Biogeography is, next to systematics, the most fundamental discipline underlying evolutionary biology. Systematics is primary because biogeography cannot be undertaken without it. Given the present emphasis on the multifarious field of population biology, the assertion that systematics and biogeography are the prime components of evolutionary biology may sound anachronistic. The statement is not meant to polarize or challenge population biology but merely to reaffirm the indispensability of systematics and biogeography and to suggest that their current role in evolutionary biology must be enlarged. The reason for this is simple. The goals of systematic and biogeographic analysis are, first, to define the units of evolution—any monophyletic group from the subspecific level on up—and, second, to describe patterns of form (including phenotype and genotype) through space and time. In other words, without systematic and biogeographic analysis, evolutionary biology would have little, if anything, to explain. The focus of evolutionary biology is ultimately the description and explanation of diversity, which can take two forms: patterns of taxonomic diversity and patterns of diversity in form. Systematic and biogeographic analysis reveals those patterns and thereby lays the groundwork for their explanation.

In its broadest sense, biogeography is the study of the distributions of organisms, but such a simple definition is not really informative. Biogeography today is usually seen from two perspectives. The first, historical biogeography, encompasses much of the subject matter classically included in the discipline for the last 150 years. The second perspective, usually called island biogeography (or equilibrium biogeography) has a much more recent inception (MacArthur and Wilson 1963, 1967).

It is instructive to consider the relationship between these two perspectives of biogeography. Island biogeographic theory is often viewed—as having transformed classical biogeography into a more modern, scientific discipline:

[Island biogeography] represents an effort to take biogeography out of its present natural-history setting and place it in a new one, more conducive to experimentation and more amenable to theoretical analysis. (Hamilton 1968:71)

[Island biogeographic theory has] revolutionized biogeography... spawned a mass of research which has given biogeography general laws of both didactic and predictive power. (Simberloff 1974:163)
Is this an accurate evaluation? Has island biogeographic theory, in fact, transformed classical biogeography? The answer probably depends upon one’s point of view. Nevertheless, although granting the significance and widespread influence of island biogeographic theory within ecology, it is also possible to argue that the approach has had little, if any, influence on the traditional domains of biogeographic thinking. Fundamental conceptual advances within a discipline usually have two major effects. They provide a theoretical basis for solving diverse problems already indigenous to the field, but for which there is as yet no unifying solution. Also, they permit the older data to be seen in a different light by using them to answer entirely new kinds of questions. Although island biogeographic theory may satisfy these criteria within ecology, it has not done so within biogeography.

Some workers have suggested that biogeography is becoming unified as a discipline, with historical and island biogeographic analyses occupying the ends of a continuous methodological spectrum, distinguished only by differences in the time and geographic scales under investigation (Simberloff 1974; Simberloff et al. 1981; Chapter 11). Thus, historical biogeography is said to concern itself with evolutionary time and broad geographic scales, whereas island biogeography applies to ecological time and local geographic situations. For those accepting this view, perhaps it is reasonable to see a synthesis just over the hill and to perceive that island biogeographic theory represents a conceptual advance within the discipline of biogeography. I believe this view is false, however, not only from a historical standpoint but also when examined in terms of contemporary research in biogeography. The primary reason why the equilibrium theory does not constitute an advance within biogeography is simple: When formulated, it was directed toward a question that never was a primary concern to classical biogeography (see also Rosen 1978).

Three observations persist in the writings of biogeographers of the last 200 years (Nelson 1978; Nelson and Platnick 1981), and each leads to specific questions.

1. Taxa are not distributed at random nor are they found everywhere: What are the areas of endemicism or provinciality? Early in the history of biogeography, it was discovered that most taxa are very localized in their distributions and that distributions are clustered. Much of nineteenth-century biogeographic analysis was directed toward defining these areas of endemicism. The concept of zoogeographic realms (Sclater 1858), for example, was one of many attempts to do this. Despite a deemphasis by contemporary ecologically oriented biogeographers on delimiting areas...
of endemism and understanding their significance, in recent years the study of endemism has taken on increasing importance.

2. An area of endemism often exhibits more similarity to a second area than either does to a third: What are the interrelationships of areas of endemism? It was an expectation of many early biogeographers that as long as the climate and topography of areas were more or less similar, so too would be their biotas. This expectation was not confirmed upon careful investigation, and it was soon realized that historical continuity, not climate and topography, was the most important determinant of biotic similarity. A measure of similarity among biotas has two components: the numbers of shared widespread species and the numbers of species whose close relatives are distributed in the areas under consideration. Historical relationships among areas cannot be established by comparison of the shared widespread species but only by the degrees of relationship among closely related species endemic in those different areas (Platnick and Nelson 1978; Nelson and Platnick 1978, 1981).

3. Areas of endemism often exhibit more similarity to areas that are far away than they do to those relatively closer: How could such similarities have developed? This third observation was derived not only from analyses of the biotas of numerous areas of endemism but also from systematic study of individual groups (the ratite birds, for instance).

These three observations and questions about areas of endemism have by no means formed the content of all biogeographic studies, but they represent classes of observations calling for general explanations. Without a doubt, most work in historical biogeography has been dominated by a concern for "tracing the distributional history" of individual groups of organisms. The highly influential works of Darwin, Matthew, Darlington, Mayr, and Simpson characterize this viewpoint. Nevertheless, even if biogeographic analysis is directed toward understanding the geographic history of individual groups rather than the interrelationships of entire biotas, both approaches focus on history, and the core concept of historical biogeography is the problem of endemism: Where is each taxon distributed? Do these distributions cluster to form shared areas of endemism? What is the history of these taxa and their areas? How is that history of endemism related to earth history? How has that history of endemism influenced the taxonomic composition of biotas through time? Whereas it is entirely possible to interpret distributional history from either a dispersalist or vicariance point of view—although such interpretations will be significantly different—the theme of historical analysis still remains the problem of endemic taxa and areas of endemism.
Conversely, the literature pertaining to equilibrium biogeography seldomly addresses the question of endemism. MacArthur and Wilson (1967), for example, mention endemism only once and then with regard to an illustration of the percentage of endemics on islands. MacArthur’s (1972) highly influential book, *Geographical Ecology*, does not even raise the issue; neither does Simberloff (1974) in his extensive review. This may or may not be significant, depending upon whether one thinks the subject of endemism plays a relevant role in the phenomena that island biogeography is supposed to explain.

One of the most important questions addressed by island biogeography has been, How can the number of species on islands (or “patches”) be explained? Expressed somewhat differently, the question becomes, How is the taxonomic and ecological structure of communities assembled? As originally formulated, the question was directed toward understanding the species richness of biotas, independent of their specific taxonomic composition. In other words, endemism and patterns of relationship among the taxonomic components can be ignored. Species number, then, is said to be a function of immigration and extinction rates, which are, in turn, a function of island size and distance from the “source” area (MacArthur and Wilson 1967). At some point in time, each island reaches an equilibrium number of species, that number being characterized by a dynamic balance between immigration and extinction to produce a given turnover rate.

It is not the purpose of this commentary to present an extensive criticism of island biogeographic theory. That there are exceedingly few empirical data, after nearly 20 years of research, to support its predictions has been forcefully argued by others (Simberloff 1976; Connor and McCoy 1979; Gilbert 1980). It is sufficient to note that one of the central questions posed by island biogeographic theory—How can the numbers of species on islands be explained?—has not been a pressing problem within biogeographic research for the last 200 years. Thus, in a sense, the question of whether there are two approaches to biogeography is a non sequitur: Island biogeography can be considered a major subdiscipline of biogeography only if one accepts its central question as being substantially important within the field as a whole, which it has not been.

What is it about the biotas of “islands”—whether oceanic or continental—that attracts our attention? From an evolutionary perspective, it is that these biotas designate centers of differentiation or areas of endemism. Upon reflection, that must be the crucial observation, if our perspective is evolutionary. Of course, it is possible to look upon these biotas
in terms of the widespread taxa they may or may not share with other areas, but by definition these taxa have undergone no evolutionary change and, from that standpoint at least, are not terribly noteworthy. In terms of its research strategy, the field of geographical ecology typically emphasizes the distributional patterns of widespread species, and the taxonomic composition of biotas is interpreted in terms of the presumed ecological characteristics of the component species (Diamond 1975; Gilpin and Diamond 1982). In the words of Diamond and Gilpin (1982:65), "The reasons why particular combinations were observed to exist in nature, while others did not, were interpretable in terms of ecological attributes of the species, such as their resource overlap, dispersal ability, proneness to local extinctions, and distributional strategy."

Connor and Simberloff (1979) have criticized this approach, claiming that the particular species combinations found by Diamond (1975) also could have been assembled even if the species were distributed at random. It would appear there is indeed some cause for worry when virtually any distributional pattern can be "explained" by invoking dispersal ability, proneness to local extinction, or distributional strategy, and it is unclear how such explanatory tools could be applied in a manner that is not inherently ad hoc. Furthermore, it does not help to respond to this apparent problem by advocating the replacement of a falsificationist philosophy of science with a pluralist philosophy (Diamond and Gilpin 1982:73), a move seemingly designed to justify an approach to distributional data that is less then rigorous. The "null" hypothesis formulations of Simberloff and his colleagues cannot be equated with a falsificationist approach to scientific explanation, and one can reject the former while accepting the latter. Instead of doing this, Diamond and Gilpin give the appearance of rejecting both, seemingly because they do not want to be forced to relinquish hypotheses in the face of conflicting data. Surely the point is not that hypotheses must always be abandoned when faced with conflicting data. Rigid falsificationism need not be followed if we admit that patterns in nature, and their explanations, will always be less than perfectly rendered; some conflicting data are always to be expected. On the other hand, an admission of this sort does not justify a pluralist position when formulating and testing hypotheses; if hypotheses are not susceptible to critical evaluation and rejection, then any progress these hypotheses seem to confer may be only illusionary.

Although proponents of rigorous testing have raised valid criticisms about much of the literature of geographic ecology, it is questionable whether a null hypothesis evaluation of biotic distribution (Simberloff
1978; Connor and Simberloff 1978, 1979, Chapter 11), in which a "deterministic" explanation is judged relative to a "random" alternative, will necessarily prove enlightening in deciphering distribution patterns (see Grant and Abbott 1980; Farris 1981; Diamond and Gilpin 1982; Gilpin and Diamond 1982). Questions of statistical treatment aside, two problems arise with the use of random null hypotheses. The first is the dubious nature of the philosophical argument that claims these hypotheses have "logical primacy" in attempts to evaluate a particular deterministic hypothesis (Strong et al. 1979:910). Others have noted that (1) the identification of a hypothesis as being null is not altogether a simple and easily justifiable procedure, (2) the designation of a hypothesis as being truly random depends upon a host of assumptions, and (3) preference for a random hypothesis over alternative deterministic hypotheses as the null hypothesis is not clear (Grant and Abbott 1980; Farris 1981; Diamond and Gilpin 1982). The second problem relates to the latter point just raised. Because many of the assumptions often underlying discussions of island biogeographic theory (geographic ecology) lack biological realism (e.g., random dispersal, community structure rigidly controlled by competition), null hypotheses based on those assumptions scarcely can possess greater validity than do deterministic hypotheses.

In their attempts to explain the distributional patterns of species, geographic ecologists often allude to a contrast between the ecological and historical determinants of those patterns (e.g., MacArthur 1972; Vuilleumier and Simberloff 1980). Not surprisingly, it is usually concluded that nature is complex, with distributions being an intricate combination of short-term ecological factors and long-term historical events. The problem, it is claimed, is with nature, not with the nature of our science: "The reason why we have some trouble disentangling ecology from history (or from chance) is not so much necessarily due to a methodological hurdle as perhaps to the very nature of the problem" (Vuilleumier and Simberloff 1980:344). If we accept this assessment, then surely there is little we can do except catalog nature's complexity and construct scenarios to explain it. If, as it is claimed, our methods of analysis are essentially correct, then there is little or no hope our approach to the problem will be changed: It will always remain at the level of narrative scenario, which in fact is exactly what the methods of geographic ecology often entail. In testing hypotheses within a given theoretical-methodological framework, we are restricted to the same theory and methodology used to construct the hypotheses in the first place; new data are interpreted the same way (although they
do not necessarily have to give the same results, in which case the hypothesis is cast into doubt.

If we accept, however, that the theory and methodology is wanting for one or more reasons, it is then possible to approach the problem in an altogether different fashion. This is what I would like to do in the remainder of this commentary.

The problem we wish to investigate is how the taxonomic and ecological structure of an avian community might have been assembled. The analytical procedures could apply either to the entire avifauna or to selected taxonomic or ecological components of that community. To begin, it is assumed the following basic data have been collected for the sample of species: (1) A species list has been compiled, and the taxonomic status of each differentiated form (at the species or subspecies level, whichever is appropriate) has been established. (2) the distribution of each form is mapped, as are those of all taxa potentially closely related to the taxa of the sample, and (3) the relevant ecological parameters of each species have been noted.

Using these basic data, it is now possible to outline a research strategy capable of generating testable hypotheses about the history of community assembly:

1. From the taxonomic and distributional data, determine the centers of endemicism not only for the taxa in the community but also for their close relatives in other areas.

2. Perform cladistic analyses on individual clades within the community sample (Eldredge and Cracraft 1980; Nelson and Platnick 1981; Wiley 1981), then reconstruct the general area cladogram for the centers of endemicism (Rosen 1978; Platnick and Nelson 1978; Nelson and Platnick 1981; Platnick 1981; Wiley 1981). This area cladogram constitutes a general historical hypothesis for all the taxa endemic in the areas of endemicism under consideration.

3. Compare the distributions of the species found in the community being investigated with the locations of the areas of endemicism. Then, taking into account the general area cladogram and the phylogenetic relationships of the species being studied, establish which of those species had an autochthonous origin (by vicariance) within the area of endemicism containing the community and which species had an allochthonous origin and subsequently dispersed into the area.

4. After characterizing the ecological structure of each area of endemicism, use the general area cladogram (and the paleogeographic and paleoclimatic data used to explain it) to construct a hypothesis for the historical changes in ecology for these areas. This procedure is a logical
extension of using cladistic analysis to infer historical changes in ecology within a clade (Cracraft 1974; Morse and White 1979; Andersen 1979; Andrews 1982). Combined, these two procedures make it possible to erect a hypothesis about the history of species interactions by comparing the ecologies of the autochthonous species with those of the allochthonous species. If the comparison is extended to communities in other areas, testable hypotheses can be constructed regarding the historical pattern of species interactions when different combinations of species are sympatric in different areas. To the extent that we understand the phylogenetic relationship and vicariance biogeography of the species of any community, we can piece together the ecological history of that community.

This historical component has been missing from the discipline of geographic ecology. Needless to say, the difficulty of such an analysis increases as more species are included, therefore, in practice we may not be able to apply it to the entire avifauna of a community. On the other hand, the procedure is particularly feasible when analyzing a specific ecological substructure of a community such as different guilds (e.g., all foliage gleaners or frugivores) or of a taxonomic subset such as all antbirds, warblers, or tanagers.

As I have argued, the key to understanding both historical biogeography and geographic ecology is the history of areas of endemism. These areas can arise in two primary ways. First, areas can be subdivided by a geological or climatic event, with subsequent taxonomic differentiation producing two or more descendant areas of endemism. Second, an area may already by separated from a "source" area and receive colonists by long-distance dispersal across a preexisting barrier, with colonizers then differentiating. Thus, there are two modes of dispersal, each having significantly different biological implications, that can produce autochthonous species within a community. The first is the gradual enlargement of species ranges, a process regulated by various ecological rules acting at the populational level. The second mode is long-distance dispersal across barriers, which, at least as presently understood, is not governed by any identifiable, predictable ecological regularities but instead seems to reflect chance-based characteristics of individual organisms. It is this second kind of dispersal that is invoked by geographic ecologists and dispersalist biogeographers to explain the "ecological" component of areas of endemism.

Critics of vicariance biogeography have failed universally to understand the biological differences and systematic implications of these two types of dispersal (e.g., McDowall 1978; Briggs 1981; Mayr 1982;
Chapter 11). The first type of dispersal produces widespread species until they become geographically subdivided; the second may also, but more often it produces isolated, random occurrences of species in places of compatible habitat. Leaving this distinction aside, there is another aspect of this controversy in need of emphasis. Science attempts to explain the nonrandomness of nature. Given a single observation, one cannot assert whether it is part of a more general pattern or simply "noise," an observation that has been shaped by its own unique contingent circumstances. In biogeography, as in all science, it is first necessary to identify the general patterns, for only then can we specify the unique component within the system. Geographic ecologists and dispersalist biogeographers advocate a methodology that assumes that patterns of nature are statistical summations of many unique species histories (i.e., they assume biotas are assembled primarily as a result of long-distance dispersal). Epistemologically, this assumption will not permit biologists to reconstruct the history of biotas or community assemblages.

Considerable theoretical work has been undertaken on the analysis of area cladograms (see references cited earlier), and much more certainly will follow in the future. One potentially influential critique of these studies is the work of Simberloff and his colleagues (Simberloff et al. 1981; Chapter 11). They attempt to establish a null hypothesis for evaluating the postulated congruence of area cladograms by treating areas of endemism as if they were random draws from a metaphorical biological urn of all possible cladograms. For example, given four areas of endemism, what is the probability that the cladistic patterns we observe could not have been randomly drawn if we assume there are 15 different cladistic patterns for four areas and \( X \) number of clades to be examined? The problem with this approach is that the null hypothesis is weakly formulated, because it omits the primary systematic data supporting the original cladistic hypotheses, that is, the character distributions. The null hypothesis constructed by Simberloff et al. apparently assumes either that each possible cladistic hypothesis is devoid of supporting data or that each possible cladistic hypothesis has equal empirical support. I am unaware of a single study in which either assumption holds. Furthermore, I cannot imagine any serious vicariance biogeographer postulating general patterns on this basis as it would be biologically unrealistic.

To illustrate this point more emphatically, consider the following. Assume there are three areas of endemism, A–C, and assume we have three clades with species endemic in each area. Suppose the first clade
exhibits a pattern of relationships \((A + B) + C\), the second \((A + B) + C\), and the third \((A + C) + B\). From these results, we might postulate that \((A + B) + C\) is a general pattern. Simberloff in Chapter 11 notes that if there were 50 clades, there would be 19,600 trios to choose from, consequently the congruence of our first two clades may not be "statistically" significant. If one accepts this method of establishing a null hypothesis, then Simberloff may have a point. However, assume there are seven well-defined derived characters linking A and B in the first clade, five linking A and B in the second clade, and only one linking A and C in the third. Given these additional data, how would we construct a null hypothesis?

Lest I be misunderstood, let me state that it is not the use of null hypothesis that is at issue. Philosophically speaking, a null hypothesis does not have to be random. If, however, such hypotheses are so simplified as to make comparisons with empirically supported hypotheses unrealistic, then the efficacy of the "null" hypothesis is impaired. At the present, null hypotheses in biogeography appear incapable of providing a realistic standard against which to compare competing hypotheses.

To summarize, we now have the theoretical and analytical tools to reconstruct the history of island and continental biotas (for a didactic example, see Cracraft 1982). In the past, biologists have viewed island biotas as calling for different methods of analysis, presumably based on the assumption that the only way endemics could have arisen is through long-distance dispersal. Given what we now know about earth history, this is clearly an unwarranted assumption. Many, if not most, of the islands of the world probably have shared a contiguous geographic history with continental mainlands or with nearby islands. It is a mistake to assume that the positions, size, or the numbers of present-day islands have remained unchanged and, consequently, that their biotas may not be older than previously assumed. If we are to decipher these complexities, we must adopt a research program that directs attention first to the general patterns of endemism and then to second-order hypotheses about the unique components of these biotas. Coupled with evidence from paleogeography, paleoclimatology, and ecology, these methods can provide a basis for hypotheses about community evolution.

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Literature cited


