Ernst Mayr and the Origin of Species

Jerry A. Coyne


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ERNST MAYR AND THE ORIGIN OF SPECIES

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Evolutionary biology has a punctuated history. It arose as a conceptual macromutation on November 24, 1859—"disgorge," as Mencken (1931) put it, "in one stupendous and appalling dose"—and has undergone stasis or slow anagenesis ever since. Indeed, much of the field still consists of repeated demonstrations of phenomena first described by Darwin, or of epiphenomena derived from them.

The study of speciation, however, is a conspicuous exception. Despite the title of his famous book, Darwin was notably unsuccessful in solving the real problem of organic diversity: why plants and animals in a habitat fall into discrete, nonoverlapping packages. It is widely accepted that his failure came from his inability to conceptualize species as noninterbreeding groups (see Mayr 1959) and to recognize that the origin of species was identical to the origin of the barriers to interbreeding. Because Darwin considered species to be only highly evolved morphological varieties (indeed, The Origin of Species should have been called The Origin of Adaptations), he confused adaptation within lineages with the origin of new lineages. Although the two are connected, the former does not automatically produce the latter. Understanding how one species of warbler becomes adapted to its habitat does not explain why four other distinct species—and no intermediates—occupy the same patch of forest.

One solution was suggested by geneticists like Bateson and Goldschmidt, who correctly conceived the species problem to be the explanation of organic gaps, but then mistakenly ascribed them to single mutations causing large morphological change. This idea foundered on the lack of a convincing scenario for fixing these mutations and on the evidence that species differed in not one but many genes. For many years after Darwin, the origin of species remained the most important unsolved problem of evolution.

The mathematical evolutionists of the modern synthesis had little to say about this problem, and much of what they did say was wrong. Our modern theories of speciation derive almost entirely from a naturalist and an experimentalist, Ernst Mayr and Theodosius Dobzhansky, and their two classic books, Genetics and Origin of Species (Dobzhansky 1937) and Systematics and the Origin of Species (Mayr 1942), later rewritten and expanded as Animal Species and Evolution (Mayr 1963).

On the occasion of Mayr's ninetieth birthday, I am pleased to pay him tribute by discussing and evaluating his four major contributions to the species problem. Three of these—the emphasis on discontinuous organic forms, the encapsulation of such discontinuities in the "biological species concept," and the theory of allopatric speciation—are milestones of evolutionary biology that constitute the modern dogma of speciation. Mayr's fourth contribution, the idea of "genetic revolutions" in isolated populations, is decidedly less important, and, it seems to me, probably incorrect. It will be impossible to discuss Mayr's work without also mentioning that of Dobzhansky, whose genetic expertise made the theory of speciation a true product of the modern synthesis.

ORGANIC DISCONTINUITIES

Many field naturalists find it hard to doubt that organisms in any habitat fall into discrete groups, which have a reality not shared by higher levels of classification like genera and families. The idea of organic discontinuity has a long tradition, beginning with Linnaeus' classification, and was recognized by even Darwin in The Descent of Man (1871): "Independently of blending from intercrossing, the complete absence, in a well-investigated region, of varieties linking together any two closely-allied forms, is probably the most important of all the criteria of their specific distinctness" (1871, p. 215).

Nevertheless, some biologists contend that these discontinuities are purely subjective artifacts of human perception. One such dissenter was, surprisingly, J. B. S. Haldane, who observed that "the concept of a species is a concession to our linguistic habits and neurological mechanisms . . . a dispute as to the validity of a specific

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distinction is primarily a linguistic rather than a biological dispute" (1956, p. 96). The idea that species are not real is particularly popular with systematists (e.g., Sokal and Crovello 1970; Mishler and Donoghue 1982; Nelson 1989) and botanists (e.g., Raven 1976; Levin 1979), who emphasize the lack of easily recognized species in plants. Those entertaining this view, of course, require no theory of speciation beyond that given by Darwin.

The recognition of the reality of species is the key to explaining organic diversity, and it was largely Mayr and Dobzhansky who impressed this reality upon evolutionists: "Only after the naturalists had insisted on the sharp definition of local species was there a problem of bridging the gap between species. And only then did the problem arise whether or not the species is a unit of evolution, and what sort of unit" (Mayr 1963, p. 30). The emphasis here is on "local," for, as Mayr noted, these discontinuities are most evident in sympatric groups, and largely disappear under the inclusion of geographic populations. This disparity between local and isolated populations was a major inspiration for his theory of allopatric speciation.

Mayr discussed the reality of species at length in his first major paper on speciation (1940), supporting the idea with evidence from bird taxonomy, and produced a longer discussion in chapter 7 of Systematics and the Origin of Species. Dobzhansky, on the other hand, solved the problem by fiat at the very beginning of Genetics and the Origin of Species: "Discrete groups are encountered among animals as well as plants, in those that are structurally simple as well as in those that are very complex. Formation of discrete groups is so nearly universal that it must be regarded as a fundamental characteristic of organic diversity." (1940, p. 5.)

Given the importance of the problem and the vocal minority of critics, it is surprising that there are few studies of the reality of species in a single locality. Existing work falls into two categories. The first notes the remarkable concordance between species described by Western taxonomists and the "kinds" recognized by indigenous peoples. Such concordance has been demonstrated for both plants (Berlin 1992) and birds (Mayr 1963; Diamond 1966), although the geographic sampling is limited.

This evidence has not convinced everyone. In response, Ridley noted, "However, the fact that independently observing humans see much the same species in nature does not show that species are real rather than nominal categories. The most it shows is that all human brains are wired up with a similar perceptual cluster statistic." (1993, p. 404.) His criticism, echoing that of Haldane, fails to recognize that all scientific progress comes from the agreement of independent observers. (Is the distinction between chemical elements, for example, an artifact of the way our brains are wired to perceive matter?) If nothing else, these congruent classifications give strong evidence that species are real, although they do not prove them more real than other categories of classification. One could test this last idea by asking nonbiologists to place all local organisms into seven hierarchical categories, and then comparing the result to traditional Western taxonomy. (I would bet a substantial sum that the congruence seen for species would largely vanish at higher levels.)

Perhaps a more convincing approach would involve cluster analysis of either genetic or morphological diversity within one area. Although such analyses are themselves designed to separate groups, they cannot create such groups when they do not exist. There are many multivariate analyses of both morphological and genetic variation showing fairly distinct differences among sympatric groups (e.g., Grant 1957; Neff and Smith 1978; Humphries et al. 1981; Futuyma 1991). These investigations, however, are often performed on species already known to differ morphologically and are usually limited to two groups. One would like to see such analyses performed on every individual bird or plant within one habitat. Mayr himself (1992b) conducted a valiant though nonstatistical study of this kind, concluding that 90.8% of the plant species in Concord, Massachusetts were clearly delimited.

My own opinion vacillates between Dobzhansky's view that the reality of species is evident to any reasonable person, and a wish that someone would settle the issue through detailed study of at least a few sympatric groups. (I cannot imagine, however, that funding agencies would rush to support this work). Such studies would be particularly useful in plants, in view of botanists' repeated claims that plant "species," such as oaks, often form intergrading, hybridizing units. It is entirely possible that many such "species complexes" are actually ecotypes of a single species, differentiated in only a few characters by intense habitat selection (Coyne et al. 1988).

A major unsolved question about the reality of species is whether discrete groups also occur
in asexually reproducing taxa. The answer would have major implications for understanding why organic forms are discontinuous, particularly in estimating the relative contributions of sexual reproduction versus discrete ecological niches. Only a few studies of eukaryotes have addressed this problem. Holman (1987) concluded that asexually reproducing groups of bdelloid rotifers were actually recognized more consistently than their sexually reproducing relatives. This conclusion, however, was based not on morphology or genetics, but on stability of nomenclature through successive taxonomic revisions. Analyzing mosses of the genus Tortula, Mishler (1990) found no difference in the amount of morphological variation among populations of two sexual versus two asexual "species," although he examined only 10 or 20 individuals per species. There is a clear need for much more work of this kind, using phenetic and not systematic criteria.

**The Biological Species Concept**

The recognition that discrete groups exist in one location immediately demands a definition, or rather a concept that encapsulates these groups in words. Although morphological species concepts were dominant until the 1930s, some biologists, such as Karl Jordan, suggested criteria based on interbreeding (for a summary of this early work, see Mayr 1942, 1957, 1982). However, it was Dobzhansky and especially Mayr who provided the definitive rejection of phenetic concepts, replacing them with what has become known as the "biological species concept," or BSC (table 1). In later publications, Mayr (1963, 1982) slightly revised the BSC, emphasizing that it is best applied to sympatric taxa. This removed the problematic words "potentially interbreeding" from his definition, although allopatric taxa that produce sterile or inviable hybrids in captivity are surely biological species.

Because the observation of discrete sympatric groups almost immediately suggests a species concept based on interbreeding and its absence, it is surprising that such a view did not become popular until about 1940. Perhaps this idea occurs most readily to the geneticist, explaining why the first explicit version of the BSC came from Dobzhansky (table 1). As he explained, "Any discussion of these problems should have as its logical starting point a consideration of the fact that no discrete groups of organisms differing in more than a single gene can maintain their

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<th>Table 1. The biological species concept and some recently proposed alternatives.</th>
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<td><strong>Biological Species Concept</strong></td>
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<td>A species is a group of individuals fully fertile interse, but barred from interbreeding with other similar groups by its physiological properties (producing either incompatibility of parents, or sterility of the hybrids, or both) (Dobzhansky 1935).</td>
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<td><strong>Species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups (Mayr 1942).</strong></td>
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<td><strong>Evolutionary Species Concept</strong></td>
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<td>A species is a single lineage of ancestral descendant populations or organisms which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate (Wiley 1978).</td>
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<td><strong>Phylogenetic Species Concepts</strong></td>
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<td>A phylogenetic species is an irreducible (basal) cluster of organisms that is diagnosably distinct from other such clusters, and within which there is a parental pattern of ancestry and descent (Cracraft 1989).</td>
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<td>A species is the smallest monophyletic group of common ancestry (de Queiroz and Donoghue 1990).</td>
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<td><strong>Recognition Species Concept</strong></td>
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<td>Species are the most inclusive population of individual biparental organisms which share a common fertilization system (Paterson 1985).</td>
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<td><strong>Cohesion Species Concept</strong></td>
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<td>A species in the most inclusive population of individuals having the potential for phenotypic cohesion through intrinsic cohesion mechanisms (Templeton 1989).</td>
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<td><strong>Ecological Species Concept</strong></td>
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<td>A species is a lineage (or a closely related set of lineages) which occupies an adaptive zone minimally different from that of any other lineage in its range and which evolves separately from all lineages outside its range (Van Valen 1976).</td>
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<td><strong>Internodal Species Concept</strong></td>
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<td>Individual organisms are conspecific in virtue of their common membership of a part of the genealogical network between two permanent-splitting events or between a permanent split and an extinction event (Kornel 1993).</td>
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identity unless they are prevented from interbreeding with other groups. . . . Hence, the existence of discrete groups of any size constitutes evidence that some mechanisms prevent their interbreeding, and thus isolate them" (Dobzhansky 1935, p. 281).

Mayr, of course, gets the credit for refining,
popularizing, defending, and working out the consequences of the BSC in his numerous writings on species concepts. Besides the original definition, Dobzhansky’s major contribution to this notion is his classification of the biological factors preventing hybridization, the so-called “reproductive isolating mechanisms,” and their division into categories acting before (prezygotic) and after (postzygotic) fertilization. A major portion of *Genetics and the Origin of Species* is devoted to describing and illustrating these mechanisms.

The BSC has become the dominant evolutionary view of species for at least three reasons. First, it is able to handle problems that cannot be solved by phenetic concepts, such as morphologically identical species, polymorphism, sexual dimorphism, and phenotypically different stages of the life cycle. Second, it shows that the species is an evolutionary unit in that it delimits the spread of a generally advantageous allele, such as one raising fecundity by 0.2%. In this sense, the species is the entity that evolves, and hence the locus of micro- and macroevolutionary change (see Gould 1994). Finally, and most important, it provides a research program for understanding the genesis of biological diversity: The origin of species is now seen as the origin of reproductive isolating mechanisms. The problem then translates immediately to understanding the evolution of factors like microhabitat preference, mate discrimination, and hybrid sterility. It is a testament to the power of the BSC that virtually everyone studying the origin of species concentrates on reproductive isolating mechanisms.

The BSC has nevertheless encountered severe opposition, usually from systematists, and many alternative concepts have been proposed. Table 1 gives only a sample of the more recent ones, and each year brings new contenders. Moreover, there is a disturbingly large literature filled with acerbic attacks and defenses of all of these concepts (for recent examples, see Coyne et al. 1988; Masters and Spencer 1989; Otte and Endler 1989; Ereshefsky 1992; Mayr 1992b); much of this argument leaves the solid ground of biology for the marshy hinterlands of philosophy.

No alternative concept, however, has displaced the BSC among evolutionists, although systematists seem increasingly to embrace typological views in which species are defined as possessing one or more diagnostic or apomorphic features (so-called “phylogenetic species concept”). I believe that the failure of alternative concepts comes largely from their inability to offer an entrée into the problem of biological diversity and to inspire interesting new research. The evolutionary and phylogenetic concepts, for example (table 1), distinguish species by phenotypic difference—and would split every morphologically diagnosable population into a new species—but suggest no program for understanding the coexistence of phenotypically distinct but related species. Proponents of the recognition concept maintain that it is not “relational”; that is, species are not detected or defined by their reproductive isolation from one another (Paterson 1985). It thus offers no way to study the evolution of mating discrimination among species. The ecological species concept may be an exception, as the discreteness of species could be ascribed to the discreteness of niches. It is not clear, however, whether niches really are discrete, and, at any rate, the concept is impossible to use given the difficulty of categorizing “minimally different adaptive zones.” Mayr (1992b) noted that many systematists proposing alternative species concepts actually revert to the BSC when dealing with problems like sibling species.

I have no idea why the BSC, which despite its difficulties has inspired so much valuable research, also seems to ignite so much controversy, nor why many biologists are intent on replacing it with concepts even more problematic. Some systematists apparently fear that acceptance of the BSC will trivialize their research program. For example, “The militant view that systematists need to embrace is that the responsibility for species concepts lies solely with systematists. If we continue to bow to the study of process over pattern, then our endeavors to elucidate pattern become irrelevant” (Wheeler and Nixon 1990, p. 79). It is clear, however, that the many pages of argument have not increased our understanding of evolution, and that the best advice may be that proffered half a century ago by the prescient Hogben (1940): “We need not prolong a barren controversy about the various definitions of species.”

Accepting that species do exist and correspond to interbreeding groups separated by reproductive gaps, one may still wonder what feature of organisms inevitably produces these gaps. Why aren’t there just a few extremely variable species? This is one of the most important and least considered questions of speciation. Mayr and Dobzhansky both had answers, but they verged on the teleological, implying that nature somehow engineers these gaps to protect adaptive gene complexes: “Hence maintenance of life is pos-
sible only if the gene patterns whose coherence is tested by natural selection are prevented from disintegration due to unlimited hybridization. It follows that there must exist discrete groups of forms, species, which consist of individuals breeding inter se, but prevented from interbreeding with individuals belonging to other groups of similar nature.” (Dobzhansky 1937, p. 405.)

“The division of the total genetic variability of nature into discrete packages, the so-called species, which are separated from each other by reproductive barriers, prevents the production of too great a number of disharmonious incompatible gene combinations. This is the basic biological meaning of species, and this is the reason why there are discontinuities between sympatric species.” (Mayr 1969, p. 316.)

These explanations, probably influenced by Sewall Wright’s concept of the adaptive landscape, do not rest on the firm populational thinking so important in the other writings of Mayr and Dobzhansky, nor do they square with the notion that some isolating mechanisms, such as hybrid sterility, cannot be the direct target of natural selection. There is still no good explanation for the ubiquity of organic gaps. The solution may involve pleiotropy, trade-offs, and sexual reproduction (adapting to one environment reduces fitness in others, causing problems in hybrids), the discreteness of ecological niches (there is a limit to the similarity of competing forms), or a combination of these factors. Several theoretical studies (Rosenzweig 1978; Hopf and Hopf 1985; Brown and Vincent 1992) have suggested that ecological factors alone can create phenotypic gaps between taxa, but the answer is not yet clear. Observing whether asexually reproducing taxa fall into discrete groups will go a long way toward solving the problem.

**Allopatric Speciation**

Mayr’s explanation for the origin of biological species was allopatric speciation: geographically isolated populations of a single species evolve reproductive isolating mechanisms that later allow them to coexist in sympathy. To describe Mayr’s multifarious evidence for this process would deprive the student of the great joy of reading chapter 7 of *Systematics and the Origin of Species*, an experience that turned many of us toward the study of speciation. The exhaustive biogeographic evidence given in this chapter reminds one strongly of *The Origin of Species* and immediately convinced most evolutionists of the importance of allopatric speciation. The novelty of Mayr’s argument was the explanation of reproductive gaps as the incidental byproduct of evolutionary divergence between isolated populations, gaps that can only be seen when the newly evolved species become sympatric. With this argument, organic diversity had at last received a convincing explanation.

Dobzhansky contributed to this theory by summarizing the genetic evidence for the importance of geographic isolation. In a famous five-page discussion in *Genetics and the Origin of Species* (1937, pp. 254–258), he refuted the notion that speciation results from single mutations, demonstrating that most forms of reproductive isolation involve epistatic interaction between alleles fixed in different demes. If an ancestral population has the two-locus genotype *aabb*, one isolated population might evolve to *aaBB* and another to *AAbb*. If individuals carrying the *A* allele are sexually isolated from the carriers of *B*, or the hybrid genotype *A*B is sterile or inviable, reproductive isolation would be a pleiotropic by-product of purely adaptive evolution. Dobzhansky concluded that geographic isolation is required for speciation, as the incompatibility between *A* and *B* alleles segregating in one population would prevent the evolution of linkage disequilibrium between the epistatically acting loci. This deductive argument for allopatry nicely complements the inductive biogeographic arguments of Mayr. (One cannot discuss Dobzhansky’s contribution without at least mentioning that of H. J. Muller, who, in two brilliant but obscure papers [1940, 1942], expanded Dobzhansky’s discussion, illustrating it with examples from his own work on *Drosophila*.) The value of the genetic argument is the demonstration that reproductive isolation, an adaptive valley between populations, evolves incidentally while each population is scaling an adaptive peak. There is thus no need to embrace the common misconception that speciation involves loss of fitness within a population.

An important difference between Mayr and Dobzhansky was their appraisal of reinforcement, the idea that natural selection can directly increase reproductive isolation between two incipient species that become sympatric. Dobzhansky held that if some hybrid sterility or inviability evolved in allopatry, natural selection in subsequent sympathy would favor mating discrimination, increasing the frequency of alleles preventing maladaptive hybridization. Reinforcement could then complete speciation by re-
ducing gene flow to zero. To the end of his life, Dobzhansky believed that this process was part of nearly every speciation event, a belief that sometimes forced him into awkward positions. In 1940, for example, he floated the idea that an island invader might become a new species only when its ancestor invaded a second time, providing the selective pressure to finish the job. Dobzhansky's influence led to the widespread acceptance of reinforcement, which was widely taught (as I learned it) to be the final step in speciation. We now know that much of the approbation was uncritical: theory shows that reinforcement is difficult to achieve, and much of the supporting data from natural were ambiguous or wrongly interpreted (see, e.g., Butlin 1987; Spencer et al. 1987; Rice and Hostert 1993). Although there is still suggestive evidence for reinforcement (Coyne and Orr 1989), it will take years of work to determine whether it is common.

Mayr has been far less enthusiastic about reinforcement, maintaining instead that most reproductive isolation is an accidental byproduct of genetic divergence in allopatry: “The question is, however, whether or not this [reinforcement] is the only way by which reproductive isolation can be established. Naturalists, from von Buch down to our contemporaries, have always believed that good species can complete their development in isolation. They find an abundance of cases in nature which seem to permit no other interpretation. The most conclusive evidence is, of course, presented by the multiple invasion of islands by separate colonizing waves coming from the same parental stock.” (Mayr 1942, p. 157; see also Mayr 1959, 1963.)

Mayr's insistence on the primacy of allopatric speciation was accompanied by his famous critiques of sympatric speciation, beginning with chapter 8 of Systematics and the Origin of Species, continuing in his first paper in Evolution (Mayr 1947), and culminating in chapter 15 of Animal Species and Evolution. These analyses, inspired by the widespread idea that reproductive isolation could easily evolve in the presence of gene flow, focused on both theoretical models, all of which Mayr diagnosed with “fatal flaws,” and the biogeographic data, which Mayr thought more parsimoniously interpreted as favoring allopatric speciation.

With the possible exception of the founder-effect theory, no aspect of Mayr's work has caused more controversy, or motivated more research, than his criticism of sympatric speciation. Entire books, such as M. J. D. White's Modes of Speciation (1978), were written to counter Mayr's arguments, these rebuttals often suffused with anger at Mayr's supposed dogmatism. The controversy also inspired a body of theoretical work, beginning with the paper of Maynard Smith (1966) and summarized recently by Rice and Hostert (1993). While confirming that sympatric speciation is more difficult to achieve than the allopatric alternative, newer theories do not support Mayr's belief that speciation nearly always requires the absence of interbreeding. Moreover, recent laboratory experiments, particularly those of Rice and Salt (1990), have achieved a surprising amount of reproductive isolation in the presence of gene flow, though it is arguable whether they are realistic models of nature. Sympatric speciation hence cannot be questioned as a theoretical possibility, at least not with the vigor shown by Mayr. (It is a mistake, however, to think that Mayr completely ruled out sympatric speciation. On several occasions [e.g., 1976, p. 144; 1982, p. 605; 1988, p. 376], he noted that it might not be rare in host-specific insects.)

The most important task for supporters of sympatric speciation, however, is to demonstrate that it occurs in nature. Although allopatric speciation can be confirmed from the biogeographic evidence adduced in Systematics and the Origin of Species, the same is not true for sympatric speciation, which also requires historical observation or measurements of gene flow. This has been achieved in allopolyploid species of Tragopogon (Novak et al. 1991; Soltis and Soltis 1991), and it is almost certain that allopolyploidy is a frequent cause of sympatric speciation in plants. But, despite ardent debate, there is still only one reasonable candidate for the sympatric evolution of reproductive isolation in animals: the host races of Rhagoletis pomonella (Feder et al. 1988). Even these races, however, have not become full species.

The only fairly convincing evidence I can imagine, save actually witnessing sympatric speciation, is finding sister species of highly mobile organisms on small and remote oceanic islands. The discovery of two sister species of Geospiza on Cocos Island, the most isolated of the Galápagos, would be hard to explain by any sort of allopatric speciation. Cocos, alas, harbors only one species of finch. As far as I know, there have been no thorough studies of this problem, although data for such an analysis surely exist.
A recent study of monophyletic cichlid groups in two small African crater lakes (Schliewen et al. 1994), which are aquatic islands, strongly suggests the possibility of sympatric speciation. White (1978) argued that adaptive radiations of wingless insects on oceanic islands prove sympatric speciation. The weakness of this argument is that such sedentary creatures might speciate allopatrically in a very small area.

It is possible that, except for allopolyploid plants, we will never know how often sympatric speciation occurs in nature. It is clearly more difficult to achieve sympatric than allopatric reproductive isolation, but perhaps the ecological opportunity for the former is far more frequent. (Can geographic isolation really account for our millions of species?) We are thus faced with an epistemological problem, leading to Mayr's (1963, p. 480) conclusion that "the burden of proof rests, however, on supporters of this alternative mode of speciation." This burden will only be eased when we find ways to distinguish sympatric from allopatric speciation in nature.

**FOUNDER-EFFECT SPECIATION**

Although the three ideas discussed above were highly salubrious, I regret that the same cannot be said of Mayr's theory of founder-effect speciation, which has infected evolutionary biology with a plague of problematic work.

According to Mayr, this theory had two sources: "One was the observation that aberrant populations of species almost invariably are peripherally isolated and that, more often than not, the most aberrant population is the most distant one. . . . By contrast, the amount of geographic variation in contiguous species ranges is usually minor. The other reason, pointed out by Haldane (1937, 1957) is that large, widespread populations—in fact all more populous species—are evolutionarily inert, because new alleles, even favorable ones, require very long periods of time to spread throughout the entire species range." (1982, p. 604.)

The geographic patterns were first described, without an explanatory theory, in *Systematics and the Origin of Species*. The theory appeared in 1954, and was discussed at length in *Animal Species and Evolution*. Mayr's basic idea is that genetic drift and epistasis play a key roles in the speciation of small, colonizing populations. This drift would supposedly cause genome-wide homozygosity, imposing novel selective pressures on alleles originally selected on heterozygous genetic backgrounds. This would in turn set off a "genetic revolution," producing large changes in the frequencies of still-segregating alleles, and establishing new polymorphic "balanced systems" when the colonizing population increased in size. The genetic divergence between ancestor and descendant was said to cause not only reproductive isolation, but also profound morphological change not achievable by conventional Darwinian selection: "The genetic reorganization of peripherally isolated populations, on the other hand, does permit evolutionary changes that are many times more rapid than the changes within populations that are part of a continuous system. Here then is a mechanism which would permit the rapid emergence of macroevolutionary novelties without any conflict with the observed facts of genetics" (Mayr 1954, p. 176).

The influence of this theory has been profound. It spawned several similar theories with confusing names, including founder-flush speciation, flush-founder speciation, flush-crash speciation, and genetic transilience. The subtle differences among these theories were described by Carson and Templeton (1984) and Provine (1989). Their common elements are the colonization of an empty habitat by a few individuals, followed by expansion (and sometimes crashes) of population size, and the existence of epistasis, genetic drift, and maladaptive evolution within the colonizing population. These theories have, in turn, buttressed the claim of punctuated equilibrium that nonadaptive gene frequency change in peripheral populations is an important part of speciation and morphological change, helping explain the sudden appearance of evolutionary novelties. (This claim, however, has apparently been jettisoned by its proponents, who now suggest that a punctuated fossil record may result from conventional natural selection after all [Gould and Eldredge 1993]). Finally, founder-effect theories have inspired a number of laboratory experiments examining the connection between founder events and reproductive isolation.

These theories and experiments have encountered strenuous objections, usually from population geneticists. Mayr's observation that isolated populations are morphologically deviant can, for example, be explained by the more parsimonious theory that isolated populations experience strong selection in a novel environment, with speciation a byproduct of adaptive change. This is the classic tale of adaptive radiation, once the favored explanation for luxuriant and rapid
speciation on islands (Coyne 1993). Moreover, there is no evidence that proposed examples of founder-effect speciation, such as the Hawaiian Drosophila, have experienced strong genetic drift (they have ample genetic polymorphism), nor any reason to suppose that they are not simply examples of adaptive radiation like the Galapagos finches or New Guinea birds of paradise.

Mayr criticized the adaptive-divergence explanation by claiming that the environment of many aberrant island populations was nearly identical to that of their more widespread relatives. The evidence for such identity, however, consisted of only two observations. Mayr noted that the islands around New Guinea, which harbor divergent populations of birds, “lie in the same climatic district as the nearest part of the mainland of New Guinea” (1954, p. 158). Referring to the divergent species of Tanysiptera on Numfor Island, he further observed that “The climate of Numfor is much like that of the opposite coast of New Guinea, thus the selection-pressure by the physical environment will remain much as it was in the previous range. The flora is somewhat different and the fauna is somewhat impoverished, but the only potentially serious predator, Accipiter novaehollandiae, occurs both on Numfor and New Guinea. The physical and biotic environments are rather similar in both places.” (1954, p. 168.) These observations provide a rather shaky foundation for a new theory of speciation! Even very similar environments, moreover, can select for dissimilar phenotypes if gene flow is completely absent. This is particularly true of sexual selection, which seems to be involved in many adaptive radiations.

The theoretical basis of founder-effect speciation has also been questioned, as all of the models are verbal, lacking a convincing mathematical demonstration that founder events can produce full reproductive isolation with reasonable probability (Lande 1980; Charlesworth et al. 1982; Barton and Charlesworth 1984). The supposed evolutionary inertness of large populations, an argument also used by Wright (1931) to support his shifting-balance theory, is based on no evidence save Haldane’s calculation that one cannot impose strong selection on many characters at once. This cost-of-selection argument, however, does not prove that large populations cannot evolve, only that no population can evolve too quickly. There is still no theoretical reason to claim that mass selection is unable to produce evolutionary novelties.

Reviewing the laboratory studies of founder events, Rice and Hostert (1993), concluded that some experiments produced small amounts of reproductive isolation, but that this isolation did not necessarily require genetic drift. More important, repeated foundings and flushings have failed to yield even moderate reproductive isolation, casting doubt on the view that the process can quickly produce full species. Although proponents of founder-effect speciation sometimes argue that it is a very rare event, Rice and Hostert note that “such a philosophy makes the model virtually impossible to reject experimentally.”

The popularity of founder-effect theories, however, seems curiously immune to these criticisms. Provine (1989, p. 72) observed—correctly, I think—that “some version of Mayr’s founder effect and genetic revolution has been the favored explanation for at least island speciation since 1954.” Since the mid-1980s, many questions of speciation, some of them tractable, have been neglected in favor of seemingly endless debates about this process.

I am not sure why genetic-drift theories of speciation have outcompeted more conventional Darwinian ideas of adaptive radiation. Unlike the case of black-body radiation, in which a new observation could not be explained by existing paradigms of physics, there is no observation about nature that demands a new theory of speciation. The popularity of founder-effect theories recalls that of another complicated and hard-to-test alternative to mass selection, Wright’s shifting-balance theory of evolution. Instead of considering only natural selection, founder-effect and shifting-balance theories involve combinations of selection, drift, and population structure, conjuring up Wright’s seductive picture of the adaptive landscape. The penchant for new and more elaborate theories may stem from a general malaise provoked by the apprehension that Darwin and Fisher may have been correct in emphasizing the ubiquity of simple, garden-variety mass selection. Unlike that of physics, the fundamental paradigm of evolutionary biology has not changed in over a century, and it is sometimes depressing to think that we may be forever sweeping up behind the Darwinian elephant. Dissatisfaction with traditional Darwinian explanations can be seen in many areas of biology, probably contributing to the popularity of saltationism in developmental biology, species selection in paleobiology, and “adaptive mutation” in molecular biology.

Of course, it is not easy to get conclusive ev-
idence for even the conventional process of adaptative radiation (do we really understand speciation in Darwin's finches?), so it would clearly be inappropriate to reject founder-effect theories out of hand. But until we find explicit ways to test them against their Darwinian alternative, the literature will remain filled with inconclusive debate.

**Conclusion**

Reading the works of the modern synthesis, one is struck by how much clarity was brought to the species problem by Mayr and Dobzhansky, and how little by their major theoretical colleagues, Fisher, Haldane, and Wright. Of these three, only Fisher (1930, chap. 6) proposed his own theory of speciation, an unfortunate model of sympatric or clinal divergence caused by disruptive selection, with reproductive isolation completed by reinforcement. Like his adherence to a morphological species concept, Fisher's view of speciation descended directly from Darwin, who believed that new species arose to better fill the niches in a single habitat: "the more diversified the descendants from any one species become in structure, constitution, and habits, by so much will they be better enabled to seize on many and widely diversified places in the polity of nature, and so be enabled to increase in numbers" (Darwin 1859, p. 112). Fisher explicitly acknowledged this inheritance by beginning *The Genetical Theory of Natural Selection* with a quotation from William Bateson: "As Samuel Butler so truly said: 'To me it seems that the 'Origin of Variation,' whatever it is, is the only true "Origin of Species."’"

Haldane, as we have seen, was not convinced that species were real, and in the *Causes of Evolution* (1932) limited his discussion of speciation to the genetics of morphological differences between taxa. Wright, who accepted both the biological species concept and allopatric speciation quite early, nevertheless largely ignored the issue; his two papers on speciation (1940a,b) are tendentious arguments for the shifting-balance theory. His ideas did surface, however, in founder-effect models of speciation.

Mayr (1992a) ascribed theoreticians' meager contribution to the species problem to their lack of experience with natural populations and consequent inability to see that speciation begins as variation among geographic isolates. I believe, however, that there is another important reason. During the modern synthesis, the major job of theoretical population genetics was to provide the mathematical framework for Darwinism: genetic and phenotypic change within a lineage. Fisher is best known, of course, for his fundamental theorem of natural selection, the most famous equation of adaptive change. Even Wright's shifting-balance theory, which introduced the novelities of genetic drift and multiple populations, deals essentially with the diffusion of an adaptation through a single interbreeding unit. When applied to the problem of speciation, such a program can do no better than suggest that natural selection directly favors an increase in the number of species and the size of gaps between them. This led Darwin and Fisher to propose that species resulted from selection to reduce intraspecific competition, and may explain the continuing popularity of reinforcement and sympatric speciation.

Although these processes might occur, they are ancillary to the true problem of speciation, which simply cannot be framed as a process occurring within one lineage. The solution requires one to recognize a phenomenon not encompassed by classical Darwinism: reproductive isolation. A reproductive isolating mechanism is a composite character of two species considered together, and, except in cases of reinforcement, not the direct product of natural selection. (It is hard, for example, to envision a selective advantage to evolving hybrid sterility and inviability). It was the genius of Mayr and Dobzhansky to first recognize that the origin of species was equivalent to the origin of a genetic interaction, and then to explain its evolution by conventional Darwinian means. (Perhaps this notion was inspired by their experience as naturalists, which allowed them to observe the coexistence of related species.) The success of this whole approach rests, of course, on adopting the biological species concept. As Mayr observed, "The word species thus became a word expressing relationship, just like the word brother, which does not describe any intrinsic characteristics of an individual but only that of relationship to other individuals; that is, to other offspring of the same parents. This new species concept meant a complete change in the ontological status of species taxa." (1992b, p. 223.)

Under this view, species are merely evolutionary accidents, the pleiotropic and nonadaptive byproducts of evolutionary change within lineages. I think that this idea is unpalatable to some, and unable to replace the belief that natural selection must somehow favor an increase in organic diversity. Such an adaptationist bent may
motivate much of the opposition to Mayr’s theories.

Speciation, then, is an epiphenomenon of Darwinism in only the trivial sense that, like nearly all evolutionary phenomena, it occurs by gradual change of populations, usually impelled by natural selection. But recognizing the importance of reproductive isolation opens up a whole range of questions beyond the realm of classical Darwinism. I mention only a few: the ecology and biogeography of polyploid plants (Soltis and Soltis 1991), the rate of origin of postzygotic isolation among isolated populations (Coyne and Orr 1989), and the explanation of the large effect of the X chromosome on hybrid sterility and inviability (Charlesworth et al. 1987).

Mayr is sometimes criticized for becoming famous by popularizing the ideas of others, and he readily admitted (1955, 1982) that both the biological species concept and allopatric speciation were suggested by earlier workers. (The founder-effect theory, however, is truly original, as are many other ideas of Mayr; see Futuyma 1994). But this criticism could also be leveled at Darwin—after all, evolution was mentioned by his own grandfather, and natural selection by Patrick Matthew in 1831. Mayr and Darwin earned their fame for the same reason: each recognized the importance of earlier suggestions, worked out their consequences in detail, and showed how they were consistent with the known facts of biology. When Mayr erred, as I think he did with founder-effect speciation, his errors were adopted widely; but his successes were far more numerous and spectacular.

The currency of science is truth, and all biologists are ultimately valued by their contribution to our understanding of nature. Ernst Mayr’s explanation of the origin of species is surely one of the greatest achievements of evolutionary biology.

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LITERATURE CITED


