Complexity of Tropical Rain Forests

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Tropical forest ecosystems represent the most complex assemblages of organisms on earth. In a given community thousands of organisms interact with one another and form an intricate web of energy flow and productivity. These forests differ greatly from one locality to the next and have been assigned a variety of names such as: humid tropics, tropical evergreen alluvial forest, dry tropics, white sand forests, etc. (Walter, 1971). Botanists throughout the world now classify these forests into 30-40 types (Caulfield, 1984). The term "tropical rain forest" which was coined by Schimper (1898, 1903), is used by many biologists as a general designation of these various forests. In "The Primary Source", Myers (1984) defines tropical forests as, "forests that occur in areas that have a mean annual temperature of at least 75 degrees Fahrenheit and are essentially frost free in areas receiving 2,000 mm or more of rainfall per year and not less than 100 mm of rainfall in any month for two out of three years. They are mainly, if not entirely, evergreen. We generally find such forests at altitudes below 1,300 meters, though sometimes in Amazonia up to 1,800 meters and usually in Southeast Asia up to only 750 meters. In mature tracts of forest, there are several more-or-less distinct strata, and the canopy is made up of almost continuous interlocking tree crowns".

Apparently the first person in western society to describe tropical rain forests was Christopher Columbus in 1493 upon visiting the island Espanola (Hispaniola)—the island that is now politically divided into Haiti and the Dominican Republic (Caulfield, 1984). Subsequently European explorers of the American tropics were the sixteenth-century conquistadors (Jordan, 1982) and several centuries later the great naturalists such as Bates (1892) and Wallace (1889).

LOCATION. Tropical rain forests exist essentially as a band around the middle of the earth concentrated on land areas between the Tropic of Cancer and the Tropic of Capricorn (Rumney, 1968). *Tropos* is Greek for "turning point" referring to the sun's zenithal position in the sky. Tropical rain forests occur in three major areas: 1) In Central and South American and the West Indies, 2) In Africa, essentially in the Congo, Niger, and Zambezi river basins and Madagascar, 3) In the Indo-Malay-Borneo-New Guinea regions of Southeast Asia.

Originally approximately 12% of the earth's surface (5 billion acres) was covered with tropical vegetation (Table 1). An estimated 50% of this vegetation has been destroyed (Table 1). The Amazon valley bounded by the Guyana and Brazilian Shields (Sterling, 1973) contains the largest continuous tract of tropical rain forest in the world with about 3.6 million square kilometers (Myers, 1979). South-east Asia has the next largest concentration of tropical rain forest followed by Africa (Table 1).

TABLE 1. Area, biomass, diversity and destruction of tropical rain forests of the world. Excerpts taken from Caulfield (1985) and Myers (1984).

	Caulfield	Myers
AREA		
	Originally 12% of earth's surface (5 billion acres now 50% destroyed).	Once covered 16 million sq. km. now ca 9 million sq. km. Maximum 5.1 million sq. km. in Latin America, 2.1 million in Asia, 1.8 million in Africa, Indian Ocean and Pacific Ocean islands. 1/3 of world's forest with 4/5 of Earth's land vegetation.
BIOMASS		
	Average dry weight (biomass 180 tons/acre) (temperate deciduous forest 120 tons/acre).	1,000 tons of plant biomass/ha, dipterocarp forest of Borneo. 30,000 tons on 45 ha (760 tree sp) Brunei 165 kg fauna/ha.
DIVERSITY		
	Plants	Plants
	40-50% of world's living things. 40-80 tree species/acre; temperate deciduous forest 4 species/acre (trees). New Caledonia—3,000 species of plants; Great Britain (13.5 x larger) has 1,800 species. Madagascar—2,000 tree species; North America temperate zone, has 600 tree species. Panama has as many plant species as all of Europe. Mt. Makiliang, forested volcano in Philippines, has more species of woody plants than United States.	4,000 orchid species in S. E. Asia (1/4 of Earth's total). S. E. Asia supports 1 in 10 of all plant speies in just 3% of the planet's land surface. 2,500 tree species on 126,000 sq. km. in Brunei and Sarawak. Amazonia—30,000 plant species; 10,000 species in all temperate S. America. Brazil, 20,000 plant species, Costa Rica, 8,000 Ecuador, 15-20,000 plant species (Great Britian, 1,433 species). Peninsular Malaysia equal 0.09% of Earth's surface supportst 8,500 species of plants or 3.4% on planet. Mt. Kinabalu has 5 times as many oak species as the whole of Europe. Highest diversity—Rio Palenque (western Ecuador (1.7 sq. km.) 1,025 plant species followed by Choco regions in Colombia with 208 tree species in 1/10 ha. Next largest center in S. E. Asia.
	Animals	Animals
	16% of all bird species in world occur in Indonesia (1480 out of 9,000). Papua New Guinea—320 endemic species of birds. 300 sq. miles in Panama/Costa Rica has 500 resident species birds (4 times as many as in temperate forests of eastern U. S.). 500 insect species in 2,000 net sweeps in understory of Central America. 1 sq. m of leaf litter—50 species of ants, Central America.	Amazonia has 1 in 5 of all bird species on Earth. Peninsular Malaysia—675 bird species and 200 mammals. S. E. Asia (whole 656 mammal species, 850 amphibians and 700 butterfly species. 2,000 fish species in Amazon River and tributaries (10 times as many as in all Europe: 8 times that of Gunung Mulu Park (Sarawak)—20,000 species of invertebrates (529 sq. km.). Panama—1,200 species beetles on a single tree (*Luehea seemannii*). About 41,000 arthropods/ha in Panama.
DESTRUCTION		
	1/5 of remaining tropical forest will be destroyed or severely degraded by end of century. Individual losses: (% of remaining) Philippines 20% Indonesia 10% Nigeria 100% Madagascar 30% Costa Rica 8% Mexico 35%	Tropical forest ecosystems have been in existence for at least 50 million years. Within a period of half a century they will be eliminated. The destruction period—one-millionth part of their history.

Tree heights and stratification of the tropical rain forest vary depending upon rainfall and other environmental factors. The structure of a typical tropical rain forest is discussed by Richards (1952). In general tree heights do not exceed 50-55 meters (Walter, 1971). The trees are straight and slender; they begin to branch only just below the apex and thus crowns are small. Commonly, the trees form buttress-like roots. These plants tend to have a large number of epiphytes and lianas attached to them (Walter, 1971; Putz, 1984).

Thus viewed, a typical rain forest has the following stratification: 1) Scattered very tall emergent trees that project above the general canopy, 2) The canopy layer which forms a continuous aerial carpet, 3) One or several understory layers, 4) A seedling layer on the forest floor. As noted by Janzen (1977), the relatively uniform green color of the vegetation disguises its true nature from the prospective herbivores. Mature tropical rain forests tend to be open and park-like and easy to walk about in. The most frustrating factor about visiting a tropical rain forest is that most of the biological activity takes place in the canopy and one only catches a glimpse of the activity. In recent years special rope climbing techniques have been employed to put observers in the canopy (Perry, 1984).

In terms of aerial phytomass (wet weight) the various components of the forest are distributed as follows: leaves, 2-3%; branches and twigs, 26-30%; stems, 60-65%; other plants, (lianas, epiphytes, etc.), 5-8%. Although liana biomass generally represents < 10% of the forest biomass, up to 40% of the total leaves in the canopy may be formed by lianas (Ogawa, Yoda, Ogino and Kira, 1965). A large proportion of the living material of the forest may be located in the roots. In some forests, such as the white sand vegetation of the Amazon basin, roots comprise 60% of the total biomass, compared to other Amazon forests having only 20% (Anderson, 1981).

DIVERSITY AND DISTRIBUTION. The tropical rain forests of the world are noted for their high diversity of plants and animals. Visitors from the temperate zone are overwhelmed by the great numbers and interactions of the organisms. Popular and technical articles (Sterling, 1973; Prance, 1982; White, 1983) repeatedly discuss the diversity and distribution of plants and animals. Table 1 presents some of the more striking statistics and comparisons of diversity in tropical rain forests.

The destruction by man of tropical rain forests throughout the world in the next fifty years will result in the extinction of a great number of these plant and animal species. The estimates of the number of species that will become extinct varies greatly (400,000 to over a million) depending upon the authority (Harwood, 1982) but all seem to think it will be the greatest extinction of species in the history of life on earth (Myers, 1984). Why the discrepancy in estimates? No one knows the number of species of organisms existing on the planet. Approximately 1.5 million species of organisms have actually been described by taxonomists (Harwood, 1982). Most of the organisms already described live in areas outside of the tropical rain forests. How many species await discovery and description? Paul and Anne Ehrlich suggest between 2 and 20 million (Harwood, 1982). Myers (1984) estimates something like 3-10 million species. Peter Raven, director of the Missouri Botanical Garden, estimates 4.5 million species as the smallest possible total for the earth (Harwood,

1982). Most of the undescribed species of plants and animals live in the tropics. All of the above suggested figures may be incorrect. In a study of Coleoptera and other arthropod species in tropical forest Erwin (1982) states, "It should be noted that there are an estimated 50,000 species of tropical trees (R. Howard and R. Eyde, pers. comm.). I suggested elsewhere (Erwin and Adis, 1981) that tropical forest insect species, for the most part, are not highly vagile and have small distributions. If this is so, and using the same formula as above starting with 162 host-specific beetles/tree species then there are perhaps as many as 30,000,000 species of tropical arthropods, not 1.5 million". With the destruction of the tropical rain forest within the next fifty years a very large number of organisms will become extinct before they are even known to man.

MAN, SOILS AND AGRICULTURE. There is a great deal of controversy surrounding the fertility of soils in tropical rain forests and the ability to sustain agriculture. Can the tropical rain forest be utilized for intensive agriculture without allowing the land to lay fallow for a period of time? The slash and burn technique of agriculture has been used by man for thousands of years to grow food in the tropics. The first year's crop is very good but the subsequent crops display a dramatic decline in production. Currently large areas in the Amazon basin are being cut and burned by large multi-national corporations for cattle raising. In many cases the cut trees are not salvaged for lumber but simply burned and the land planted with a single species of grass seed (Silva, 1979). In Brazil pasture land is 85% *Panicum maximum* (Toledo and Serrao, 1981). Myers (1984) refers to this as the hamburgization of the Amazon Basin. This noninflationary beef supplies the fast food restaurants of the world, particularly in the United States. The pasture cannot be sustained after 5-7 years and then more vegetation must be cut and burned (Myers, 1984). There are reports, however, that maintain the pastureland can be sustained indefinitely if fertilized (Toledo and Morales, 1979; Sanchez, 1981).

The soils of the tropical rain forest vary in structure and fertility (Richards, 1952). The distribution of soils in the tropical rain forests of the world shows a dominance of acid, infertile soils. The smallest proportion of fertile, well drained soils occur in Latin America (Sanchez, 1981). Southeast Asia has a large percentage of fertile soils (with many "problem soils") with the soils of Africa falling between these two areas (Sanchez, 1981). Technical descriptions of tropical soils have been reported by Sanchez and Cochrane (1980) for tropical America, Dent (1980) for tropical Asia, and Moormann and Greenland (1980) for tropical Africa. The knowledge of soils of the Amazon basin is more complete than for any other tropical region of the world except peninsular Malaysia (Sanchez, 1981); Cochrane, *et al*, 1979; Cochrane and Sanchez, 1981).

The classification and nomenclature of soils is confusing. The following paragraphs briefly discuss the major soils of tropical rain forest areas using the terminology employed by FAO (Food and Agriculture Organization of the United Nations). Information in this listing was taken primarily from Sanchez (1981) and Hecht (1981).

Oxisols– low fertility but with favorable physical properties. Red or yellowish. Acid, deficient in P, K, Ca and micronutrients—often with toxic levels of Al. In the New World mainly in areas affected by the Guyana and Brazillian Shield.

Pacific Coast of Colombia. In Africa in Cameroon, Gabon, central Zaire and Madagascar. Not extensive in tropical Asia.

Ultisols– low fertility, poor physical qualities (increase of clay with depth). Red or yellow. Acid, susceptible to erosion. Predominant soils of the Amazon basin west of Manaus. Dominant on Atlantic Coast of Central American and humid coastal Brazil. Abundant in tropical Asia and Africa.

The above two soil types are not susceptible to laterite formation. These two soil types occur in 63% of the world's humid tropics. In tropical America 82% of soils are either oxisols or ultisols (56% in Africa and 38% in Asia).

Inceptisols– young soils.

aquepts– (poorly drained). In Asia these soils are devoted to rice production. Half of the aquepts soils in the Amazon basin are in varzeas; the rest are aquajales (mainly palm swamps).

andepts– (volcanic origin). Lack high phosphorus fixation capacity. Important in Philippines, Java, Sumrata and parts of Central America.

tropepts– (well drained, non-volcanic). Moderate to high fertility. Not extensive in tropical America or Africa.

Entisols– recently developed.

fluvents– along major river valleys. Common in Asia.

psamments– deep sandy, acid, low fertility. Western portion of Congo Basin, some areas of Brazil and Asia.

Alfisols– many cannot be separated from oxisols and ultisols without chemical analysis. Most are deep, well drained and red or yellow. Occur in spots surrounded by oxisols and ultisols in the Amazon Basin. Fertile. In Africa, however, they have a sandy gravelly surface underlaid by plinthite. This soil becomes acidic when fertilized and are the dominant soil of the forested zone of West Africa.

Vertisols– heavy clay soils that shrink and crack with changes in moisture. They are well supplied with nutrients except for nitrogen and phosphorus. Not abundant in tropical rain forest.

Mollisols– are highly fertile, typical of temperate grasslands, with a spotty distribution in the tropics.

The alfisols, vertisols and mollisols, plus andepts, tropepts and fluvents are the best soils of the humid tropics but account for only 221 million hectares or 15% of the area of the humid tropics (7% in tropical America but 33% in Africa).

THE COUNTERFEIT PARADISE. A review of any general ecology text will show that the natural productivity of tropical rain forests exceeds or equals that of any ecosystem on the planet (Odum, 1971; Whittaker, 1975). If the soils are poor and sustained European and North American agriculture is not possible, why is the natural forest so productive? The entire nutrient capital necessary for continued growth is tied up in the living matter itself (Walter, 1971). One way of viewing this is to compare the distribution of carbon in a typical coniferous forest versus a typical tropical rain forest (Odum, 1971). Approximately 50% of the carbon in the ecosystem of the northern coniferous forest is located in the soil versus less than 20% in the soil of the tropical rain forest. The tropical rain forest may be viewed as epiphytic upon the soil (Anderson, 1981). The concept of great fertility was supplied by early conquistadors (Jordan, 1982) as Europeans commonly equated the sizes of trees with soil fertility. However, the tropical rain forest, although very productive in the natural state, gives a false impression of fertility from man's temperate agricultural point of view; thus the term "counterfeit paradise" (Meggers, 1971) is used to express the contradiction.

Sustained agriculture does not seem to be possible in most regions of the tropics, for with removal of the vegetation the soil nutrients, low to begin with, are leached by the heavy rains to levels that cannot sustain a harvest to justify the energy input needed. How does a tropical rain forest ecosystem manage to maintain the nutrients in the living biomass? The theory that nutrients are

intercepted and taken up rapidly before they are lost from the system is called direct nutrient cycling and was put forth by Went and Stark (1968). It is direct because the nutrients move directly from decomposing organic matter to roots via mycorrhizae (Jordan, 1984) and by-pass the soil. Very few workers have tested this theory but in a study of nutrient retention in the Amazon Basin, Stark and Jordan (1978) sprayed radioactive labeled P and Ca directly on the root mat. Less than one tenth of 1% of the radioactivity applied to the study plots was recovered. One month after application no levels of radioactivity could be detected in the study plots. In this area of study (oxisol soil type) the roots occurred primarily in the humus layer, near the surface, and in some places formed a mat 10-30 cm thick on top of the mineral soil. Indeed in some areas the root mat could be peeled from the soil like a carpet (Stark and Jordan, 1978).

There are other means whereby trees in the tropical rain forest conserve and allocate minerals. In some types of tropical rain forest, such as moist subtropical montane forest, canopy lichens are a source of nitrogen (Forman, 1975). Lichens containing blue-green algae (*Nostoc*, *Gloeocapsa*) capable of fixing atmospheric nitrogen are common in Colombia. An estimated 13,600 macrolichens per hectare were found to contain *Nostoc* (biomass 5.7 k.7 kg/ha). Fixation of nitrogen by these lichens yielded an estimated 1.5-8 kg N/ha/yr. The death of lichens and steady precipitation would presumably distribute nitrogen in the ecosystem (lichens are rare in forests with a pronounced dry season).

Another means whereby trees in tropical rain forests gain access to nutrients has recently been elucidated. In the montane cloud forest of Costa Rica, twenty-two species of trees have been found with canopy roots (Nadkarni, 1981). Epiphytes (particularly bromeliads) are common in the tropical rain forest and have been considered by some workers to be "nutrient pirates". The roots and leaves of many epiphytes accumulate organic material (fallen leaves, tissue produced by the growth of the epiphyte, etc.). The host trees in some instances put forth adventitious roots that run beneath these mats of accumulated organic matter and utilize the minerals (Nadkarni, 1981).

Although the root mat of the tropical rain forest is very good at capturing minerals there is leakage from the ecosystem. An important source of minerals to replace the leakage, particularly in the Amazon Basin, is precipitation (Jordan, 1982). In an area at Rio Negro (Jordan, 1982) which receives 3,500 mm annual rainfall (with no month receiving less than 100 mm), nutrient input via precipitation was measured over a two year period. It was concluded that input of minerals via rainfall exceeded loss of minerals via leaching (raining fertilizer). Therefore weathering of rock really is not contributing to the nutrient economy of the forest.

CONSEQUENCES OF DESTRUCTION. The climax tropical rain forests of the world are being destroyed at a tremendous rate (Table 1). The slash and burn method of agriculture is being abandoned in large areas in favor of cattle ranching, or forest is simply totally cut to make composite wood (De'Ath, 1980). Man has been utilizing the tropical rain forest for a long time. The oldest evidence of human presence in the interior Amazon Basin for example is 3,750 years B. P. + 20 (Sanford, Saldarriaga, Clark, Uhl and Herrera, 1985).

In the method of slash and burn agriculture, small areas of forest are cut, allowed to dry and are then burned. After growing crops for one to two years, the plot is abandoned and allowed to revert again to forest. Thus plant succession is allowed to repair the damage to the original forest. In the succession process, seeds that remained in the soil germinate (Ewel, Berish, Brown, Price and Raich, 1981), and stump sprouting may occur if the fire was not too intense; seeds of primary tree species are brought in by animals (Foster and Brokaw, 1982). Actually, disturbance of vegetation, especially by fire, appear to have played major roles in the history of tropical rain forest vegetation. Earthquakes occasionally denude large areas of tropical forest especially in mountainous areas such as New Guinea and Central America (Garwood, Janos and Brokaw, 1979). Recent evidence indicates that charcoal is common in the soils of mature rain forest in the north central Amazon Basin. The fires which formed the charcoal may have been common for the past 6,000 years (Sanford, *et al*, 1985). Treefalls in mature tropical rain forests occur often enough (one per hectare every 5.3 years) and create large gaps over 150 sq m to allow pioneer trees to colonize (Brokaw, 1982). Also aridity in the Pleistocene has apparently affected the evolution of tropical rain forest. Ten thousand years ago, in the Peten in Guatemala, vegetation consisted of marsh, savanna and juniper scrub (Leyden, 1984). Thus the rain forests of Guatemala are no older than 10,000–11,000 years (Leyden, 1984).

The point is that tropical rain forests have been disturbed for thousands of years and plant succession has been a factor in the repair process. Slash and burn agriculture has been successful for man because it imitates the natural disturbances of the forest. However, what is going to happen to the forest and the people now that large areas are being cut and losing contact with uncut regions?

Gomez-Pompa and Vazquez-Yanes (1972) suggested that the primary trees of the tropical rain forest would be incapable of regenerating under present land-use strategies. The primary trees originate from neighboring uncut areas. As large expanses of land are utilized the sources of seeds become smaller and the numbers of dispersal agents also diminish. After a period of time only secondary species are capable of surviving. These species are generally lower in stature and the biomass lower. Indeed there may already be areas in the world where only secondary vegetation can occur. As a result there is a great loss in diversity and gradual erosion of the ecosystem. Recent work on ecosystem decay (Lovejoy, Rankin, Bierregaard, Brown, Emmons, and Van der Voort, 1984) suggest that the above theory is correct.

In wet tropical rain forest there are two main groups of seeds according to their germination behavior. One group comprises seeds (canopy species) which germinate in stable conditions on the forest floor. The trend is for rapid formation of partially or totally dormant seedlings that are less susceptible to predators (Vazquez-Yanes and Segovia, 1984). The second group of seeds has delayed germination adapted for establishment in gaps and other disturbances (secondary species; Vazquez-Yanes and Segovia, 1984). With the cutting of large areas of tropical rain forest, rainfall patterns may be greatly altered. It has long been observed in tropical areas of the world that the cutting of vegetation seems to decrease rainfall. Another con-

sequence of destroying the vegetation is an increase in water runoff from the land followed by erosion. For example, the Amazon River has a discharge (5.5 N 10 m yr) five times that of the Congo and represents 15-20% of the *global* freshwater supply (Salati and Vose, 1984). In the Amazon Basin about 50% of the rainfall is evapotranspired as water vapor back into the atmosphere, of which 48% falls again as rain. This represents a recycling rate of about 5.5 days. Detailed studies at Manaus (2,000 mm/yr) indicate a much higher evapotranspiration rate. In one study 18.7% of rainfall was intercepted by the forest and evaporated back, 62% was transpired and 19.3% was runoff; in another study the figures were 25.6%, 48.5% and 25.9% respectively (Salati and Vose, 1984). The implication is that large-scale deforestation, if continued at current rates, must inevitably affect the present equilibrium of the water cycle (Salati and Vose, 1984). The effects could be continental or global. As noted earlier the tropical rain forests in Africa occupy the smallest area of the three areas of concentration. Compared with rain forests on other continents, the African tropical rain forest is relatively dry and receives between 1600 to 2000 mm rainfall per year (distribution is also uneven; Tucker, Townshend and Goff, 1985). The areas receiving more than 3,000 mm per year are largely confined to the coast. Analysis of the African rain forest throughout the year using satellite data dramatically displays the large areas that are affected by seasonal dry patterns. If rainfall is indeed reduced by cutting of the forest, fire may begin to play a major role and desertification processes set in motion.

INTERACTIONS–MOSTLY INSECTS. Tropical rain forests are not only structurally and physiologically very complex but the interactions organisms are perhaps even more complex. As Myers (1984) states, "After all, if there are 1,000 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". Ecological interactions have long been recognized as important factors influencing the evolution of species, but few explicit models of the evolution of these interactions exist. One possible way of explaining this lack of information is that the interactions are more ephemeral and less tangible than species, but certainly must be the result of evolution (Thompson, 1982; Futuyma and Slatkin, 1983). It is important, in terms of evolutionary ecology, to study the origin of interactions (Thompson, 1982) and their patterns.

Gilbert (1980) suggests that patterns of chemical defenses (and of insect feeding) are generated by a process of coevolution between plants and their parasites. He coined the terms "mobile links" and "keystone mutualists" to describe interactions between certain key organisms in tropical rain forests (Gilbert, 1980). Animals (as Euglossine bees) that are major factors in the presistence of certain plant species which also support separate food webs are called mobile links. Keystone mutualists are those organisms which provide support to large complexes of mobile lines (many are successional species of plants, as species of *Heliconia* and members of the Solanaceae).

The various kinds of interactions can be divided roughly into negative or antagonistic, and mutualistic (Thompson, 1982). Antagonistic in-

teractions occur between species because living organisms are concentrated packages of energy and nutrients and because resources are limited (competition; Thompson, 1982). The most common categories of these interactions are parasitism, grazing, and predation. Competition differs greatly from other kinds of interactions because species that initially have similar use of a resource diverge in time (Thompson, 1982). This makes competition generally less likely to lead to long-term coevolution of sets of species than other forms of antagonistic or mutualistic interaction (Thompson, 1982).

In mutualistic interactions associated members receive some sort of benefit which enhances their general fitness. Mutualisms seem to be more common in tropical areas, particularly in regard to pollination systems, seed dispersal and extrafloral nectary systems. However, species richness, biomass, diversity, and productivity also increase in the tropical rain forest and there must be an increase in the number of interactions.

A good example of the change of interactions from antagonistic to mutualistic is the interaction between plants and the animals that pollinate them. The habit of feeding on spores is very old for terrestrial arthropods (Malyshey, 1968, in Strong *et al*, 1984) and apparently early insects pollinating angiosperms fed on pollen, ovules, etc; undoubtedly the vast majority of these interactions provided a basis for natural selection. The transition from antagonism to mutualism, favoring pollination by insects over pollination by wind may have been a consequence of changing climates selecting against wind-pollination. Benefits of insect pollination may have outweighted pollen and ovule loss and conferred a net energy gain compared to decreasing efficiency from wind pollination (Raven, 1977; Thompson, 1982). Furthermore, the development of floral nectaries reduced the cost of interaction relative to the gain.

As noted in Table 1 ants are abundant in tropical rain forest. Spectacular mutualistic interactions have been described in which ants act as protective agents of plants against herbivores and competing plants (Dirzo, 1984; Janzen, 1966). Ants interact widely with a variety of other life forms, doing or performing such activities as seed harvesting, leaf cutting, tending ant-gardens, or pollinating. These interactions between plants and ants have been classified in different ways using a variety of categories (Huxley, 1978; Buckley, 1982; Schemske, 1983).

An example of mutualistic interaction between ants and a plant is given below, in which the ants receive domantia and food; presumably the plant receives an increase in fitness.

Schomburgkia tibicinis (Orchidaceae) occurs throughout Central America in a variety of habitats (Jones, 1965). The plants are most often found growing high in large trees throughout tropical regions of Central America making observation difficult; however, a unique shrub community with a maximum height of 2 m on the Yucatan Peninsula, offers easy access to large numbers of *S. tibicinis*. This area, called a matorral by Miranda (1958), stretches across the northern coast astride a series of old parallel beachheads and is bracketed by sand beach and mangrove swamp or mixed tropical deciduous forest. The interactions occurring between the ants and plants on the matorral are assumed to be similar to those in wetter habitats throughout Central America.

Although a few plants can be found in anthesis throughout the year, the peak flowering period of *S. tibicinis* occurs from the middle of the dry season to the beginning of the wet season (April-June). Orchid clumps may be readily spotted from great distances as their flowering peduncles rise 1.5 to 2 m above the tops of the shrubs (ca 138 clumps per ha).

The plants of *S. tibicinis* have large, hollow pseudobulbs (to ca 4 cm in diameter and 40 cm long) with a coin-like slot at the base that are inhabitated by ants. A wide variety of animals may also live among or in old and new pseudobulbs, including snakes (boas are common), mole crickets, millipedes, and bees. Thirteen species of ants live in the hollow pseudobulbs, in old inflorescence spikes or in the soil directly beneath the plants. The ant species are as follows: *Azteca* sp, *Brachmyrmex* sp, *Camponotus* (*Myrmobrachys*) *planatus* Roger, *Camponotus* (*Myromcladoecus*) *rectangularis* Emery, *Camponotus* (*Myrmothrix*) *abdominalis* Fabricius, *Crematogaster* (*Orthocreama*) *brevispinosa* Mayr., *Ectatomma tuberculatum* (Oliver.), *Monomorium* (*Carbonarium*) *ebeninum* Forel, *Paratrechina longicornis* (Latreille), *Pseudomyrmex* sp A, *Pseudomyrmex* sp B, *Pheidole* sp, *Zacryptocerus* (*Harnedia*) *maculatus* (Fr. Smith). Although in most cases several species of ants occupy the same plant, strong territoriality separates the species; two species of ants never occur or nest in the same pseudobulb. Only six species of ants utilize the inflorescences of the plant: *Camponotus rectangularis, Camponotus planatus, Crematogaster brevispinosa, Ectatomma tuberculatum, Pseudomyrmex* sp, and *Pheiodole* sp. All these ants take nectar from developing peduncles, floral buds and parts of the mature fruit. If the ants are removed from the inflorescences, nectar drips from these various plant structures. However, only one species of ant occupies a given peduncle of inflorescence. The same species will dominate all such structures produced by a given orchid plant (clump).

One species, *Crematogaster brevispinosa*, herds the common citrus mealybug, *Plannococcus citri,* and perhaps other species, on the developing peduncles of *S. tibicinis*. Of the plants dominated by *C. brevispinosa*, 80% have mealybugs on some of their peduncles. The ants guide or carry the mealybugs to the apical meristem of the peduncle and the mealybugs feed by inserting the proboscis into the sieve cells of the outer layer of tissue. The ants take the honeydew from the anus of the mealybugs. As the peduncle grows (rate of ca 1 cm/day) the tissue becomes woody and the ants then move the mealybugs to the tip. Upon molting, the mealybugs leave their exoskeletons with proboscis inserted into the peduncle and the liquid that exudes is also harvested by *C. brevispinosa* until all the stalk tissue becomes woody and dripping ceases.

It is obvious what the ants receive from this relationship, but do the plants receive any benefit? Observations suggest the ants drive off herbivorus insects that feed on the peduncles, flowers and fruits of the orchid. The fruit and flowers of plants without ants are usually partially or wholly eaten. Perhaps the ants increase the reproductive fitness of the plants and the plants derive nutrients from material carried by ants into pseudobulbs.

Undoubtedly there are thousands (or ten or hundred of thousands) of mutualistic interactions taking place in the tropical rain forest, involving not only ants but many other types of insects. An example of ants protecting sa-

plings from herbivores was only recently elucidated. Koptur (1984) determined that *Inga densiflora* and *Inga punctata* have foliar nectaries that are visited by a variety of ants. Extrafloral nectar secretion on new leaves is continuous throughout the day and night; ant activity on both old and new leaves is also continous. Experiments were performed to compare the effectiveness of the five ant species in removing caterpillars and other insects from the leaves. All ant species tested could remove herbivores, but *Pheidole biconstricta* was the most effective. Leaves from saplings with ants excluded suffered substantially greater damage than control leaves.

Interactions of saplings and insects in tree gaps appear to be important in determing the structure and function of tropical rain forests. The evolution of different antiherbivore systems may depend on the risk of discovery by herbivores (escape). In a study of herbivory on Barro Colorado Island, Panama, Coley (1983) showed that saplings of the pioneer and permanent trees in the gap are equally easy for insects to locate. She suggests specialized herbivores and not escape is the major factor in herbivory. Apparently pioneer species are simply able to tolerate high rate of herbivory because of cheaper leaves and faster growth rates (Coley, 1983). Habitat quality is suggested as a major selective force behind the evolution of different defensive systems. A high quality habitat is one in which rapid growth is possible. Thus in low-quality habitats the vast majority of plants would have defensive systems (chemicals, leaf fibers, etc.) whereas a mixture of defensive and non-defensive systems would prevail in a high quality habitat (Coley, 1983).

As noted by Gomez-Pompa and Vazquez-Yanes (1972), any isolated tree from a temperate forest has a greater probability of survival than an isolated tree from a tropical rain forest (primary species); this is due to the complex and delicate net of relationships of each individual with the environment.

THE FUTURE. The success of the 300,000 species of angiosperms has been largely attributed to the evolution of the mutualistic interactions of insect pollination (Burger, 1981). The future for thousands of organisms in the tropical rain forests of the world is dim. A great deal is at stake, for if these species are lost, so is the chance for discovery of new drugs. Furthermore, we may see a change in the climate of the world and collapse of the human population.

Good insight into what will be lost if large portions of the tropical rain forest are not preserved is offered by the example of the plants preserved in the Rio Palenque research station on the western coast of Ecuador (Dodson and Gentry, 1978). The entire tropical rain forest on the western coast of Ecuador has been converted by man into plantations. All that remains is 1.7 km. However, this area supports 1,025 plant species, the highest recorded concentration of plant diversity on Earth (Myers, 1984). One of these plants in the small reserve, which is gradually being undermined by the local people who are illegally cutting fire wood, is a relative of the cultivated avocado which, by supplying a rot-resistant root stock, could offer commercial benefit to avocado growers in many parts of the world. Another species of plant is a relative of cocoa which reputedly yields a tastier form of chocolate. Yet another species is a fast-growing tree (endemic to the station) which used to be the tree most favored by timber harvesters in the region (Myers, 1984). Approximately 20% of the plant species occurring at Rio Palen-

que are endemic to the station (Dodson and Gentry, 1978). The loss of vast areas of tropical rain forests throughout the world would clearly be a decline in the stability and quality of life for man. As Prance and Elias (1977) so well stated "Extinction is Forever".

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