EVOLUTIONARY BIOLOGY

Life on the Edge: Rainforest Margins May Spawn Species

With millions of life-forms crawling, flying, and slithering about, the world's rainforests have become the icon of biodiversity, as well as a living laboratory for researchers studying how new species appear. But a study on page 1855 of this issue suggests that many of these species may arise not in the rainforests themselves, but rather in their frayed edges. Led by evolutionary biologist Thomas Smith of San Francisco State University, the study of small forest birds in Cameroon suggests that "ecotones," the transition zones between rainforest and savanna, may be important to generating biodiversity. If so, the authors argue, these oft-forgotten habitats deserve some attention from conservationists.

What's more, the study—"a clever blend of ecology, biogeography, and molecular genetics," as University of British Columbia evolutionary ecologist Dolph Schluter puts it—offers empirical support for a controversial theory of speciation. The work suggests that populations may diverge into different species even when some interbreeding occurs between them. "This really is a major first observation to support that kind of hypothesis," says evolutionary biologist John Endler of James Cook University in Townsville, Australia, who has been promoting this idea for 20 years. Indeed, says Guy Bush, an evolutionary biologist at Michigan State University in East Lansing, the study is "probably the best piece of work so far" on this question.

Smith, with co-workers from San Francisco State, the University of California, Los Angeles, and the Zoological Society of London, set out to examine a contentious issue in evolutionary biology: How isolated must populations of a species be before they can start to develop physical differences—and so take the first steps on the road to becoming separate species? For decades, the dominant theory was that such a split could occur only when there was almost no interbreeding, or gene flow, between populations. Even when natural selection in different environments pushed populations apart, it was thought that a small amount of gene flow would mix the genetic pool enough to prevent speciation.

However, a growing number of lab experiments with the fruit fly *Drosophila* have suggested that different selection pressures can create populations with different traits even in the face of moderate gene flow, says Smith. When researchers exposed different populations of flies to different selection regimes and allowed some gene flow between them—for example, by connecting their cages via narrow tubes—the populations started to diverge. Over time, the flies began to mate preferentially with flies within their own population. The theory predicts that this would eventually lead to reproductive isolation and thus to the birth of a separate species. But most biologists thought that this style of speciation rarely if ever occurred in nature.

T. B. SMITH

Cradle of speciation? Little greenbuls *(top)* living in the transition zone between savanna and rainforest *(above)* may be on the road to becoming a new species.

To test this model in the wild, the researchers chose Cameroon's little greenbul (*Andropadus virens*), a small green bird that feeds on insects and fruits and inhabits both the tropical rainforest and patches of forest surrounded by grasslands in the ecotone. Although transition areas like the ecotone aren't as species-rich as the rainforest proper, they include different types of environments close together and are often zones of contact between subspecies or closely related species. So biologists have suspected since the 1930s that these transitional areas may somehow be important in speciation, although there have been several competing theories as to just how such species would arise.

Using mist nets, the team trapped birds from six forest and six ecotone sites between 1990 and 1996. They measured a number of physical traits that are important to fitness and known to be under selection in other bird species—weight, the depth of the beak, and the length of the wing, leg bone, and upper jaw. They also drew a few drops of blood for genetic analysis.

Most of the ecotone-dwelling little greenbuls turned out to be quite different in size and shape from their rainforest counterparts. They were heavier and had deeper bills and longer wings and legs. At least one of those traits, longer wing length, offers an advantage in open ecotone environment because it allows the birds to fly faster and so escape aerial predators, which are more common in the ecotone, says Smith. In some cases, the morphological gulf between little greenbuls from the forest and those from the ecotone was larger than that between two different bird species sharing the same habitat.

But the results of the genetic part of the study, which compared birds from different sites using both mitochondrial and nuclear DNA, revealed many similarities between the populations. The team used the amount of similarity and a population-genetics model to estimate that there was considerable gene flow between the two habitats—about one to 10 migrants per generation in each population of birds.

Taken together, Smith says, the findings mean that selection pressure in different environments can offset gene flow and create differences in populations, even when individuals travel back and forth frequently. Only in populations that experienced very high gene flow—eight to 10 migrants per generation—were the effects of natural selection washed away. In these cases, the morphological differences between an ecotone and a rainforest greenbul were much smaller, about the same as between two ecotone or two rainforest birds. Of course, morphological divergence isn't the same as speciation. "But it is evidence for strong differentiation in the presence of gene flow," says Endler. "So it's a first step in speciation."

Other researchers say they are impressed by the study's hard data on what has been a mostly theoretical debate. "I think they're the first to go out and test some of these hypotheses," says Bush. Endler, who in 1977 was one of the first to point out that selection might overcome the effects of gene flow, says it's "exciting" to have one of his theories confirmed.

Still, evolutionary biologist Nick Barton at the University of Edinburgh in the United Kingdom warns that the study hasn't quite sewn up the case for this model of speciation. He points out that the amount of gene flow the team found is quite small and says he's not surprised that it wasn't enough to swamp selection: "Four to five migrants per generation … that's very weak relative to selection." Smith acknowledges that because he doesn't know the little greenbul's population sizes, it's hard to prove just how significant the one to 10 migrants are. His team is now censusing the birds to find out.

While its implications for evolutionary theory are under debate, the study, if it holds up, might also have implications for the fight to save the world's biodiversity. If gene flow isn't a barrier to new species formation, then the ecotone is a likely source of new diversity, argues Smith. Species spawned in the ecotone might use forest resources in new ways that would be advantageous in the rainforest proper. Moreover, because migration between ecotone and rainforest is so common, over millions of years many of these new species might have moved back from their ecotone cradle to the rainforest. Thus, the patchy ecotone may generate species that find long-term homes in the adjacent rainforest, says Smith: "Maybe the rainforest is a sink for new species, rather than an area where new species are generated."

Yet conservationists have tended to neglect ecotones, because they are typically much less diverse and also less pristine than the central rainforest. The Australian ecotone between dry forest and rainforest, for example, is sometimes considered "not pure" and therefore difficult to protect, says Endler. In Cameroon, the transition zone—which at some points is over 965 kilometers wide—is currently being devastated by cattle grazing, burning, and wood cutting, according to Smith. In the 6 years of the study, the team lost three sites to fire. In addition, Exxon and Shell oil companies are planning to build a huge pipeline from the oil fields in Chad to the Atlantic Ocean. In an attempt to protect the rainforest, the line is to run right through the Cameroon ecotone. While Smith says the pipeline itself probably won't harm the ecotone much, he is concerned about the increased access of people to the area. "If we are to protect biodiversity, we should also protect the processes that generate it," he says. "The study suggests we need to look at what's happening at the periphery as well. … I'm hoping this paper might be a wake-up call."

–Martin Enserink

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MEETING BRIEFS

Geophysicists Ponder Ancient Chills and Elusive Quakes

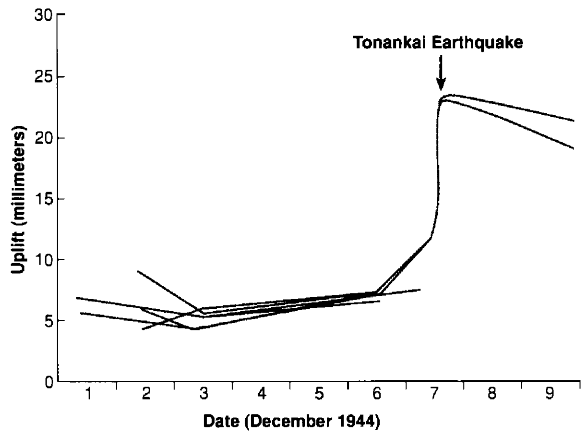
BALTIMORE—The spring meeting of the American Geophysical Union (AGU) here late last month attracted the usual assortment of presentations on climate and space science (*Science*, 13 June, p. 1648), but there was also much discussion of seismology, a subject usually more popular at the fall meeting in earthquake country in San Francisco. Here is a selection from each area: a series of reports that focuses new attention on "silent" earthquakes and a climate modeling study that takes the middle ground in a dispute over ice age cooling.

Listening to Silent Earthquakes

Seismologists have developed increasingly sophisticated means of watching and waiting, but they have yet to find a sure warning sign that a fault is about to rupture in an earthquake. At AGU, researchers had no magic solution to this problem, but they did offer persuasive new evidence of a potentially helpful phenomenon to which they had previously turned a deaf ear: so-called slow or "silent" earthquakes. These are fault movements so slow—taking days instead of seconds as in ordinary earthquakes—that they produce no seismic waves and hence can't be picked up by the listening ears of seismometers.

Silent earthquakes had seemed little more than rare curiosities, but as a flurry of presentations at the meeting showed, reanalysis of old records and use of additional instruments are revealing many more of these slow groanings of the crust. The new data also suggest that these slow movements can provide a window into the secret life of faults. A silent quake may defuse a fault that has been building toward failure—or transfer stress to part of the fault already near failure and trigger a normal earthquake. Detecting a silent precursor might thus give a few days' warning before a quake strikes. "There's enough evidence of slow and silent earthquakes to make them credible," says seismologist Paul Segall of Stanford University. "The grand prize in all this would be seeing something occurring before earthquakes" and so allow quake prediction.

No one has captured that prize yet, but a new analysis of data collected southwest of Tokyo just before the magnitude-8.1 Tonankai earthquake of 1944 suggests that a silent quake presaged that killer. Geophysicists Alan Linde and Selwyn Sacks of the Carnegie Institution of Washington's Department of Terrestrial Magnetism reexamined data collected by Japanese seismologist A. Imamura of the University of Tokyo. Fearing a great quake, Imamura had requested a survey to gauge the slow flexing of the land southwest of Tokyo. On the night of 6 December 1944, the surveyors were surprised to note that one end of an 800-meter survey line was 3 millimeters higher than it had been 3 days before. They resurveyed the next morning, only to find an additional 4-millimeter difference. Either their surveying was badly awry, or the southeast end of the line was rising extraordinarily fast. They got their answer that afternoon when the great quake struck.



A silent quake speaks. Surveyors saw the land rising days before the great 1944 Tonankai earthquake.

SOURCE: EARTHQUAKE PREDICTION, BY KIGOO MOGI, ACADEMIC PRESS, 1985.

At the meeting, Linde and Sacks reported that the survey data fit a silent quake that triggered the devastating quake from below. They found that the sharp rise of the land implied about 2 meters of silent slip along a deep, 60-by-50-kilometer patch of the fault during the few days before the earthquake. Such slip, equivalent to a magnitude-7.5 quake, would have loaded stress on the upper part of the fault, apparently bringing it to the point of failure.

It's not clear how often silent quakes presage normal ones or whether Japan's next great quake will issue a silent warning. To find