

Differentiation of Populations

Gene flow seems to be less important in speciation than the neo-Darwinians thought.

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Most contemporary biologists think of species as evolutionary units held together by gene flow. For instance Mayr (1) writes "The nonarbitrariness of the biological species is the result of . . . internal cohesion of the gene pool." Merrell (2) states "The species is a natural biological unit tied together by bonds of mating and sharing a common gene pool." This idea is founded in the pioneering work of Dobzhansky, Mayr, Stebbins, and others integrating the theory of population genetics with laboratory and field experiments and observations to produce the neo-Darwinian or synthetic theory of evolution. These workers quite logically concluded that differentiation of populations would be prevented by gene flow, and they focused their discussions of speciation on various means of interrupting that flow. In other words, they emphasized the role of mechanisms isolating populations from one another. Until quite recently there has been little reason to question this view. In the past few years, however, growing evidence from field experiments has led us to reevaluate the processes leading to organic diversity, and to conclude that a revision of this section of evolutionary theory is in order.

In this paper we suggest that many, if not most, species are not evolutionary units, except in the sense that they (like genera, families, and so forth) are products of evolution. We will argue that selection is both the primary cohesive and disruptive force in evolution, and that the selective regime itself determines what influence gene flow (or isolation) will have. Threefold evidence is presented for this. We will show that (i) gene flow in nature is much more restricted than commonly thought; (ii) populations that have been completely

isolated for long periods often show little differentiation; and (iii) populations freely exchanging genes but under different selective regimes may show marked differentiation.

We finally reiterate the point (3) that a vast diversity of evolutionary situations is subsumed under the rubric "speciation," and that this diversity tends to be concealed by an extension of a taxonomic approach from the products of evolution to the processes leading to the differentiation of populations. *Euphydryas editha* and *Festuca rubra* are both species to the taxonomist, but knowing this does not tell us if they are evolutionary units or how they evolved. Nor does it permit us to guess how similar are their evolutionary pasts, in what way they are similar today, or to predict anything about their evolutionary futures.

Gene Flow in Nature

To what extent do populations considered to be conspecific ordinarily share a common gene pool? Mayr (4) estimated that "genetic exchange per generation . . . due to normal gene flow is at least as high as 10^{-3} to 10^{-2} for open populations that are normal components of species." He considered that gene flow was the principal source of genetic variation in natural populations, and we would agree that the introduction of genetic novelties into natural populations, even at a low level, may be important in supplying raw material for selection (5). The problem of testing Mayr's estimates and the conclusions to be drawn from them is complex. First, we must ascertain how much gene flow ordinarily occurs in nature. Second, we must determine the

amount of gene flow at which significant sharing occurs. That is, we must find the amount at which subpopulations of a species affect the evolution of other subpopulations. Both questions are difficult to answer, but at least a general picture of patterns of gene flow in nature has started to emerge recently.

Movement and Gene Flow in Animals

For many animals there is information on the movement of individuals. For instance, butterflies (except those few species which are migratory) seem to be quite sedentary as compared with what one might expect in view of their powers of movement (6). Birds also often seem to show less movement than they are capable of—the young of migratory species often nest near the parental nest site (7). There also is some evidence that birds may be stopped by "psychological barriers" (8). Similar restriction of movement not associated with insurmountable physical barriers has been observed in many nonaerial organisms, such as the rusty lizard (9). Twitty's (10) studies demonstrate that California newts show great perseverance and navigating ability in returning precisely to a particular stretch of stream to breed. Individuals displaced several miles in mountainous country have successfully returned to their "home pool." And, of course, the great accuracy with which salmon return to their birthplace to breed is well documented (11).

On the other hand, there also is abundant evidence in the literature that individuals may travel very long distances, such as in Bishopp and Laake's (12) release-recapture experiments with flies in which individuals were recovered as far as 17 miles (27 km) from the point of release. Small wind-dispersed terrestrial organisms may travel tremendous distances, as may some mammals (13). It is also clear (14) that extremely careful work covering the entire life history under a variety of weather conditions is necessary before reasonably definitive statements on amounts of individual movement may be made.

Of course, movement of individuals does not necessarily indicate gene flow. Anderson (15) has shown that the pres-

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ence of wandering individuals of *Mus musculus* as emigrants from granary populations does not indicate significant gene flow, since in general the granary demes do not admit immigrants. Ehrlich and his co-workers (16) have produced evidence indicating that the reproductive success of emigrant *Euphydryas editha* individuals is less than that of stay-at-homes, a situation which also probably pertains among small mammal populations (17).

Even reproduction by migrants or propagules may not constitute evolutionarily significant gene flow. Only if the migrants are carriers of alleles or arrangements of alleles not represented in the recipient population has gene flow occurred. In addition, if a new allele is to be passed from population to population by gene flow, one must consider the probability of its spread in each new population and its possibility of being included in the genome of migrant individuals leaving that population. Its fate in the first instance will presumably be governed by the kind of gloomy odds facing mutant genes (18); in no small part it will rest with its fitness in that population. One would normally expect selective barriers to the movement of genetic novelties.

Movement and Gene Flow in Plants

In plants, we have some actual estimates of gene flow between populations. Here the chances of crossing diminish rapidly with distance. In wind-pollinated species, one might expect a great deal of gene flow even between well-separated populations, but this assumption is not borne out by the available data. In *Zea mays* and *Beta vulgaris*, whose pollen is carried far and wide by wind, measurements have been made of contamination because of their agricultural importance. At distances greater than 60 feet (18.3 m), contamination by distant outcrossing in *Zea* was only 1 percent. In *Beta* plants separated by 200 meters, contamination was only 0.3 percent (19). Colwell (20) studied the dispersal of pollen of Coulter pine (*Pinus coulteri*) labeled with radioactive phosphorus. The bulk of the dispersal was within 10 to 30 feet (3 to 9 m) downwind from the source, with very little beyond 150 feet (46 m). It is obvious that, although pollen can be dispersed great distances at times, the chances of its falling on a receptive stigma at any great distance are slight.

On the other hand, a given plant normally will be completely pollinated, even in an outcrossing species, with pollen from nearby sources. A very short distance therefore will form the basis for nearly complete genetic discontinuity, even in a wind-pollinated plant.

In insect-pollinated species, Bateman (21) found that beyond 50 feet (15 m) there was less than 1 percent contamination between two varieties of turnips or radishes. Similarly, Roberts and Lewis (22) cite examples in several species of the herbs of the genera *Clarkia* and *Delphinium* where no more than 50 feet (15 m) seems to be an effective barrier. In *Linanthus parryae* the pattern of variation suggests that a very short distance effectively isolates these insect-pollinated plants (23). On the other hand, insects may occasionally carry pollen to somewhat greater distances. Because of their relative specificity, they actually may do so at a much higher frequency than occurs in plants whose pollen is carried by wind. An interesting demonstration of this is provided by Emerson's (24) studies of *Oenothera organensis*. This species is a local endemic of the Organ Mountains in New Mexico, where it occurs in isolated small colonies in the bottom of several steep-walled canyons. The colonies are separated by high ridges and are from 600 feet (183 m) to about 3 miles (5 km) apart. Emerson was able to demonstrate that this species had a system of self-sterility (S) alleles, the majority of which occurred in more than one colony, and some of which occurred in all of the colonies. Wright's (25) analysis of these data led to the conclusion that intergroup crossing had to have occurred about 2 percent of the time to account for this distribution. The plants are pollinated by strong-flying hawkmoths (Sphingidae), and Gregory (26) believes that this figure is consistent with the known behavior and power of flight of these insects.

In tropical rain forest, trees of a given species are often separated by considerable distances. Here it would appear that either strong-flying selective pollinators must actively seek out individuals or self-pollination must be prevalent. It is of interest to distinguish between these two possibilities, but little is understood of the structure of tree populations in the tropical rain forest at present.

In plants, therefore, there is consid-

erable evidence that distances of from 50 feet (15 m) to a few miles (several kilometers) may effectively isolate populations, and there is no evidence of longer-range gene flow. Beyond these limits, there is no suggestion of gene flow at or near the amounts suggested as "normal" by Mayr (4).

The possibilities of gene flow between natural populations of most species are sharply limited by their wide separation. Both plants and animals are usually highly colonial, the populations being separated by relatively great distances. For example, colonies of the butterfly *Euphydryas editha* occur scattered throughout California, many of them separated by distances of several kilometers and some by gaps of nearly 200 kilometers. It has been demonstrated that there is almost no gene flow in this species over gaps of as little as 100 meters (27). For this reason, there seems no possibility that gene flow "holds together" its widely scattered populations. The cave-dwelling collembolan *Pseudosinella hirsuta* occurs in a series of populations in the southeastern United States. There is no gene flow between them (28), yet they resemble one another. *Clarkia rhomboidea* occurs in the Great Basin of the western United States as a disjunct series of similar populations in widely separated mountain ranges. These are separated by gaps of scores or hundreds of kilometers and they are genetically highly differentiated (29). Gene flow can have no bearing on their evolution under present conditions, and we suggest that these three examples are representative of the vast majority of plant and animal distributions.

What then is the evidence for gene flow as a cohesive force holding together plant and animal species? Basically, the evidence seems to be that they are "held together"—populations considered to belong to a given species resemble one another. But the taxonomic decision to consider them members of one species is inevitably based on the fact that they do resemble one another and does not in itself provide an explanation for the resemblance. It may be that in certain continuously distributed species—if there are such—the regular exchange of genes between populations prevents differentiation in the face of different kinds of selection pressures at different places. But such a situation has never, to our knowledge, been demonstrated convincingly in either plants or animals.

The Origin of Species

One can see that, at the very least, it is unwise to view species of sexual organisms in general as the largest group of organisms sharing a common gene pool, although it may be true in particular instances. Yet this notion is important in the history of evolutionary biology, because it has promoted the idea that a species is an evolutionary unit, and that gene flow among its populations makes it such a unit. It led also to the conclusion that sharing the gene pool gives a species "cohesion" which must be broken if further speciation is to occur.

It is appropriate now to consider what processes are critical to the multiplication of species. There is an abundance of inferential evidence indicating that, at least in many cases, gene flow is of little or no importance in maintaining many of the phenetic units we call "species." Some of the strongest evidence, of course, comes from the wide variety of organisms with asexual reproduction. When this is obligate there is, by definition, no gene flow either within or between populations. And yet these organisms tend to occur as phenetic species—presumably groups of individuals being kept similar by their continued existence under similar selective regimes. And, as Mayr (30) points out, the existence of groups of sibling species indicates that gene flow is not necessarily the cause of phenotypic uniformity.

It is not necessary, however, to turn to asexual organisms (with, presumably, sharply restricted genetic variability) or sibling species to find evidence of selection rather than gene flow maintaining phenetic units. This is clearly what is happening in *Euphydryas editha* in California as well as in many other butterflies with populations that are totally isolated from one another. *Erebia theano* populations in Alaska are only slightly differentiated from those isolated in Colorado, indeed from those in Europe. Yet we would be greatly surprised if the Colorado populations (occurring as scattered isolates) receive a gene originating in Alaska once per hundred millennia. *Lycaena phlaeas* remains *Lycaena phlaeas* in the Sierra Nevada of California, although almost certainly no alleles from its European or eastern American relatives have reached this area for thousands of generations. The sand crab *Emerita analoga* has a strongly disjunct Northern-Southern Hemisphere distribution with

apparently no possibility of significant gene flow (31). In spite of this the two populations are not obviously differentiated. This is just one of many cases of a phenomenon known to marine biogeographers as "bipolarity" (32). Similarly, many species of plants have disjunct ranges in temperate North and South America, with varying amounts of differentiation despite a distributional gap of thousands of kilometers (33). Another case in point is the extreme resemblance of the marine faunas of the east and west sides of the Isthmus of Panama, which includes organisms considered to occur as pairs of relatively undifferentiated "twin species" (32). The close resemblance of the faunas remains, although the organisms on either side of the isthmus (that is, those which are restricted to warm seas) have presumably not exchanged genes for two million generations or more. Similarly, reef fishes often are remarkably similar throughout tropical seas, although gene flow among their populations is probably very reduced. The same can be said for plants on the numerous low atolls scattered through the Pacific. The plants which occur on them are identical everywhere, as contrasted with the plants on the high islands which present different selective regimes. Similar examples of lack of obvious differentiation in the absence of gene flow we suspect will prove to be common in all groups of organisms, just as will examples of rapid and prominent local differentiation (34) with or without gene flow.

In view of these considerations, we should reexamine the commonly observed situation in which island populations are more different from mainland populations than mainland populations are from one another. This difference is usually attributed to interruption of gene flow, but may more often be a function of a very different selective regime—for example, a milder climate—on the islands. Similar reasoning might be applied to other instances of differentiation on islands, for example, the case of the Galápagos finches (35). Isolation is always assumed to play the major role in this case, and indeed it may. But the islands, although superficially similar are ecologically very different and had depauperate faunas at the time of the original invasion (that is, there were many empty niches). Furthermore, the higher islands also show great internal diversification. If this explanation is correct, then we might expect relatively slow

differentiation in the future, since much of the "ecological opportunity" is gone, and the various species have now spread over the islands.

A word is necessary here about the function of isolating mechanisms, which have received so much attention from evolutionists (36). There is now no reason whatever to believe that such mechanisms evolved to somehow "protect" the genetic integrity of species. Incompatibility arises because two populations are subjected to differing selective regimes, and it is often reinforced by selection operating against hybrids. It is a common but not universal result, not a cause, of the process of speciation.

The similarity of populations that are obviously isolated from one another is conventionally attributed to their existence under similar selective regimes. But similarity where isolation is thought not to have been of long duration, or where isolation is not obvious, is almost always attributed to gene flow. This assumption seems untenable in the light of our knowledge of how rapidly differentiation can occur, gene flow or no, when selection promotes it. *Biston betularia* in England in 1825 would doubtless have been considered to be uniform in appearance because its populations were exchanging genes. We now know how fallacious that conclusion would have been, since whatever level of gene flow existed was insufficient to prevent dramatic local differentiation when the selective situation changed (37). Similarly the butterfly *Maniola jurtina* maintains stable genetic configurations selectively over vast areas (38) and maintains sharp borders between the different types in spite of strong gene flow (39). Genetic "area effects" are also well known in *Cepaea* populations (40) with boundaries not coinciding with barriers to gene flow.

The formation of very local races of plants and animals is commonplace even in extreme outcrossers such as the self-incompatible wind-pollinated grasses *Festuca rubra* and *Agrostis tenuis* (41). Such races, which may be sharply differentiated genetically, may occupy areas in nature only a meter or so in diameter—with these races surrounded by plants of another race. The differentiation of such localized populations dependent on the interplay between natural selection, the breeding system, and gene flow, has been analyzed (42). The advantage of particular genotypes in reproducing under a particular, often extremely local, set of conditions may be such that recombinants and other

variants are systematically eliminated. In spite of the opportunity for high levels of gene flow, the selection pressures determined experimentally in such cases seem theoretically adequate to explain the very local patterns of differentiation found, for example, in *Agrostis stolonifera* (43).

The increasingly refined methods of genetic analysis that are being applied to natural populations are revealing more and more instances of unexpectedly local differentiation even when the organisms concerned are highly mobile and the populations appear to be continuous. In *Drosophila aldrichi*, Richardson (44) analyzed three populations within a 40-mile (64 km) radius of Austin, Texas, for the frequencies of six alleles concerned with a particular esterase system. The frequencies differed slightly from locality to locality but remained constant at each locality during a year. Using a similar approach, Selander (45) showed "microgeographic" variation between populations of the house mouse (*Mus musculus*) in a single large barn.

Thus, there is increasing evidence of extremely local patterns of differentiation in both plants and animals. We predict that such patterns may prove to be the rule, rather than the exception, for most populations of organisms.

Evidence from natural populations is supported by experimental work such as that of Thoday and his co-workers (46) which indicates that selection can override the effects of gene flow even when the amount of that flow is greater than would ever occur in nature. Evidence of this sort would undermine arguments about "gene flow" as a cohesive force binding together all the populations of some widespread species into a genetic entity, even if such binding were not patently impossible for most organisms on purely distributional grounds. Indeed, gene flow eventually might be discovered to play a rather insignificant role in evolution as a whole. There is substantial evidence that populations can be changed rapidly by selection. Similarly there is evidence that selection often resists such change—presumably in part because of genetic homeostasis. The most basic forces involved in the differentiation of populations may be antagonistic selective strategies, one for close "tracking" of the environment and one for maintaining "coadapted" genetic combinations—combinations which have high average fitness in environments which are inevitably variable through time.

Of course final answers about the relative evolutionary roles of selection and gene flow will not come until we have more thorough studies of natural situations. Some of the cases commonly presented as showing gene flow preventing differentiation need careful re-examination, for example, those of Hooper (47) and others on the development of dark-lava races in mice. If this, indeed, is a case of gene flow swamping selection, then we must learn the magnitude of both factors. In cases such as that of *Euphydryas editha*, laboratory and field experiments must be devised to determine the exact selective regimes which produce relative uniformity among populations along with temporal variability within populations, in the absence of gene flow. In this, and virtually all other situations cited in this paper, further genetic analysis is needed to determine how well phenetic uniformity or variability reflects genetic uniformity or variability. It is well known that there is no one-to-one relationship (48), but in general we are profoundly ignorant of the degree of overall genetic similarity, however defined (49), at all levels of phenetic differentiation.

Our suspicion is that, eventually, we will find that, in some species, gene flow is an important factor in keeping populations of the species relatively undifferentiated, but that in most it is not. As this becomes widely recognized we will see the disappearance of the idea that species, as groups of actually or potentially interbreeding populations, are evolutionary units "required" by theory. Modern evolutionary theory requires local interbreeding populations, far smaller groups than those normally called species, as evolutionary units in sexual organisms. It recognizes that such units will vary greatly in their genetic properties and may have a vast diversity of relationships with other such units. The evolution of larger phenetic clusters—the species, genera, orders, and so forth, of taxonomists—is easily derived from the theory, but it seems unwise to consider any of these as evolutionary units except in those cases where they can be shown to react to evolutionary pressures as units (50).

Summary

Evidence is presented from a variety of sources which indicates that species should not be thought of as evolutionary units held together by the cohe-

sive force of gene flow. Gene flow in nature is much more restricted than commonly thought and experimental evidence is badly needed to document the extent to which it does occur. Selection itself is both the primary cohesive and disruptive force in evolution: the selective regime determines what influence gene flow has on observed patterns of differentiation. Populations will differentiate if they are subjected to different selective forces and will tend to remain similar if they are not. For sexual organisms it is the local interbreeding population and not the species that is clearly the evolutionary unit of importance.

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