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Growing back after hurricanes

Catastrophes may be critical to rain forest dynamics

Hundright through the Caribbean and onto the US coast in September 1989 was front-page news. Readers learned once again how natural disasters, although rare, are a recurring aspect of life even in the so-called temperate zone. This reminder of nature's unpredictability came just as ecologists are beginning to see catastrophes as critical to the dynamics of ecosystems.

Ecology's recognition of the importance of hurricanes, earthquakes, volcanic eruptions, and similar disasters represents a major shift. Until recently, the field had interpreted areas undisturbed by humans as unchanging climaxes. Equilibrium theories developed in the 1950s and 1960s emphasized the role of millenia of evolution in structuring a balance of nature. But now the pendulum has swung toward seeing periodic disturbances as preventing equilibria from being reached, thereby casting doubt on the idea of the climax.

Two major hurricanes in the fall of 1988, Hurricane Gilbert in Jamaica and Mexico and Hurricane Joan in Nicaragua, led to studies that reinforce the nonequilibrium view. The relation between storms and tropical forests had long been recognized, with the palm brakes of Puerto Rico's montane rain forest and the storm forest of Kelantan in Malaysia showing storms' long-lasting effects on forest structure. In the Solomon Islands of the western Pacific, differences between forests on windward and lee shores were ascribed to periodic typhoon effects. But such examples were considered atypical.

by Douglas H. Boucher



Rain forest in eastern Nicaragua, three weeks after Hurricane Joan. Photos: D. H. Boucher.

Hugo and the forests

s rebuilding began and the damage to property inflicted by Hurricane Hugo was tallied up, scientists found that nature, too, had suffered considerably. In both Puerto Rico and South Carolina, forests were badly damaged, and there is concern for the fate of endangered animal species.

Hugo's eye passed almost directly over the largest rain forest in Puerto Rico, on the slopes of the mountain named El Yunque (The Anvil). The Forest Service estimates that 22,000 acres of the 28,000-acre Caribbean National Forest around El Yunque were heavily damaged, with nearly complete defoliation. Although the canopy was not destroyed as with Hurricane Joan in Nicaragua, there are areas with many trees fallen or snapped off. El Yunque, formerly a luxuriant green, now appears a desolate brown.

Damage to the forest is estimated at \$6.5 million, but the picture is not totally bleak. As Ariel Lugo, director of the Forest Service's Institute of Tropical Forestry pointed out, "Hurricanes are part of the ecology of El Yunque." Estimates of hurricane frequency in Puerto Rican rain forest range from a few years to several decades, but the last major storm at El Yunque before Hugo was in 1932.

Now scientists have an opportunity to study a hurricane's effect on a forest that was already well known. More than 15,000 trees had been marked for research at El Yunque, and data is now being collected on their survivorship. "From a scientific point of view, this is a great opportunity," said Lugo.

The outlook is bleaker in South Carolina, where Hugo struck a heavy blow to the pine forests along the coast. Timber loss is estimated at several billion board feet, with a value of many millions of dollars. In the Frances Marion National Forest, half of the saw timber stands are downed or heavily damaged. Efforts are being made to salvage some of the fallen wood, but most logging roads were blocked by the storm and local sawmill capacity is inadequate to deal with the enormous volume.

Scientific facilities suffered badly, too. The Forest Service's yellow pine seed orchard at Monck's Corners was nearly wiped out; only 12 of its 20,000 seed trees remained standing. The Belle Baruch Marine Lab of the University of South Carolina was completely swept away.

With the immense amounts of timber downed, there is concern about fire and insect outbreaks. Southern pine beetles and ips beetles are likely to be serious problems next year, and the fire hazard level is extreme.

As with Hurricane Gilbert, bird populations seem to have suffered from Hugo. The rare Puerto Rican parrot numbered only approximately 100 individuals before the storm hit its rain forest home. Those in captivity all survived, but only approximately half of the 45 in the wild have been seen since Hugo struck. Immediate prospects for the wild survivors is worrisome; the species is frugivorous, but most of the fruit on the forest's trees was blown down. As with Gilbert in Jamaica, the species suffering most from Hugo appear to be those that eat fruit and nectar.

In South Carolina, Hugo severely damaged 90% of the local habitat of the red-cockaded woodpecker, an endangered species that nests only in large pine trees. The species is unusual in that it excavates nest holes in live trees. Most of the pines old enough to be so inhabited were knocked down by the hurricane. Wildlife biologists are now experimenting with two techniques to allow nesting: drilling large holes in live trees and installing artificial nest boxes.

Direct regeneration in Nicaragua

The initial stages of recovery after Hurricane Joan, however, seem to indicate that rain forests growing back after major hurricanes can appear to be primary climax types. An international expedition to southeastern Nicaragua four months after Hurricane Joan reported that primary forest trees, rather than the expected secondary pioneer species, dominated the regeneration. Although the canopy over an area of half a million hectares had been destroyed by Joan's 250 km/hr winds, more than threefourths of the downed trees had resprouted. Colonization of the enormous light gap by pioneers was sparse, perhaps because of the reduction of seed-dispersing bird populations and the direction of predominant trade winds off the ocean, rather than from areas of remaining forest.

The rain forest destroyed by Joan showed little change in species composition despite massive damage, and it is not yet undergoing the expected secondary succession. The members of the February expedition, sponsored by the Nicaraguan Center for Atlantic Coast Studies (CIDCA), speculate that such "direct regeneration," rather than the classic patterns of succession after agriculture or logging, may typify posthurricane recovery. Their estimate of a 100-year return time for hurricanes hitting Nicaraguan rain forests suggests that they are nonequilibrium systems, despite their climax appearance.

Changes in forest shape

Gilbert, despite having the lowest pressures ever recorded in a hurricane's eye, seems to have been somewhat less destructive than Joan. In Jamaican montane forests, approximately 25% of the trees were felled or snapped off, compared to more than 80% in the Nicaraguan lowlands damaged by Joan. However, a similar reduction of bird populations was found, with nectar and fruit eaters such as orangequits and tanagers being affected the most.

In Jamaica, a long-term study of bird relationships to the forest physical structure was under way before the hurricane. This research, by Bob Waide and Joseph Wunderle of Puerto Rico's Center for Energy and Environmental Research, made it possible to show that the foliageheight diversity, a measure of the physical complexity of the vegetation, was altered substantially by the hurricane. Bird diversity has been known since the 1960s to correlate well with foliage-height diversity, so the observed foliage changes are likely to lead to changes in the avifauna.

The rain forest giants

One of the enigmas of rain forests has been the presence of occasional giant trees, called emergents, that tower above the forest canopy. Emergents can poke up as much as 20 meters higher than their canopy neighbors, giving rain forests an irregular, bumpy appearance from the air. Ecologists have speculated that the trees are the survivors of past disturbances, getting a head start by remaining upright when the rest of the forest was knocked down.

The CIDCA expedition's results support this idea. Although small trees survived Hurricane Joan better than middle-sized ones, the tallest trees actually survived best. Some of the emergent species, such as *Dipteryx panamensis*, had as many as half their individuals standing after the storm, compared to an overall average of less than 20%. These species seem to be characterized by slow growth rates but very dense wood, which may explain their resistance to strong winds.

On the other hand, disturbances may not be necessary to explain emergents. David and Deborah Clark, working at the La Selva Biological Station in Costa Rica, have found that the growth and survivorship rates of *D. panamensis* are sufficient to maintain its emergent population



Resprouting rain forest trees, four months after Hurricane Joan.

even without disturbances. Thus the presence of emergents in rain forests, while perhaps favored by hurricane damage, cannot be taken as evidence of past catastrophes.

Does disturbance favor palms?

Another unusual characteristic, which may be related to periodic damage, of some rain forests is the dominance of small palms in the understory. Shade-adapted palm species, which reach maturity and reproduce when only 1 or 2 meters high, predominate in rain forests such as La Selva. They are often more abundant than dicot shrubs and herbs.

The CIDCA expedition found extremely high rates of survivorship of understory palms in forest damaged by Hurricane Joan. Whereas loss of leaves was often heavy, the palms protect their principal buds. Thus they had high survivorship rates, averaging 94%, and were more predominant after the hurricane than before it.

Vulnerable pines

Both hurricanes Gilbert and Joan hit areas of tropical pine forest as well as rain forest. In Jamaica, pine forests and plantations hit by Gilbert seem to have been damaged more than other kinds of vegetation. This difference may have been due to the location of the pines on particularly steep slopes.

Slope, however, is not a factor in Nicaragua, where Joan hit flat lowland areas along the Caribbean coast. Here the initial damage to pine forests was considerably less than to rain forests. More than half the pine trees survived the hurricane standing up, according to the CIDCA expedition, compared to only a fourth of the trees in nearby rain forest.

Although almost all of the injured rain forest trees have resprouted, practically none of the damaged pines have. Also, seedlings of primary forest species are abundant in the damaged rain forest, but few pine seedlings are found. Thus the members of the CIDCA expedition predict the long-term prospects for the rain forest areas in Nicaragua to be considerably brighter than prospects for the pine forest.

Types of deforestation

The initial studies of hurricanes Ioan and Gilbert, both of which will also be the subjects of long-term research, seem to confirm the importance of hurricanes to forest structure. Other disturbances, too, have been shown to be important to rain forests. Nancy Garwood and her co-workers found substantial areas of Panamanian rain forest to be damaged by landslides after an earthquake, and Thomas Veblen has suggested that the composition of temperate rain forests in the Chilean Andes is determined by regrowth after earthquake-induced landslides.

As the nonequilibrium view becomes more acceptable, ecologists are beginning to see implications for deforestation. Rain forests may have developed mechanisms to reestablish themselves rapidly, without loss of diversity, after hurricanes and landslides. But this resilience does not necessarily imply that they can bounce back easily after deforestation by humans.

What seems to matter is not merely the damage to the forest, but the opportunity for regrowth. Logging, agriculture, and the establishment of pastures produce disturbances of considerable duration, and resprouting trees and seedlings are often eliminated by weeding for months or years. This weeding can wipe out most of the regenerative capacity that the rain forest has developed in response to natural disturbances. Thus, human deforestation may produce much more long-term change than nature's catastrophes.

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