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ON THE ROLE OF SPECIES IN ANAGENESIS

Speciation is central to the hypothesis of punctuated equilibria as developed by Eldredge and Gould (1972; see also Gould and Eldredge 1977, 1986; Gould 1982) and by Stanley (1975, 1979). Without the claim that evolutionary change is associated with speciation, punctuated equilibria would consist merely of the statement (to which no one would take exception) that rates of evolution vary. Population geneticists have generally been skeptical about punctuated equilibria (e.g., Templeton 1980; Lande 1980*a*; Stebbins and Ayala 1981; Turner 1981; Charlesworth et al. 1982), in part because genetic theory and data appear to offer no support for the postulate that evolutionary change in, for example, morphological characters is contingent upon or associated with speciation (i.e., acquisition of reproductive isolation). These authors doubt that speciation should increase the rate of morphological evolution and are particularly skeptical of the punctuationists' supposition that lineages are static between speciation events because of an inability to respond to selection.

Here I point out a consequence of speciation that supports a highly qualified version of punctuated equilibrium. None of the ideas explored below is in itself original, but I am not aware that they have been explicitly developed in the present context. In brief, I propose that because the spatial locations of habitats shift in time, extinction of and interbreeding among local populations makes much of the geographic differentiation of populations ephemeral, whereas reproductive isolation confers sufficient permanence on morphological changes for them to be discerned in the fossil record. Long-term anagenetic change in some characters is then the consequence of a succession of speciation events. I have briefly referred to this argument before (Futuyma 1986*a*, pp. 404, 406; Futuyma 1986*b*, p. 377), without having developed the reasoning, evidence, and contrasts with alternative hypotheses presented here.

Eldredge and Gould (1972) hypothesized that punctuated patterns follow from Mayr's (1954, 1963) neo-Darwinian but not universally accepted hypothesis of peripatric speciation, according to which rapid shifts in morphology occur in highly localized populations in concert with the acquisition of reproductive isolation from the main body of the species, which remains little changed. The morphological shifts envisioned by both Mayr and the punctuationists are typically not so pronounced as to mark the origin of higher taxa; they are of the magnitude that usually distinguish congeneric species; and it is shifts of this magnitude that I discuss in the first part of this note.

Authors who have offered population-genetic explanations for rapid shifts between stable morphological states (e.g., Kirkpatrick 1982*a*; Newman et al. 1985)

grant that populations in which such shifts occur may incidentally acquire reproductive isolation as well, but they have not suggested that speciation is a necessary concomitant of the morphological shift. In contrast to those who view genetic homeostasis and gene flow as the agents of stasis from which speciation liberates a population, many population geneticists have been inclined to attribute stasis to stabilizing selection (Stebbins and Ayala 1981; Charlesworth et al. 1982), although at first surmise it seems surprising that stabilizing selection could favor the same phenotype over many thousands or even millions of years despite manifest changes in the environment.

Some evolutionary changes (“general adaptations”; Brown 1959) doubtless are selectively advantageous throughout the range of a species—perhaps increases in digestive efficiency or fecundity, for example. I assume, however, that such changes are rare compared with the evolution of “special adaptations” to a population’s ecological niche (in the sense of Hutchinson 1957), which have a more narrowly context-dependent advantage. For example, the host plant used by a phytophagous insect affects the course of adaptation respecting chemical and physical properties of the host, phenology, dispersal, microclimate, and host-associated parasitoids and predators. In animals, habitat selection (or comparable behavioral traits such as host selection in phytophagous insects) is a critical proximate mechanism maintaining (and even defining) the association between an organism and the elements of its niche. By habitat selection, the organism therefore largely determines the selection pressures to which it is subject; it creates much of its own environment (Lewontin 1983). If habitat selection remains constant, it confers some stabilizing selection on numerous morphological and physiological traits (Maynard Smith 1983; Slatkin and Kirkpatrick, in press). Habitat selection can therefore contribute to such stasis as is observed in the fossil record, providing at least a partial answer to the question of how stabilizing selection can operate in an apparently changing environment. The phenomenon of habitat selection reinforces the argument that follows but is not essential to it.

The constellation of characters associated with adaptation to an ecological niche will generally not be maintained intact in a sexual population if it is locally sympatric with and interbreeds with another such population that is likewise adapted to another niche. Even for a single locus, a stable multiple-niche polymorphism (e.g., in a phytophagous insect that occupies two species of hosts) can ordinarily be maintained only under restricted conditions, including intense selection (Felsenstein 1976, 1979; Maynard Smith and Hoekstra 1980). Maintenance of linkage disequilibrium among loci governing the several traits appropriate to one or another niche requires strong selection and/or tight linkage (Lande 1980*b*). That is, recombination breaks down associations among traits—including associations between alleles for habitat selection and other traits—such that these associations remain intact only if reproductive isolation exists. In this sense, reproductively isolated species are “coadapted gene pools” (Mayr 1963) and are “necessary” (Hutchinson 1968).

It is likely that shifts to new ecological niches, and consequently changes in relevant characters, occur in local populations in response to locally prevalent resources or microhabitats. If the niche shift happens to be accompanied by the

acquisition of reproductive isolation from populations that remain associated with the ancestral niche, the newly formed species can spread, retain its association with its resource even if this is generally less abundant than in the species' site of origin, and retain its distinctive constellation of characters even when sympatric with the ancestral form. This part of the familiar theory of speciation is central to the argument.

As long as spatial differences in selection are stable and gene flow is not excessive, local populations of a species can develop any degree of difference in any number of characters: the evidence from geographical variation tells us that character evolution does not require speciation. But in the absence of speciation, much of the geographical variation we observe is ephemeral, leaving little imprint on evolution in the long term. This is chiefly because most local populations are ephemeral; over even moderately short spans of evolutionary time (tens or hundreds of thousands of years), the habitats to which populations are adapted shift, often over large distances, in consequence of climatic change. The most recent dramatic instance—dramatic in magnitude but not exceptional in kind—is seen in the Pleistocene, during which the distribution of both temperate and tropical species changed markedly and repeatedly (e.g., Cushing 1965; Livingstone 1975; Davis 1976; Coope 1979; Graham and Lundelius 1984 and numerous references therein). The critical consequence of these changes in the distribution of a species' habitat is that habitats in new localities are colonized from preexisting populations that subsequently are likely to become extinct. To the extent that the founders of new populations are drawn from separate, differentiated populations, the consequence is occasional (perhaps at intervals of thousands of years) but massive gene flow (i.e., hybridization), on a scale far greater than the trickle that often characterizes populations at equilibrium (Slatkin 1977; Maruyama and Kimura 1980). Instances of hybridization in regions of secondary contact often illustrate the breakdown in distinctiveness of formerly isolated populations. Thus, in the absence of reproductive isolation, differentiation is broken down by recombination. Given reproductive isolation, however, a species can retain its distinctive complex of characters as its spatial distribution changes along with that of its habitat or niche.

Thus, speciation can facilitate morphological change not by liberating a population from genetic homeostasis or accelerating the response to selection, but by enabling a gene pool to remain subject to consistent selection pressures even as it moves about in space. By isolating gene pools from other gene pools that they encounter as they move about, speciation enables them to retain characters that evolved in a localized context. It provides them, as Simpson (1961) pointed out, with a distinct evolutionary trajectory.

The fossil record, except when it is unusually detailed, probably records little of the evolution that occurs within populations, because these evolutionary events are spatially highly localized and are obliterated by extinction and interbreeding with other populations over the course of even a few thousand generations. Although speciation does not accelerate evolution within populations, it provides morphological changes with enough permanence to be registered in the fossil record. Thus, it is plausible to expect many evolutionary changes in the fossil record to be associated with speciation.

It will be useful at this point to expand on the kind of evidence that supports certain elements of this argument.

That considerable ephemeral change occurs but is not recorded in coarse fossil records is evident from finer records, in which rapid fluctuations about relatively unchanging character means are typical (Charlesworth 1984). This pattern may represent the action of fluctuating selection on a local gene pool, but it could just as well stem from occasional episodes of massive gene flow. For example, Williamson (1981) reported that several molluscan species in a Pleistocene lake basin diverged during isolation, but returned to the ancestral morphology after reestablishing contact with the main populations of the species. Assuming the excursion in morphology had a genetic basis (see Fryer et al. 1985 and associated papers), the reversal could equally be explained by a reversal of selection or by gene exchange with the larger population. It is safe to say that if the divergent characters had a polygenic basis, a bimodal character distribution would not have persisted locally in the face of substantial gene flow.

For species with low equilibrium levels of gene flow (e.g., land snails, many plants, inhabitants of desert pools), substantial geographic differentiation can develop over short distances, and regionally localized changes in the spatial distribution of habitats will likewise suffice to reverse or erase differentiation. In contrast, large-scale patterns of geographical variation in widespread, vagile species, such as many North American birds, will probably break down under hybridization only if climatic changes bring about massive changes in the species' distribution, as when temperate-zone species became restricted to southern refugia during Pleistocene glacials.

My argument for the importance of reproductive isolation applies to characters that evolve in a local adaptive context but are retained as the species moves geographically with its habitat. For character changes that are adaptive throughout the range of a species, in all the habitats that its various populations may occupy, simple phyletic transformation of the entire species may be expected. Such general, "progressive" adaptations, however, probably represent a minority of adaptive changes. Characters that distinguish closely related species (i.e., characters at the level we are concerned with here) appear frequently to be context-dependent adaptations to the species' respective niches. Many other species differences can plausibly be ascribed to sexual or social selection, which depends strongly on context because it depends on frequency (Lande 1981; Kirkpatrick 1982*b*; West-Eberhard 1983). Although adaptations to a food type or microhabitat may arise in a local context of interspecific competition or resource abundance, they may be retained when a reproductively isolated species moves into different communities. Every ecologist is familiar with species that, having acquired a specialized habit, are rare in regions where their resources are rare and they have not adapted to alternative resources. Similarly, if they confer reproductive isolation, characters that evolve in a local population by sexual selection are retained after sympatry with other populations is established.

For example, the chief characters that distinguish species of hummingbirds are differences in male plumage characters that have doubtless evolved by sexual selection and differences in beak, leg, and wing dimensions that are adaptations to

species-specific modes of feeding (Feinsinger and Colwell 1978). The chief differences among geospizine finches are food-related differences in beak form (Lack 1947; Abbott et al. 1977). Many differences among populations or congeneric species of plants are adaptations to different pollinators or microhabitats (Grant and Grant 1965; Stebbins 1974). Among West Indian species of *Anolis*, slight skeletal differences distinguish a few of the species, but most are distinguished by size, color, leg and head dimensions, scalation, and the size and color of the dewlap (Williams 1976, 1983). The dewlap is surely subject to sexual and social selection and may evolve in response to interspecific interactions (Webster and Burns 1973; Williams and Rand 1977). The other external characters correlate strongly with macrohabitat (forest, grassland, etc.) or microhabitat (canopy, trunk, etc.) and have evolved repeatedly within the West Indian radiation (Collette 1961; Williams 1983; G. C. Mayer, pers. comm.), perhaps partly in response to interspecific competition (Schoener 1970; Roughgarden et al. 1983; Williams 1983). Such niche-specific characters that distinguish species are more likely to have arisen in a local environmental context than throughout a broad, environmentally variable geographic region.

I turn now to long-term anagenetic change, which advocates of punctuated equilibria propose to explain by species selection (differential speciation and extinction rates). For characters that provide a general, relatively context-independent advantage, a consistent long-term regimen of directional selection can often be envisioned, and no role for speciation need be invoked. Many synapomorphies of higher taxa, such as the plumose hairs of bees, the ear ossicles of mammals, and the digital lamellae of *Anolis*, are possible examples. Some major anagenetic changes, however, represent extreme adaptations to special resources in a small branch of a larger clade. In some such instances, speciation may facilitate the evolution of an extreme morphology, because the variance among a set of sympatric species can exceed the variance in any one population (Arnold and Fristrup 1982; see also Wright 1932).

Consider as a heuristic example the extraordinary hummingbird *Ensifera ensifera*, with a beak length of 83 mm or more, which feeds in flowers with corollas that may exceed 100 mm in length (Snow and Snow 1980). Suppose it evolved from a "typical" hummingbird of roughly the same body size, such as *Sericotes holosericeus*, with a beak-length mean and standard deviation of 22.2 mm and 2.2 mm, respectively (Kodric-Brown et al. 1984). If this ancestral population encounters an abundant plant with 80-mm corollas, it cannot be directionally selected for an equally long beak, because the maximal beak length is about 28.8 mm (three standard deviations above the mean), permitting few if any individuals to feed on this plant at all. But if there are numerous species with different means, the distant optimum (>80 mm or so) is more likely to fall within the range of variation of one or another of the species, such that directional selection is possible. The population in which such selection occurs (with mean and standard deviation of perhaps 70 mm and 3 mm) is likewise a specialist on unusually long flowers (relative to those used by a *Sericotes*-like ancestor) and likewise is more likely to have arisen if there previously existed a constellation of species than if there existed a single one.

In this scenario (which, being heuristic, ignores the possible role of coevolution; see Feinsinger 1983), the evolution of an *Ensifera* morphology has proceeded stepwise, each step being specialized for an ever more extreme resource. But each step has had a more than ephemeral existence only because reproductive isolation prevented the slippage consequent on interbreeding with other populations adapted to less extreme resources. (This scenario is very like that of Mayr [1963, pp. 588, 621] and may be implicit in Stanley's [1979, pp. 195–197] discussion of "isolate selection.") Thus, even without species selection in the sense of differential speciation and extinction rates, speciation may facilitate anagenesis by retaining, stepwise, the advances made in any one direction. If we envision an adaptive landscape not of gene frequencies but of character values (Lande and Arnold 1983; Slatkin 1983), successive speciation events are the pitons affixed to the slopes of an adaptive peak.

I have mainly attempted to offer here a role for speciation not requiring the punctuationalists' suppositions that periods of apparent stasis represent inability to respond to selection and that speciation somehow enables response. Although the punctuationalists and I envision different roles for speciation, the evidence favoring the present hypothesis is the same as that favoring the postulated process of punctuated equilibria: substantial character change (of more than a few standard deviations) should be associated in the fossil record with speciation (bifurcation of lineages). It is far from clear (to say the least) that the fossil record supports this prediction or that the record will often be good enough to test it (Gingerich 1976; Levinton 1983; Cope and Skelton 1985). The association of character change with speciation should hold especially for alterations of character state that are temporally and geographically extended after their origin (i.e., not brief, reversed excursions in a single section). The theory of punctuated equilibria does not claim greater applicability to any classes of characters over others; granted the difficulty of inferring function from structure in fossil material, I would expect punctuated patterns more frequently of specially adaptive than of generally adaptive characters.

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