Article

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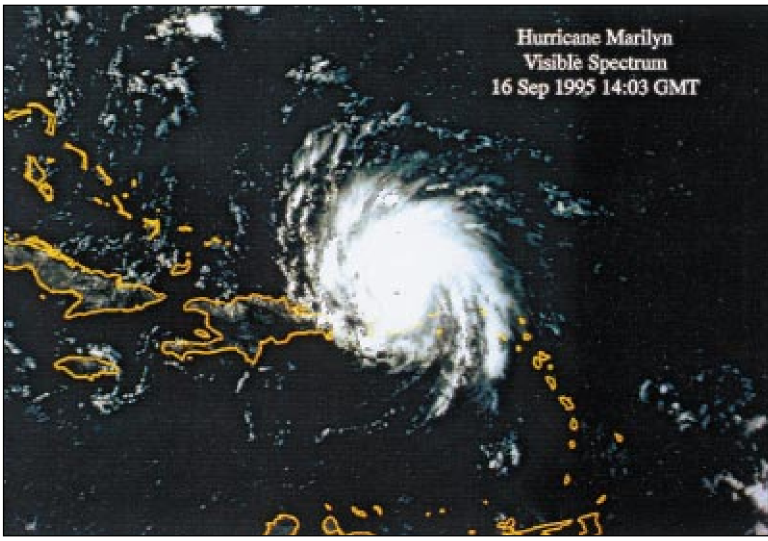
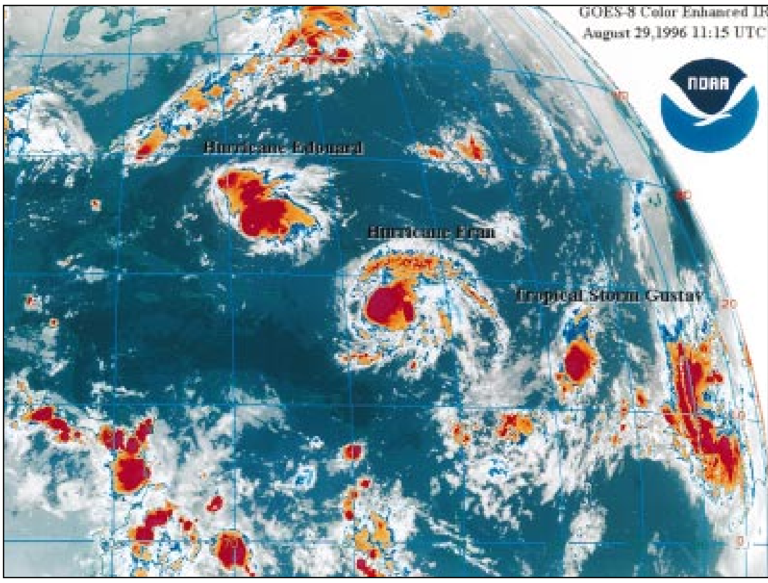
Hurricanes, Coral Reefs and Rainforests: Resistance, Ruin and Recovery in the Caribbean

The coexistence of hurricanes, coral reefs, and rainforests in the Caribbean demonstrates that highly structured ecosystems with great diversity can flourish in spite of recurring exposure to intense destructive energy. Coral reefs develop in response to wave energy and resist hurricanes largely by virtue of their structural strength. Limited fetch also protects some reefs from fully developed hurricane waves. While storms may produce dramatic local reef damage, they appear to have little impact on the ability of coral reefs to provide food or habitat for fish and other animals. Rainforests experience an enormous increase in wind energy during hurricanes with dramatic structural changes in the vegetation. The resulting changes in forest microclimate are larger than those on reefs and the loss of fruit, leaves, cover, and microclimate has a great impact on animal populations. Recovery of many aspects of rainforest structure and function is rapid, though there may be long-term changes in species composition. While resistance and repair have maintained reefs and rainforests in the past, human impacts may threaten their ability to survive.



Satellite image of Hurricane Marilyn as it passed over the U.S. Virgin Islands on September 16, 1995. Photo: Courtesy of NOAA.



Satellite image of two hurricanes, a tropical storm, and a tropical wave over the Atlantic Ocean. All these systems originate off the coast of Africa—as illustrated by the tropical wave on the right of the image—and travel in a westerly direction towards the Caribbean or the North American mainland. The Caribbean is on the bottom left of the image shrouded in clouds. Image courtesy of NOAA.

The sea was far away in Villavicencio, but curiously I spent a deal of time there thinking about it, reading about it, wondering about the similarities, the biological analogies, between the forest and the sea. There I first began to realize the essential similarities in plan and function among all the diverse living landscapes and seascapes of our planetary surface — the essential unity of the living world. Marston Bates (1).

INTRODUCTION

The great naturalist Marston Bates was neither the first nor the most recent observer to recognize similarities between landscapes and seascapes (e.g., 2–4), but his extended essay on *The Forest and the Sea* is the most popular and poetic writing on the subject. Although our knowledge of terrestrial and marine environments has increased dramatically during the past century, and especially since Bates' essay in 1960, there have been few attempts to compare the emerging views of how different ecosystems on land and in the sea function. As John Steele (4) put it, "Terrestrial and marine ecological research are usually carried out in different institutions, published in different journals and funded from different sources." In spite of these obstacles and the authors' very different areas of focus (tropical forests, coral reefs, and coastal ecology), we have been brought together by luck and circumstance numerous times. Over the years, we have found ourselves returning again and again to discussions comparing the forest and the sea, an exercise that has proven to be stimulating and rewarding regardless of whether we see differences or similarities.

Our purpose in this article is to concentrate on two of the most complex and beautiful of marine and terrestrial environments, coral reefs and tropical rainforests, and to explore the paradox that such diverse and highly structured ecosystems can persist, in spite of recurring exposure to the enormous destructive energy of tropical hurricanes. (We use the term "rainforest" generically to include tropical moist and wet forests as well as the "true" rain forest with its particular rainfall and temperature regime as defined by Holdridge (5)). Because most of our experience is in the Caribbean, we have confined our attention to that region. Where rainfall is adequate, the tropical Caribbean climate is very favorable for supporting biological activity. The region lacks frost in the lowlands, its trade winds moderate air temperature, and solar radiation is abundant throughout the year. The Caribbean is thus a region of contrasting conditions: favorable for ecosystem development most of the time, but with powerful forces that may periodically disrupt the structure and functioning of its ecosystems.

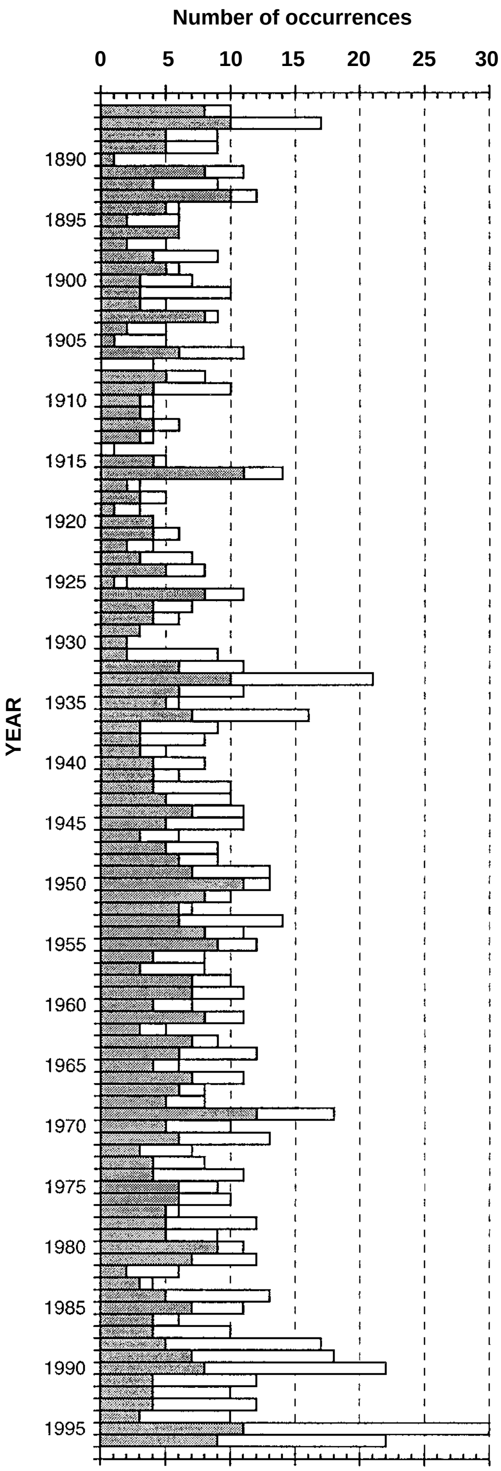


Figure 1. Total numbers of tropical storms (open bar) and hurricanes (solid bar) each year in the Atlantic for the period 1886–1996. Tropical storm numbers prior to about 1950 may be underestimates. Data from Neumann et al. (76) updated using Pielke and Pielke (77).

Neither the coral reefs nor the rainforests of the Caribbean are as diverse and complex as those found in the Old World Tropics (6–8), and the geologic history, climate, and destructive storm regimes of the Caribbean are different from the Indo-Pacific, the Indian Ocean region, and the lowland tropics of South America. But the diversity and complex structure of Caribbean coral reefs and rainforests are remarkable, and their interaction with severe storms has been studied more thoroughly than anywhere else in the world. Even within the Caribbean, however, there is great variability in the structure and composition of coral reefs and rainforests, and the number of sites studied remains small. Unfortunately, there are also very few long-term data sets that document the impact of hurricanes on these systems and their rates of recovery following the event. The information that is available, however, suggests that coral reefs and rainforests, the most complex and productive ecosystems in the Caribbean, experience hurricanes in very different ways.

HURRICANES

The word hurricane comes from the Central American Taino language, in which the word hurucan was said to mean "God of evil."

T. P. Eichler (9).

Hurricanes are particularly intense tropical cyclonic storms. The distinguishing features of a tropical cyclone include a central core or "eye" of very low atmospheric pressure, which usually forms over areas where the temperature of the surface ocean water exceeds 26°C. Moisture-laden air flows into the low pressure area and is turned into a counter-clockwise spiral in the Northern Hemisphere by the rotation of the earth. As the warm air rises in the low pressure, it cools and its relative humidity increases, thus leading to dense cloud formation around the eye and, often, very intense rainfall. While there is virtually no wind or cloud within the eye itself, the winds rotating around the core can become extremely strong. If they develop sustained speeds exceeding 33 m s^{-1} (74 mph), the storm is classified as a hurricane in the Atlantic and Caribbean, a typhoon in the western Pacific, and a cyclone in the Indian Ocean (9).

The criteria by which hurricane intensity are defined are summarized in the Saffir/Simpson (SS) scale. These criteria include atmospheric pressure in the core, maximum sustained winds, storm surge, and a relative index of potential destruction. The range of maximum sustained wind speeds in the SS scale is from 33 m s^{-1} (74 mph) for a category 1 hurricane to over 69 m s^{-1} (154 mph) in a category 5 hurricane. Central pressures range from 980 mb to less than 920 mb and storm surges range from 1 m to over 5 m above normal high tide. Another type of cyclonic storm, the tornado, has stronger winds of 90 to 235 m s^{-1} (200–525 mph) and travels faster than hurricanes (10 to 20 m s^{-1} *vs*. 3 to 8 m s^{-1}), but tornadoes usually cover less than 2 km^2 and travel less than 300 km. Hurricanes commonly impact areas many thousands to many millions of square kilometers, last for 7 to 10 days, and travel over thousands of kilometers (9). "Because of its great size and intensity, the tropical cyclone, when fully developed, is the most destructive of all storms" (10).

About 80 tropical cyclones develop over the world ocean each year, with 10 of those forming in the North Atlantic. On average, 6 of the 10 develop into hurricanes, though the actual number of storms varies greatly from year to year (Fig. 1). The frequency of hurricanes also varies considerably in different areas of the Caribbean–Gulf of Mexico region (Fig. 2). Historically, over 80% of the hurricanes in the Caribbean have occurred during the three months from August through October (11).

It is difficult to quantify the destructive power of hurricanes as they are experienced by rainforests and coral reefs. The speed of the wind is of fundamental importance and it varies markedly within a given storm. According to Emanuel (12), "The wind speed rises rapidly from nearly zero at the storm center to its maximum value at a radius between 10 and 100 km . . . . The winds then fall off more gradually with radius, roughly declining inversely with the square root of the distance from the center, and decreasing more rapidly near the outer limit of the storm circulation . . . between 100 and 1000 km from the storm center." While the kinetic energy that can be extracted from moving air by a device such as a windmill is proportional to the cube of the wind speed, there is evidence that damage to buildings and other structures may be proportional to the fifth power of the wind speed (13). The impact of the wind will also depend on the overall size of the hurricane, the speed of its forward movement, the direction from which it approaches, the aspect of the reef or forest that is exposed, and the elevation or depth of the forest or reef (14, 15). For example, since hurricanes in the Caribbean have a counter-clockwise rotation, areas exposed to the right-hand side of the storm will experience winds enhanced by the forward motion of the system.

The exposure of coral reefs is particularly difficult to assess, since they are impacted by wind-driven storm waves and surge rather than by the wind itself. While measurements of wind velocity during hurricanes are relatively common, no one has yet measured the power of hurricane waves on coral reefs. Since storm waves propagate more rapidly than hurricanes move, reefs may experience rough water for days before and after a hurricane passes. On the other hand, groups of islands may produce an archipelago effect in which fetch is reduced and many reefs are sheltered from storm waves.

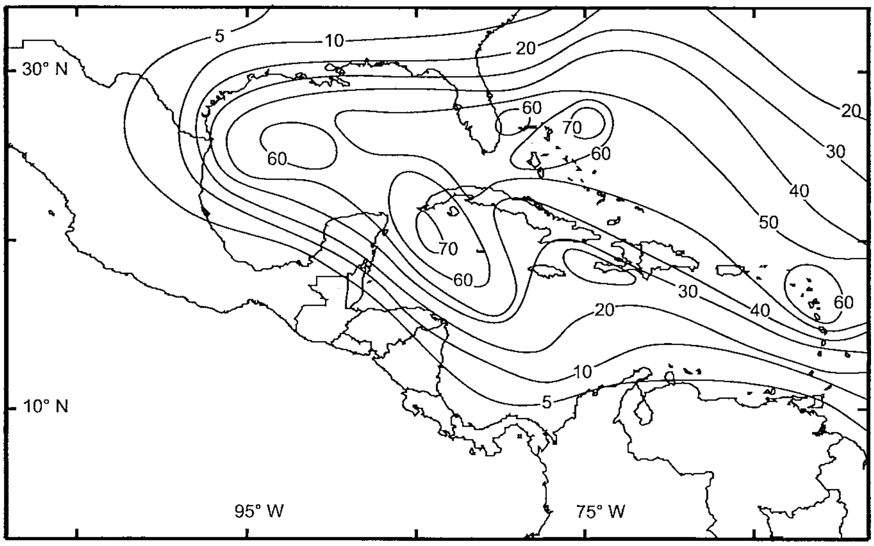


Figure 2. Spatial distribution of hurricanes and tropical storms over the Caribbean region. Isopleths show lines of equal numbers of storms between 1871 and 1986 according to Neumann et al. (76). Figure prepared by G.R. Camilo.

The question of fetch is important because the height of the waves increases with fetch (up to a limit that varies with wind speed), and the power of the waves is proportional to the square of their height. With normal trade winds, Adey (16) estimated that the waves were "saturated" at a fetch of 50 to 100 km and concluded that ". . . fetch is probably not a factor in wave height on a regional scale" in the Caribbean. However, according to Denny (14), "Hurricane winds need nearly three days to raise waves to their equilibrium height and require a fetch of more than 2250 km." Where fetch plays a role in severely limiting the height of hurricane waves, the relative increase in energy input to reefs during storms may be much less than the very large increase experienced by forests from the wind. In other cases, the power of hurricane waves may be several orders of magnitude greater than normal wave energy (Table 1).

The energy content of a hurricane is enormous, and the popular literature contains some startling comparisons to make the point, including Helm's (17), "The average hurricane that sweeps across the Atlantic Ocean contains an equivalent of up to five hundred thousand atomic bombs of the Nagasaki type!" In spite of such frightful statistics, most hurricane energy is involved with latent heat rather than destructive mechanical work. Early calculations (11) showed that while typical storms might have a latent heat energy release of about 3.5×10^{14} joules s^{-1}, only a few percent of this would be felt as kinetic or mechanical energy on the ground. But a few percent of 10^{14} joules s^{-1} is still a lot of energy.

The first detailed energy analysis of a hurricane by Riehl and Malkus (18) showed that the total kinetic energy of Hurricane Daisy in 1958 was almost 10^{17} joules and that it was dissipated and replaced every two to three hours. This is equivalent to a loss of mechanical energy of roughly 10^{13} joules s^{-1} for the storm as a whole. Potentially destructive kinetic energy dissipation on the ground amounted to about 3.2×10^{12} joules s^{-1} or 32% of the total kinetic loss.

Since any part of a rainforest is exposed to a small part of a hurricane and any patch of a coral reef experiences only a small segment of a wave front, it is the dissipation of kinetic energy per unit area that may best describe the input of mechanical energy to these ecosystems (Table 1). Notice that the mechanical energy flux per unit area due to hurricane winds is less than half the solar energy input to these systems. Because waves represent the work of the wind over a large area, they are more powerful than the wind itself. The average dissipation of non-hurricane wave energy per unit area on the reefs of Grand Cayman Island in the western Caribbean appears to be about 10 times greater than that of the wind during a severe winter storm on Long Island Sound off the northeast coast of the United States (Table 1). The most powerful waves from Hurricane Allen in Jamaica may have dissipated 1000 times more energy per unit area of reef than the winds in the most intense inner portions of a major hurricane (Table 1).

It is clear that coral reefs develop and thrive in extremely high energy environments where they are regularly exposed to rates of kinetic energy dissipation equal to or exceeding those felt by tropical rainforests during hurricanes. The importance of waves in coral reef formation and ecology has been recognized for a long time (e.g., 8, 16, 19, 20), but the quantitative comparison with hurricanes and the winds experienced by terrestrial systems

Table 1. Approximate kinetic energy dissipation rates from wind and waves. For comparison, the 24 hr mean solar energy input to the rainforest or coral reef is about 185 joules $m^{-2} s^{-1}$.

	Kinetic Energy (joules $m^{-2} s^{-1}$)
Winds	
Global yearly average wind[1]	0.014
Wind over Lake Mendota, Wisconsin, USA[2]	0.003–0.015
Winter storm wind, Long Island Sound, USA[3]	2
Winds from Hurricane Daisy[4]	
0 to 37 km radius core	1.6
37 to 74 km radius ring	72
74 to 111 km radius ring	38
111 to 148 km radius ring	27
Area-weighted mean	47
Waves	
Yearly average waves on Grand Cayman Island coral reef, Caribbean Sea[5]	20–25
Zones of maximum wave energy from Trade Winds, Bikini Atoll reef, Pacific Ocean[6]	200–300
Waves on exposed rocky coast, Northeast Pacific[7]	3000
Maximum waves from Hurricane Allen on Jamaican coral reefs[8]	550 000–750 000

[1] Lettau (70).
[2] Stauffer (71), lower value is for summer, higher for winter.
[3] Bokuniewicz and Gordon (72).
[4] Calculated from Riehl and Malkus (18) Table 9 estimates for dissipation on the ground (sea surface), Aug. 27, 1958. Daisy was a fully developed category 4 hurricane with winds of 213 km h^{-1}.
[5] Roberts et al. (73).
[6] Munk and Sargent (20) assuming wave energy is distributed over a reef front 60 to 90 m wide corresponding to the length of reef groves.
[7] Leigh et al. (74).
[8] Kjerfve et al. (75) calculations of maximum power per unit wave crest distributed over reef widths of 300 m and 750 m, respectively (27). Allen was "the strongest Caribbean hurricane of this century" (27). These are overestimates because some energy was reflected from the reef and shore and not dissipated on the reef (B. Kjerfve, pers.comm.).

provided a surprising new perspective for us.

The destructive impact of hurricanes is not limited to wind and wave energy alone. Many storms are characterized by prolonged and intense rainfall. For example, Hurricane Daisy had rainfall exceeding 80 cm d^{-1} in the inner core (18). Since the hurricane system is usually moving, a fixed point on the ground will not experience such intense deposition for very long. Nevertheless, rainfalls associated with hurricanes are usually the most intense deposition events recorded by meteorological stations. For Hurricane Daisy, Simpson and Riehl (21) computed that a rain gauge fixed beneath the center track of the storm would have collected 35 cm of rain in two days — a very impressive amount. Actual rain gauge measurements usually under-collect waterfall during hurricanes because it is estimated that at wind speeds above 25 m s^{-1}, no more than half the falling water is caught by the typical gauge (21). If a hurricane stalls, a meter or more of rain may fall on one area and cause a flood. In addition to causing tree falls, landslides, and mass wasting events in the forest, hurricane rains often produce a large amount of freshwater runoff, which can expose reefs to short-term salinity reduction and sediment deposition, both significant stresses for corals.

Table 2. Some similarities and contrasts between coral reefs and rainforests.

Similarities	
High diversity of reef and rainforest types Large number of species	Fast development of photosynthetic tissue High respiration
Complex food webs	Resistance and resilience strategy for storms
High species dominance	Life history traits of dominant species reflect responses to disturbances
Day/night shifts in activity	Asexual reproduction of corals and resprouting of trees after storms
High photosynthesis	Delayed mortality after storm damage

Contrasts	
Coral Reefs	Rainforests
Topography is mostly biogenic	Topography is tectonic
Carbonate substrate does not provide nutrients	Soil provides most of the nutrients
Low biomass of organisms	High biomass of organisms
Plants inconspicuous	Plants conspicuous
Animals easily visible	Animals less visible
Algae controlled by herbivores	Producers not controlled by herbivores
High degree of symbiosis	Moderate degree of symbiosis
Low coral species turnover at 0.1 ha level	High tree species turnover at 0.2 ha level
30 animal phyla represented	15 animal phyla represented
Alien species not important	Alien species are a concern
Disease conspicuous	Disease not conspicuous
Larvae are pelagic, dispersed by currents	Animals disperse seeds
Larvae disperse 1000s of km	Seeds disperse 100s of km
Water, nutrients, larvae and fish transported by currents	Water, gases, and some nutrients transported by wind
Close physical proximity between photosynthesis and respiration	Photosynthesis and respiration physically distanced
Low nutrient accumulation on sediments	High nutrient accumulation below ground
Slow turnover variables[1] are wave regime and calcium carbonate structure	Slow turnover variables are topography and soil
Intermediate turnover variables include large fish and organic sediments	Intermediate turnover variables are large trees
Fast turnover variables include water, plankton, algae, and microbes	Fast turnover variables include leaves, animals, and microbes

[1] The rate of turnover is classified relative to other rates within each system. There are also potentially interesting and important comparisons of rates between systems.

CORAL REEFS AND RAINFORESTS

Coral reefs and rainforests are both highly structured environments that are markedly different from surrounding ecosystems. For the great numbers of species that live within, coral reefs and rainforests provide food, shelter, and protection from predation.

Reefs owe their existence to a highly specialized symbiotic relationship between the coral animals and photosynthetic algae, the microscopic dinoflagellates (zooxanthellae) within their tissues. Corals function as both autotrophs and heterotrophs, obtaining energy from zooxanthellae and zooplankton. Corals also make use of dissolved organic substances in the water column. These dissolved materials originate from diverse sources, including excretions from other living organisms, and the decomposition of organic matter within the reef. Some coral reefs also receive inputs of organic matter from adjacent mangrove and seagrass ecosystems.

The metabolism of the corals is responsible for the deposition of the calcium carbonate framework of the living reef that provides much of the three-dimensional structure of the environment. In shallow water, the growth of coralline algae also contributes to carbonate deposition. The resulting structure is a highly heterogeneous rock platform with many fissures, pockets, and crevices. The reef is cracked, eroded, and modified by the combined activities of reef animals (termed bioerosion) and the powerful ocean currents and waves that impinge on the reef (physical erosion).

Living corals make up less than 50% of the substrate on most Caribbean reefs (22). Most of the hard bottom on coral reefs is actually covered by algae, which are a primary food source for fishes and other "grazers." Coralline algae are also found on the exposed faces of Caribbean reefs, where their development is "directly related to wave action" (16). In an extensive review of Caribbean coral reef growth and development, Adey (8) found that wave energy was a primary factor in regulating growth rates of both coralline algae (*Porolithon* and *Lithophyllum*) and the common scleractinian corals, *Acropora palmata* (elkhorn coral) and *A. cervicornis* (staghorn coral). He concluded that ". . . moderate wave energy favors vertically rapid growth that is porous and uncemented; high wave energy favors slow but compact growth . . ." Others have also shown that the zonation and overall morphology of coral reefs are strongly influenced by their exposure to waves (e.g., 23, 24) and hurricanes (25).

While the details of reef structure and taxonomic composition vary from place to place and even within an individual reef, there is general recognition of three reef zones — a very shallow back reef area, the reef crest, and a forereef slope of increasing depth to seaward. When the reef crest is well developed, it can reduce wave energy by over 90% (26). Massive "head" or "brain" corals, such as *Montastraea annularis* and *Diploria strigosa*, are far less susceptible to wave damage than branching species such as elkhorn coral (*Acropora palmata*) and staghorn coral (*A. cervicornis*). On many Caribbean reefs, *Montastraea annularis* is the most, or among the most, abundant species in terms of numbers of coral colonies or living "cover." *Montastraea* is often found growing in deeper water seaward of the shallow elkhorn zones on fringing reefs. However, on some reefs, *M. annularis* also dominates in the shallowest waters nearshore and no elkhorn zone is present.

In contrast with the coral reef, virtually all of the three-dimensional structure of the rainforest is alive in the form of tree trunks and leaf canopy. Just as the structure of the reef moderates waves

Top — Elkhorn coral fragments on the reef flat at Discovery Bay, Jamaica, after Hurricane Allen (1980). Photo: J. Woodley.
Bottom — Smashed elkhorn coral at Buck Island Reef National Monument, St. Croix, after Hurricane Hugo (1989).
Photo: D. Hubbard.

and currents and modifies the light microclimate, the canopy of the rainforest creates an environment in which light energy decreases exponentially toward the floor, temperature is lower and less variable than above the forest, and air humidity is much higher than outside the forest. The canopy also protects the inside of the forest from winds, and the forest floor from the direct impact of pounding rain (6). Like the reef, the rainforest has a gradient of environmental conditions, including soil characteristics, topography, and exposure to wind increasing from valley to slope to ridge.

In the spirit of Bates' (1) "essential unity" of the forest and the sea, we can identify important structural and functional similarities in the rainforests and coral reefs of the Caribbean, but there are many contrasts as well. We have developed a list of what appear to us to be some of the more interesting and provocative comparisons in the hope that others will explore them further (Table 2).

HURRICANE EFFECTS

To the casual eye, the immediate effects of hurricanes on both coral reefs and rainforests often appear devastating. Coral reefs may look as though they had been turned into piles of rocks pushed up against the beach or scattered over the shallows. Forests can lose virtually all their leaves and drop limbs, tree trunks may be snapped or overturned, and the landscape may appear as if scorched by a gigantic fire. Closer examination, however, usually shows that the impact is patchy, and that some areas of both the reef and rainforest survive without any apparent damage.

Coral Reefs

Damage to reefs can vary from almost total destruction to no effects at all over a distance of just a few meters. Shallower portions of reefs usually suffer the greatest impact (27–29), even though many back reef areas are protected by reef crests from the full brunt of the storm seas (30, 31). It is not clear whether the elkhorn and staghorn corals are broken mostly by the force of the water itself, or by point loads from storm-tossed reef front and crest debris striking them (14, 32).

The massive head or brain corals generally resist the power of the waves and suffer less damage overall than branching corals (27). Often, more fragile organisms survive in the lee of these massive corals, although the large corals can be transported by storm waves leaving distinct paths of destruction (27). Intact coral colonies typically survive near overturned and fractured corals, but in extreme cases, significant reef areas (on the scale of 100 m^2) are scoured and little or no hard coral remains (29). In general, changes in the microclimate of the reef are less than in the forest.

Hurricanes appear to have only short-term or minor impacts on reef fishes, though different species can be affected in different ways (33), and only a few long-term quantitative studies are available (34, 35). In general, few fish are killed outright by hurricanes. At least some species apparently redistribute themselves, moving from shallow to deep water or from damaged to unaffected areas of the reef (36). Although fish abundance has been correlated with the amount of living coral cover in some locations, reductions in the amount of live coral following storms apparently do not usually result in long-term decreases in the abundance or diversity of reef fishes, presumably because the reef continues to provide both food and shelter. Predation probably increases at least temporarily after the storm as many cryptic fish species are found out in the open (27, 34).

The primary effects of hurricanes on fishes are through physical disruption or rearrangement of corals and the opening up of new surfaces for colonization by algae upon which many of the fishes feed. In the Caribbean, only about three fish species out of over 500 feed directly on coral, but many of these depend on the reef structure for shelter. Sometimes storm rubble provides new habitat for fishes (36). One of only a few long-term studies of reef fishes demonstrated that most species on a reef off St. John, U.S. Virgin Islands, returned to pre-storm abundance within a few months of Hurricane Hugo (34).

Even fewer studies are available on the effects of storms on mobile invertebrates or on sessile, non-coral, invertebrates (e.g., 31). Hurricane Allen in Jamaica killed about half of the gorgonian colonies at one site through burial and abrasion, but surviving colonies began to regenerate rapidly. Almost 50% of the ropelike sponges were broken off near the substrate, while some of the other sponges were less affected (27). The sea urchin, *Diadema antillarum*, suffered greater losses in shallow water (27). Echinoderms in back reef areas in St. Croix and Jamaica suffered no damage from hurricanes Hugo and Gilbert, two extremely powerful storms, apparently because reef crests shielded the back reef areas (31).

Hurricanes can also have complex indirect effects on reef organisms. For example, after Hurricane Allen, surviving fragments of staghorn coral were killed by damselfishes that established territories around the algal encrusted coral (30, 36). In St. Croix, Hurricane Hugo smashed standing dead colonies of *A. palmata* which were occupied by two species of blennies, caus-

Eastern slopes of the Luquillo Experimental Forest in Puerto Rico, several days after the passage of Hurricane Hugo on November 18, 1989. The absence of leaves is striking. These slopes are the focus of long-term ecological research by scientists of the USDA Forest Service and the National Science Foundation.

ing a decline in the abundance of the spinyhead blenny which prefers cavities higher off the substrate (37).

Rainforests

The loss of rainforest structure after a hurricane has been documented in some detail in the Caribbean (38, 39). Surprisingly, ridge vegetation in the Luquillo Mountains of Puerto Rico is more resistant to damage than valley or slope vegetation in spite of greater exposure to wind on ridges (40). The reason for the higher resistance is the dominance of tree "unions" on ridges (41). Tree unions contain dozens of trees interconnected by root grafts. The unions build organic matter "benches" that effectively isolate the stand from mineral soil, while other deep roots wrap around rocks near the surface of the ridge. When exposed to hurricane winds, the tree unions lose their leaves and main branches, resulting in a low crown diameter to stem diameter ratio and less resistance to wind. Few trees are toppled over on ridges and trees attain larger size and biomass there than at any other location along the elevation gradient. Trees on slopes tend to tip over as the soil gets soggy and land movements occur. In valleys, the vegetation is continuously turning over because of frequent flooding, soil movement, and soil saturation. The younger trees lack deep roots and are very susceptible to wind damage even though they are in a relatively sheltered part of the forest.

The most important result of hurricane damage in rainforests is a dramatic change in the microenvironment of the forest. When a large fraction of the forest canopy is destroyed, its biomass and nutrients are transferred to the forest floor, and the light, temperature, and humidity profiles of the forest change dramatically. The dark, cool, isothermal calm of the forest interior is converted into a high solar energy environment with high temperature, low humidity, increased exposure to wind and rain, and wide fluctuations in all microclimatic parameters. Fruits, flowers, and leaves disappear for varying periods of time. In effect, the forest understory disappears, and animals must forage for food in a smaller space.

The compression of the forest has implications for birds, lizards, and other rainforest animals. After Hurricane Hugo struck the rainforest of El Verde, Puerto Rico, bird species and bats that fed on fruits or nectar exhibited large reductions in their numbers because those food items were not available (42, 43). Part of the decline was the result of migration to areas less affected by the hurricane. Insectivore and omnivore bird species increase in abundance after hurricanes because insects are readily available and concentrated on the forest floor (42–47). Predatory birds find it easier to capture prey because the complex forest structure no longer provides cover. Lizards in El Verde were concentrated after Hugo, and the separation between those that foraged in the canopy and those that foraged in midcanopy or on the forest floor no longer occurred (48). Adult frogs of the species *Eleutherodactylus coqui* were not affected by the hurricane, but juveniles of the species suffered large reductions immediately after the hurricane because of the drier conditions that then prevailed inside the forest (49). Invertebrates, such as snails and walking sticks, also suffered dramatic reductions in populations (50).

RESISTANCE AND REPAIR

While the coral reef and the rainforest both use the abundant solar energy of the tropics to build ecological systems of great beauty and complexity, it is clear that reefs have adapted to a regime of more rigorous physical energy input (Table 1). The growth rates and forms of the corals and the reefs they create are influenced by the waves, and the waves are, in turn, molded to an important extent by the architecture of the reef (8, 16, 20). For the most part, coral reefs appear to resist hurricanes, to endure by reason of strength. As Darwin (19) recognized long ago:

. . . the vital energies of the corals conquer the mechanical power of the waves: and the large fragments of reef torn up by every storm are replaced by the slow but steady growth of the innumerable polypifers which form the living zone on its outer edge — it is certain that the strongest and most massive corals flourish where most exposed.

The more fragile branching corals may appear as a weak link, but they can recover surprisingly quickly because they have high growth rates and because they have the ability to regenerate from fragments that reattach to the bottom (28, 51–53). Even in cases of extreme destruction, for example in shallow zones where elkhorn and staghorn corals are smashed, it is likely that the three-dimensional topographical complexity of the reef can be rebuilt over a relatively short time (perhaps less than 15 to 20 years) because of the rapid growth rates of these dominant branching species. Estimates for growth rates of *A. palmata* and *A. cervicornis* include a range of 47 to 100 mm yr^{-1} and 71 mm yr^{-1}, respectively (51, 54).

Storms "rearrange" the physical structure in localized areas of the reef and thus change light conditions and water flow patterns. However, the reef can immediately start to recover through regeneration of surviving corals, attachment and growth of viable coral fragments (from both branching and massive species), and from colonization of new substrate. The post-storm environmental conditions, in the absence of additional anthropogenic or natural stresses, will usually be conducive to regrowth and recovery. Hard corals do not contribute the majority of the food resources or primary productivity on the reef, so decreases in coral cover do not have as drastic consequences as one might assume. Most primary production is carried out by free-living algae, which are invariably among the earliest colonizers of new hard substrate exposed by hurricane waves (e.g., 27, 28). The algae appear within a few weeks after a storm's passage, immobilizing or accumulating nutrients in their tissues, and providing more food for herbivores. When grazing is intense enough, algal growth is kept in check and recruits of various reef species can settle and survive on the new substrate (e.g., 28).

There have been very few long-term, quantitative measures of reef regeneration following major storms. In many cases, damage was noted, but conditions on the reef were followed for only a few months. Studies of the effects of Hurricane Allen on Jamaican coral reefs are the most comprehensive, but the confounding effects of overfishing and the 1983 dieoff of the major herbivorous sea urchin *(Diadema antillarum)* may have overwhelmed the reef's regenerative capabilities (55). A study of the effects of Hurricane Donna (1960) on staghorn corals on Key Largo Dry Rocks Reef in Florida (52), which showed recovery of the reef after only five years, is frequently, and sometimes exclusively, cited as documentation of the ability of branching corals to recover quickly.

Unfortunately, most of the quantitative studies of the effects of hurricanes on Caribbean coral reefs have been done in the last two decades, a period during which the fast-growing acroporid corals have suffered extreme losses from white-band disease (56, 57). Throughout much of the Caribbean, *A. palmata* colonies have died from this disease which was first observed in the 1970s and which, to date, has not been correlated with pollution or any other stress associated with humans (56). Our understanding of this, and other, coral diseases lags considerably behind our observations of their general impacts on reefs (58). On some reefs, white-band disease has had more devastating impacts on *A. palmata* than storms. This disease, and other factors, including the delayed mortality from predation of staghorn corals following storms (59), may be overwhelming the ability of these corals to regenerate. Although there are informal reports that *A. palmata* is reestablishing itself in some locations, many shallow reef zones in the Caribbean have "standing dead" colonies of elkhorn and are littered with branches of elkhorn and staghorn corals, victims of disease and the violence of the waves.

Unlike fishes and corals on a reef, rainforest plants and animals must cope with dramatic changes in habitat and food supply after exposure to a severe storm. This is true of even those resistant components of the rainforest — like the tree unions and palms. The impact of the hurricane is felt first by the vegetation as the storm passes over the forest. Animals can usually survive the storm itself, but they must then cope with the consequences of the changes in forest structure, especially changes in food availability, microclimate, and predation. After a severe storm such as Hurricane Hugo, the environmental conditions in the rainforest are very favorable for the regrowth of vegetation and variable for animals and microbes. Rainforests have most of their nutrients and organic matter reserves below ground, and these reserves allow for the rapid regrowth of vegetation. Initially, most of the nutrients are bound by microbial populations that rapidly immobilize nutrients and thus prevent leaching and nutrient loss (60). A thicket of grasses, herbs, and vines develops very quickly and continues to immobilize nutrients in vegetation (61). Wood boring insects and decomposers have a clear advantage after the hurricane because of the large masses of dead wood and decaying leaves on the forest floor. Most of the nutrients liberated by their activity are recycled back to the fast growing vegetation.

The dramatic alteration and rapid rebuilding of vegetative structure in the rainforest have many effects on animal populations. Some animal populations are harmed, others benefit, and still others are not affected by the ruin and recovery of forest structure. Frogs are an example of animals that benefit. With the regrowth of vegetation following Hurricane Hugo in Puerto Rico (particularly heliconias and the common successional tree, *Cecropia*), frogs increased rapidly in numbers and reached values six times higher than pre-hurricane conditions (62). This peak production of frogs also appeared to coincide with depressed populations of invertebrate predators, which then increased following the recovery of the frogs. The endangered Puerto Rican boa (*Epicratres inonatus*) only eats about once a month and sleeps much of the time. Studies of tagged snakes suggest that they appear completely unaware of a hurricane's passage.

Many bird species are capable of migration to less impacted areas as a way of coping with food reductions. When fruit production increased some 90 to 150 days after Hurricane Hugo, the numbers of fruit-eating birds increased rapidly (45). Arendt (63) found that the recovery of frugivores and other bird species following a hurricane was a function of the recovery of vegetation, availability of food, and whether alien species had established themselves at sites and thus increased competition. Furthermore, some bird species, called "tramp species" increase their reproductive output after major storms by reproducing year-round as opposed to only part of the year, and thus maintain a relatively constant reproductive output in spite of having a lower population density (64).

After dramatic reductions, some species of snails and walking sticks in El Verde failed to exhibit any recovery five years after Hurricane Hugo (65). Some bat species showed a steady decline in numbers, others remained at low population densities two years after the hurricane, and still others increased their numbers or expanded their territory, depending on their dietary needs (66).

Because the redevelopment of a pre-disturbance understory may take decades, animal populations have to be flexible in terms of the size of their home range and ability to forage for food in close proximity to other species. For example, for some months after a storm, canopy dwellers have to feed on the forest floor and coexist with the forest floor species they find there. Overall, the metabolism of the rainforest returns to pre-hurricane conditions relatively quickly, along with superficial forest structure as leaves reappear and fast growing species recreate a canopy and forest microclimate. The replacement of large trees and taxonomic composition takes much longer. In fact, the path to recovery can lead to innovation and surprise as species importance values change, new species enter at the patch scale, and others exit patches. Full recovery may take as long as 60 years, and the timing of the recovery varies with the forest component or function under consideration.

HUMAN IMPACTS

The long-term historical coexistence of hurricanes, rainforests, and coral reefs in the Caribbean is unequivocal evidence that elaborate ecological structure with great complexity and high biological diversity can persist in spite of recurring exposure to intense destructive physical energy. The mechanism by which this persistence is achieved may be resistance, rapid repair, or both. For marine and terrestrial ecologists alike, the most pressing question is how these mechanisms may be compromised by human actions, as well as by unexplained phenomena such as coral diseases, episodes of coral bleaching, and mysterious declines in forest amphibian populations.

Some human impacts are so widespread and of such long standing that we have no image of what prehistoric nature was really like in the Caribbean (67). Intense fishing pressure is an ongoing uncontrolled experiment in which people have drastically reduced the numbers and sizes of many carnivorous and herbivorous fish species associated with most Caribbean reefs (68). If herbivory is reduced, algae may grow at the expense of reef-building corals and reef systems may become more vulnerable to storms. There is little doubt that nutrient inputs to tropical coastal waters will continue to increase in coming decades, and this fertilization is likely to stimulate algal growth and/or shading of corals by phytoplankton (69). On land, human activities have fragmented large areas of rainforest, over harvested trees, and reduced populations of some animal species. In some areas, alien species have expanded into the forests. Human impacts in the Caribbean range from local damage by dragging boat anchors to global warming and potential changes in hurricane frequency. It remains to be seen if either resistance or ruin and repair will continue to work in the future.

CONCLUSIONS

At the outset we asked how Caribbean coral reef and rainforest ecosystems maintain structure and complexity in spite of the catastrophic conditions created by hurricanes. Our comparison showed that both ecosystems have considerable resistance to hurricanes — neither is completely destroyed by even the most intense storms. The effects of hurricanes are patchy, and significant areas of both coral reefs and forests remain undamaged. After a hurricane both ecosystems exhibit regrowth and recovery.

There are numerous mechanisms for rapid recovery. Life history traits of many coral reef and rainforest species allow them to re-grow rapidly, and to reproduce either sexually or asexually. Recolonization of damaged areas from those that survived is also important, and conditions after a hurricane are generally favorable for fast recovery in both ecosystems. On land and in the sea, nature appears resilient when faced with a natural disturbance that recurs in a particular geographic area with a predictable long-term frequency and intensity (Figs 1 and 2). However, when exposed to recent chronic disturbances, such as coral reef overfishing or rainforest land conversion, reefs and forests both suffer dramatic changes in structure and species composition. These changes may be less reversible than those resulting from hurricanes and may compromise the ability of the systems to continue to resist and recover from storms.

Differences in the responses of coral reefs and rainforests to hurricanes and anthropogenic disturbances suggest an answer to the question of how complexity coexists with disturbance. The acute nature of hurricanes, compared to the chronic nature of some anthropogenic disturbances, appears to make the difference in whether a complex system can or cannot coexist with disturbance. The passage of a hurricane over a particular area of reef or forest is usually followed by decades of recovery, while overfishing and recurrent clearcutting do not allow for repair. As a result, both coral reefs and rainforests of the Caribbean can restore their majestic complexity between hurricanes, while both fail to do so when humans chronically interfere with their recovery mechanisms.

Hurricanes also play a role in explaining why Caribbean coral reefs and rainforests are less complex than their analogs outside the hurricane belt. The structure, species composition, and resilience of Caribbean coral reefs and rainforests have, in part, been shaped by the hurricane disturbance regime, and this is also part of the explanation of how complexity and disturbance coexist. Through evolutionary time, organisms in these environments have evolved with particular life history traits that lead communities to exhibit high species dominance and a reef structure or canopy capable of either resisting the destructive forces of the hurricanes or rebuilding in time to reproduce before the next destructive event.

The turnover rates of various parts of coral reefs and rainforests also shed light on the long- and short-term adjustments of these ecosystems to the periodic effects of hurricanes (Table 2). The slow variables in each system (for example, the calcium carbonate reef structure and the soil of the rainforest) are the critical ones providing long-term stability in these ecosystems. The slow variables survive hurricanes with very little change (piles of rubble in the reef and landslides in the rainforest) and thus provide the substrate resources on which quick recovery depends. The intermediate variables (for example, large fish and organic sediments in reefs and large trees in the rain forest) are the ones responsible for the long-term biological response or biotic legacy following the hurricane. The fast variables (for example, algae on the coral reef and microbes and weeds in the rainforest) provide the mechanisms for quick recovery immediately after the event.

These variables complement each other and assure the recovery and survival of the familiar coral reef and rainforest. When disturbances are chronic, as with some anthropogenic stresses, one or two of the complementary variables can be suppressed in either of these ecosystems. For example, the harvest of large fish or corals on coral reefs or large trees in rainforests leaves only fast variables available for recovery, resulting in degraded forms of these ecosystems. We must come to understand how different manifestations of biodiversity complement each other in natural ecosystems and assure that our use of these ecosystems doesn't deplete any particular group of species required for the sustainability of the systems we need and value.

References and Notes

1. Bates, M. 1960. *The Forest and the Sea*. Vintage Books, New York. 277 pp.
2. Johnstone, J. 1908. *Conditions of Life in the Sea.* Cambridge University Press. Reprinted by Arno Press, New York, 1977, 332 pp.
3. Steele, J.H. 1989. The ocean 'landscape'. *Landsc. Ecol. 3*, 185–192.
4. Steele, J.H. 1991. Can ecological theory cross the land-sea boundary? *J. Theor. Biol. 153*, 425–436.
5. Holdridge, L.R. 1967. *Life Zone Ecology.* Tropical Science Center, San José, Costa Rica, 106 pp.
6. Odum, H.T. 1970. An emerging view of the ecological system at El Verde. In: *A Tropical Rain Forest*, Odum, H.T. and Pigeon, R.F. (eds). National Technical Information Service, Springfield, Virginia, pp. I-191 to I-289.
7. Milliman, J.D. 1973. Caribbean coral reefs. In: *Biology and Geology of Coral Reefs*, James, O.A. and Endean, R. (eds.). Academic Press, N.Y, pp. 1–50.
8. Adey, W.H. 1978. Coral reef morphogenesis: A multidimensional model. *Science 202*, 831–837.
9. Eichler, T.P. 1996. Hurricanes. In: *Encyclopedia of Climate and Weather*, Vol. 1. Schneider, S.H. (ed.). Oxford University Press, New York, pp. 407–411.
10. Tannehill, I.R. 1938. *Hurricanes.* Princeton University Press, 257 pp.
11. Riehl, H. 1954. *Tropical Meteorology*. McGraw-Hill Book Co. New York, NY. 392 p.
12. Emanuel, K.A. 1996. Cyclones: Tropical Cyclones. In: *Encyclopedia of Climate and Weather*, Vol. 1. Schneider, S.H. (ed.). Oxford University Press, New York, pp. 231–236.
13. Miller, D.H. 1981. *Energy at the Surface of the Earth*. Academic Press, Vol. 27 in Internal Geophysics Series, 516 pp.
14. Denny, M.W. 1988. *Biology and the Mechanics of the Wave-Swept Environment.* Princeton University Press, Princeton, NJ, 329 pp.
15. Boose, E.R., Foster, D.R. and Fluet, M. 1994. Hurricane impacts to tropical and temperate forest landscapes. *Ecol. Monogr. 64*, 369–400.
16. Adey, W.H. 1978. Algal ridges of the Caribbean Sea and West Indies. *Phycologia 17*, 361–367.
17. Helm, J.H. 1967. *Hurricanes: Weather of its Worst*. Dodd, Mead and Company, NY, 234 pp.
18. Riehl, H. and Malkus, J. 1961. Some aspects of Hurricane Daisy, 1958. *Tellus 13*, 181–213.
19. Darwin, C. 1842. (Republished in 1984). *The Structure and Distribution of Coral Reefs*. The University of Arizona Press, 214 pp. plus plates.
20. Munk, W.H. and Sargent, M.C. 1954. Adjustment of Bikini Atoll to ocean waves, pp.275-280. In: *Bikini and Nearby Atolls*, Part 2. Oceanography (physical). Geological Survey Professional Paper 260-C. U.S. Government Printing Office, Washington.

21. Simpson, R.H. and Riehl, H. 1981. *The Hurricane and Its Impact*. Louisiana State University Press, Baton Rouge, LA, 398 pp.
22. CARICOMP. 1997. CARICOMP monitoring of coral reefs. *Proc. 8th Int. Coral Reef Symp. 1*, 651–656.
23. Geister, J. 1977. The influence of wave exposure on the ecological zonation of Caribbean reefs. *Proc. 3rd Int. Coral Reef Symp. 1*, 23–39.
24. Hubbard, D.K.H. 1997. Reefs as dynamic systems. In: *Life and Death of Coral Reefs* . Birkeland, C. (ed.). Chapman and Hall, pp. 43–67.
25. Hubbard, D.K. 1988. Controls of modern and fossil reef development: common ground for biological and geological research. *Proc. 6th Int. Coral Reef Symp.* 243–252.
26. Roberts, H.H. 1989. Physical processes as agents of sediment transport in carbonate systems: examples from St. Croix USVI. In: Hubbard, D.K. (ed.). *Terrestrial and Marine Geology of St. Croix, US Virgin Islands.* WIL Special Publication No 8, West Indies Laboratory, St. Croix, USVI, pp. 95–104.
27. Woodley, J.D., Chornesky, E.A., Clifford, P.A., Jackson, J.B.C., Kaufman, L.S., Knowlton, N., Lang, J.C., Pearson, M.P., Porter, J.W., Rooney, M.C., Rylaarsdam, K.W., Tunniffliffe, V.J., Wahle, C.M., Wulff, J.L., Curtis, A.S.G., Dallmeyer, M.D., Jupp, B.J., Koehl, M.A.R., Neigel, J. and Sides, E.M. 1981. Hurricane Allen's impact on Jamaican coral reefs. *Science 214*, 749–755.
28. Rogers, C.S., Suchanek, T.H. and Pecora, F.A. 1982. Effects of Hurricanes David and Frederick (1979) on shallow *Acropora palmata* reef communities: St. Croix, US Virgin Islands. *Bull. Mar. Sci. 32*, 532–548.
29. Hubbard, D.K., Parsons, K.M., Bythell, J.C. and Walker, N.D. 1991. The effects of Hurricane Hugo on the reefs and associated environments of St. Croix, US Virgin Islands—a preliminary assessment. *J. Coastal Res. 8*, 33–48.
30. Williams, A.H. 1984. The effects of Hurricane Allen on back reef populations of Discovery Bay, Jamaica. *J. Exp. Mar. Biol. Ecol. 75*, 233–243.
31. Aronson, R.B. 1993. Hurricane effects on backreef echinoderms of the Caribbean. *Coral Reefs 12*, 139–142.
32. Tunnicliffe, V. 1981. Breakage and propagation of the stony coral *Acropora cervicornis. Proc. Natl Acad. Sci. 78*, 2427–2431.
33. Jones, G.P. 1991. Post recruitment processes in the ecology of coral reef fish populations: a multifactorial perspective. In: *The Ecology of Fishes on Coral Reefs*. Sale, P. (ed.). pp. 294–328.
34. Beets, J. 1993. Long-term monitoring of fisheries in Virgin Islands National Park: Chapter I. Baseline data, 1988-1992, with emphasis on the impact of Hurricane Hugo. Technical Report to the National Park Service. 17 pp.
35. Bohnsack, J.A., McClellan, D.B., Harper, D.E., Bolden, S.K., Eklund, A., and Sandorf, S. 1994. Effects of Hurricane Andrew on reef fishes in Biscayne National Park. *Bull. Mar. Sci. 54*, 1072.
36. Kaufman, L. 1983. Effects of Hurricane Allen on reef fish assemblages near Discovery Bay, Jamaica. *Coral Reefs 2*, 43–47.
37. Clarke, R.D. 1996. Populations shifts in two competing fish species on a degrading coral reef. *Mar. Ecol. Prog. Ser. 137*, 51–58.
38. Walker, L.R., Brokaw, N.V.L., Lodge, D.J. and Waide, R.B. 1991. Ecosystem, plant, and animal responses to hurricanes in the Caribbean. *Biotropica 23*, 313–521.
39. Walker, L.R., Silver, W.L., Willig, M.R. and Zimmerman, J.K (eds). 1996. Long-term responses of Caribbean ecosystems to disturbance. *Biotropica 28*, 414–613.
40. Scatena, F.N. and Lugo, A.E. 1995. Geomorphology, disturbance, and the soil and vegetation of two subtropical wet steepland watersheds of Puerto Rico. *Geomorphology 13*, 199–213.
41. Basnet, K., Scatena, F.N., Likens, G.E. and Lugo, A.E. 1993. Hurricane Hugo: damage to a tropical rain forest in Puerto Rico. *J. Tropical Ecol. 8*, 47–55.
42. Waide, R.B. 1991. The effect of Hurricane Hugo on bird populations in the Luquillo Experimental Forest, Puerto Rico. *Biotropica 23*, 475–480.
43. Waide, R.B. 1991. Summary of the response of animal populations to hurricanes in the Caribbean. *Biotropica 23*, 508–512.
44. Wunderle, J.M., Lodge, D.J. and Waide, R.B. 1992. Short-term effects of Hurricane Gilbert on terrestrial bird populations on Jamaica. *Auk 109*, 148–166.
45. Wunderle, J.M. 1995. Responses of bird populations in a Puerto Rican forest to Hurricane Hugo: the first 18 months. *The Condor 97*, 879–896.
46. Wiley, J.W. and Wunderle, J.M., Jr. 1993. The effects of hurricanes on birds, with special reference to Caribbean islands. *Bird Conserv. Int. 3*, 319–349.
47. Wauer, R.H. and Wunderle, J.M. Jr. 1992. The effect of Hurricane Hugo on bird populations on St. Croix, U.S. Virgin Islands. *Wilson Bull. 104*, 656–673.
48. Reagan, D.P. 1991. The response of *Anolis* lizards to hurricane-induced habitat changes in a Puerto Rican rain forest. *Biotropica 23*, 468–474.
49. Woolbright, L.L. 1991. The impact of Hurricane Hugo on forest frogs in Puerto Rico. *Biotropica 23*, 462–467.
50. Willig, M.R. and Camilo, G.R. 1991. The effect of Hurricane Hugo on six invertebrate species in the Luquillo Experimental Forest of Puerto Rico. *Biotropica 23*, 455–461.
51. Shinn, E.A. 1966. Coral growth-rate, an environmental indicator. *J. Paleontol. 40*, 233–240.
52. Shinn, E.A. 1972. Coral reef recovery in Florida and the Persian Gulf. Environmental Conservation Department. Shell Oil Company. Houston, Texas. 9 pp.
53. Highsmith, R.C., Riggs, A.C. and D'Antonio, C.M. 1980. Survival of hurricane-generated coral fragments and a disturbance model of reef calcification/growth rates. *Oecologia 46*, 322–329.
54. Gladfelter E.H., Monahan, R.K., and Gladfelter, W.B. 1978. Growth rates of five reef-building corals in the northeastern Caribbean. *Bull. Mar. Sci. 28*, 728–734.
55. Hughes, T.P. 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science 265*, 1547–1551.
56. Gladfelter, W.B. 1982. White -band disease in *Acropora palmata*: implications for the structure and growth of shallow reefs. *Bull. Mar. Sci. 32*, 639–643.
57. Peters, E. 1997. Diseases of coral reef organisms. In: Birkeland, C. (ed.). *Life and Death of Coral Reefs*. Chapman and Hall, pp. 114–139.
58. Richardson, L.L. 1998. Coral diseases: what is really known? *TREE 13*, 438–443.
59. Knowlton, N., Lang, J.C., Rooney, M.C. and Clifford, P. 1981. Evidence for delayed mortality in hurricane-damaged Jamaican staghorn corals. *Nature 294*, 251–252.
60. Sanford, R.L. Jr., Parton, W.J., Ojima, D.S. and Lodge, D.J. 1991. Hurricane effects on soil organic matter dynamics and forest production in the Luquillo Experimental Forest, Puerto Rico: results of simulation modeling. *Biotropica 23*, 364–372.
61. Scatena, F.N., Moya, S., Estrada, C. and Chinea, J.D. 1996. The first five years in the reorganization of aboveground biomass and nutrient use following Hurricane Hugo in the Bisley Experimental Watersheds, Luquillo Experimental Forest, Puerto Rico. *Biotropica 28*, 424–440.
62. Woolbright, L.L. 1996. Disturbance influences long-term population patterns in the Puerto Rican frog, *Eleutherodactylus coqui* (Anura: Leptodactylidae). *Biotropica 28*, 493–501.
63. Arendt, W.J. 1994. Effects of Hurricane Hugo on Montserrat's forest birds and their habitats. *Pitirre 7*, 5–6.
64. Arendt, W.J. 1993. The pearly-eyed thrasher distribution, ecology and life history strategy of an avian supertramp. Dissertation. University of Wisconsin at Madison, USA.
65. Secrest, M.F., Willig, M.R. and Peppers, L.L. 1996. The legacy of disturbance on habitat associations of terrestrial snails in the Luquillo Experimental Forest, Puerto Rico. *Biotropica 28*, 502–514.
66. Willig, M.R. and Gannon, M.R. 1991. The effect of Hurricane Hugo on bat ecology with emphasis on an endemic Puerto Rican bat (*Stenoderma rufum*) in the Luquillo Experimental Forest. Research Report, USDA Forest Service, Southern Forest Experiment Station, Río Piedras, PR.
67. Jackson, J.B.C. 1997. Reefs since Columbus. *Coral Reefs 16*, Suppl. S23–S32.
68. Hixon, M.A. 1991. Predation as a process structuring coral reef fish communities. Chapter 17. In: *The Ecology of Fishes on Coral Reefs.* Sale, P.F. (ed.). Academic Press, Inc., pp. 475–508.
69. Nixon, S.W. 1995. Coastal marine eutrophication: A definition, social causes, and future concerns. *Ophelia 41*, 199–219.
70. Lettau. H. 1954. A study of the mass, momentum and energy budget of the atmosphere. *Arch. Meteorol. Geophysik Bioklimatol. Ser. A. 7*, 133–157.
71. Stauffer, R.E. 1980. Windpower time series above a temperate lake. *Limnol. Oceanogr. 15*, 513–528.
72. Bokuniewicz, H.J. and Gordon, R.B. 1980. Storm and tidal energy in Long Island Sound. In: *Studies in Long Island Sound*, Adv. Geophys. Edition, Vol. 22. Academic Press, NY, pp. 41–67.
73. Roberts, H.H., Murray, S.P. and Suhayda, J.M. 1975. Physical processes in a fringing reef system. *J. Mar. Res. 33*, 233–260.
74. Leigh, E.G., Jr., Paine, R.T., Quinn, J.F. and Suchanek, T.H. 1987. Wave energy and intertidal productivity. *Proc. Natl Acad. Sci*. *84*, 1314–1318.
75. Kjerfve, B., Magill, K.E., Porter, J.W. and Woodley, J.D. 1986. Hindcasting of hurricane characteristics and observed storm damage on a fringing reef, Jamaica, West Indies. *J. Mar. Res. 44*, 119–148.
76. Neumann, C.J., Jarvinen, B.R., Pike, A.C. and Elms, J.D. 1987. Tropical cyclones of the North Atlantic Ocean, 1871–1986. Historical Climatology Series 6-2, National Climate Data Center, Asheville, NC. 186 pp.
77. Pielke, R.A., Jr. and Pielke, R.A., Sr. 1997. *Hurricanes – Their Nature and Impacts on Society*. John Wiley and Sons, NY, 279 pp.
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