the differential college attendance, paternal vocational motivations, and their implied correlates among high-aptitude students. This formulation appears to be more probable for males than for females. The institutional productivity hypothesis proposed in previous studies is not supported by the present evidence (*14*).

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Comparison of Closely Related Faunas

Eugene Munroe

Zoogeography is the science of the distribution of animals as influenced by present and past causes. One of its important tasks is to study differences between faunas that inhabit different geographic areas. Although rough qualitative comparisons can be made fairly easily, their interpretation is beset with pitfalls. When quantitative comparison is attempted, the difficulties are greatly multiplied, and special attention must be given to the methods used. The subject of comparison of faunas is large and complex and cannot be surveyed fully here. This article (*1*) deals primarily with a method useful for comparing closely related faunas, but to place this method in perspective, a short discussion of the general nature of differences between faunas is necessary.

Differences between Faunas

The differences between whole faunas are best thought of as aggregates of differences in the representation of individual taxa (*2*). These differences are of several kinds, with different zoogeographic meanings: (type A) a taxon of one fauna may be unrepresented in another fauna—for example, the pronghorn is present in North America but absent in Eurasia; (type B) a single taxon of one fauna may represent a group of taxa in another fauna—for example, the butterfly genus *Calisto* has one species in Puerto Rico but a considerable number of species in Hispaniola (*3*); (type C) there may be a one-to-one correspondence between groups of taxa, such as the Old-World and New-World monkeys; (type D) there may be a one-to-one correspondence between two individual taxa, such as the European elk and the American moose.

The significance of the simple presence-and-absence differences of type A has been over-emphasized. A taxon may be absent from a locality for any of three reasons: (i) it may never have reached it because of some barrier (most higher mammals are absent from Australia); (ii) having reached a locality, the taxon may have found it unsuitable for colonization (numerous species of insects arrive fairly regularly as strays or migrants in England but fail to become established, *3*); or (iii), having become established, it may subsequently have suffered local extinction (the large copper butterfly has disappeared in England). These causes cannot ordinarily be distinguished on direct evidence, and the absence of taxa, even if established beyond doubt, is an uncertain basis for zoogeographic conclusions—witness, for instance, the controversy over the insular or oceanic nature of the West Indian fauna (*4, 5*), in which arguments based solely on the absence of elements in the present fauna are inconclusive.

Differences of type B, where a single taxon in one place is the counterpart of a group of taxa in another, may also arise in different ways. The isolated taxon may be a colonist from a center of dispersal in which a group of similar taxa survives—the Hawaiian butterfly *Vanessa tameamea* is a segregated species of a genus with several continental representatives. Conversely, the single taxon may be a relict in an otherwise abandoned ancestral habitat—the raccoon is the only surviving procyonid in North America, the original home of the group, but there are a number of species in South America. In such cases the present center of abundance of the group may be a secondary one, quite distinct from the true center of origin or dispersal. Or, finally, the vicarism of single and multiple taxa may be the result of a difference in evolutionary, or, more strictly speaking, of radiative, rates—as already noted, the butterfly genus *Calisto* is represented by

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Table 1. Degree of differentiation within superspecies of Papilionoidea between certain West Indian islands.

Degree of difference within superspecies	Cuba and Cayman Islands	Cuba and Bahamas	Bahamas and Cayman Islands	Cuba and Hispaniola
Specific	0	1	0	9
Subspecific	5	11	10	23
None	23	24	13	35
Not compared	3	5	4	0
Total superspecies in common	31	41	27	67

a single endemic species in Puerto Rico, but by an array of about 20 species in Hispaniola (*3*). Puerto Rico and Hispaniola had a common fauna in the Pliocene (*5*), and at least some of the Hispaniolan species appear to be radiants from a common ancestor shared with the Puerto Rican species, which has not radiated. In this type of vicarism, the group of taxa may have originated either contemporaneously with the vicarious single taxon, as in the example given, or subsequently as a colony from it; the important feature is that radiative differentiation has proceeded more rapidly in one segregate than in the other.

More rapid radiative evolution may sometimes be the result of inherent differences, but it probably is caused most often by characteristics of the environment. Relaxation of biotic competition and geographic compartmentalization are environmental factors favoring radiation. Animals that succeed in colonizing oceanic archipelagoes frequently radiate rapidly to fill empty niches—for example, Hawaiian honey-creepers (*6*) and Galapagos finches (*7*), in contrast to similar animals in continental areas or single islands which do not commonly radiate to the same extent. Indeed, it is a plausible hypothesis that the explosive evolution that characterizes the early history of many successful groups (*8*) follows on the reduction of effective competition by the development of some striking selective advantage. From the foregoing discussion it will be seen that differences of type B, like those of type A, are likely to be of uncertain significance because of the different ways they may have arisen.

Differences of type C, where groups of taxa represent one another without shared elements, almost without exception imply isolation for a time long enough to permit independent radiative evolution of the degree observed. Conceivably, serious reduction of a large homogeneous population could lead to the segregation of wholly different relict arrays of taxa in different refugia. However, such occurrences must be rare, and no convincing example occurs to me. The length and degree of isolation needed for independent radiation vary with groups and circumstances; snails have formed separate endemic faunas on the major islands of the West Indies (*9*), whereas birds (*10*) and most butterflies (*11*) have not; fish perhaps radiate quickly in large tropical lakes (*12*), but evolve slowly in temperate rivers.

By suitable choice of taxa, differences of type C can be reduced to those of type D. I shall therefore restrict type D to instances where the vicarious taxa are of species or lower rank. In closely related faunas, a large proportion of the differences are of this class.

Assessment of Differences between Closely Related Faunas

It is well known that faunas that in reality are closely related may, because of accidental or environmental factors, have very different compositions. Mount Katahdin, Mount Washington, and the different peaks on the Gaspé Peninsula have insect faunas that differ appreciably. These differences almost all result from the accidents of survival, and the arctic and subarctic components of the different faunules all have their close counterparts in the much larger fauna of Labrador. Again, faunas of a sandy and of a forested island might be very different, and yet each be fully matched in a single adjacent mainland fauna. A common method of coping with this problem is always to consider the percentage of taxa in the smaller fauna that also occur in the larger, rather than to analyze the larger fauna in terms of the smaller. This method would work well in comparing the two island faunas with the mainland fauna, but would break down in comparing the fauna of the sandy island with that of the wooded one.

There is a simple way of overcoming the difficulty, although it is not in general use. This is to compare only species that occur or are represented in both faunas—that is, to base the comparison on differences of type D. The average degree of taxonomic difference between vicarious populations is then a measure of the differences between the faunas.

Mayr's concept of the superspecies (*13*) is a useful one in this connection. However, it is necessary to admit the existence of monotypic superspecies—those containing only one species—in addition to the polytypic ones conceived by Mayr. The way this method works can be seen qualitatively by a comparison of the hemispheres. For instance, in Lepidoptera, in the Arctic Zone, practically all superspecies that occur in both hemispheres are represented by the same or closely similar subspecies. In the subarctic there are more distinct subspecies and some distinct species. As we go south in the Temperate Zone, the proportion of distinct species rises, and in the Tropics almost all species except those introduced by man are distinct. Between tropical Africa and tropical Asia, on the other hand, there is much less difference. Although many superspecies are represented by different species in the two continents, many others are represented by the same species, often as indistinguishable populations.

This method of comparison is capable of much more subtle discriminations. Consider the array shown in Table 1 (*14*). The frequency-distribution of the degree of differentiation between Cuba and the Cayman Islands is fairly similar to that between Cuba and the Bahamas, showing that the faunas of the Bahamas and the Caymans have much the same degree of relationship to the fauna of Cuba. The somewhat larger proportion of subspecific differences between the faunas of the Bahamas and Caymans reflects the fact that the faunas have been derived independently from the fauna of Cuba and have had no direct influence on each other. On the other hand, the Cuba-Hispaniola distribution shows a definite shift, with more in the specifically different class and fewer in the identical class, indicating a more distant relationship between these islands, a conclusion with which most zoogeographers would agree. The sensitivity of the method increases with the number of superspecies considered and with the number of grades of difference that can be distinguished.

When applied to such widely different faunas as those of Africa and Asia, the superspecies-comparison method obviously does not tell the whole story. Although a comparison of superspecies may reveal the rank of differences between widely separated faunas, it does not accurately represent their extent. The reason is, of course, that differences of types B and D—that is, differences resulting from radiative evolution—are important in these faunas. This suggests a simple distinction between closely related and distantly related faunas.

Closely related faunas are those whose differences are mainly of the presence-and-absence and simple vicarism types; distantly related faunas are those in which an important part of the differences are the result of independent radiative evolution. As suggested earlier, faunas may on this definition be closely related with respect to one group of organisms but distantly related with respect to another. This presents no logical difficulty; the difference is inherently one of mobility. Cuba is an island for birds but a continent for snails.

For closely related faunas, superspecies comparison is a primary, and, for many purposes, a sufficient, method. However, its limitations must be recognized. It is, for instance, unsuitable for assessing differences caused primarily by differences in environment. Indeed, its very strength is that it tends to minimize or eliminate such differences, revealing the underlying differences of historic origin. Other problems are posed by interpretation. Accurate measurement of differences is one thing; accurate explanation of them is quite another. We tend to think of differentiation within superspecies as being the result of gradual divergence of geographically separated populations. However, with respect to two given localities, this explanation is not necessarily correct.

A superspecies may be represented by different species because they have differentiated *in situ,* implying a long period of isolation. On the other hand, the difference may be one of origin, not of history: the two species may have arrived ready-made from different sources, perhaps contemporaneously and perhaps very recently; or one species may have supplanted the other in one locality but not in the second, again perhaps very recently. Of course, the preservation of distinct populations from different sources may itself be a sign of strong isolation between two localities, but there is considerable evidence that, even in the absence of a serious barrier, immediately related species do not readily coexist in the same restricted area. In the West Indies, for instance, species of northern and southern origin in the Lesser Antilles often meet but seldom overlap—for example, *Pyrgus syrichtus* F. and *Pyrgus orcus* Cr. (*15*). Geologic evidence and the fact that different species pairs meet at different levels in the island chain rule out the possibility that the failure to overlap is caused by an important present or past barrier.

Comparison on a superspecies basis does not in itself distinguish endogenous from exogenous differences. This must be done by studying individual patterns of distribution. The presence of distinct populations in each of a series of well-separated localities is evidence of autochthonous differentiation; certain geographic patterns, and especially similarity to the representative in a suitable source region, suggest immigration of a taxon developed elsewhere. Not all cases are clear-cut, and a considerable proportion of doubtful ones can be expected in the study of an actual fauna.

Even if a series of purely endogenous differences can be isolated, its statistics are not free from bias. What is being measured in such a purified series is the amount of evolutionary differentiation between faunas. Apart from the weakness of purely phenotypic comparison, which can be minimized by the use of sufficiently large series of superspecies, there are certain sources of systematic error. One class of errors arises from differences in evolutionary rate in different populations. It is well known from the work of Wright (*16*) and his followers that different conditions of selection and population size influence rates of evolution. In addition, differential selection in different environments has an effect opposite to that of parallel selection in similar environments. Unfortunately, we usually cannot apply this theoretical knowledge to concrete situations, because we are almost always ignorant of the quantities involved. Another type of systematic error is caused by extinction. Extinction has both a general and a differential effect. On the law of averages, older components of a fauna are more likely to have become extinct than younger ones. Evolutionary differences between isolated habitats therefore tend to be minimized. Extinction is more rapid in small habitats than in large ones (*17*). The fauna of a small habitat is therefore likely to be more youthful and less strongly differentiated than that of a large habitat with a similar history. If colonization from an outside source is possible, these effects may be reinforced, for to the attrition of old superspecies is added the continual arrival of new ones, adding to the undifferentiated element of the fauna.

Conclusion

The comparison of vicarious elements of shared superspecies provides a reasonably accurate and objective measure of the degree of difference between faunas in which autochthonous radiative evolution is not an important factor, but historical interpretation of the differences is beset with errors and bias inherent in the differences themselves rather than in the method of measuring them.

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