Diversity in Tropical Rain Forests and Coral Reefs

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niques is taking place, and new information is already yielding fresh insights into chemical, physical, and biological systems.

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Diversity in Tropical Rain Forests and Coral Reefs

High diversity of trees and corals is maintained only in a nonequilibrium state.

Joseph H. Connell

The great variety of species in local areas of tropical rain forests and coral reefs is legendary. Until recently, the usual explanation began with the assumption that the species composition of such assemblages is maintained near equilibrium (*1*). The question thus became: "how is high diversity maintained near equilibrium?" One recent answer for tropical bird communities is given as follows: "The working hypothesis is that, through diffuse competition, the component species of a community are selected, and coadjusted in their niches and abundances, so as to fit with each other and to resist invaders" (*2*). In this view, the species composition of tropical communities is a consequence of past and present interspecific competition, resulting in each species occupying the habitat or resource on which it is the most effective competitor. Without perturbation this species composition persists; after perturbation it is restored to the original state (*3*).

In recent years it has become clear that the frequency of natural disturbance and the rate of environmental change are often much faster than the rates of recovery from perturbations. In particular, competitive elimination of the less efficient or less well adapted species is not the inexorable and predictable process we once thought it was. Instead, other forces, often abrupt and unpredictable, set back, deflect, or slow the process of return to equilibrium (*4*). If such forces are the norm, we may question the usefulness of the application of equilibrium theory to much of community ecology.

Summary. The commonly observed high diversity of trees in tropical rain forests and corals on tropical reefs is a nonequilibrium state which, if not disturbed further, will progress toward a low-diversity equilibrium community. This may not happen if gradual changes in climate favor different species. If equilibrium is reached, a lesser degree of diversity may be sustained by niche diversification or by a compensatory mortality that favors inferior competitors. However, tropical forests and reefs are subject to severe disturbances often enough that equilibrium may never be attained.

In this article I examine several hypotheses concerning one aspect of community structure, that is, species richness or diversity (*5*). I first explore the view that communities seldom or never reach an equilibrium state, and that high diversity is a consequence of continually changing conditions. Then I discuss the opposing view that, once a community recovers from a severe perturbation, high diversity is maintained in the equilibrium state by various mechanisms.

Here I apply these hypotheses to organisms such as plants or sessile animals that occupy most of the surface of the land or the firm substrates in aquatic habitats. I consider two tropical communities, rain forests and coral reefs, concentrating on the organisms that determine much of the structure, in these cases, trees and corals. Whether my arguments apply to the mobile species, such as insects, birds, fish, and crabs, that use these structures as shelter or food, or to nontropical regions, remains to be seen. I deal only with variations in diversity within local areas, not with large-scale geographical gradients such as tropical to temperate differences. While the hypotheses I present may help explain them, such gradients are just as likely to be produced by mechanisms not covered in the present article (*6*).

Various hypotheses have been proposed to explain how local diversity is produced or maintained (or both). I have reduced the number to six, which fall into two general categories:

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1) The species composition of communities is seldom in a state of equilibrium. High diversity is maintained only when the species composition is continually changing. (i) Diversity is higher when disturbances are intermediate on the scales of frequency and intensity (the "intermediate disturbance" hypothesis). (ii) Species are approximately equal in ability to colonize, exclude invaders, and resist environmental vicissitudes. Local diversity depends only on the number of species available in the geographical area and the local population density (the "equal chance" hypothesis). (iii) Gradual environmental changes, that alter the ranking of competitive abilities, occur at a rate high enough so that the process of competitive elimination is seldom if ever completed (the "gradual change" hypothesis).

2) The species composition of communities is usually in a state of equilibrium; after a disturbance it recovers to that state. High diversity is then maintained without continual changes in species composition. (iv) At equilibrium each species is competitively superior in exploiting a particular subdivision of the habitat. Diversity is a function of the total range of habitats and of the degree of specialization of the species to parts of that range (the "niche diversification" hypothesis). (v) At equilibrium, each species uses interference mechanisms which cause it to win over some competitors but lose to others (the "circular networks" hypothesis). (vi) Mortality from causes unrelated to the competitive interaction falls heaviest on whichever species ranks highest in competitive ability (the "compensatory mortality" hypothesis).

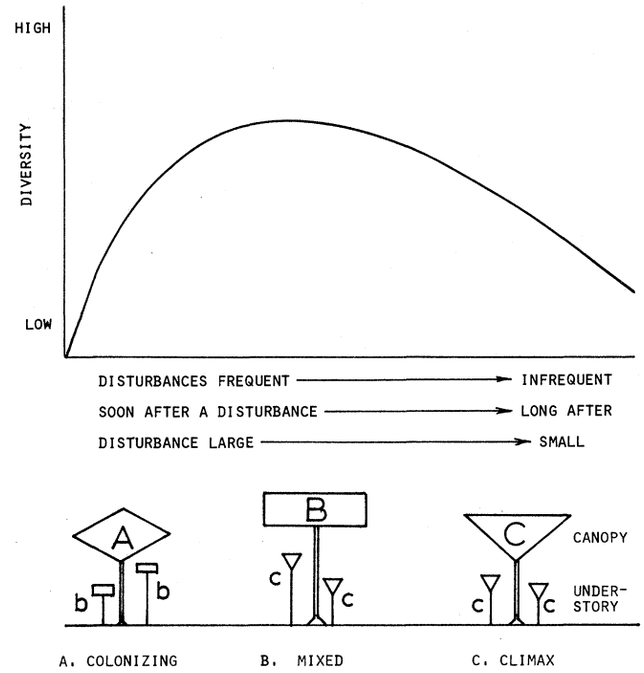

Fig. 1. The "intermediate disturbance" hypothesis. The patterns in species composition of adults and young proposed by Eggeling (*8*) for the different successional stages of the Budongo forest are shown diagrammatically at the bottom.

Nonequilibrium Hypotheses

The intermediate disturbance hypothesis. Organisms are killed or badly damaged in all communities by disturbances that happen at various scales of frequency and intensity. Trees are killed or broken in tropical rain forests by windstorms, landslips, lightning strikes, plagues of insects, and so on; corals are destroyed by agents such as storm waves, freshwater floods, sediments, or herds of predators. This hypothesis suggests that the highest diversity is maintained at intermediate scales of disturbance (Fig. 1).

The best evidence comes from studies of ecological succession. Soon after a severe disturbance, propagules (for example, seeds, spores, larvae) of a few species arrive in the open space. Diversity is low because the time for colonization is short; only those few species that both happen to be producing propagules and are within dispersal range will colonize. If disturbances continue to happen frequently, the community will consist of only those few species capable of quickly reaching maturity.

As the interval between disturbances increases, diversity will also increase, because more time is available for the invasion of more species. New species with lower powers of dispersal and slower growth, that were excluded by more frequent disturbances, can now reach maturity. As the frequency declines further and the interludes between catastrophes lengthen, diversity will decline, for one of two reasons. First, the competitor that is either the most efficient in exploiting limited resources or the most effective in interfering with other species (or both) will eliminate the rest. Second, even if all species were equal in competitive ability, the one that is the most resistant to damage or to death caused by physical extremes or natural enemies will eventually fill much of the space. This process rests on the assumption that once a site is held by any occupant, it blocks all further invasion until it is damaged or killed. Thus it competitively excludes all potential invaders, which are by assumption incapable of competitively eliminating it (*7*).

Thus, diversity will decline during long interludes between disturbances unless other mechanisms, such as those given in the other hypotheses below, intervene to maintain diversity. Disturbances interrupt and set back the process of competitive elimination, or remove occupants that are competitively excluding further invaders. Thus, they keep local assemblages in a nonequilibrium state, although large geographic areas may be stable in the sense that species are gained or lost at an imperceptible rate.

Evidence that this model applies to tropical rain forests comes from several sources. Eggeling (*8*) classified different parts of the Budongo forest of Uganda into three stages: colonizing, mixed, and climax stands. Using observations made many years apart, he showed that the colonizing forest was spreading into neighboring grassland. In these colonizing stands the canopy was dominated by a few species (class A in Fig. 1), but the juveniles (class B in Fig. 1) were of entirely different species. Adults of the class B species occurred elsewhere as canopy trees in mixed stands of many species. In these mixed stands, the juveniles were also mainly of different species (class C, Fig. 1), those with even greater shade tolerance. Adults of class C species occurred in the canopy of other climax stands where a few species dominated (mainly ironwood, *Cynometra alexandrei*, which comprised 75 to 90 percent of the canopy trees). However, in these stands, the understory was composed mainly of juveniles of the canopy species. Thus, an assemblage of self-replacing species (that is, a climax community of low diversity) had been achieved. This is not a special case; the Budongo forest is the largest rain forest in Uganda, and one-quarter of it is dominated by ironwood. Later and more ex-

Table 1. Mortality of young trees (between 0.2 and 6.1 meters tall) in relation to their abundance for two rain forests in Queensland. Not all species had enough young trees to analyze; only those whose adults were capable of reaching the canopy and that had at least six young trees are included. The mortality rate between 1965 and 1974 was plotted against the original numbers mapped in 1965; the least-squares regression slope and correlation coefficient are shown.

Site	Number of species	Regression of mortality (%) on abundance	
		Slope	r*
Tropical, North Queensland, 16°S	49	0.039	0.217
Subtropical, South Queensland, 26°S	46	0.002	0

*Neither correlation coefficient is significantly different from zero at $P < .05$

tensive surveys (*9*) showed that the proportion so dominated in other forests in Uganda is even higher and have confirmed that, where *Cynometra* dominates the canopy, its juveniles also dominate the understory.

Another excellent example is the work of Jones (*10*) in Nigeria. In this diverse tropical forest, many of the larger trees, aged about 200 years, were dying. They probably became established in abandoned fields in the first half of the 18th century, a time when the countryside was depopulated by the collapse of the Benin civilization. These trees had few offspring; most regeneration was by other species, shade-tolerant and of moderate stature. This mixed forest was in fact an "old secondary" forest that had invaded after agricultural disturbances. It was in about the same state as Eggeling's mixed forest in Uganda. In both Nigeria and Uganda, high diversity was found in a nonequilibrium intermediate stage in the forest succession.

In many studies of forest dynamics, the abundance of juvenile stages constitutes the evidence as to whether a species is expected to increase or to die out. Such inferences are of course open to the criticism that, if the mortality rate of juveniles increases with their abundance, it is not necessarily a good indicator of more successful recruitment. I tested this for young trees in two rain forest plots in Queensland that several colleagues and I have been studying since 1963 (*11*). Over a 9-year period, mortality showed no correlation with abundance (Table 1). Thus, it seems safe to assume that species which now have many offspring will be more abundant in the next generation of adult trees as compared to those species which now have few offspring.

In most of the mixed, highly diverse stands of tropical rain forests that have been studied, some species are represented by many large trees with few or no offspring, whereas others have a superabundance of offspring (*8, 10–12*). (Of course, many species are so rare as adults that one would not expect to find many offspring.) My interpretation of this finding is that these mixed tropical forests represent a nonequilibrium intermediate stage in a succession after a disturbance, in which some species populations are decreasing whereas others are increasing. Since mixed rain forests are common in the tropics, this hypothesis suggests that disturbance is frequent enough to maintain much of the region in the nonequilibrium state.

If this is so, tropical forests dominated by a single canopy species that has abundant offspring in the understory must not have been disturbed for several generations. Such forests, similar to the ironwood climax of Eggeling (*8*), also occur commonly elsewhere in Africa as well as in tropical America and Southeast Asia (*13*). Two lines of evidence indicate that they have been less frequently disturbed than have mixed forests. First, the only papers that I have found in which the incidence of storms was described in relation to single-dominant forests state that destructive storms "never occur" in these regions (*8, 14*). Second, many of these forests are unlikely to have been disturbed by man, because they lie on poor soils, in swamps or along creek margins, on steep stony slopes, or on highly leached white sands (*12, 15*). All of these are soils that the farmers of shifting cultivation in forests avoid since they produce very poor crops (*12*). Such agriculture is confined mainly to the well-drained good soils, and these are the soils where the mixed diverse forests exist. Thus, mixed forests occur in the places most likely to have been disturbed by man, whereas single-dominant forests occur in those least likely to have been disturbed.

Since single-dominant forests often (though not always) lie on poor soils, it has usually been assumed that this is because only a few species have evolved adaptations to tolerate them (*12, 15*). However, the difference between forests on good soils and those on poor soils lies in the dominance of a single species in the canopy rather than in the total number of species. Thus, in comparing plots in rain forests in Guyana, the commonest species constituted 16 percent of the large trees (more than 41 centimeters in diameter) on good soils and 67 percent on poor soils (leached white sands), yet the number of species of trees more than 20 centimeters in diameter was 55 and 49, respectively [table 27 in (*12*)]. Thus, a large number of moderate- to large-sized tree species occupy poor soils, even though only a few are common. The best evidence that single-species dominance is not necessarily due to poor soils is the example of the Budongo forest. Here, various forest stands, ranging from ones of mixed high diversity to those with single-species dominance, each occur on similar soils. Single-species dominance seems to be explained more satisfactorily by the absence of disturbance rather than by poor soil quality.

On coral reefs, the relation between disturbance and diversity is similar to that in tropical forests. At Heron Island, Queensland, the highest number of species of corals occurs on the crests and outer slopes that are exposed to damaging storms. Since I began studying this reef in 1962, two hurricanes have passed close to it, one in 1967 and one in 1972. Each destroyed much coral on the crest and outer slopes but failed to damage another slope protected by an adjacent reef. The disturbed areas have been recolonized by many species after each hurricane, but colonization has not been so dense that competitive exclusion has yet begun to reduce the diversity (Fig. 2A). Other workers on corals have witnessed the same phenomenon; disturbances caused both by the physical environment and by predation remove corals and then recolonization by many species follows (*16, 17*).

In contrast, in permanently marked quadrats observed over several years without disturbance at Heron Island, I found that competitive elimination of neighboring colonies was a regular feature, either by one colony overshadowing or overgrowing another, or by direct aggressive interactions (*18*). Here competition is by interference, rather than by more efficient exploitation of resources. On one region of the south outer slope, protected from storm disturbance by an adjacent reef, huge old colonies of a few species of "staghorn" corals occupy most of the surface (Fig. 2B). Since these are able to overshadow neighbors (*18*) at a height sufficient to be out of reach of the mesenteric filaments used as defenses (*19*), I infer that such staghorns have in fact competitively

eliminated many neighbors during their growth. Here competitive elimination has apparently gone to completion, with a consequent reduction in local diversity. A similar situation has been described for Hawaii (*16*) and for the Pacific coast of Panama (*17*).

The discussion so far has concerned mainly the frequency of disturbance. However, the same reasoning applies to variations in intensity and area perturbed; diversity is highest when disturbances are intermediate in intensity or size, and lower when disturbances are at either extreme. For example, if a disturbance kills all organisms over a very large area, recolonization in the center comes only from propagules that can travel relatively great distances and that can then become established in open, exposed conditions. Species with such propagules are a small subset of the total pool of species, so diversity is low. In contrast, in very small openings, mobility is less advantageous: the ability to become established and grow in the presence of resident competitors and natural enemies is critical. In addition, recolonizing propagules are more likely to come from adults adjacent to the small opening. Therefore, colonizers will again be a small subset of the available pool of species, and diversity will tend to be low. When disturbances create intermediate-sized openings, both types of species can colonize and the diversity should be higher than at either extreme.

Not only the size, but also the intensity of disturbances makes a difference. If the disturbance was less intense so that some residents were damaged and not killed, in a large area recolonization would come both from propagules and from regeneration of survivors, so that diversity would be greater than was the case when all residents were killed and colonization came only from new propagules.

Direct evidence linking diversity with variations in intensity and total area of disturbance in tropical communities is meager. However, there is evidence that the processes described above do occur. For example, a 40-kilometer-wide swath of reef in Belize was heavily damaged by a hurricane in 1961, with lesser damage on both sides. Four years later, in the middle of the swath, new colonies of a few species were present, but the only significant frame-building corals, mainly *Acropora palmata*, were the survivors of the original storm (*20*). Ten years later many of the new colonies were of this species. In contrast, in the zone of lesser damage, colonies and broken fragments of many species had survived the storm and had regenerated quickly so that recovery was complete.

Likewise, in rain forests, the size and intensity of a disturbance influences the process of recolonization. In a long-term study of a small experimental opening made in a Queensland rain forest, the most successful colonists after 12 years were either stump sprouts from survivors of the initial bulldozing or seedlings that came from adult trees at the edge of the clearing (*21*). Farther from the forest edge, in a much larger clearing, only species with great powers of seed dispersal had colonized (*22*).

It has recently been suggested (*23*) that in a nonequilibrium situation, any conditions that increase the population growth rates of a community of competitors should result in decreased diversity (since faster growth produces faster competitive displacement). In places with a lower rate of competitive elimination, there is also a greater chance for interruption by further disturbances. This "rate of competitive displacement" hypothesis is an extension of the intermediate disturbance hypothesis and should be true, other things being equal. How relevant it is for explaining differences in local diversity remains to be seen. However, present evidence from tropical communities does not support it. Forests on extreme soils (such as leached white sands, heavy silt, or steep stony slopes) that have slower growth rates than those on less extreme soils have either few species or strong single-species dominance (*24*). Likewise, coral diversity shows little correlation with growth rates. Coral diversity varies with increasing depth, sometimes decreasing, sometimes increasing, or sometimes being greatest at intermediate depths. Coral growth rates tend to be faster at intermediate depths (*24*). Thus, among neither tropical rain forest trees nor corals is there a consistent correlation of diversity and growth rates, as predicted by the hypothesis.

In summary, variations in diversity between local stands of these tropical communities are more likely to be due to differences in the degree of past disturbances than to differences in the rate of competitive displacement during recovery from the disturbances. The high diversities observed in tropical rain forest trees and in corals on reefs appear to be a consequence of disturbances intermediate in the scales of frequency and intensity.

The equal chance hypothesis. In contrast to the previous model, let us assume that all species are equal in their abilities to colonize empty spaces, hold them against invaders, and survive the vicissitudes of physical extremes and natu-

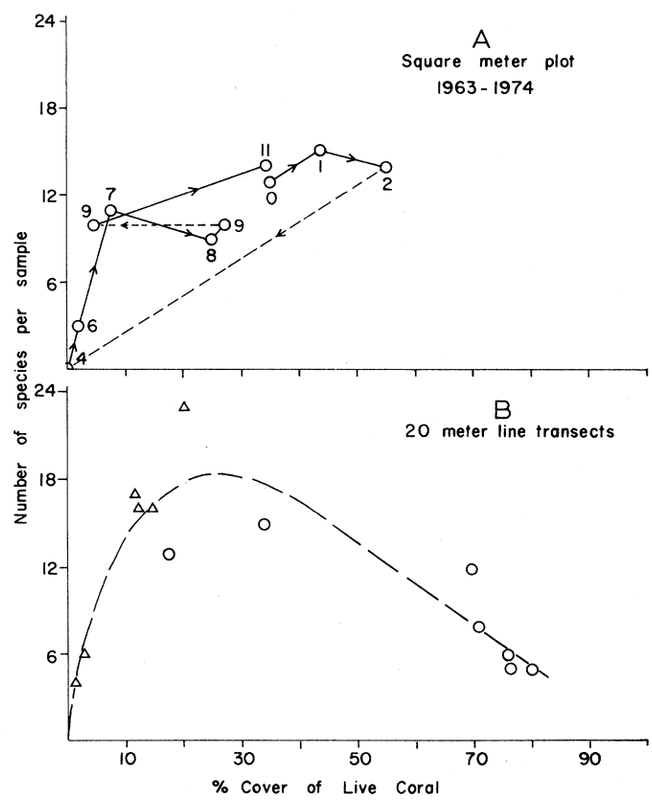

Fig. 2. Species diversity of corals in the subtidal outer reef slopes at Heron Island, Queensland. (A) Changes over 11 years on one of the permanently marked plots on the north slope. The number at each point gives the years since the first census at year 0 (no censuses were made in years 3, 5, and 10). The dashed lines indicate changes caused by hurricanes in 1967 and 1972. (B) Results from line transects done 3 to 4 months after the 1972 hurricane. (△) Data from the heavily damaged north slopes; (○) data from the undamaged south slope; the line drawn by eye. Where disturbances had either great or little effect (very low or high percent cover, respectively) there were few species, with maximum numbers of species at intermediate levels of disturbance.

ral enemies. Then local diversity would simply be a function of the number of species available and the local population densities. The species composition at any site would be unpredictable, depending upon the history of chance colonization.

What conditions would produce this? First, for all species the number of young (such as larvae and seeds) invading empty places must be independent of the number produced by the parent population. Otherwise, any species that increased its production of offspring per parent would progressively increase at the expense of those with lesser production. Second, any occupant must be able to hold its place against invaders until it is damaged or killed. Otherwise, any species that evolved the ability to oust an occupant would also progressively increase. Last, all species must be equal in ability to resist physical extremes and natural enemies. Otherwise, the most resistant species will gradually increase, as was discussed in the previous hypothesis.

Do communities exist that satisfy these conditions? Sale (*25*) has proposed that certain guilds of coral reef fish do. He assumes that, as with some temperate fish, recruitment to newly vacated sites is independent of the stock of eggs released into the plankton. One must probably assume that the fecundity and mortality of all species are equal. The juveniles grow quickly after they colonize to vacant places, and thus they are able to hold their territory against further invasion by smaller juveniles of any species from the plankton. Space is limiting, as judged from the rapid colonization of vacated sites. Since the juvenile fish seem to be generalists in the use of food and space, Sale suggests that local diversity would be a function of chance colonization from the available pool of species. Clearly, the initial assumption of independence of stock and recruitment is critical and needs to be tested for these tropical fish.

Likewise, for rain forest trees, Aubreville (*26*) has suggested that many species have such similar ecological requirements that it would be impossible to predict which subset would occur together on a site. He based this suggestion on the observation that some of the commoner large trees on his study plot in the Ivory Coast had few or no offspring on the plot. He inferred that their offspring must be elsewhere, so that the species composition of the forest would continually shift in space and time. While this might be so, his original observation of few offspring could be explained if the forest was an old secondary one, similar to Jones' (*10*) in Nigeria.

Other characteristics of trees and corals do not satisfy the requirements of the equal chance hypothesis. For example, dispersal of propagules of many trees and corals is quite restricted so that local recruitment of juveniles may not be as independent of local production of propagules as it apparently is in some fish populations. Likewise, species differ in fecundity, competitive ability, and resistance to environmental stresses, and the differences often result in predictable patterns of species distribution along environmental gradients (*27*). Therefore, it seems unlikely that either rain forest trees or corals conform to the equal chance hypothesis.

The gradual change hypothesis. This model was suggested by Hutchinson (*28*) to explain why many species coexist in phytoplankton assemblages. Seasonal changes in, for example, temperature and light, occur in a lake, and different species are assumed to be competitively superior at different times. It is postulated that no species has time to eliminate others before its ability to win in competition is reduced below that of another species by changes in the environment.

Climates change on all time scales from seasonal to annual to millennial and longer, and hence, this hypothesis may apply to organisms with any length of generation. With long-lived organisms such as trees or corals, gradual changes in climate over several hundred years represent the same scale as seasons do to a phytoplankton community. Drier periods producing a savanna vegetation in regions now covered with rain forest occurred about 3000 and 11,000 years ago in the Amazon basin; similar changes occurred in Africa and Australia (*29*). As Livingstone (*30*) pointed out, "Climates change and vegetational adjustments are not rare and isolated events, they are the norm." As climates changed, marine transgressions shifted and altered coral reef environments (*31*).

Whether such gradual transitions would also produce the highly intermingled diverse assemblages seen in present forests and reefs depends on the rate of competitive elimination compared to the rate of environmental change. If the time required for one tree species to eliminate another in competition is much shorter than the time taken for an environmental change that reversed their positions in the hierarchy, they would not coexist. Therefore, very slow changes would not maintain diversity, but higher rates might do so.

Equilibrium Hypotheses

The niche diversification hypothesis. The key point in this model is the degree of specialization to subdivisions of the habitat. For a given range of habitat variation, more species can be packed in the more they are specialized. The question is: Are the species so often observed living in diverse local assemblages sufficiently specialized to coexist at equilibrium? Some ecologists believe that motile animals have reached the required degree of specialization, particularly if different aspects of habitat subdivision are considered (*32*). The different aspects such as food, habitat space, and time of activity are called "niche axes."

Specialization along niche axes does not seem to have evolved to this extent in plants and in sessile aquatic animals such as corals. For long-lived organisms there exists no regular temporal variation to which they could have specialized. Plants in general have not specialized along the food niche axis. They all have similar basic resource requirements (such as light, water, carbon dioxide, and mineral nutrients). Niche subdivisions are made on degrees of tolerance to different quantities of these resources. As a consequence, plants subdivide space along gradients of quantitative variations in light, water, and nutrients. These variations are often associated with variations in elevation, slope, aspect, soil type, understory position, and so on. Exceptions to this idea are marine algae that have adapted to the qualitative changes in wavelength of light at different depths. General observations and some statistical analyses (*12, 15, 33*) have revealed associations between sets of species and certain subdivisions of the habitat in tropical rain forests, for example, to broad variations in soil properties (such as parent material, drainage, and tip-up mounds and hollows at the roots of fallen trees), and topography (ridges, steep slopes, creek margins, and so on). Other analyses have shown little association between species and local soil types (*15*, p. 188). As was discussed earlier, plants are also specialized according to differences in habitats caused by variations in the frequency and intensity of disturbance. The aftermath of a disturbance presents a new local environment in which species with different traits are at an advantage. It has been suggested that tropical trees may have subdivided this niche axis finely (*34*); at present there is little direct evidence to support this view. It seems unlikely that tropical trees are so highly specialized to such small differences in

the local physical environment that more than 100 species of trees could coexist at equilibrium on a single hectare of rain forest. In fact, the forests closest to equilibrium are those dominated by a single tree species, as was discussed earlier.

Corals seem as general in their requirements as trees; for example, although some of their energy comes from feeding on zooplankton, much comes from photosynthesis by their symbiotic zooxanthellae, which consist of a single species in all coral species studied to date, although several different strains detected by electrophoresis show some degree of specificity (*35*). It has been suggested (*36*) that corals have differentiated along the food niche axis between the extremes of autotrophy and heterotrophy. However, in shallow water where both light and species diversity is high, this differentiation could promote the coexistence of several species on the same space only if they were stratified vertically, autotrophs above, heterotrophs in the understory. Yet the layering observed thus far has not revealed specialized "shade" species adapted for life in the understory. Corals have been seen beneath open-branched species such as the Caribbean *Acropora cervicornis* (*37*) but, to my knowledge, never beneath close-branched species. One might expect that hetertrophy would be advantageous where light is reduced by deeper water. Yet there is evidence that a predominantly autotrophic coral was able, over a day's time, to meet its energy requirements down to a water depth of 25 meters (*38*). Thus, the proposed niche differentiation along the food axis has apparently contributed little to coexistence, and corals seem very generalized in their use of resources. On the habitat niche axis, corals are also generalized. Although some species are confined to certain zones, most corals have broad ranges of distribution with respect to depth and location on reefs, which indicates little precise specialization in habitat (*39*). Thus, like rain forest trees, corals do not seem to have specialized to the degree required to maintain the observed high diversities at equilibrium.

The circular networks hypothesis. This model suggests that, instead of the linear and transitive hierarchy (A eliminates B, B eliminates C, implying A eliminates C) presumed in the other hypotheses, the competitive hierarchy is circular (A > B > C, but C eliminates A directly). This hypothesis was first applied to sessile invertebrates living beneath ledges on coral reefs (*40*). Since it seems unlikely that the same competitive mechanism could apply throughout such circular interactions, the reverse pathway acting against the highest ranked species is likely to be a different mechanism. For example, if species A and B overshadow the species below them in the hierarchy, but C poisons A, the network is biologically more plausible. A difficulty arises if the interactions are not exactly balanced: if A eliminated B first, then C, no longer reduced by B, would quickly eliminate A. However, if the species in this network competed only in pairs, none would be eliminated.

I tested this hypothesis (*18*) for interactions between adjacent coral colonies on a permanently marked plot (12 species, 55 colonies, 82 interactions observed over 9 years) and found no circular pathways, even though two mechanisms, overshadowing and direct extracoelenteric digestion, were acting. It is more likely that these networks would operate between more distantly related organisms. The original observations involved different phyla of invertebrates (*40*).

Among trees of the rain forest this hypothesis has not been examined. Shading, root competition, and allelopathy are different mechanisms, so that some circular networks might be possible. However, trees may also be too similar for this to maintain diversity.

The compensatory mortality hypothesis. If mortality falls most heavily on whichever species is ranked highest in competitive ability, or, if they are all of approximately equal rank and it falls heaviest on whichever species is commonest (that is, mortality is frequency-dependent), competitive elimination may be prevented indefinitely. In tropical forests, if herbivores attack and kill seeds or seedlings of common species more frequently and to a greater extent than they attack those of less common or rare species competitive elimination could be prevented. For example, if herbivores attack the offspring of a species more heavily nearer than farther from the parent tree, that species would probably not be able to form a single-species grove (*41*). This possibility has been tested by either observations or field experiments and rejected for four out of five species of seeds of rain forest trees and vines, but not rejected for seedlings in two other species (*41, 42*). In the analysis reported in Table 1, the mortality of seedlings or saplings did not increase significantly with their abundance. Thus, mortality of young trees is not generally frequency-dependent. Destruction of trees by elephants also does not seem to be compensatory. In Ugandan rain forests it has been observed (*43*) that elephants preferentially destroy young of the fast-growing early and middle succession trees, leaving the young of the late succession ironwood alone, thus hastening progression toward the low-diversity forest. Therefore, contrary to my own earlier work on this aspect (*41*), I feel that while compensatory mortality may occur in some instances it does not seem to be a generally important factor in maintaining the high diversity of mixed tropical rain forests.

Watt's (*44*) "cyclic succession" is probably an example of this mechanism. The dominant species does not replace itself; other species intervene before the dominant becomes reestablished. This process has never, to my knowledge, been demonstrated in the tropics, but there seems no reason not to expect it to happen there.

In coral reefs, some predation does not act in a frequency-dependent fashion. An earlier claim (*45*) that the starfish *Acanthaster planci* might act in this way has now been demonstrated to be in error. Studies in Hawaii and Panama (*46*) indicate that the starfish attacks rarer species preferentially, which would reduce diversity. Studies in a much more diverse coral community on Saipan (*47*) suggest that *Acanthaster* might eliminate certain preferred species, although no data were given which indicated whether these were the common or rare species. In Panama, evidence indicates that other types of predators may possibly act in a compensatory manner, increasing diversity (*17, 46*).

In my studies of corals I found that the physical environment can inflict mortality in a manner that compensates for the competitive advantage of branching species that overshadow others. I measured the mortality of corals over a 4-year period that included a hurricane at Heron Island in Queensland (*18*). As described above, I had ranked these species in competitive ability by observing dynamic interactions over a period of 9 years on permanent quadrats. On the part of the reef crest that was badly damaged by the hurricane, the mortality of those species of corals that ranked high in the competitive hierarchy was much greater than those that ranked low. In contrast, the high-ranked species on an undamaged part of the reef crest had a lower mortality than low-ranked species, over the same period. The reason for the difference was that the high-ranked corals were branching species observed to grow above their neighbors, overshadowing and thus killing them. However, these branching species were more

heavily damaged in the storms. Thus, species of corals that ordinarily win in competition suffer proportionately more from storm damage, compensating for their advantage.

In certain situations, diversity, instead of decreasing with high coral cover (Fig. 2), increases. This occurs on the very shallow reef crests at Heron Island and is due to compensatory mortality. The larger colonies that are spreading horizontally and eliminating their neighbors tend to die in the center, where they have grown up above the low tide level. This provides open spaces in which new species can colonize. Thus, on the reef crest no species is capable of monopolizing the space, in contrast to the slope situations shown in Fig. 2B.

High diversity at high cover has also been found in the Caribbean, and it was proposed that a balance in competitive abilities exists at equilibrium (*48*). Last, it occurred in the deepest samples at Eilat, Red Sea (*49*). Although no explanation was suggested for this last-mentioned instance, it and the Caribbean one could be explained by the intermediate disturbance hypothesis. In both cases, the slope is steep where diversity is highest. In such places, small-scale disturbances occur by slumping of coral blocks (*17, 46*). The deep corals at Eilat are very small (more than 100 colonies in some 10-meter line transects), which might indicate that they are recent colonists after local disturbances.

Tests of the Hypotheses

Hypotheses are made to be tested, and, in ecology, field experiments are often an excellent way to do so (*50*). The intermediate disturbance hypothesis can be tested in various ways. It will be necessary to verify that the sequence observed by Eggeling (*8*) also occurs in other rain forests. Probably the best way to do this would be to examine gaps of various sizes within forests dominated by a single species. In very small openings the shade-tolerant offspring of the dominant should grow and survive better than other species, whereas in larger openings, juveniles of less shade-tolerant species should perform better. To estimate the probability of replacement, one would need to measure the abundance and sizes of each species having juveniles in the light gap, and if possible their rates of growth and mortality.

Even better than such observations are experimental transplants into different-sized light gaps of seedlings of species whose adults live in mixed and in single-dominant stands. These experiments would test the prediction that the species of the single-dominant stands will be more successful in small openings near the parent tree, whereas those of mixed stands will be more successful in larger openings. The alternative hypothesis, that single-dominant stands are due to poor soils, could be tested by experimentally improving soils (by draining, for example, or by fertilizing) and then planting seedlings of species that do or do not live in poor soils, in these plots and in unmodified control plots.

Tests of the equal chance hypothesis involve determining whether recruitment is (i) independent of adult stock, and (ii) equal among the different species. This is a difficult problem if propagules are distributed widely. In addition, equality in ability to resist invaders, extremes of the physical environment, and natural enemies must be established. Sale (*25*) has made a start on this in his experiments with coral reef fish.

The hypothesis of continual change is difficult to test because of the impracticality of determining the fate of organisms as long-lived as trees or corals. Pollen records in lake sediments are seldom precise enough to distinguish species, although genera are often identifiable.

Attempts to test the niche-diversification hypothesis are sometimes made by postulating how the different species could divide up resources and then seeing whether the coexisting species overlap significantly in their use of resources. The degree of overlap is sometimes judged indirectly by the range of variation in those aspects of morphology associated with resource use, such as root depth in plants, or degree of branching and polyp size in corals. However, these indirect measures are open to the criticism that the particular resource chosen (or the structure used to indicate it) may not be the one for which the species are competing. Another criticism is that competition may not be taking place through superior efficiency in exploiting resources, but by superior ability in interfering with competitors. Until a precise definition of the range of resources of each species is specified, this hypothesis will remain untestable.

The circular networks hypothesis might be tested either by observing as many interactions as possible, or better, by transplanting individuals into mixed and single-species groups. Since circular networks are apparently rare, many replicate observations must be made if such a network is found. For example, if a single set of observations indicated that ($A > B > C > A$), further observations might uncover an instance where ($A > C$), indicating "equal chance," which I found in observing coral interactions (*18*).

The compensatory mortality hypothesis can be tested in various ways. Observations of density and mortality before and after storms or predator attacks would reveal whether highly ranked species suffered greater mortality (*18*). Experiments in which seeds were placed both near and far from adult trees, or in both dense clumps and sparsely, have been done with several species of tropical trees (*41, 42*). Observations on the mortality of naturally occurring seedlings and on experimental plantings both near and far from adults have also been made (*11*). In addition, I have used cages to exclude insects and larger herbivores from seeds and seedlings, using open-sided cages as controls. The purpose was to establish whether natural enemies act in a compensatory way. The experiments done so far should be regarded as pilot ones, since they were done with few replicates on a few species. More experiments need to be done before the role of compensatory mortality can be established.

Conclusion

This article discusses two opposing views of the organization of assemblages of competing species such as tropical trees or corals. One is that stability usually prevails, and, when a community is disturbed, it quickly returns to the original state. Natural selection fits and adjusts species into this ordered system. Therefore, ecological communities are highly organized, biologically accommodated, coevolved species assemblages in which efficiency is maximized, life history strategies are optimized, populations are regulated, and species composition is stabilized. Tropical rain forests and coral reefs are generally regarded as the epitomes of such ordered systems. The last three hypotheses presented in this article detail the mechanisms that may maintain these systems.

In the contrasting view, equilibrium is seldom attained: disruptions are so common that species assemblages seldom reach an ordered state. Communities of competing species are not highly organized by coevolution into systems in which optimal strategies produce highly efficient associations whose species composition is stabilized. The first three hypotheses represent this view.

My argument is that the assemblages

of those organisms which determine the basic physical structure of two tropical communities (rain forest trees and corals) conform more closely to the nonequilibrium model. For these organisms, resource requirements are very general: inorganic substances (water, carbon dioxide, minerals) plus light and space, and, for corals, some zooplankton. It is highly unlikely that these can be partitioned finely enough to allow 100 or more species of trees to be packed, at equilibrium, on a single hectare (*12*). Instead, if competition is allowed to proceed unchecked, a few species eliminate the rest. The existence of high local diversity in the face of such overlap in resource requirements is a problem only if one assumes equilibrium conditions. Discard the assumption and the problem vanishes.

Although I have presented these ideas as separate hypotheses, they are not mutually exclusive. Within a local area, there are usually enough variations in habitats and resources to enable several species to coexist at equilibrium as a result of niche differentiation. In addition, a certain amount of compensatory mortality probably occurs, as some evidence from rain forests indicates (*41, 42*). In special circumstances, circular networks might also increase diversity. Thus, a certain amount of local diversity would exist under equilibrium conditions.

However, climates do change gradually, which probably results in changes in the competitive hierarchy. On a shorter time scale, disturbances frequently interrupt the competitive process. These variations prevent most communities from ever reaching equilibrium. In certain special cases, species may be so alike in their competitive abilities and life history characteristics that diversity is maintained by chance replacements.

Thus, all six hypotheses may contribute to maintaining high diversity. My contention is that the relative importance of each is very different. Rather than staying at or near equilibrium, most local assemblages change, either as a result of frequent disturbances or as a result of more gradual climatic changes. The changes maintain diversity by preventing the elimination of inferior competitors. Without gradual climatic change or sudden disturbances, equilibrium may be reached; diversity will then be maintained by the processes described in the hypotheses of niche diversification, of circular networks, and of compensatory mortality, but at a much lower level than is usually observed in diverse tropical forests and in coral reefs.

Although tropical rain forests and coral reefs require disturbances to maintain high species diversity, it is important to emphasize that adaptation to these natural disturbances developed over a long evolutionary period. In contrast, some perturbations caused by man are of a qualitatively new sort to which these organisms are not necessarily adapted. In particular, the large-scale removal of tropical forests with consequent soil destruction (*51*), or massive pollution by biocides, heavy metals, or oil, are qualitatively new kinds of disturbances, against which organisms usually have not yet evolved defenses. Tropical communities are diverse, thus species populations are usually smaller than those in temperate latitudes, which increases the chances that such new disturbances will cause many species extinctions.

References and Notes

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Reputational Ratings of Doctoral Programs

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Undoubtedly the best-known efforts to assess the quality of doctoral programs in recent years have been the collection of prestige or reputational ratings by the American Council on Education (ACE) in 1964 (*1*) and 1969 (*2*). In those surveys the ACE obtained from samples of university faculty members ratings of the quality of graduate faculties in their own fields at other U.S. institutions. In addition to serving their primary purpose in the graduate education community, these surveys produced data that have been used to gain a better understanding of the meaning of reputational ratings, particularly how they are related to other characteristics of doctoral programs. As a result, we have learned that the reputational ratings—often called peer ratings—tend to be fairly highly related to program size (*3, 4*) and various indices of research productivity (*4, 5*), though the magnitude of these relationships varies considerably across disciplines. In particular, it appears that the ratings are more highly correlated with various traditional measurements (for example, number of Ph.D.'s produced, levels of funding) in the biological and physical sciences than in the social sciences or the humanities. One plausible explanation for this is that in the biological and physical sciences there tends to be greater consensus about accepted knowledge and standards (*6*).

There has been a good deal of concern about the use of reputational ratings in making judgments about program quality. The chief objections have been (i) that the ratings are unfair to doctoral programs which do not place primary emphasis on doing research and preparing their students to do research; (ii) that there is a strong halo effect, the ratings of a department being unduly affected by the prestige or reputation of the university of which it is a part; (iii) that there is a time lag, that is, the ratings are usually based on impressions of what a department used to be like, not on knowledge of its current strengths and weaknesses; and (iv) that the rating information seldom makes for a better understanding of a specific program's strengths and weaknesses and therefore is not useful for program improvement.

It was largely in response to some of these dissatisfactions with reputational ratings that the Council of Graduate Schools (CGS) and Educational Testing Service (ETS), in 1975, conducted a multidimensional study of quality in doctoral programs in three disciplines (*7*). This project was designed primarily as a study of the feasibility of employing information about a wide variety of characteristics in making judgments about the quality of programs. An important feature of the project was the idea that a single ranking is too simplistic, that it does not allow for the possibility that doctoral programs relatively strong in one respect (such as publication rates of the faculty) might be less strong in another (such as the quality of their teaching). A major procedural characteristic was that most of the information collected from respondents had to do with their own departments; for example, faculty members reported their own publication rates or journal-refereeing activities, students their opinions about the quality of teaching they received, alumni their dissertation experiences, and so on. These reports were obtained from students, faculty, and alumni by means of questionnaires. A general conclusion of the study was that such reports can be obtained without great difficulty, are usually reliable, and augment the description of characteristics relevant to appraisals of doctoral program quality.

Though they were not a crucial element in the CGS/ETS study, peer ratings were also obtained from the faculty respondents, each of whom was asked to rate the quality of the faculties of the other departments in his or her discipline which participated in the study. This aspect of the CGS/ETS study paralleled the two earlier ACE surveys, and it is this aspect of the CGS/ETS study that is the focus of this article.

The primary reason for obtaining the peer ratings was to examine their relationship to the broader array of program characteristics reported in the main part of the survey, a line of inquiry that was not possible with either of the earlier ACE studies. But interest in peer ratings per se remains strong. The Conference Board of the Associated Research Councils convened a planning conference, in the fall of 1976, to investigate issues involved in conducting another peer rating survey (*8*). In spite of ACE's announced intention of refraining from further efforts of this kind, it appears likely that some agency concerned with graduate education in the United States will conduct some kind of reputational rating survey in the not too distant future. Our interest in an improved understanding of the nature and meaning of peer ratings therefore goes beyond pure intellectual curiosity.

This article draws on the data gathered in the CGS/ETS study (*7*) and the two earlier ACE studies (*1, 2*) to address

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