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# Recovery of the Rain Forest of Southeastern Nicaragua after Destruction by Hurricane Joan[1]

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## ABSTRACT

Hurricane Joan badly damaged the rain forest of southeastern Nicaragua in October 1988, toppling or snapping off 80 percent of the trees and completely destroying the canopy over an area of 500,000 ha. An international expedition to the area in February 1989 found an unexpected pattern of recovery, with a large majority of damaged trees resprouting. Regeneration is dominated by sprouts and seedlings of primary forest species, rather than secondary pioneers. Little or no reduction in tree species richness has occurred, although bird and bat populations seem to have decreased considerably. The "direct regeneration" observed after this large disturbance of primary forest, challenges previous views of both the pattern of secondary succession and the nature of primary rain forest.

"*Behold, the Lord, the Lord of hosts, lops off the boughs with terrible violence;*
*The tall of stature are felled, and the lofty ones brought low;*
*The forest thickets are felled with the axe, and Lebanon in its splendor falls.*

*But a shoot shall sprout from the stump of Jesse, and from his roots a bud shall blossom.*"

Isaiah 10:33–11:1

THE LARGEST AREA OF SURVIVING RAIN FOREST in Central America, near Bluefields on the east coast of Nicaragua, was struck by Hurricane Joan on October 22, 1988. The hurricane's winds, which topped 250 km/hr (Cortés and Fonseca 1989), badly damaged approximately 500,000 ha of rain forest, destroying the canopy and stripping leaves from the few trees which remained standing.

Initial surveys of forest damage were done by the Nicaraguan Ministry of Agriculture's Division of Natural Resources (DIRENA) in November, 1988. An international expedition to the rain forest, funded by Oxfam America, was organized by the Nicaraguan Center for Studies of the Atlantic Coast (CIDCA) in February 1989. The expedition's purpose was to assess the destruction to the rain forest and its prospects for recovery. Recommendations were to be made on long-term plans for management of the damaged forest, including assessment of alternatives such as forest replanting, extraction of downed logs, and management of regeneration.

The hurricane's effects were also relevant for concepts of community ecology. In recent years, ecological theory has recognized that even natural ecosystems are not at equilibrium; rather, they are constantly being disturbed by storms, fires, floods, droughts, and earthquakes (Lewin 1983). Non-equilibrium models emphasizing recovery after disturbance rather than stability are now in vogue (Connell 1978, Huston 1979, Sousa 1984, Pickett and White 1985), and forests are seen as shifting mosaics of different successional stages, rather than as an unchanging "climax."

Non-equilibrium models are based on patches of various sizes caused by disturbance, ranging from the "light gaps" caused by the fall of a single tree to the much larger gaps caused by occasional disasters. Succession in small gaps in moist tropical

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forests is dominated by primary forest species, but as gap size increases, secondary or "pioneer" species become more common, while the density of primary forest species either decreases (Lawton and Putz 1988) or remains the same (Brokaw 1985, Uhl *et al.* 1988). The "supergap" created by Hurricane Joan was about seven orders of magnitude larger than what previous researchers have considered a large gap (5000 $km^2$ versus 500 $m^2$), suggesting that both pioneers and primary forest species would be important in its early regeneration.

A different model for post-hurricane regeneration is secondary succession after forest clearing by humans. Typically, human-disturbed Central American rain forest areas in the early stages of succession are dominated by pioneers such as *Cecropia, Ochrōma, Piper, Heliconia* and *Calathea.* Primary forest species do not colonize in substantial numbers until years or decades later. It has been feared that if disturbed areas are large enough, primary forest species will not be able to regenerate, and the rain forest will become extinct (Gómez-Pompa *et al.* 1972). In light of the rapid destruction of rain forest by humans over much of the earth (Buschbacher 1986), we were interested in how initial recovery processes after a large natural disturbance would compare to those after large-scale artificial disturbances (*e.g.*, logging, conversion to pasture).

## METHODS

Initial observations were made by DIRENA staff in November, 1988 at five sites in the hurricane-damaged forest. All trees greater than 5 cm diameter at breast height (dbh) in 24 10 by 10 m plots (from 3 to 8 per site) were identified by common name, and their condition (standing, snapped off, or completely fallen) was recorded. Additionally, the presence of leaves was recorded, and animals seen in the area were noted.

The CIDCA expedition in February 1989, consisting of nine persons from Nicaragua, Costa Rica, and North America, visited six forest sites in the hurricane-damaged area and intensively sampled at La Bodega (11°53′N, 83°58′W, 20 m altitude) and Las Delicias (12°16′N, 83°53′W, 30 m altitude) (Fig. 1). At each of these two sites, we located, noted the condition, and measured the diameter and height of every tree greater than 5 cm dbh, in two 100 m by 10 m (0.1 ha) transects. We also noted whether each tree had leaves and/or new sprouts. All understory monocots above 0.5 m in height were located and measured in an area of 100 m by 5 m within each transect. Ten 2 m by 2 m subplots were spaced systematically along the transect on either side of the midline, and all tree seedlings within them were identified and counted.

Most plant species found by the expedition were field-identified by scientific name. Two species of trees could not be identified, and another was identified only to family.

For the purposes of analysis, trees were considered to be alive in February if they had green leaves. Trees completely felled or snapped off were collectively referred to as "damaged," although even standing trees had suffered some branch and leaf damage.

We present the results in three sections. The first section looks at the characteristics of the forest before destruction by the hurricane. This analysis combines the data for all damaged and undamaged plants. Only fallen trees, whose state of decomposition made it clear that they had already fallen before the hurricane, were excluded. The second section describes how trees of different species and sizes were affected by the hurricane. And finally, we consider how the forest has regenerated during the several months following the hurricane, including both sprouting by adult trees and growth of seedlings. Detailed data on each species are given in Vandermeer *et al.* (1990).

THE FOREST BEFORE THE HURRICANE.—The four rain forest transects intensively sampled in February were very species-rich, with a total of 79 species of dicots among 374 individuals of 5 cm or more dbh (Fig. 2b). Each of the two most abundant species (*Pseudolmedia spuria* and *Qualea* sp.) had a density of 52 individuals/ha, or less than 6 percent of the total tree density. The 10 most abundant species made up only 43 percent of the forest.

The two sites differed in both species richness and composition, with the La Bodega site having more dicot species (61) than the Las Delicias site (38). Only 20 species were found at both sites, while 41 were present only at La Bodega and 18 only at Las Delicias. *Vochysia ferruginea, Inga thibaudiana,* and *Qualea* sp. were the most abundant species at La Bodega, while *Galipea granulosa* and *Pseudolmedia spuria* were the most abundant at Las Delicias. Both sites included species characteristic of swamps (*e.g., Carapa guianensis, Pterocarpus officinale*), moderately drained areas (*e.g., Dendropanax arboreus, Tetragastris panamensis*), and well-drained areas (*e.g., Vochysia ferruginea, Brosimum utile*), indicating that the transects covered a broad range

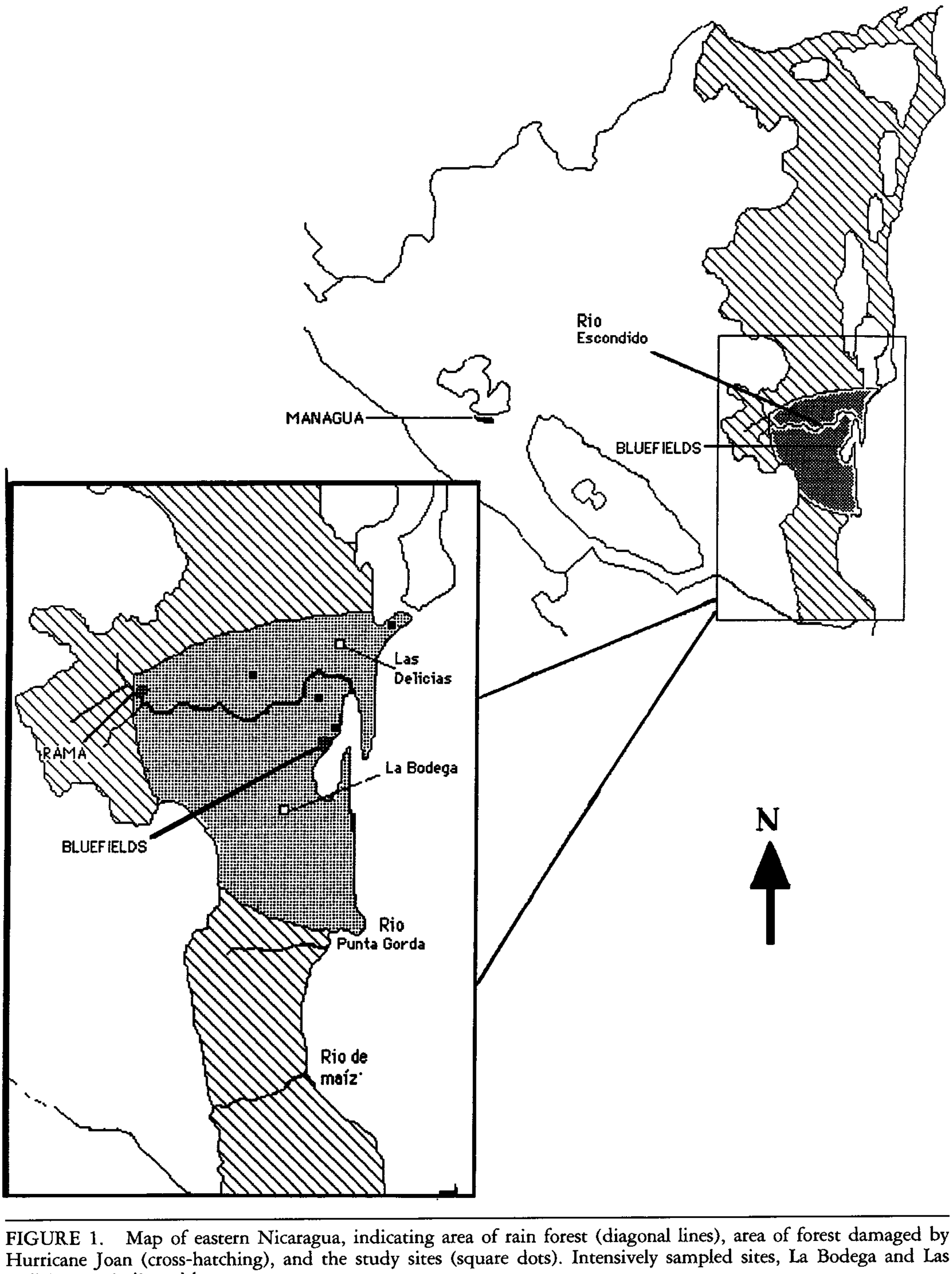
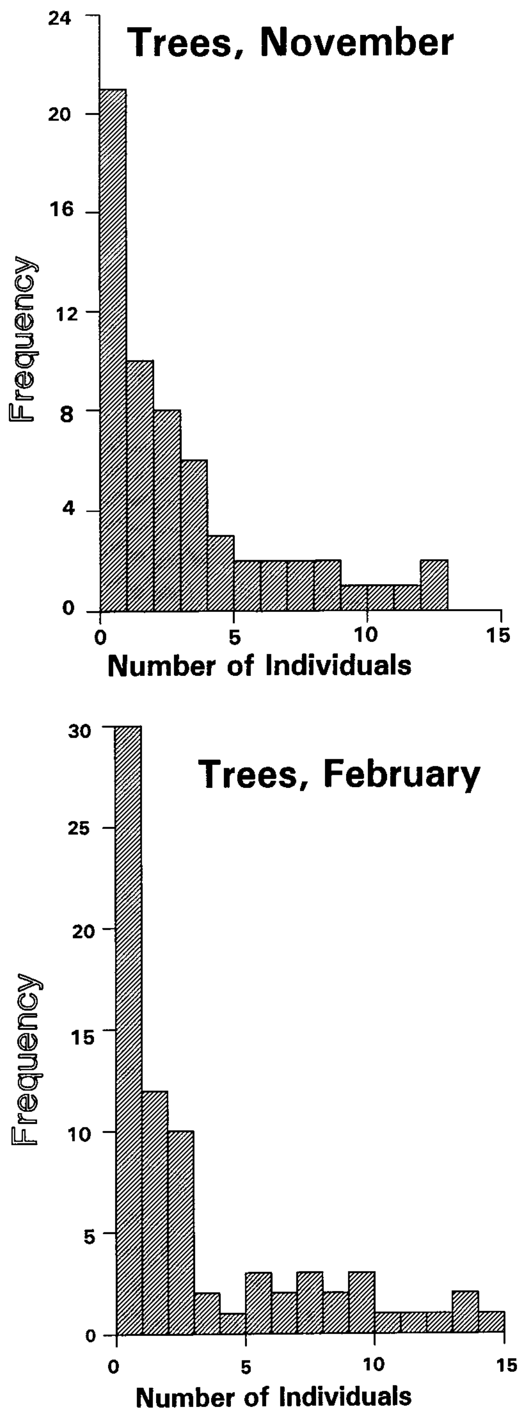



FIGURE 1. Map of eastern Nicaragua, indicating area of rain forest (diagonal lines), area of forest damaged by Hurricane Joan (cross-hatching), and the study sites (square dots). Intensively sampled sites, La Bodega and Las Delicias, are indicated by open squares.



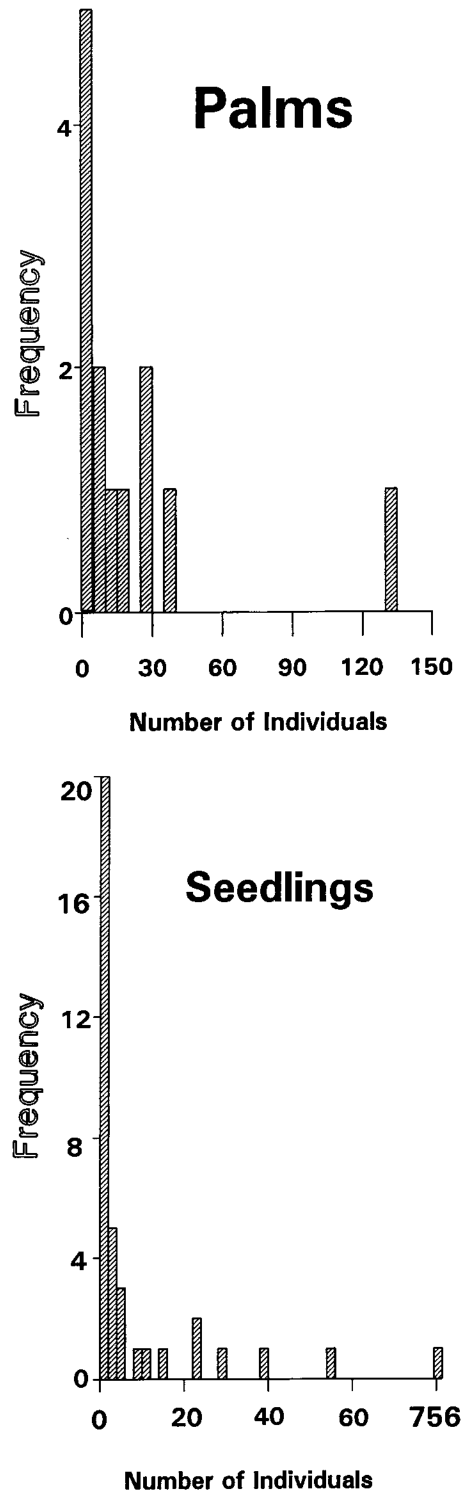




FIGURE 2. Frequency distributions of the species' abundances (total number of individuals in all areas sampled): a) trees, November 1988 plots; b) trees, February 1989 transects; c) palms, February 1989 transects; d) seedlings, February 1989 subplots.

TABLE 1. *Condition of the rain forest (number of trees in each category) in November 1988 (top) and February 1989 (bottom). November 1988 data are pooled results of twenty-four 10 by 10 m plots at five sites; February 1989 data are pooled results of four 10 by 100 m. transects at two sites. Results of G-tests of independence of the categories "Presence of Leaves" and "Status of Tree" are: for November 1988, $G = 128.7$, $df = 2$, $P < .001$; for February 1989, $G = 23.6$, $df = 2$, $P < .001$.*

| | Presence of leaves | | |
|---|---|---|---|
| Status of tree | Present | Absent | Percent |
| November 1988 | | | |
| Standing | 43 | 23 | 27 |
| Snapped off | 2 | 90 | 38 |
| Fallen | 0 | 86 | 35 |
| Percent | 18 | 82 | |
| February 1989 | | | |
| Standing | 69 | 4 | 20 |
| Snapped off | 152 | 47 | 53 |
| Fallen | 67 | 35 | 27 |
| Percent | 77 | 23 | |

of conditions. The pattern of species' abundances in both the November and February censuses was highly skewed to the right, with the largest number of species being found only once (Fig. 2a, b).

Diameter distributions were also highly skewed to the right. Mean diameter was about 15 cm for both the November and February samples, indicating an abundance of individuals of sapling and small tree size.

The understory was dominated by 13 species of palms, with small members of the genus *Geonoma* being the most common (42% relative density). Among larger species, *Welfia georgii* was most common (10% relative density). Total palm density was 1325/ha, or about a third greater than that of dicots (942/ha). The frequency distribution of monocot species' abundances was highly skewed to the right (Fig. 2c).

Based on the February data, very few pioneer species were found in the transects before the hurricane. Only *Miconia elata,* another *Miconia* sp., and *Pouruma aspera* were typical of early secondary forest (total relative density 5%), and no pioneer species such as *Cecropia peltata* or *Ochroma lagopus* were seen in the transects. Nor were there the genera of monocots typical of disturbed areas, such as *Heliconia* and *Calathea*. Pioneer species were present, however, in agricultural areas within a few km of the forest transects.

DAMAGE BY THE HURRICANE.—The immense destruction of the forest by the hurricane was confirmed by the initial census in November, three weeks after the storm (Table 1). Only 27 percent of the trees remained standing, and only 18 percent had leaves. Approximately equal numbers of trees were snapped off and felled completely.

This initial plot census of damage was confirmed by the more detailed sampling of transects in February. Twenty percent of the trees were found to be standing, although in this sample there were considerably more snapped trees (53%) than completely fallen ones (27%). As in November, there was less damage to small (under 15 cm dbh) and large (over 45 cm dbh) trees than to intermediate sizes.

The distribution of "Percent Standing" among species tended toward bimodality. Several common species had no individuals standing erect (*e.g., Dendropanax arboreus, Byrsonima crispa, Otoba novagranatensis*); others had over 35 percent standing (*e.g., Guarea kunthiana, Brosimum guianensis*). *Dipteryx panamensis,* which is known for its very hard wood, was especially notable in the latter category. Fifty percent of the species' trees were standing, even though they were among the largest in the forest (mean dbh 24.5 cm).

Damage was considerably less among the understory palms, with only 19 percent snapped off and 14 percent fallen. Only among those palms large enough to have an above-ground trunk, were a majority of the individuals damaged.

POST-HURRICANE REGENERATION.—By the time of the February expedition, most of the trees had resprouted. Fully 77 percent of the trees had leaves, including most of the standing trees and a majority of the snapped-off and fallen ones (Table 1). Although the areas censused in February were different from those censused in November, their trend of better survivorship among the largest and smallest size categories was the same (Fig. 3).

Of the 79 species found, all but two had some resprouting individuals. These two were *Vochysia hondurensis,* of which only a single individual was found in the transects, and *Vochysia ferruginea,* a common and large species (density 42.5/ha, mean diameter 22 cm dbh), of which none of the 17 individuals found had leaves. *Vochysia ferruginea* also had a low proportion of individuals still standing (6%).

Survivorship was even better among the 13 species of understory palms, with 94 percent of the individuals having leaves. Survivorship was high even among fallen and snapped off palms (84% and 82%, respectively), and nearly 100 percent among those still standing.

Of the 37 species and 1019 individuals found in the seedling subplots, 89 percent of the species and 94 percent of the individuals were characteristic of primary forest. The only pioneer species found was *Croton killipianus,* representing only about 6 percent of the seedlings. Such common pioneer genera as *Cecropia* and *Ochroma* were totally absent, despite being present in nearby agricultural areas.

By far the most common species in the seedling subplots was *Vochysia ferruginea,* representing 75 percent of the seedlings found. As noted above, none of the 17 adults of this species had survived to February. The frequency distribution of seedling species was strongly skewed to the right, with most species being represented by only one or two individuals (Fig. 2d). Most seedlings appeared to be advance regeneration rather than new germinants, but we had no reliable criteria for distinguishing these two groups.

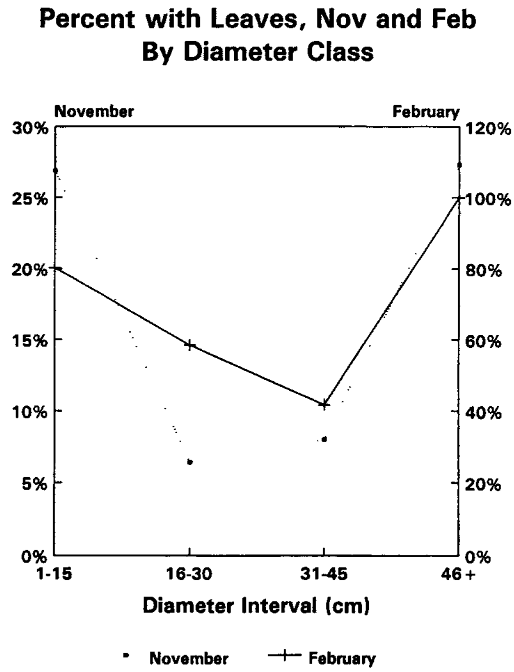



FIGURE 3. Tree survivorship, estimated as the percent of individuals which had leaves, by diameter class, November 1988 and February 1989.

## DISCUSSION

Theories concerning the effect of disturbance on species richness in tropical rain forest differ in their predictions concerning the pattern of recovery (Fig. 4), but all agree that the initial effect of disturbance will be to reduce species richness significantly. Although Hurricane Joan caused heavy damage to primary forest, essentially no initial reduction of plant species richness had occurred. Despite serious damage to the trees and complete elimination of the forest canopy, the high species richness of primary rain forest was maintained after the hurricane, with most species resprouting and many also being represented by seedlings.

Secondary species were rare, and pioneers almost totally absent. This result may be related to the diminution of the bird and bat populations, since some pioneer species are dispersed by these animals. Colonization of wind-dispersed species would also have been limited, since the prevailing trade winds enter the damaged area from the Caribbean Sea to the east, rather than from land which could serve as a source of seeds. In any case, the area did not appear to be beginning the secondary succession sequence of pioneers–other secondary species–primary species. Rather, there was a "direct regeneration" of primary forest species. Most of this regeneration was by resprouting, but there were also large numbers of seedlings (most of which were probably present before the hurricane).

Succession after Hurricane Joan seems to be fundamentally different from the patterns observed after logging, cropping, or abandonment of pasture. These differences may occur because:

1) The disturbance was a single dramatic event rather than an ongoing perturbation lasting months or years (*e.g.,* weeding of fields, browsing by cattle).
2) The soil remained protected by a thick (although quite patchy) layer of organic matter, including large branches and trunks as well as leaf litter.
3) The biomass of the forest was not reduced by fire or severe erosion, although its distribution was certainly rearranged drastically.
4) The root systems of most trees remained intact, providing sources of energy for resprouting.
5) Colonization by some secondary species may have been delayed by the absence of seed dispersal.

All these factors combined to favor primary forest species, leading to the "direct regeneration" of the rain forest rather than the abundance of pioneers which we had expected. While the effect of the hurricane was extensive (5000 km²) and dramatic (80% of trees damaged), it was not "se-

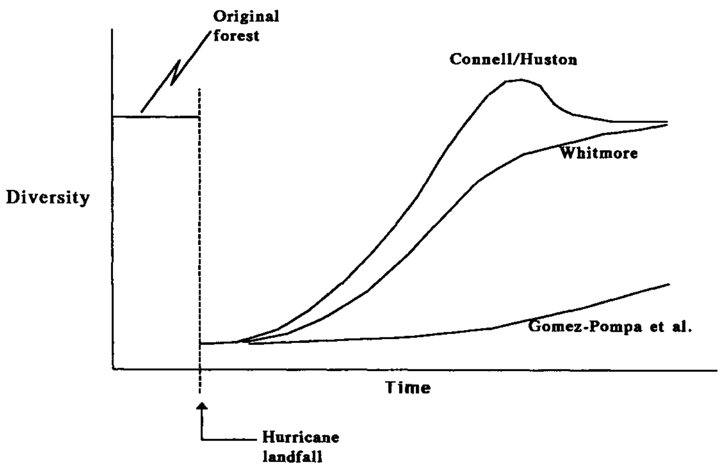



FIGURE 4. Theoretical trends of species richness over time after a disturbance, according to various authors: Huston 1979, Connell 1978, Whitmore 1974, and Gómez-Pompa *et al.* 1972.

vere" in the sense of disturbance theory, since biomass or soil cover was not removed (Pickett and White 1985). The initial pattern of regeneration is thus similar to that found in gaps (Denslow 1987, Brokaw and Scheiner 1989) rather than that found in secondary succession.

The pattern of regeneration also challenges the widespread notion of Central American rain forests as stable equilibrium communities. The frequency of hurricane damage to the rain forest at a given point on the Atlantic coast of Nicaragua has been estimated at once per 100 years (Boucher, in press); in 1971 another hurricane, Irene, struck the area just south of that damaged by Joan. Periodic hurricane disturbance every century or so could explain such features of primary rain forests as dominance of the understory by palms and the presence of large "emergents" such as *Dipteryx panamensis.* (See, however, the study of Clark and Clark (1987) which indicates that the presence of emergents does not require a disturbance-related explanation.)

While hurricane damage did not reduce species richness, it has decreased competition by eliminating shading and lowering the amount of living biomass. Overall species composition seems to have remained the same, but the proportions of the different species and their size distributions have been altered. So while hypotheses relating species richness to disturbance (Fig. 4) were not sustained, it is still reasonable to propose that periodic hurricane disturbance helps maintain high species richness by altering competitive relations and preventing competitive exclusion.

One important *caveat* is necessary. We do not know how well the resprouting trees and the seedlings will survive, nor how fast pioneer species will colonize the area. Heavy mortality or a sudden upsurge in colonization could change the path of succession. For this reason, permanent plots have been established for long-term study. However, at least in the first several months after the disturbance, the path of recovery has been different from what we had expected.

## CONCLUSIONS

The forest after Hurricane Joan did not behave as we had expected, and the initial stages of succession are very different from those hypothesized. Direct regeneration is the predominant pattern, with little or no change in species composition despite drastic alteration of the forest's physical structure. The pattern of recovery from a large natural disturbance may prove to be completely unlike both theories and observations based on artificial disturbances such as logging, cropping, and pasture.

If disturbances like Hurricane Joan have occurred repeatedly in the history of Central American rain forests (on a scale of centuries), we can no longer view them as stable equilibrium communities. As with many other ecosystems (Pickett and White 1985), their structure depends on patterns of natural damage and recovery. The appropriate metaphor for natural ecosystems is not eternal constancy, but rather cycles of death and resurrection.

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