



## Hurricane Disturbance and Tropical Tree Species Diversity

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decay rate, thus effectively increasing the donor oscillator strength. In the nonradiative Förster process, the transfer rate is dependent on this oscillator strength and so is similarly enhanced by the PMD, as shown here. The situation is different for radiative transfer. Because the evanescent donor dipole near-field components are negligible for separations appropriate to radiative transfer, the mode acts directly as a mediator, being the only way of transporting energy from donor to acceptor. This process does not alter the donor decay rate because donor and acceptor are decoupled by the mediating photon. This situation was studied by Folan *et al.* (22), who investigated transfer between donors and acceptors positioned on the surface of a microdroplet. Enhanced acceptor emission was observed because of a two-stage process; the donor excited a Mie resonance of the droplet, which was in turn damped by excitation of the acceptor. The high field strength associated with the Mie resonance allowed efficient transfer over large donor-acceptor separations (~10 μm).

The enhanced transfer we observe for small donor-acceptor separations is not predicted in recent theoretical work (11, 12). These reports concentrate on the effect the cavity has on the photons that mediate the transfer and in doing so ignore the important effect of the cavity on the donor; they appear to assume unit donor oscillator strength. Summarizing their picture, when donor and acceptor are close and transfer is efficient, the cavity has little effect on the evanescent mediating photon, so transfer is unaltered. In contrast, when donor and acceptor are well separated, the mediating photon is real or propagating and strong transfer enhancement is predicted. Unfortunately, transfer is much less likely at these large separations; consequently, observation of this enhancement requires the use of either a high-quality factor cavity (22) or a large number of acceptor molecules (16, 17). By assuming unity donor oscillator strength, the theories discussed above miss the important role the cavity plays in modifying the Förster transfer process. The dependence of the Förster process on the donor oscillator strength has been known since the first reports on energy transfer (9). With the current interest in the use of photonic materials to control optical processes, it is surprising that enhancing transfer by modifying the donor oscillator strength seems to have been overlooked.

This new understanding can be put to practical effect. In many device architectures, fabrication is simplified by the deposition of active layers containing a random distribution of dye molecules, rather than as an ordered nanostructure. In such systems, the Förster process is likely to be the dominant transfer mechanism because any excited donor will have a number of acceptor molecules in close proximity. Indeed, Förster transfer has already been used to

increase the efficiency of light-emitting devices based on organic materials by recouping energy lost to nonradiative triplet states (3). This was achieved by transferring the excitation energy from the triplet state to radiative singlet states of dopant dyes. Another application is in solid state polymer dye lasers, Förster transfer being used to spectrally shift the lasing wavelength away from the strong absorption losses of the host materials (23). In both these applications, increasing the donor oscillator strength through the use of microcavities resonant at the transfer wavelength could enhance the rate of Förster transfer still further and may be particularly important in lasing schemes where transfer is the rate-limiting step. It is interesting to note that a recent report indicates that in the process of photosynthesis, Förster energy transfer already benefits from increased donor oscillator strength, here brought about by the aggregation of dye molecules (24). Our demonstration that Förster energy transfer depends on the local optical environment means that the multiplicity of reports using confining structures to alter spontaneous emission also provide suitable strategies to control energy transfer.

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## Hurricane Disturbance and Tropical Tree Species Diversity

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The debate over the maintenance of high diversity of tree species in tropical forests centers on the role of tree-fall gaps as a primary source of disturbance. Using a 10-year data series accumulated since Hurricane Joan struck the Caribbean coast of Nicaragua in 1988, we examined the pattern of species accumulation over time and with increased sampling of individuals. Our analysis shows that the pattern after a hurricane differs from the pattern after a simple tree-fall disturbance, and we conclude that pioneers are limited in large disturbances and thus do not suppress other species the way they do in smaller disturbances.

A persistent issue in ecology is how tree species diversity is maintained in tropical rainforests (1, 2). Studies have proposed (3,

4) and then challenged (5) the idea that disturbances, in the form of tree-fall light gaps, set back the process of competitive exclusion, thus conforming to the intermediate disturbance hypothesis (1). This hypothesis states that neither very large nor very small disturbances can deter the eventual extinction of species, either through competition or through the disturbance event itself, and that only disturbances of intermediate intensity can have this effect. Central to the intermediate disturbance hypothesis is a higher spe-

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cies richness within the disturbed forest (in this case tree-fall gaps) compared to undisturbed forest.

An analysis of a large data set from Panama (5, 6) compared the number of species per individual in light gaps and in undisturbed forest of equal area (5) and contrasted species-individual curves for light gaps and undisturbed forest (6). From this analysis, it was concluded that the necessary assumption that more species exist in the disturbed area than in the undisturbed area appears to be a consequence of the simple fact that there are more stems in light gaps than in undisturbed forest. A possible explanation for this pattern may be that pioneer trees rapidly colonize disturbed areas and usurp space that might otherwise be occupied by nonpioneers. This fact may account for the observed increase in mortality of shade-tolerant species in larger gaps (6). Thus, the reasonable expectation that the large numbers of species banked as seedlings and saplings in the understory of the undisturbed forest would rapidly grow into the light gap (7) may not be realized in nature, at least partly because of the recruitment of pioneer tree species (8). Whether this might be true for other, larger, disturbances could have important implications for the

intermediate disturbance hypothesis. Here, we examined this possibility with an analysis of a data series from a hurricane-damaged forest in eastern Nicaragua.

In many tropical regions, catastrophic disturbances are common, usually in the form of large storms (9, 10). Storm damage may cover hundreds of square kilometers (9, 11), whereas tree-fall light gaps are usually measured in tens or hundreds of square meters. Although the intermediate disturbance hypothesis is usually thought to operate similarly whether the independent variable is frequency or intensity, earlier literature (12) suggests that there is an important difference between frequency and intensity as represented by spatial scale.

Hurricane Joan was a large storm (category 4) that severely damaged about 500,000 ha of rainforest when it struck the Caribbean coast of Nicaragua in October 1988 (11, 13). Studies of post-hurricane forest succession were initiated in eight small plots at four sites in the damaged area (Fig. 1) and have continued since February 1989 (14). In 1996, comparative plots were established in the nearest intact forest available (Kurinwas, Fig. 1).

For each plot in the hurricane-damaged area, there was a pronounced increase in species richness during the 10 years after the hurricane (Fig. 2). Assuming that the species richness at the Kurinwas site is similar to what would have been the case before the hurricane in the other sites (15), a twofold to threefold increase in species richness has oc-

curred in the damaged area over the past 10 years of the study.

Comparing species richness in a disturbed area to that in a nondisturbed area may give a false impression because the disturbed area will typically have more individual stems than the nondisturbed area, making the larger number of species only a statistical artifact (5, 7). Comparing curves of species versus individuals from site to site corrects for this bias. Examining such graphs, we find a pattern that, as suggested earlier (7), would be characteristic of a disturbed area (Fig. 3). Accumulation of species with increased sampling of individuals is greater for the hurricane-damaged forest sites than for the nondamaged site [ $t = 3.869$ ,  $P = 0.005$ ; Kruskal-Wallis comparison,  $P = 0.036$  (16)]. This pattern contradicts the results reported for some tree-fall light gap data (6). Species-individuals curves for tree-fall light gap data are below those for the undisturbed forest, whereas here (Fig. 3) the species-individuals curves for the hurricane-damaged area are always above those for the undisturbed forest. It is worth noting that the pattern shown in Fig. 3 need not remain constant as succession proceeds. The details of intermediate disturbance are poorly understood in tropical forests and depend on the vegetation size classes that are considered as well as the time since disturbance (17, 18).

The increase of tree species over time (Fig. 2) and with increased sampling of individuals (Fig. 3) is as expected if large storms

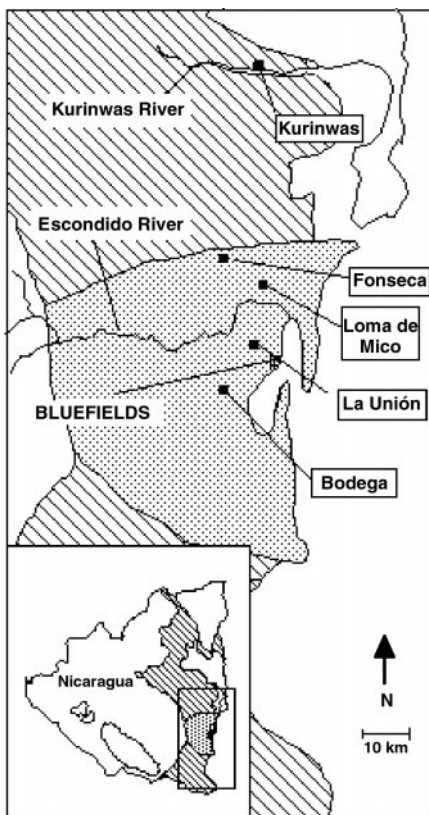


Fig. 1. Map of study area. Central shaded area is approximate area of damage from Hurricane Joan in October 1988. Hatched area is approximate area of original lowland tropical rainforest. Solid squares indicate locations of all study sites.

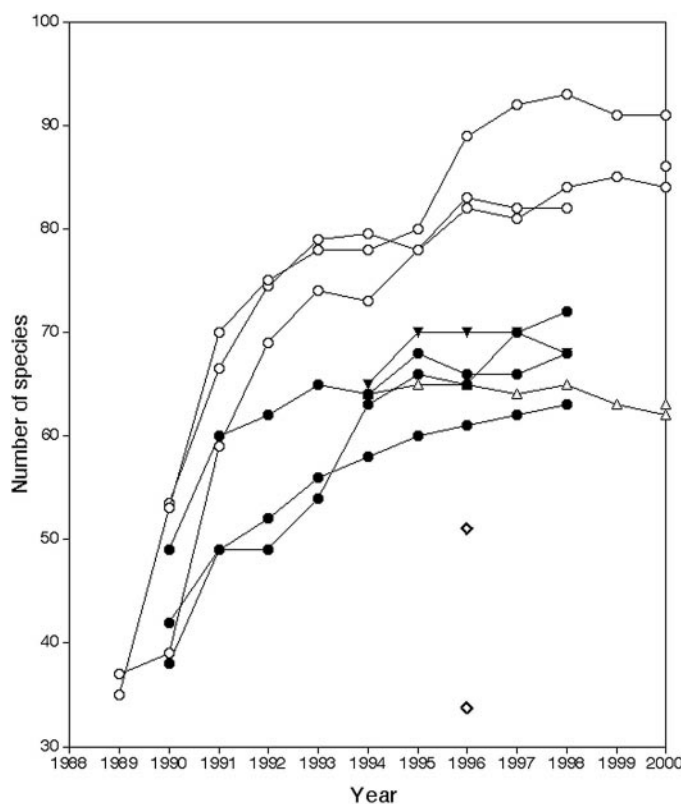


Fig. 2. Number of species during each year of the study. Each species richness estimate is based on a sampling area of 0.1 ha and includes individuals >3.2 DBH in the year concerned. Because the raw data samples at La Unión, Loma de Mico, and Kurinwas are from an area of 0.15 ha, subsampling was done to estimate the average number of species per 0.1 ha. Open circles, Bodega; solid circles, Fonseca; open triangles, La Unión; solid triangles, Loma de Mico; open diamonds, Kurinwas. The two sites at Kurinwas were only sampled once, but it is unlikely that much of a change in number of species occurred during the time of the study (12).

are diversity-preserving. These findings suggest that the intermediate disturbance hypothesis requires modification. In its most widely accepted form, the intermediate disturbance hypothesis considers number of species as a function of either intensity or frequency (or both) of the disturbance event (19). In the present application, the intensity in spatial extent of damage is the important force. This may be due to recruitment limitation of pioneers, all of which must be dispersed into the newly created light gap. Few pioneers were banked as seeds or seedlings in the prehurricane forest, as documented in previous studies (11, 20). With such a large area damaged, the few pioneers that survived the storm did not produce enough recruits to saturate the area, as they are able to do in a typical year in the comparatively small total area of all the tree-fall gaps in a given forest. The percentage of stems that are pioneers in light gaps (5) and at the four damaged sites in our study (21) supports this idea. When the disturbance is so extensive, seed recruitment of the entire population of reproductive adult pioneers is not sufficient to saturate the damaged area, and thus other species may flourish.

Other mechanisms for maintaining canopy tree species richness should not be discounted. Recruitment limitation of nonpioneers (5) as well as light gap specialization (3, 4) may be important under typical circumstances. On the other hand, forest dynamics occurs over long periods (decades to centuries), and many catastrophic disturbances may be rare but critical even though researchers often miss seeing them. Although tree-fall

gaps may not fit the pattern predicted from the intermediate disturbance hypothesis (5), larger disturbances may indeed fit that pattern and could thus be essential to the maintenance of species richness. In addition, the details of forest succession will depend on the exact nature of the disturbance event [e.g., a landslide that effectively initiates primary succession (22) will differ from a hurricane, in which resprouting of individual trees is dominant (11, 20, 23)]. Furthermore, there are local storms and other forms of disturbance that affect scales between the 400 m<sup>2</sup> and 500,000 ha contrasted here. Such events may be among the most numerous disturbances in tropical forests (24), but it is not yet known at what scale the proposed recruitment limitation of pioneers begins to operate.

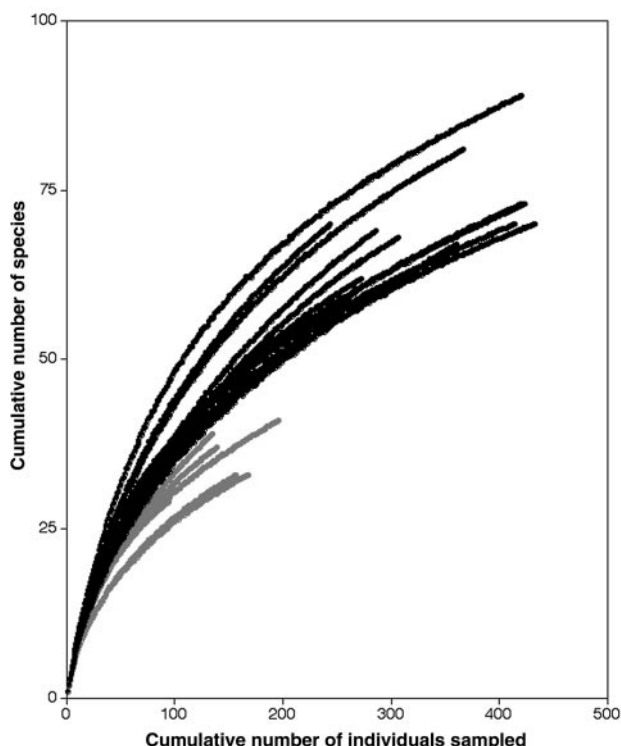
Recent evidence suggests that the frequency and intensity of El Niño events are increasing as a result of global warming. With this change, the frequency and intensity of tropical storms may also increase (25, 26). If catastrophic damage from large storms is a major contributor to the maintenance of tropical tree species diversity, the long-term indirect effects of global warming on tropical biodiversity could be important. It is likely that some areas already have storms that are so frequent that many tree species infrequently reach reproductive maturity during the interval between storms, and thus have a reduced potential for maintaining a persistent population (e.g., Puerto Rico). Increasing frequency at such sites would probably result in a lowering of species richness as species requiring more time to reach maturity become locally extinct. Conversely, other areas

exist in which storms are sufficiently infrequent that the process of competitive exclusion may operate, or other mechanisms [e.g., recruitment limitation (5) or habitat specialization (3, 4)] may dominate the suite of factors determining local species richness (e.g., Panama). In such areas, increased hurricane frequency could increase local species richness. Thus, the ultimate effect of increased frequency and/or intensity of large tropical storms depends on the specific location.

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13. In this case 100% of the canopies were removed, 27% of the stems were topped, and 53% of the stems were truncated in a pattern that was remarkably homogeneous because of the flat, largely uninterrupted nature of the landscape (17).
14. Since February 1990, we have annually monitored all stems >3.2 cm DBH (diameter at breast height) in six plots (100 m by 10 m) at two sites, one in the center of the damaged area (Bodega) and one near the edge of the damaged area (Fonseca). In 1994, two additional sites, La Unión and Loma de Mico, both located between Fonseca and Bodega, were added to the study. Here, single plots of 30 m by 50 m were established. Two plots (30 m by 50 m) were established in a nondamaged primary forest site, Kurinwas. Voucher specimens for all species were deposited in herbaria (INB in Costa Rica, HNMN in Nicaragua, and MICH at the University of Michigan).
15. Nothing suggests that the forests at the Kurinwas site differed significantly in species composition from any of the other sites more than those sites differed from one another. For example, the proportion of species found at Loma de Mico that were also found at Bodega was 43%, whereas the proportion of species found at Loma de Mico that were also found in Kurinwas was 42%.
16. Statistical tests were conducted under conservative assumptions. Of the six curves in the undisturbed forest, the highest values were chosen, one from each of the plots at Kurinwas. Of the three curves at each of La Unión and Loma de Mico, the smallest number of species was chosen. The highest values from the nondamaged site and the lowest values from the damaged sites were chosen because we expected that those for the nondamaged site would be lower than for the damaged sites, and thus the biased sampling had the most chance of rejecting the hypothesis of that difference. All comparisons were done at an individual accumulation number of  $N = 94$ , because that is the largest  $N$  for which all six curves for the nondamaged site still exist. At 94 individuals, the numbers of species observed were 31

**Fig. 3.** Number of species as a function of number of individuals. Black data points denote hurricane-damaged forest; gray data points denote undamaged forest. All data were gathered by randomly resampling 500 times (at each "number of individuals" category) from the collection of individual trees in each plot in 1996. For La Unión, Loma de Mico, and Kurinwas, the 30 m by 50 m plots were divided into three 10 m by 50 m plots and species-individuals curves were constructed for each combination of two 10 m by 50 m plots (thus contributing three individual curves for each 30 m by 50 m plot). This gives rise to six curves for Kurinwas (three for each of the two 30 m by 50 m plots) and 12 curves (three each for Bodega, Fonseca, La Unión, and Loma de Mico) for the hurricane-damaged sites. All curves are thus based on a sampling area of 0.1 ha.



and 32 for Kurinwas and 34, 34, 35, 36, 37, 42, 44, and 47 for the other sites.

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21. In 1991, the proportions of stems that were pioneers were 0.05, 0.13, 0.17, and 0.19 for Bodega, La Unión,

Loma de Mico, and Fonseca, respectively. In 1996, the corresponding figures were 0.09, 0.14, 0.15, and 0.16, respectively. Note that the order of sites ranging from farthest to nearest to the edge of the nondamaged forest (i.e., a potential source of pioneer seeds) is also Bodega, La Unión, Loma de Mico, Fonseca.

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27. We thank students from Universidad de las Regiones Autónomas de la Costa Caribeña de Nicaragua, Bluefields Indian Caribbean University, University of Central America, Hood College, University of Guelph, and University of Michigan for help in data collection; D. Goldberg for guidance on data analysis; and L. Curran, R. Burnham, and S. Levin for advice on the manuscript. The Centro de Investigaciones y Documentación de la Costa Atlántica (CIDCA) contributed logistic and intellectual support. Supported by NSF and the University of Michigan.

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## A Low Temperature Transfer of ALH84001 from Mars to Earth

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The ejection of material from Mars is thought to be caused by large impacts that would heat much of the ejecta to high temperatures. Images of the magnetic field of martian meteorite ALH84001 reveal a spatially heterogeneous pattern of magnetization associated with fractures and rock fragments. Heating the meteorite to 40°C reduces the intensity of some magnetic features, indicating that the interior of the rock has not been above this temperature since before its ejection from the surface of Mars. Because this temperature cannot sterilize most bacteria or eukarya, these data support the hypothesis that meteorites could transfer life between planets in the solar system.

Large-body impacts are the only known natural processes capable of ejecting a rock from Mars. It has been suggested that some rocks could be ejected without being shocked and heated (1, 2), and laboratory shock experiments have spalled lightly shocked material moving at about 20% of Mars' escape velocity (3). Thermal conductivity calculations (4) demonstrate that passage through Earth's atmosphere will not heat the interior of meteorites larger than ~0.3 cm above 100°C.

ALH84001 is a meteorite composed of ~95% orthopyroxene that accumulated in a magma chamber on Mars ~4.5 billion years ago (Ga) (5). Carbonate blebs, which may contain evidence for ancient life on Mars (6), formed in its fractures at about 4 Ga (7). During its first few billion years, ALH84001 experienced several shocks, probably from minor planet impacts (8). It was launched from the surface of Mars at ~15 million years ago by another impact (9) and after

wandering through space, landed in Antarctica at about 11 thousand years ago (ka) (10).

Transmission electron microscopy imaging of the rims of the carbonate blebs in an ultrathin section prepared by focused ion beam detected single domain (SD) and superparamagnetic (SP) (11) magnetite (Fe<sub>3</sub>O<sub>4</sub>) and monoclinic pyrrhotite (Fe<sub>7</sub>S<sub>8</sub>) with characteristic lattice fringes. Because magnetic minerals have not been positively identified outside the carbonate bleb's rims, the blebs probably carry most of the magnetization in ALH84001. Other studies (12) have shown that this magnetite is stoichiometric (impurities <0.1%). After exposure to a 5-T field at room temperature, a 20-mg pyroxenite grain from ALH84001,236 containing multiple carbonate blebs exhibited a remanence transition at 112 K and a possible weaker remanence change at ~35 K, diagnostic of low-Ti magnetite (Fe<sub>3-z</sub>Ti<sub>z</sub>O<sub>4</sub> with z < ~0.01) and pyrrhotite, respectively. The grain's magnetization increased during cooling and then recovered ~90% of its original magnetization upon warming to room temperature, indicating the presence of SP and SD crystals and a lack of multidomain (MD) crystals. Anhyseretic remanent magnetization (ARM) and isothermal remanent magnetization (IRM) acquisition and demagnetization experiments on this grain also provide evidence of pyrrhotite (it acquires an IRM up to and beyond 1000 mT) and a small fraction of pseudo-

single domain (PSD) crystals (alternating-field demagnetization is more effective at removing an IRM than an ARM). X-ray maps obtained by electron microprobe analysis detected Fe-sulfide crystals dispersed through the pyroxene matrix, suggesting that pyrrhotite may also be present outside the carbonate. We have thus detected two major magnetic minerals in ALH84001, located in the carbonate blebs and also probably in the pyroxene: magnetite and pyrrhotite ranging in size between SP, SD, and PSD. This confirms a previous identification of these magnetic minerals (13) and argues against the presence of titanomagnetite (14).

Kirschvink *et al.* (13) suggested that the interior of ALH84001 has been cooler than 110°C since before the formation of the carbonate. To obtain more precise thermal constraints, we imaged the perpendicular (east/west in the meteorite orientation system) component of the magnetic field of eight oriented slices of ALH84001 (15) using the Ultrahigh Resolution Scanning SQUID Microscope (UHRSSM). This magnetometer has a sensitivity of better than 0.1 nT and is capable of making two-dimensional images of the magnetic field of materials at room temperature with a resolution of 500 μm (16).

The fusion crust on the top-south surface of ALH84001,228b formed during its high-temperature passage through Earth's atmosphere and magnetic field, and is associated with an intense magnetic anomaly (Fig. 1). Moment magnetometry measurements of this and two additional samples with fusion crusts indicate that the meteorite initially came to rest in the ice with its east-southeast axis pointing up. Much weaker (~1% intensity) positive and negative magnetic features are present at distances of <5 mm in from the surface, implying that the heat pulse from atmospheric deceleration did not travel further than this into the meteorite. This shallow depth of heating is typical of most meteorites of this size (4). This suggests that the heterogeneous magnetization in the interior (Fig. 2) predates arrival at Earth.

Using the same technique, we made multiple magnetic images of ALH84001,232e, which was extracted from the interior of the

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