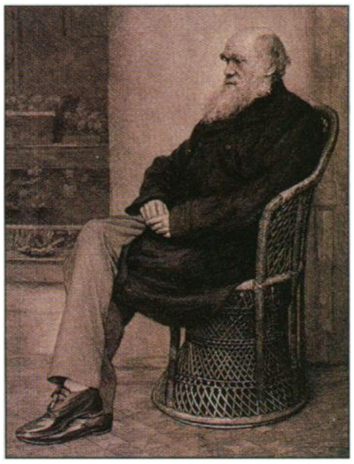
Ecology Returns to Speciation Studies

Evolutionary biologists rediscover their roots, as field studies highlight the importance of ecology in the formation of species

Charles Darwin got his ideas about how species arose by poring over his voluminous notes taken aboard the *Beagle* and from hours of observation in his native England. He watched to see what pollinators visited particular orchids, grew 233 cabbages of different varieties near each other to see how many offspring were true to their kind, and counted the number of Scotch fir seedlings that filled the gaps between adult trees.

For Darwin, such loving attention to the details of nature was the underpinning of his theory, but such ecological minutiae have had little place in this century's more sophisticated evolutionary science. Among evolutionists trying to understand how species arise, "ecology has been out of favor" for over 2 decades, says James Patton, an evolutionary biologist at the University of California (UC), Berkeley. Ecology was neglected, he and others say, as researchers buoyed by the power of new genetic techniques were "swept up in creating molecular family trees," focusing on the relationships among species, not what drove them apart in the first place.



The master's idea. Darwin thought ecology drove speciation.

Now, however, Darwin's obsessive attention to ecological detail is making a comeback. Researchers probing the mechanics of how one species splits into two are once again taking copious notes about such things as the number of predators lizards face in different forests and the angle at which bottom-dwelling fish feed. It's a back-to-basics approach that has led to some sophisticated and surprising science—and revived an old idea: the ecological speciation model.

In the dominant picture of speciation, put forth in 1942 by Harvard University's Ernst Mayr, a geographic barrier develops between two populations, interrupting gene flow between them. Even if the populations live in identical environments, gradually they diverge through random mutations, so that if they ever encounter each other later, they will be unable to mate—a condition called reproductive isolation, the sine qua non of speciation. But the ecological speciation model offers another possibility: The barriers that spawn species can be ecological rather than geographic, and selection may be paramount. Different ecological pressures will favor changes in body shape and function that eventually make populations unable or unwilling to mate with each other, even if they have never been physically separated.

Thus, researchers studying speciation find themselves paying attention to environmental factors as well as genes. Some field studies demonstrate how a particular selective factor can push two populations down separate evolutionary paths. Others try to probe the factors that keep incipient species from mating, testing whether genetic or ecological differences make the best chaperones. And a few studies are trying to put it all together to document ecological speciation. The new work "shows the importance of ecology in speciation, which has been almost entirely neglected," says John Endler, a longtime proponent of ecological speciation at UC Santa Barbara.

This view of speciation "is not new," adds David Wake, an evolutionary biologist at UC Berkeley. "It traces its roots to Darwin. But what's new and nice is the sharp focus on testing hypotheses [via] natural systems."

The shift in emphasis is allowing the field to move beyond the debate about whether speciation happens mostly when populations are geographically separated or when they are next door (*Science*, 13 September 1996, p. 1496). The new view implies that both distance and habitat differences can split a species. Also, because ecological speciation is spurred by strong selection and rapid adaptation, this model fits well with field data showing that evolution can be rapid and that a few mutations of large effect can support key adaptations (see sidebar). "We're trying to find what causes [speciation]," says Patton, "and we're finding that geographic isolation by itself doesn't always provide the best answer. Something else is driving it—and we think that 'something else' is often the ecology."

How fish choose their mates

Everyone agrees that geographically isolated populations do drift apart in the wild. But populations not isolated by geography have to be actively pushed down separate paths by natural selection. So one step in documenting the ecological speciation model is simply to show that natural selection does indeed push populations to diverge, and a number of studies have documented this with everything from Darwin's own Galápagos finches (*Science*, 26 February, p. 1255), to Trinidadian guppies (*Science*, 28 March 1997, pp. 1880 and 1934).

In some cases, selection can cause morphological change surprisingly quickly. For example, in an unpublished study of Cameroon rainforest birds called little greenbuls, Thomas Smith of San Francisco State University found that after 20 years in a secondary, more open forest, the birds evolved longer wings at the "huge rate" of 120,000 darwins. A darwin is a unit of proportional change per unit time, and artificial selection experiments on mice show rates of up to 200,000 darwins.

Such speed is important to help explain bursts of speciation, such as that seen in the cichlid fish in Africa's Lake Victoria, which have evolved into hundreds of species in only

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Size Matters: The Genes Behind Adaptation

To a fruit fly, nothing is more important than the kind of fruit it chooses to live on. Here it will hatch, dine, mate, and leave its young, and the peculiarities of a particular fruit affect almost every aspect of a fly's brief life. That's why graduate student Corbin Jones of the University of Rochester in New York expected to find a big genetic gulf between two related fruit flies of the Seychelles archipelago in the Indian Ocean: *Drosophila simulans*, which lives on a variety of succulent fruits, and *D. sechellia*, which lives only on the prune-sized *Morinda* fruit, a knobby, foul-smelling fruit poisonous to most insects. While *D. simulans* and other fruit flies struggle to evade even the scent of the *Morinda*, *D. sechellia* happily settles in to live and lay eggs.

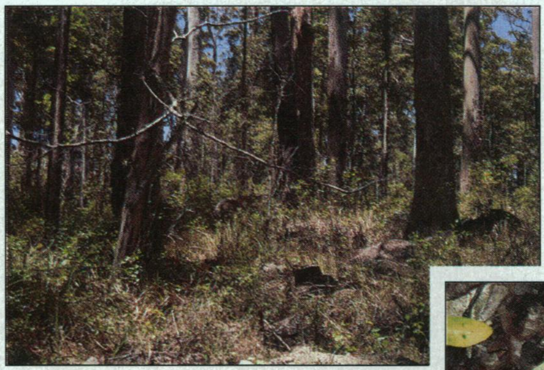
But to Jones's surprise, it appears that this dramatic switch stems from only a few genetic differences. Genetic mapping last year showed that only a handful of genes confer resistance to the *Morinda* fruit's poison. And Jones's latest mapping work shows that only a few genes may account for *D. sechellia*'s attraction to the *Morinda* scent. "It looks like this adaptation requires only a few genes, but with big effects," he says.

12,000 years. But did minute ecological differences actually trigger the formation of that rich diversity? No one has actually witnessed the birth of a species in the wild, so researchers must come up with clever experiments to see whether differences in ecology, and the adaptations they spur, can isolate species reproductively. Dolph Schluter, an evolutionary biologist at the University of British Columbia (UBC) in Vancouver, and his colleagues are addressing this question using marine and stream-dwelling stickleback fish from British Columbia and their ecologically similar but genetically distant counterparts in Japan; the freshwater fish may have speciated from marine ancestors only 13,000 years ago.

The freshwater descendants on both sides of the Pacific look nearly identical to one another—small and husky, with deep jaws and snouts that point down so they can suction food off the bottom of the stream bed. In both cases, the dumpy shape lets the fish swim while feeding from the bottom. The ancestral marine forms of all these fish are also remarkably similar, with streamlined, torpedo-shaped bodies. "It's a great example of parallel evolution; I guarantee you can't easily tell them apart," says Schluter.

Indeed, even the fish can be fooled. To see whether ecology was a strong force in causing reproductive isolation regardless of geography and shared history, Schluter teamed up with Jeffrey McKinnon of the University of Wisconsin, Whitewater, and Seiichi Mori of the University of Gifu-keizai in Ogaki, Japan, gathering Japanese and Canadian sticklebacks and putting them in his tanks at UBC. The team released female Japanese marine sticklebacks, heavy with eggs, one at a time into a tank containing a single male—a Canadian marine or freshwater form, or a Japanese freshwater form. If the female found the male acceptable as a mate, she entered his nest.

Geographic speciation would predict that fish from each continent—most similar genetically—would mate with each other and be reproductively isolated from those from the other continent, says McKinnon. But in this case, ecology won out. Japanese marine females spurned their closely related freshwater cousins but mated with their distantly related Canadian marine counterparts. Canadian freshwater females also accepted Japanese freshwater mates, and vice versa; these crosses produced viable hybrids, says Schluter. Thus, both the marine and freshwater species preferred to mate with others from their own environment rather than with more closely related fish from a different habitat.



Danger zone. Lizards in open forest *(above)* face many attacks from birds, as seen by scars on this clay model *(right)*.

CREDITS: (TOP PAIR) CHRIS SCHNEIDER; (BOTTOM) W. L. WAGNER

Such findings are a surprise to many researchers, because big, beneficial mutations were thought to come along so rarely that many models simply assumed that they play no part in adaptation. But as evolutionists begin to probe the genetic basis behind important adaptations, they are uncovering examples of such large mutations, dramatically revising how biologists think about evolutionary change. "Evolution is all about adaptation, and for the first time, we're actually getting a look at the genetics of adaptation," says H. Allen Orr, Jones's adviser and an evolutionary geneticist at Rochester. "And it seems to go against all the old models—it's faster and uses bigger genes."

Charles Darwin, of course, knew nothing about mutations—he wrote 100 years before DNA was discovered. Even so, he thought that natural selection acted on "successive slight variations," and for much of this century researchers agreed that evolution was the sum of many mutations of small effect. New species were thought to emerge from the slow accumulation of mutations (see main text). And the population genetics model put forward by R.A. Fisher in 1930, which Orr says is still the leading explanation of adaptation, argues that the accumulation of very small mutations is the essence of evolutionary change.

But as researchers begin to uncover the specific mutations that separate species, their first findings show the opposite pattern: Big mutations lead the way in adaptive events. In addition to the fly study, for example, evolutionary biologist Doug Schemske and geneticist Toby Bradshaw of the University of Washington, Seattle, have found through genetic mapping that bee-pollinated and hummingbird-pollinated monkey flowers in California's Yosemite National Park differ from each other in only a few sets of genes. But these few genes have large effects, changing flower color, petal shape, and the amount of nectar (*Science*, 13 September 1996, p. 1499)—all crucial variables for luring the two pollinators and keeping the two plant species reproductively isolated.

Acquired taste. One fly species happily lives on the poisonous *Morinda* fruit, but other flies avoid its scent.

Such studies "show how important large beneficial mutations are in the first stages of an adaptation," says Schemske. A new adaptation must be acquired fairly quickly, or else organisms will be poorly adapted to both the new and the old conditions and will not survive. So it makes sense that the first genetic changes have large effects, he explains; later, smaller mutations fine-tune the adaptation.

But these results also pose a problem, because "they contradict theory," as big mutations were thought to be mostly rare and mostly disadvantageous when they did happen, says Orr. "We're in a funny situation—we're about to have a wave of data crash down on us and no theory to hang it on." Orr has made a first stab at filling this void, presenting a mathematical model in *Evolution* last year showing how the big-adaptations-first pattern would work. "This is what we need," says Schemske: "a theoretical framework for the genetics of adaptation, something we can test." –V.M.

Further analysis of the data showed that the females were choosing their partners based primarily on size. Thus, in terms of reproductive isolation in the sticklebacks, "genetic history doesn't matter," says Schluter. "It's how they look that counts." Fish from different environments were most likely to be reproductively isolated, even if they had close genetic and geographic ties.

Other researchers praise the work. "They've shown that common environmental differences can produce common patterns of speciation," says UC Santa Barbara's Endler, right down "to the same isolating mechanisms. It's the first time we have definite evidence of this rather than speculation."

Separating skinks

Halfway around the world in Queensland, Australia, Christopher Schneider, an evolutionary biologist at Boston University, is studying similar questions in the leaf-litter skink, *Carlia rubrigulais*, a small, reddish lizard that lives in both wet rainforest and drier open forest. The setup is perfect to test whether geography or ecology drives speciation: A well-known biogeographic barrier, the Black Mountain Corridor, physically splits the skink's range into two large populations, but on each side of the mountains the lizards inhabit both closed rainforests and more open forest. Based on the differences between the two populations' mitochondrial DNA, Schneider estimates that the single ancestral population split apart several million years ago.

Lizards living cheek-by-jowl—in some cases only 500 meters apart—in the two different forest types have similar mitochondrial DNA, suggesting recent or current gene flow between them. Yet Schneider found that the neighboring lizards vary more in size and shape than do those inhabiting the same environment on the other side of the barrier. "Morphologically, the ancient isolates are very similar," he says, "but there are whopping great differences" in size and shape between lizards separated by "very short distances." Open forest lizards are smaller, with shorter limbs and bigger heads, and they become sexually mature at a smaller size than those in the rainforest.

Schneider and his colleagues believe they have found an ecological force responsible for these differences: predation. Earlier reproduction and smaller size are often found in species under high predation, as individuals that manage to reproduce before being picked off are favored. More species of lizard-eating birds hunt in the open forest, Schneider notes, and by placing clay lizard models in both environments, his team gathered evidence that lizards there are more likely to be attacked.

Of course this is only one case, but as genetic data on various organisms roll in, this pattern—of geographically separated populations being similar in size and shape, while neighboring populations in slightly different habitats vary—turns out to be quite common, says Berkeley's Patton. He cites similar findings for snails and bats across the Black Mountain Corridor in Australia and rodents in the Amazon River Basin. "We find these widespread species that have deeply divergent molecular histories yet haven't changed morphologically, apparently because they continue to inhabit the same environment. Time and isolation alone don't necessarily result in new morphologies—whereas a new environment does," he says.

And because new morphologies may lead to new species—perhaps even in the face of gene flow—the vagaries of ecology may be a driving force in more cases of speciation than researchers have imagined, Patton says. In the case of the skinks, for example, if size and shape are important in mate choice, then the ecologically distinct lizards may have taken the first step down the road to speciation, says Schneider; the critical test will be whether the geographically or ecologically separated skinks have more reproductive isolation.

Schneider's and other studies are not yet complete, and no one is ready to toss out the notion of geographic speciation. Indeed, ecology and geography may work together, says Schneider. He expects that the next round of skink studies will find the greatest reproductive isolation between populations that have been separated for a long time and also occupy different habitats. The bottom line, says Patton, is that geography alone may not be sufficient for speciation. In many cases an environmental nudge may give populations a bigger shove down the path to speciation. "That's the way to generate diversity," he says—an observation worthy of Darwin himself.

–VIRGINIA MORELL

NEWS

Test Tube Evolution Catches Time in a Bottle

By running experiments on microbes for thousands of generations, researchers are exploring the roles of chance and history in evolution

For most living things, 24,000 generations is a daunting span of time. Go back that many human generations, or about 500,000 years, and *Homo sapiens* had not yet evolved. Even for the fruit flies beloved of geneticists, 24,000 generations equals about 1500 years. But in Richard Lenski's laboratory at Michigan State University in East Lansing, 24,000 generations ago is a recent memory. The year was 1988, when he and his students first introduced 12 genetically identical populations of the bacterium *Escherichia coli* to their new homes: 50-milliliter flasks filled with sugary broth.

Since then, those bacteria have been clocking up the generations at a rate of about one every 3.5 hours, mutating and adapting right in front of Lenski's eyes. Lenski is a founding member of a subculture of evolutionary biologists—many of them his former students and colleagues—who are watching evolution unfold in laboratory cultures of microbes, where a single experiment can span enough generations for major evolutionary change. These laboratory microcosms, whether of bacteria, viruses, or yeast, can turn evolution into an experimental science, says Michael Travisano of the University of Houston. "You have the luxury of making a prediction, and then you can test it. It's almost like physics."

Researchers can subject populations to the same environmental stresses again and again—a procedure that Paul Sniegowski of the University of Pennsylvania calls "analogous to being able to revive the fossils and rerun the evolutionary events." They can thaw out ancestral forms, stored in laboratory freezers in what Lenski calls a "frozen fossil record," and compare them to their descendants. And they can monitor the microbes' genomes as they evolve, tracking the ultimate roots of those changes in DNA or RNA. "It's some of the most exciting stuff in evolution," says Stephen Jay Gould of Harvard University.

These laboratory microcosms are allowing researchers to address some of the field's biggest questions, such as how often the twists and turns of evolution are the result of chance rather than adaptation. Researchers can study how evolutionary baggage from one round of selection affects how an organism fares in the next, and how adaptive radiations can arise from a single organism. And they can address a question that has preoccupied evolutionary thinkers like Gould: How reproducible is evolution? If the history of life could be replayed from the same starting point, how differently would it unfold? So far they are finding that identical populations facing similar conditions can follow parallel courses, although the underlying genetic changes often differ. But over time, in new environments, the effects of those differences can grow, steering evolu-