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Ecological Complexity

IF I HAVE WONDERED AT the abundance of life forms during my treks around tropical forests, I have marveled even more at the intricate ways in which these organisms go about their communal activities. This tree, that flower, those insects: what parts of the ecosystem contribute to their well-being--and whose well-being do they themselves support?

The extreme biological richness of tropical forests is related to their extreme ecological complexity. With every tick of the clock, day and night, multitudes of animals seek multitudes of plants for food--the numbers of both categories being, as we have seen, far higher than in any other ecological zone of similar size. To ward off plant-eating animals, plants deploy defenses of extraordinary variety (we shall come across many examples further in this book, notably chapters 1-12). At the same time, many organisms make use of other types of organisms: trees use animals as pollinators and seed dispersers, and microorganisms transport nutrients from one individual organism to another and on to another. All the while, creatures are competing with each other for food or light, or simply for space; simultaneously, many exploit others for protection against still others. The whole scene, it seems to me whenever I survey it, resembles an arena of incessant pushing and shoving, each organism searching for advantage of whatever sort that assists its survival--and that thus offers a chance to propagate its kind by passing on its genes, its own version of the throb of life, to a further generation.

Yet however vigorous the struggles to stay alive, there are obviously checks and balances. Obviously, in that plant-eaters consume plants but seldom eliminate them, and eaters of planteaters gain enough sustenance to keep going without generally causing final harm to their prey species. Not so obviously, in that it is difficult for the observer to track down the inter-relationships that maintain the system as well as its parts. As a scientist, I recognize that there is balance, or "ecological equilibrium." But just where I can discern that balance, just how I can see it actually at work, is something else again. The various strands of life clearly make up an ecological web, which in turn constitutes a fabric with its own design imprinted on it. But what is the nature of the overall picture that we may perceive in the forest's workings? That is something we have yet to discover in detail. At best we see a blurred image. Truly spoke the scientist who said that our understanding of tropical forests resembles the forests themselves, with many fast-growing components, numerous gaps, and tangles on every side.

However hard it is for me to visualize the scale of biological richness in a tropical forest, I find it far more difficult to imagine the complexity of interactions between plants and animals, and between them and their physical environs. After all, if there are l,000 species within one

particular square kilometer of forest, their relationships with each other--their comings and goings, their incessant encounters with associates and enemies--certainly number tens of thousands of interactions, probably hundreds of thousands, possibly many more. I sometimes speculate that, given our scant understanding to date, I likely fail to recognize the very scale of a forest's complex functioning. In other words, I have little idea of how massively complex it is.

Thus it is the complexity of a tropical forest that excites me when I stand amid those stately trunks and their convoluted vegetation abuzz with creatures of myriad forms. Whereas it would take me many moons to identify and document the main species (certainly not all of the species--I would need the rest of my life for that) within l00 meters of where I stand, it would take me many times longer to trace even a portion of their interrelationships, their energy flows, their distinctive roles in the phenomenon that makes up a tropical forest. What I see is probably surpassed in complexity by only one other living entity on Earth--that which is between my ears. Yet how far short is my gray matter from gaining even an intuitive sense of the full intricacy of the scene before me.

SOURCES OF ECOLOGICAL COMPLEXITY

What has given rise to this ecological complexity? It stems largely from the exceptional amounts of light, warmth, and moisture that everlastingly foster favorable conditions for the evolution of species in their multitudes. It is climatic stability, with no seasonal hiatus in the form of winter each year, that seems--so far as scientists understand the situation--to make it work. In these tropical zones, we find abundant food all year long--food for plants in the first place, and thereafter for plant-eaters, eaters of plant-eaters, and so forth. In the temperate zones, by contrast, plant growth tapers off for several months of each year; as it does so, animal life endures a prolonged famine. But in a situation with food aplenty at all times, and food with lots of variety, we generally find that great numbers of species evolve to take advantage of what is, in many circumstances, an unceasing feast. Thus, at any rate, runs much scientific thinking on what makes a tropical forest tick to such fecund effect. *(1)*

Furthermore, in a situation where there is often--though by no means invariably--an abundance of permanent food supplies, many organisms do not have to constantly roam the forest looking for their next meal. Usually they can afford to stay in one place, since there is enough food at hand: thus the remarkably large numbers of plant species, which by definition are stationary forms of life. Thus, too, the disinclination of many forest animals to wander far from home: insects, together with other arthropods that constitute the bulk of forest animals, generally confine their activities to a limited space, often just a few square meters of forest habitat. Each takes a portion of the food supplies available, generally without over-encroaching on the feeding habits of its neighbors. The result is room for all, as long as they all do their own thing. The overall result is that the "all" becomes very numerous.

It is this division of habitats into mini-habitats, followed by subdivision into micro-habitats, that offers vast scope for species and their populations to engage in adaptive radiation, that is, throwing off new forms. These new forms can lead to new subspecies and eventually to new species. Moreover, plants and animals, developing in co-evolutionary accord, devise new niches, or ecological living space, for themselves and thereby create further variation on established

themes. In turn, the every-richer array of life forms finds ways for all to live with each other, on each other, off each other, through each other--building up, in short, the multitudes of lifestyles that constitute ecological complexity.

Yet another dimension to the situation emerges. Evolution works slowly; it has needed eons to produce such complexity. For further clues to the workings of tropical forests, then, we can look at their paleoecological pedigree. The generally stable background of their prehistory has allowed differentiation through processes of natural selection to develop undisturbed--and to do so for a very long time. Indeed, this last factor, the evolutionary ancestry of tropical forests, is so important to our understanding of present-day forests that we should look at what has been happening during a long line of yesterdays.

PALEOECOLOGICAL PAST

Tropical-forest ecosystems are almost certainly the oldest continuous ecosystems on the planet. Of course new species have come and gone, entire communities have emerged and disappeared in the process of becoming modified into fresh assemblies of plants and animals. But the fundamental configurations of the ecosystems have, in the main, persisted for very long periods of time. In parts of Southeast Asia, for instance, we know from fossil deposits of forest plants that the forest there has existed in more or less its present form for at least 70 million years, possibly l00 million years. We cannot assert as much for any other major ecosystems on Earth. This is not to suppose, however, that there have not been phases of change, occasionally drastic change--especially during the recent past. Yet far from impoverishing the forest ecosystems, these upheavals appear to have fostered an increase in biological richness and thus in ecological complexity. In short, tropical forests have generally experienced exceptional stability and continuity for much of their past, with opportunity for evolution to go its creative way undisturbed. At other times, they have undergone enough "constructive disruption" to foster fresh evolutionary departures.

The principal upheavals occurred during the late Pleistocene, when glaciations in the Northern Hemisphere were matched by repeated expansion and contraction of tropical forests, producing market local differentiation in climate and biogeography. (2) There were several such occasions, the last one about l0,000 years ago. During the times of greatest contraction of the forests of Amazonia, a few moister localities appear to have persisted as "forest refugia," serving as reservoirs of plant and animal species from which the forests were ultimately able to reestablish themselves when wetter conditions returned. Because the species communities in these refugia were cut off from each other, suspending their gene flow, each community could follow its distinctive track of evolution by responding to its own environmental circumstances in a manner that would allow natural selection to throw up new variations of the old stock. In short, each refuge would tend to produce an assembly of new species that would supplement or in other cases supplant the established species. In turn, the increased richness of species communities would serve to generate greater complexity of ecological functions in many parts of Amazonia.

In Southeast Asia the recent changes seem to have been less pronounced. During the drying-out phases of the late Pleistocene, the region did not desiccate nearly so much as did the tropical forest zones of Latin America and Africa, presumably due to the maritime effect (i.e., the

moderating effect of the surrounding seas on climatic upheavals). Southeast Asia constitutes not a continental land mass, but an archipelago with a few large islands such as Borneo, Sumatra, and New Guinea, and thousands of smaller ones. This means that local climatic regions had to have drawn sufficient moisture from the nearby oceans to maintain a consistent expanse of forests. At the same time, the archipelago effect (i.e., the influence of so many island territories of different sizes) would have stimulated speciation by virtue of the fact that the plant and animal communities were divided into thousands of distinctive units--a situation that promotes extreme differentiation.

ISLANDS

Whereas Amazonia is split into various sectors, or ecologically differentiated islands, Southeast Asia has numerous geographic islands. The Malay Archipelago, as Southeast Asia is known to biogeographers, covers 2,894,0000 square kilometers--only twice the size of Alaska. Yet the region comprises at least 20,000 islands, of which 13,000 make up Indonesia in a chain 5,000 kilometers long between Asia and Australia. The Indonesian archipelago has not always been so broken up. When the sea level has dropped, as it has several times during the relatively recent past, many of the islands have merged to form a single territory, allowing their wildlife communities to mingle. When the seas have receded again, splitting up the prehistoric forests into fragments once more, each separate sector would follow its evolutionary path in response to its own set of local environmental conditions and selection pressures. Greater diversity and complexity result. When the seas advance again, there will have been a repeated mingling of biotas and more creative tension between disparate communities of animals and plants, which often leads to some extinctions but eventually fosters more speciation. And so it continues.

The overall result is an exceptional amount of biotic diversity within Indonesia's 2 million square kilometers, almost all of it to be found in the primary forests that reputedly still cover two-thirds of national territory (roughly one-eighth of the entire biome of tropical forests). Of Indonesia's 500 mammal species, l00 exist only within the confines of that country; and Indonesia features 1 in 6 of the world's bird species, again with a good number of endemics. We know Indonesia as home to tigers, elephants, rhinos, and orangutans--but perhaps not everybody realizes that it provides living space for the Komodo dragon and a host of other bizarre-looking creatures that are native to Indonesia alone.

The insulating effect found within the Indonesia archipelago is well demonstrated by Siberut, a 4,500-square-kilometer island off the west coast of Sumatra.*(3)* This island, having been separated from the mainland for at least one million years, has enjoyed evolutionary scope to produce four endemic primates, more per unit area than any other island in the world, even Madagascar. Siberut is the smallest island in the world to have any endemic primates of its own-- and of its 31 mammal species altogether (apart from bats), 25 are native to the island alone. More remarkable still is the endemism of Maluku, the group of islands formerly called the Moluccas and sometimes known as the Spice Islands. *(4)* The several hundred islands of the group support 450 bird species, including 89 endemics, and 80 mammals, 14 of them endemics. In addition, at least 25 butterflies and several reptiles and land snails are limited to these islands. Among the endemic birds, 94 percent are confined to a single island or a small group of islands. We might

also note that nine-tenths of the forest in the wettest and hence the richest two-thirds of Maluku have been assigned to timber concessionaires.

An additional 20,000 islands are scattered across 29 million square kilometers of the southwestern Pacific, known collectively as Micronesia and Polynesia. Again, the mind can hardly entertain the uniquely varied bioecological character of these islands. On New Caledonia, for instance, an island of only 19,000 square kilometers, or smaller than Vermont, there are three thousand plant species (as many as in Canada), four out of five of them endemic. Moreover, New Caledonia's flora contains high concentrations of primitive species that illuminate our understanding of basic evolutionary processes.

So much, then, for some formative factors that contributed to the ecological complexity of tropical forests. It is important to understand the dynamic origins of today's ecosystems so that we can do a better job of ensuring them a future. At the same time, we need to balance our grasp of the bioecological components of these ecosystems with some insights into their geophysical underpinnings, particularly the mineral nutrients that feed the ecosystems.

MINERAL NUTRIENTS

Central to the workings of tropical forests is the cycling of mineral nutrients through their ecosystems. As we have noted, tropical forest soils, with the exception of recent alluvial and rich organic soils, are very old and, hence, impoverished. [(5)](#) In Amazonia, for example, where there has been no recent geologic activity (such as mountain building) to throw up new materials, the soils have long been weathered, leaving them deficient in phosphorus, potassium, sulphur, and other key minerals. Plenty of Amazonian topsoils possess only minor quantities of phosphorus, less than is generally needed for a region to qualify as fertile; or the phosphorus is chemically fixed in forms that leave it unavailable to plants. Moreover, such few minerals as have survived the lengthy periods of topographic stability in Amazonia's past tend to have lost their nutrients through leaching deep into the ground as a consequence of heavy rainfall.

All in all, three-quarters of Amazonia contains soils with high acidity and aluminum toxicity (not unusual in the humid tropics, where the overall proportion is two-thirds). A further 15 percent of Amazonia comprises younger soils, often alluvial materials, many of them fertile; while 4 percent consists of mature soils that are unusually fertile and have great agricultural potential. But many of these better soils tend to become water-logged. Only about 300,000 square kilometers of Amazonia, notably in the foothills of the Andes with their high-nutrient soils and in the alluvial territories of the floodplains, can be considered to offer both the fertility and the drainage suitable for agriculture. To grow crops in the rest of the region, farmers need to spend large sums on lime and other fertilizers.

True, some regions of the moist tropics have nutrients in underlying mountain rock, which become available as the exhausted topsoils erode. We find examples not only in the lower Andes, but in Central America and some of the Caribbean islands, where hills (defined as areas with greater than 8-degree slopes) and highlands often account for one-half of the terrain. [(6)](#) We also find nutrient-rich soils in volcanic areas of Central Africa and Southeast Asia. Soils in these

territories, with their fine stocks of nutrients, are akin to those of temperate-zone forests, where nutrients are common--in contrast to the tropics as a whole, where they are rare.

In these circumstances of infertility, it is "inefficient" for forest organisms to allow the nutrients to stay in the soil. Evolutionary processes have responded by developing a virtually leakproof system for cycling nutrients through the ecosystem. (*7*) When the main source of nutrients, rainfall, hits the forest canopy, it can bring with it (as measured at Manaus in Amazonia) 3 kilograms of phosphorus, 2 kilograms of iron, and l0 kilograms of nitrogen per hectare per year. (*8*) The multilayered structure of the forest then serves to filter out nutrients from through-falling water--a process in which epiphytic organisms, such as lichens, bryophytes, and algae, plus bacteria, play an important role. These findings are based on only a few experiments scattered through southern Venezuela, but they illustrate the many devices adopted by tropical forests to safeguard their precious stocks of nutrients.

At ground level, we encounter still more nutrient-conserving mechanisms. Tree roots, some of which extend l00 meters along the surface of the ground from the tree trunk, form a network that can be three times as dense as it would be in a temperate forest--occasionally as much as one-quarter of the tree biomass. (Some roots even emerge from the soil to climb up tree trunks, thus enabling the trees to capture nutrients before they enter the soil.) The root mat, as much as 30 centimeters thick, is extraordinarily efficient at absorbing nutrien ts washed into the soil, whether from rainfall or from rotting vegetation. Field experiments in southern Venezuela show that when calcium and phosphorus are sprinkled on these root mats, 99 percent is absorbed quickly, within six months at most. (*9*)

Closely associated with the root mats are fungus-root combinations known as mycorrhizae. (*10*) These micro-organisms of the soil, together with their associated bacteria, are essential to the well-being of many tropical trees in that they are the main way tree roots recover phosphorus, zinc, copper, molybdenum, and other minerals from leaf litter. The mycorrhizae grow on or near the surface layers of feeder roots of plants, where they work in close symbiotic relationship with their plant hosts. In a particle of soil the size of a sugar lump, there may be several meters of delicate fungal filaments (and as many bacteria as there are humans on Earth). By colonizing the roots, the fungi enhance the workings of the rhizosphere, or root world. They not only enable plants to absorb more minerals from the soil, they also help them to resist root pathogens, to withstand drought, and to tolerate other adverse conditions. In return for this support, the fungi obtain energy from their plant hosts in the form of fixed carbon. I have often gazed at a tall tree in all its stately splendor and reflected that much of the giant plant's welfare depends on tiny fungi that operate out of sight below ground level--and each dipterocarp species may have its own particular fungus.

So widespread are these mycorrhizal fungi, and so critical are they to tree growth, that some scientists wonder whether a forest, once cleared, can ever reestablish itself without them. When an extensive patch of forest is eliminated, the soil becomes drier and warmer, causing the mycorrhizae to die out. In other words, the tree species and their symbiotic fungi are entirely dependent on one another. Unless the mycorrhizae can eventually be restored from residual forest in the environs (supposing any such is close enough), the forest community will not get a

chance to re-colonize the cleared area. The ecosystem will remain disrupted, and a different assembly of plants, perhaps scrub or coarse grass, will take over.

Still other nutrient-conserving mechanisms operate in tropical forests. Evergreen trees produce leaves all through the year, rather than in a single season, which means that their nutrient demand remains constantly low. Moreover, the leaves of many trees are thick and leathery, preventing the leaching of their water-soluble elements by rainfall. *(11)*

All in all, the cycling of nutrients in a tropical forest is fast and efficient, occurring within a virtually closed ecosystem. So capable is the process that streams draining from some forests actually have smaller concentrations of certain nutrients than are found in the rainfall descending on the forest. Many plant communities store at least 75 percent, and sometimes as much as 90 percent, of their nutrient stocks in their vegetation. As a result, forest soils have virtually no exchangeable minerals such as calcium, magnesium, potassium, and phosphorus--precisely the reason they remain highly acidic and infertile and, hence, unsuitable for agriculture. Contrary to popular understanding, the forest thrives despite its soil rather than because of it.

Because the bulk of the forest's nutrients are held in the vegetation, burning the forest triggers a flood of minerals into the soil. After one or two years of heavy-rainfall leaching, this stock is washed deeply into the undersoil, where it lies beyond the reach of new plants (grasses, shrubs, etc.) that replace forest trees and that have only short roots. The nutrient cycle being broken, fertility quickly fades and can be restored only through increasing amounts of fertilizer.

Furthermore, when the forest cover is eliminated, and especially when the trees have been removed through heavy bulldozerlike equipment that compacts the soil, the exposed ground is left unprotected against the heavy beating of tropical thunderstorms. The result is massive water runoff, accompanied in some cases by soil erosion. In the main, a forest on undulating terrain allows erosion of no more than 1 ton of soil per hectare per year, whereas the same area can lose 20 to 160 tons if the forest is replaced with fairly dense vegetation such as that of a coffee plantation, 60 to 100 tons if replaced with man-established pasturelands, and l,000 tons or more with field crops. *(12)*

These, then, are some of the risks associated with large-scale clearing of tropical forests. A small clearing, however, can generally recover, because key features of the ecosystem, such as nutrients, are available from nearby patches of residual forest as colonizing vegetation comes in to cover the denuded ground. Similarly available from the forested environs are tree seeds to restore the original plant growth--and these seeds, with their specialized patterns of reproductive biology, are so important that they deserve a section of this chapter to themselves.

SEEDS AND FRUITS

The paleoecological pedigree of tropical forests has been dominated, in the main, by the phenomenon of environmental stability. With only occasional breaks, there have been millions upon millions of years of ceaseless warmth and moisture; continuity unmatched. By contrast, temperate-zone forests, with their seasonal fluctuations, have had to cope more constantly with feast-and-famine conditions during their evolutionary past. The practical consequence for

tropical forests is that when they are left undisturbed, they demonstrate exceptional stability and "survivorship." Equally to the point, they are little able to tolerate the abrupt and broadscale disruptions that modern man inflicts.

By way of illustrating how tropical forests adapt to conditions that vary only slightly, let us look at the regeneration systems of tropical trees. (*13*) Their seeds generally have little or no capacity to remain dormant: they don't need to. Whereas the seeds of a temperate-zone tree may well lie unchanged for ten years before finally sprouting, the seeds of trees in tropical forests often survive no more than twenty-five days. Having become finely tuned to unchanging conditions, they are acutely sensitive to perturbations in their environments. The dipterocarp family of trees in Southeast Asia produces seeds that germinate only so long as the microclimate varies hardly at all around the mean temperature of 73 to 80 degrees Fahrenheit. When a timber exploiter breaks open the canopy and allows the air to warm up to as much as l00 degrees F., many if not most of the seedlings die (though this is not invariably the case: in Central America, for example, seedlings of certain species respond vigorously to opening of the canopy [*14*]). By contrast, temperate-zone-tree seeds survive the heat of summer and the cold of winter year after year.

In addition, tropical trees do not all flower and seed continuously, or even regularly. Many tree flowers complete their cycle in a single day, or are receptive for only a few hours around the middle of each day. Many other trees seed heavily only every third year, some only every tenth year, and a few only every thirtieth year or so. What, we might wonder, is the reason for this curious circumstance? So far as we can tell, the tightness of the nutrient cycle does not encourage trees to produce large amounts of fruits at regular intervals.

But perhaps the most distinguishing feature of the self-regeneration systems of tropical trees is that very few of them depend on the wind to convey their pollen and seeds. This is in marked contrast to the pattern in temperate zones, where forests are more open, and there is more scope for the wind to blow through the plant community. Beneath the dense canopy of a tropical forest, there is little air movement. In the forest undergrowth of Barro Colorado Island, in Panama, the average wind speed measures only 1.6 kilometers per day, or 1/240th as much as in open fields. In this situation, there is next to no hope for pollen or seeds that would normally be carried by wind. In a survey of 40 hectares of forest in Brunei, scientists have found that only 1 out of 760 tree species relies on the wind for pollination. So most tree species and other plants depend on creatures such as insects, birds, and bats to transport pollen and seeds.

Furthermore, when the seeds of forest plants drop to the ground, they almost always have to germinate in very shady conditions. So a seedling must get a good start in life if it is ever to reach the sunlight. To survive in these unpromising conditions, it needs an immediate supply of food during its critical early phase--which helps to explain why many fruit seeds are large. We have only to think of the seed of an avocado, the size of an egg, to understand the appetite of the infant tree. But a large-sized seed needs a large-sized creature to carry it--one reason why we find, among the more regular residents of tropical forests, toucans, pigeons, monkeys, and other sizable creatures. To attract these seed carriers, the trees produce large, fleshy fruits--witness the splendid selection of outsize, juicy fruits found at stalls in marketplaces throughout the moist tropics. The forests of Southeast Asia produce well over 100 kinds of fruit that are widely consumed by humans, in contrast to Europe's forests, with less than 10 varieties.

In tropical forests, trees and other plants depend heavily on their dispersal agents. The difficulties of regeneration are illustrated by the fact that the islands of Borneo and Sulawesi are only 100 kilometers apart, yet no more than 2 of the 282 dipterocarp species on Borneo appear on Sulawesi as well. *(15)* Despite the crucial importance of large creatures in the self-regeneration systems of tropical forest plants, we generally encounter few such creatures in tropical forests. In fact the biomass of large mammals sometimes amounts to no more than the equivalent of two or three domestic cats per hectare. *(16)*

All of this has crucial implications for conservationists. Insofar as large animals exist at low densities, and with populations that are often patchy, we must anticipate that if tropical forests are ever reduced to a few parks and reserves, these protected areas will have to be very extensive if they are to safeguard not only the trees and other plants, but the rare creatures that play such a critical role in the plants' survival. On top of that, we must recognize that many fruit-eating animals turn to successional species in secondary forests for part of their food needs, on the grounds that only successional species provide the specialized types of fruits that the animals need for their year-round diets. So a protected area must take account of this further quirk. To safeguard a patch of primary forest may not be enough in itself, even though this is often the predominant goal of park planners. A protected area will often need to incorporate an associated patch of secondary forest, perhaps one-tenth of the total protected area, to supply all the needs of all members of the wildlife community. *(17)*

DURIAN AND BATS

As an illustration of the way that forest organisms make common ecological cause--and of the way in which the forest's fabric of life can be injured through marginal-seeming interventions on the part of man in the forest ecosystem--let us look at the sag of the durian fruit and its pollinator bat in the Malay Peninsula. The durian is considered a delicacy and may well have pleased the human palate for half a million years. The fruit, about the size of a small football, has a strong and distinctive taste, like a mixture of rancid garlic and best strawberries. Connoisseurs say there are few better fruits anywhere, even though the act of consuming it can be compared, because of the smell, to eating dessert in a run-down public toilet.

With the fruit selling for the equivalent of U.S. $3 a piece, the durian tree generates a crop worth as much as $35 million per year. *(18)* Whereas most of the fruits are harvested in the wild, a number are now raised on plantations. Cultivated durians cover some 12,500 hectares, with a value between $5,000 and $10,000 per hectare; throughout Southeast Asia, the crop is worth at least $120 million a year. The net annual return on investment for an orchard owner works out at between 15 and 20 percent during the twenty-five-year lifetime of a plantation--a rate of return matching that of a rubber or oilpalm plantation. For the peasantry of the Malay Peninsula, the durian represents big money.

The famous, or infamous, smell of the fruit plays a key part in the plant's life cycle. Like virtually all trees of tropical forests, the durian tree occurs only sparsely. Yet no matter how isolated the trees may be, the powerful smell attracts animals that disperse the fruit seeds. And herein lies a curious phenomenon. Together with a good number of other tree species, the durian is pollinated by a single species of bat. Conversely the bat, Eonycteris spelaea, appears to find its

main source of nectar food in durian trees. The bat spends a good part of its day roosting in caves; and large numbers of this particular species occupy caves in the environs of Kuala Lumpur, known as the Batu Caves, about 40 km. from coastal mangrove swamps in which grows a particular flower that is also favored by the bats. The swamps are being reclaimed for building land, which reduces a significant food source of the bats. Moreover, the Malay Peninsula, like most other parts of the Third World, has developed a hearty appetite for concrete. So the Batu Caves have been steadily exploited for their limestone. In the wake of these two assaults upon their life-support systems, the bat populations have declined. Fortunately the blasting of the Batu Caves has recently been halted, in order to safeguard the bats' roosts, among other reasons. But as long as the mangrove swamplands continue to be eliminated, the bat populations steadily fade away. The economic backlash affects many hundreds of people who trade in the durian fruit of the area, and many thousands who enjoy that mealtime delicacy. Much the same applies wherever bat habitats in Southeast Asia are under human assault of whatever kind.

During the lengthy stretches of the year when the durian tree is not in flower, the bat sustains itself by feeding on the nectar of several other trees, not only the mangrove species, but certain trees that occur only in primary forest. So if durian enthusiasts are to conserve the ecological network that sustains the species, they must maintain extensive patches of forest in order to safeguard not only the pollinator bat but the entire ecosystems that sustain the durian economy-- both the natural economy and the human economy.

This example of ecologic linkages within the forest community has come to light in just the past few years. If we were to trace the many dynamic relationships that constitute the full fabric of forest life, we would surely find many such instances. Meanwhile, we continue to intervene in the forest's workings, with next to no knowledge of what we are doing. We often start to learn only when we recognize the damage that we have unwittingly wrought.

For instance, we might ponder the lifestyles of other bats in tropical forests. Their popular image apart, bats are beneficial to humans in all kinds of unsuspected ways. Earth may support as many as 1,000 species of bats altogether, or almost one-quarter of all mammals; and we can reasonably reckon that a good half of them live in tropical forests. In Southeast Asia overall, at least one-third of all mammals are bats; in the Malay Peninsula, one-half; and in the La Selva Forest Reserve in Costa Rica, a full three-fifths. Bats range from the size of a bumblebee, making it the smallest mammal (weighing less than a penny) on Earth, living in limestone caves far up the notorious River Kwai in Thailand, to flying foxes with 2-meter wingspans. Because they dwell in localized refuges such as caves, and because their specialized foraging practices confine them to just a few sources of food, they are very vulnerable to man's disruption of their lifestyles. A single cave-dwelling colony can consist of millions of individuals, constituting the largest congregations of warm-blooded creatures on Earth--and leaving them susceptible to summary execution through dynamite blasting. Whereas it would take several weeks to dispatch the two million wildebeest in the Serengeti Plains, at least as many bats can be eliminated in a matter of seconds. Not such a spectacular demise, but perhaps more terminal in the long run and more insidious in its impact, is the destruction of forest ecosystems. In Thailand, for example, where 94 out of 263 mammal species are bats, forest cover has declined by well over half in the last twenty years, and much of the rest may disappear before the end of the century.

Together with the nectar-consuming bats, a good number of fruit-eating bats are likewise important to the workings of tropical forests. As we have seen above, the abundance and variety of forest fruits is complemented by an array of fruit-eaters that disperse the fruit seeds. In forests of Asia and Africa, fructivorous bat species are as numerous as all the birds, mammals, and other creatures that consume fruits. Moreover, fruit-seeking bats often visit flowers, thus pollinating them. All in all, bats pollinate hundreds of genera of tropical trees and shrubs, thereby fostering the prosperity, and often the very survival, of many plants that we encounter on our tables at mealtime, including guavas, avocados, bananas, breadfruits, mangoes, cashews, cloves, eugenol, and tequilla. In addition, we can view various other plants as "bat supported," notably the kapok tree and many timber and fiber trees.

The one-on-one link between the Batu bats and the durian tree is paralleled by mutually supportive relationships between fig trees and wasps. The fig genus, the most distinctive and widespread of plant genera in the tropics, comprises more than 900 species, each of which is pollinated by its own species of wasp. At the same time, the wasps depend on the ovaries of the figs as sites for their larvae to develop. [(19)](#) A further illustration lies with the Brazil nut tree, which is commonly known for its tasty nut, and is widely harvested in Amazonia as a source of cash. This huge tree is pollinated solely by an iridescent insect, a member of the euglossine group of bees (the busy euglossines occasionally cover as much as 20 kilometers in 65 minutes). Likewise the tree's nut depends for its germination on a sharp-toothed rodent, the agouti, which chews and softens the seed coat. So this towering tree requires, for its reproductive system, the services of a high-flying bee that pollinates flowers in its crown, and a forest-floor rodent that disperses its nuts. Of the two creatures, the euglossine bee appears to be the more important in that it also pollinates, among many other plants, orchids--and in turn, these plants often supply prime sources of food to sundry other insects, which pollinate further plants, and so on. In this crucial sense, we can view the euglossines as "mobile link" species, and their plant hosts, by virtue of supplying food to extensive associations of mobile links, as "keystone mutualists." [(20)](#)

Many other cash crops, after the pattern of the Brazil nut tree, are pollinated by obligate insects or bats or birds. Tiny midges and thrips pollinate rubber and cocoa; bees and others of the Hymenoptera order pollinate passion fruit and curcurbits; flies pollinate cashew, mango, and kola nut; nocturnal moths and bats pollinate callabash, kapok, and balsa trees; and hummingbirds pollinate wild pineapples. All these specific pollinator relationships form part of larger "food webs," often with their mobile links and keystone mutualists.

This key concept of pivotal linkages within tropical forest ecosystems can be extended to thousands of plants that through their nectar, pollen, and fruit supply critical support for multitudes of insects, mammals, and birds: for example, figs, with their several hundred species, and epiphytes, with their thousands of species. Further, if as a result of man's disturbance of the forest, a keystone mutualist is eliminated from its ecosystem, the loss may lead to that of several other species. Still more to the point, these additional losses may, in certain circumstances, trigger a cascade of linked extinctions. Eventually a series of the forest's food webs could become unraveled; developed as they are through the co-evolution of plants and animals that have sustained each other through ever-more complex relationships, [(21)](#) they can steadily become destabilized from start to finish of their workings, with a shatter effect throughout their ecosystems. Thus, the exceptional intricacy of the forest's fabric of life. Interdependency is all.

When human incursion causes the severing of a few threads, the damage can ultimately lead to a rending of the fabric from top to bottom.

While many of the species, both plant and animal, live only in primary forest, certain of them are "successional" species that depend on disturbed patches of forest, with their specialized foods and creatures, for survival. These successional species include certain figs, epiphytes, orchids, and aroids, also many euglossine bees and butterflies. Conservationists must aim therefore to protect all sorts of forest formations with their multiple habitats, if they are to preserve multiple communities of species. Furthermore, they need to bear in mind that many pollinators of tropical forests, in common with a good number of other species, exist at very low densities. (22) This leaves them unusually susceptible to sudden elimination. Not only are there obvious threats such as forest burning and other disruptions at the hand of humans, but by virtue of their sparse numbers, these species are subject to stochastic extinction (meaning, roughly, "random" extinction). The phenomenon occurs when populations, fluctuating as they normally do between high and low points, descend a demographic curve to a point from which they cannot recover. Or a population may die out because of genetic quirks. Under natural circumstances, these localized events do not matter, since a population can be reestablished by colonizers from neighboring populations. But if a park were established in a tropical forest without space enough to account for small-scale disappearances of "fragile" species, the park might be unable to sustain a complete forest community, even though it were to total hundreds of square kilometers. In temperate-zone forests, a park can generally protect a sufficient spread of ecosystems while covering a smaller tract of forest. In the humid tropics, however, we need to consider that a park should usually cover at least l,000 square kilometers, often much more, to do its job.

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4. Ecological Complexity

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