric populations diverge and speciate. (4) The new species may spread into each other's ranges. This model has specific predictions about the taxonomic relationships of the vicariant species: species resulting from recent vicariant events should be sister species (closely related), and species resulting from older vicariant events should be more distantly related. Relatedness is estimated by cladistic methods (Nelson, 1979; Eldredge and Cracraft, 1980). In addition, since many different organisms living in the same large area experience the same sequence of geological changes and vicariance events, there should be a high degree of concordance among the estimated phylogenies for each group (Rosen 1975, 1978; Platnick and Nelson, 1978; Nelson and Platnick, 1978, 1980; Nelson and Rosen, 1981; Wiley, 1981). Ecology is ignored because taxonomic characters must be non-adaptive. Dispersal is minimized because most species are assumed to have originated in their present area, or dispersal took place before the vicariant events. This model has the advantage of specific testable predictions.

The papers of the symposium do not fit easily into the three categories because I asked the speakers to consider as many alternative hypotheses as possible without setting up "straw men." They do, however, vary in their emphasis on ecology, dispersal, or vicariance.

Strong and Rey give a good definition of ecological biogeography: it is concerned with how geographical range and local success is affected by predation, disease, parasitism, and abiotic factors. Their paper is concerned with the effects of temporal changes and randomness in the immigration and extinction curves of island biogeography. They find that on a very short time scale the slopes of these curves may not be significantly different from zero, but over a long time period, or for many islands, the classical MacArthur-Wilson pattern emerges. In addition, over intermediate (ecological) time periods the slopes of the immigration and extinction

curves may change. This has profound effects on the predicted equilibrium number of species on an island or patch of habitat. The important point is that temporal changes in the probabilities of immigration and extinction can make both predictions and testing of predictions difficult.

Livingstone, Rowland, and Bailey examined fishes of African rivers and found that most of the variation in numbers of species could be explained on the basis of the total stream discharge. The annual flow through a river is correlated with terrestrial productivity. This can affect the fish because much of the food of these tropical rivers comes from the surrounding land rather than within the streams themselves, and space is not limiting. This not only explains many present-day distributions, but also some patterns in the past; periods of low discharge (such as a warm dry period) will therefore cause extinctions of many species in a given drainage. It would be interesting to know if the pattern applies to other continents, tropical or temperate. This is a good example of a simple ecological limitation which can change in space and time, with testable predictions.

Edmunds presented some interesting data on relationships, distributions, and ecology of new world mayflies. Relationships were worked out by cladistic methods. Once Laurasian or Gondwana assignments are made, it is possible to examine the effects of the merger of the two fauna after the formation of the Central American land bridge. Many South American genera have penetrated far into North America. It turns out that variation in life-history patterns largely explains the dispersal pattern. Species with tropical affinities are limited in their northward dispersal by the length of their larval period. Those with shorter larval periods can reproduce at higher latitudes than those with longer periods; if a larval period is too long the mayfly dies before it can transform to an adult and reproduce. North American species which hatch in warmer periods have southern affinities more often than those which hatch in colder periods. Thus we have a direct ecolog-

ical reason for an historical pattern of the dispersal of species, using cladistic methods and a knowledge of the biology of the animals. Edmunds also discusses vicariant patterns among the southern continents.

Davis examined the effects of dispersal, vicariance, and ecology on the large freshwater snail family Pomatiopsidae. He is able to separate out the effects of all three factors on species distributions. By comparing cladistic reconstruction to known geological events he was able to follow the divergence and radiation of the family on a large scale. The breakup of Gondwanaland, passage on India into Asia, and subsequent diversification in the newly created river systems was also reflected in the phylogenetic reconstruction. Vicariance events were detectable as a result of the splitting of Gondwanaland and also the Himalayan orogeny. Dispersal (reconstructed from relationships) was presumably responsible for spread into the river systems (such as the Mekong) which resulted from the Himalayan orogeny. Finally the presence of a large number of new ecological niches in the newly formed river systems allowed rapid adaptive radiation without vicariance events (allopatric speciation), merely because these snails have very low mobility. Speciation and adaptive radiation is thought to have occurred by parapatric and even sympatric speciation in these new rivers. The ecological factors are sufficiently important in snails that they cause strong convergence in gross morphology and shell morphology in unrelated species living in the same kinds of habitats. At the same time ecological factors cause great divergence in closely related species living in very different, but adjacent habitats. Davis shows that much more information can be obtained by considering a variety of approaches, and considering the biology of the organisms, than by blindly following the predictions and paradigms of a single biogeographic model.

Heyer and Maxson do something similar with South American leptodactylid frogs. They worked out relationships by means of microcomplement fixation instead of cladistic techniques and found that this can

help to reconstruct the sequence of vicariant events. Unlike cladistic methods, this method estimates the amount of divergence as well as the branching sequence (for a discussion of methods, see Hull, 1979). In many cases the immunological method yields similar results to morphological methods, but they found some cases where there was a lack of congruence between immunological distances and morphological distances among species. This suggests that morphology is only an approximation to molecular divergence, or at least that the evolutionary rates of morphology and albumins are different. They then discuss the problems of using morphological and molecular data in biogeography. If different kinds of characters evolve at different rates, then they will have very different effects on attempts to estimate phylogenies. Their results also imply that varying rates can affect the cladistic estimates of branching sequences. If some characters evolve more slowly than other characters then the slow characters will not record as many vicariant events as the rapidly evolving characters. If the character change rates vary in time as well as between characters, then the recording of vicariant events will be very sporadic, and an analysis of the final result (the current species) is very likely to yield very inaccurate branching sequences. Heyer and Maxson also show how ecological constraints affect species distributions, and test many different hypotheses about leptoactylid frog distributions.

Cracraft presents a very clear example of vicariance biogeography of Australian birds. More important, he shows how vicariance biogeography can help to distinguish between the various modes of speciation. This was also discussed by Wiley (1981). The most important point of this paper is that the methods of cladistic reconstruction and vicariance biogeography have never been applied to the study of speciation. This is surprising in that cladistics attempts to estimate genealogical relationships, and speciation is the process producing those relationships. Given the various modes of speciation, and the necessary assumptions of cladistic reconstruc-

tion of phylogeny, Cracraft shows that some kinds of speciation yield unique predictions about the relationships among the newly split species. He then goes on to test the predictions with Australian bird systematics and biogeography. He does not cover all the modes of speciation, so not all of the conclusions are generalizable. For example he does not discuss the main mode of parapatric speciation, which requires ecological differences among the new sister species (Endler, 1977); instead he discusses a very special case of parapatric speciation which depends upon genetic drift and no selection. This leads to his conclusion that parapatric speciation should always yield sister species. But this is a very special case of parapatric speciation and a very unlikely one since there is nothing in the system to promote isolating mechanisms. The regular form of parapatric speciation will rarely if ever result in sister species since the system depends upon very differing environments among the species *in statu nascendi*, and therefore they would share very few derived characters. This reverses his conclusions about the frequency of parapatric speciation in Australian birds. But in spite of this, the paper is one of the first attempts to apply cladistic reconstruction of speciation events to the speciation process, and an excellent example of the method of vicariance biogeography.

Chernoff presents a good test of vicariance biogeography by examining how well morphological characters work, when used in a cladistic analysis, to reconstruct known vicariant events which happened less than 50 years ago in *Menidia beryllina* fish living in the Mississippi river system. Although he used characters typically used by fish taxonomists, the recently separated populations were not sister species in the analysis. A multivariate analysis was performed on the morphological and environmental factors among all localities. Chernoff found significant canonical correlations between groups of taxonomic characters and groups of environmental factors, indicating that these characters may experience natural selection. This yields the false "vicariance patterns." Environmental fac-

tors were more important in determining the pattern of shared derived characters than history in this data set. It is therefore very important to eliminate characters subject to natural selection before proceeding with the methods of vicariance biogeography. Chernoff's results cast doubt on much of work in fish systematics and biogeography because his results are for characters typically used by fish systematists.

My paper is concerned with the problems of confounding the effects of historical and ecological factors in biogeography. Unfortunately both classes of factors can yield similar results in distributions and in genealogies. Two examples are given (1) the Pleistocene forest refuge hypotheses, and (2) vicariance biogeography. The Pleistocene forest refuge hypothesis seems to work well because only one of three predictions has been tested (Prance, 1981); centers of diversity correspond among many different groups of animals and plants. An examination of the other predictions makes the hypothesis seem doubtful, and the predictions of two alternative hypotheses—present-day ecology and differentiation of peripheral isolates—are upheld. The major prediction of vicariance biogeography, that lineages experiencing the same sequence of vicariant events should yield highly concordant estimated phylogenies, is rejected. Concordant cladograms can only result from common patterns of shared selection regimes, and these do not necessarily reflect shared vicariant patterns. Sister species in a cladogram can result either from many shared derived neutral characters and a recent vicariant event, or independent of history, from many shared derived characters under the same selection regime. This is true even if not all characters are under selection. Species experiencing different selection regimes will not be assigned to sister groups by a cladistic analysis unless *no* characters are subject to selection. This is a direct corroboration of Chernoff's results. It is necessary, therefore, to show that taxonomic characters are not under selection. The problem of distinguishing historical from present-day factors is a serious one.

Brown's paper presents one of the most extensive sets of biogeographical data and analysis ever published, as well as one of the most balanced in terms of the consideration and testing of alternative hypotheses. It deals with the distribution of neotropical butterflies, and the effects of historical and ecological factors. The major conclusions are that the distributions of species, as well as zones of high diversity, are caused by: (1) ecologically favorable conditions and resulting regional differentiation, (2) unpredictable mild disturbances over short and longer time scales, differing regionally, and (3) regional differentiation related to historical changes in climate and the distribution of the vegetation, including Pleistocene forest refuges (isolated patches of forest flora and fauna). Brown shows how ecology, dispersal, and vicariance exert varying effects, but all are detectable as important factors. This paper is a splendid example of considering many hypotheses, and with a knowledge of the biology of the organisms, testing the hypotheses in a reasonable and informative way.

It is clear from the papers that there is a great diversity of biogeographical phenomena, and a diversity of explanations for the phenomena. It is clearly important to entertain more than one hypothesis at a time, and for each consider all the predictions. A knowledge of the biology of the organisms concerned helps to eliminate incorrect results which would otherwise appear to be correct. No one method of analysis is the best in biogeography, as each only gives a part of the story. There are multiple explanations for species distributions, and some effort should be made to integrate them. Biogeography could profit by more attempts to examine the relative and joint effects of both history and ecology on distributions. One possible method would be to explore the ecological factors in sufficient detail so that these factors could be removed, leaving components of the distributions which presumably reflect historical events. But this is a formidable task. Brown's paper is a start. It is obvious that much work needs to be done in attempts to understand both historical and

ecological factors in species distributions, without losing sight of the alternative hypotheses.

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