
9 Impact of Biodiversity on Tropical Forest Ecosystem Processes

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9.1 INTRODUCTION

Organisms in tropical forests are being subjected to massive disruptions in the form of wholesale exchanges of species among regions, introduction of alien predators and pathogens, overharvesting, habitat destruction, pollution, and, in the future, climate change. Changes in land use in the tropics are creating extensive areas of agricultural land, pasture and early successional patches at the expense of late successional and mature forest communities. Accompanying these changes are major reductions in the sizes of populations, and extinctions of species that depend upon the habitats that are being destroyed. Rates of forest destruction and subsequent species loss are higher in tropical regions today than elsewhere on Earth (Sader and Joyce 1988; Whitmore and Sayer 1992; Wilson 1992; FAO 1993). The ecosystem-level consequences of these changes are not well known and, unfortunately, loss of species is irretrievable.

Relative constancy of temperature characterizes tropical regions, but total annual rainfall and the length and severity of dry seasons varies strikingly with topographic position and latitude. Seasonality of rainfall exerts a strong influence on temporal patterns in primary and secondary production (Janzen and Schoener 1968; Opler *et al.* 1976; Lieberman 1983; Leighton and Leighton 1983; Bullock and Sólis-Magallanes 1990; Loiselle 1991), and on temporal variations in rates of decomposition (Birch 1958; Jordan 1985; Leigh *et al.* 1990). Species richness in most taxa of macroorganisms is positively correlated with annual rainfall (Gentry 1988) and inversely correlated with the length of the dry season, both variables being strongly correlated in tropical regions.

Moist lowland tropical forests are characterized by both high richness of species in many taxa and complex biotic interactions and linkages. Most tropical plants are animal-pollinated (Bawa 1979, 1990; Bawa and Beach



1981; Baker *et al.* 1983; Bawa and Hadley 1990). They are fed upon by a wide variety of animals, ranging from highly specialized to generalized species (Dirzo 1987), and they also depend upon animals for dispersal of their seeds (Levey *et al.* 1993; Estrada and Fleming 1986). Many biologists have assumed that tropical animals are, on average, more specialized in their diets than their temperate counterparts (Janzen 1973, 1980; Gilbert and Smiley 1978; Beaver 1979), but there are insufficient data on the diets of most tropical organisms to either support or reject this view (Marquis and Braker 1992). Similarly, ecologists cannot yet distinguish between the competing hypotheses that "tropical ecosystems are species-rich because they are stable," that "tropical ecosystems are stable because they are species-rich", or that "tropical ecosystems are species-rich because they are unstable" (MacArthur 1972; Brown 1981; Karr and Freemark 1983; Lugo 1988a).

9.2 ENVIRONMENTAL GRADIENTS IN TROPICAL FORESTS

Gradients in moisture, soil fertility and elevation constitute the most important variables in tropical forest environments. Changes in any of these environmental attributes are likely to affect the performance of functional groups or to cause shifts in the relative abundance of functional groups within tropical ecosystems.

9.2.1 Moisture

In tropical regions, annual rainfall varies from near zero in the Atacama Desert in northern Chile, and a few centimeters in the Guajira Peninsula of northern Colombia, to more than 10 m in the upper San Juan Valley of western Colombia and in northeast India. Over much of the Neotropics there is a good correlation between total annual rainfall and the length of the wet season because the amount of rainfall during wet months is relatively constant over broad areas. However, many regions in southeast Asia have extremely high rainfall during the summer monsoon, combined with a long dry season. Other areas have low rainfall fairly evenly distributed over the year (Walter 1973).

A decreasing gradient in moisture is likely to be associated with a higher frequency of fires. Because fires affect functional groups differently, ecosystem processes may be altered accordingly. For example, if understory shrubs are more affected than trees, the resources upon which a large number of pollinators and fruit eaters depend in tropical dry forests may be extensively diminished by fire, altering the energy flow interface at the level of primary consumers. Fires also favor animals able to escape by moving out of the area or by burrowing (Braithwaite 1987).

Production of flowers, fruit and litter is more clumped temporally in regions with long dry seasons than in regions of relatively constant rainfall (Opler *et al.* 1976; Foster 1982a,b; Lieberman 1982; Leighton and Leighton 1983). Therefore, the flow of energy occurs in marked pulses in tropical dry forests, and the temporal concentration of litterfall concentrates patterns of nutrient retention and transfer (Silver *et al.* 1996). The relative importance of plants that flower and fruit during the driest season is probably also positively correlated with increasing dryness.

When tropical soils become saturated with the first heavy rains following a lengthy dry period, there is often an increased incidence of treefalls (Brokaw 1982; Brandani *et al.* 1988). Thus, as dry seasons increase in duration, the temporal clumping of treefalls becomes more pronounced. Drying/wetting cycles also accelerate the replenishment of the available soil nitrogen pool from microbial, recalcitrant or physically protected nitrogen pools. Fluctuations in soil moisture cause crashes in populations of soil microbes that induce pulses of nutrient release. These cycles in soil nutrient availability and moisture may increase the uptake of limiting nutrients by plants (Lodge *et al.* 1994). With increasing length of dry season, the drying of the soil becomes more extreme and the pulsing of microbial populations and nutrient release probably become especially marked, but the influence of this pattern on ecosystem productivity and the efficiency of natural nutrient cycling is yet to be determined. Although extreme drying of the soil is associated with long dry seasons, even relatively brief rainless intervals can cause large reductions in soil moisture. At La Selva, Costa Rica, a site without a well-marked dry season, there was a 40% reduction in total soil moisture content in the upper 70 cm of soil following a 1-month period without significant rainfall. Such reductions are sufficient to cause water stress in the forest vegetation (Sanford *et al.* 1994).

9.2.2 Fertility

Although belief that all tropical soils are red, infertile and harden irreversibly when they are cleared is widespread, soils of the lowland tropics are as diverse as those of any other region. Infertile red and yellow oxisols and ultisols are common throughout the tropics, but red, infertile soils are found on only about 7% of the tropical landmass (Sanchez 1976), and there are significant areas of highly fertile soils along rivers and in volcanically active areas. A reduction in species richness, vegetation layers, canopy height and mean leaf sizes is associated with decreases in soil fertility in tropical forests (Brunig 1983). Data from the few tropical forests that have been studied intensively enough to provide good comparative information have been summarized by Jordan (1985). The sites range from a forest on a rich dolomite soil high in magnesium- and calcium-carbonate in Darién,

Panama, to forests on infertile spodosols and oxisols at San Carlos, Venezuela. Changes in ecosystem functioning associated with the gradient from high to low soil fertility are listed below.

1. Decreasing production. Productivity of leaf litter ranged from $11.3 \text{ Mg ha}^{-1} \text{ year}^{-1}$ at Darién to $4.95 \text{ Mg ha}^{-1} \text{ year}^{-1}$ at San Carlos. Wood production data are not available from the most fertile sites, but the medium-fertility sites had nearly double the production of the least fertile site, suggesting that the range in wood production is comparable to that for leaves.
2. Reduced above-ground biomass but increased below-ground biomass. Standing above-ground biomass varied by a factor of two, whereas below-ground biomass varied by a factor of 10. As a consequence, root-shoot ratios ranged from 0.03 at Darién to 0.49 at San Carlos.
3. Reduced decomposition rates. Trees on fertile soils produce large quantities of nutrient-rich non-scleromorphic foliage that decomposes rapidly. In contrast, trees on infertile soils produce smaller quantities of nutrient-poor, scleromorphic leaves that decompose more slowly. The rate of leaf decomposition varied by nearly a factor of five along the soil fertility gradient.
4. Increased percentage of roots in a superficial mat. 20–25% of the roots in the forests at San Carlos are in a superficial mat; such mats do not exist in forests on fertile soils.
5. An increase in the relative allocation of plant resources to defense (Coley *et al.* 1985) and a reduced allocation to reproduction (Gentry and Emmons 1987). These differences in resource allocation contribute to the slower decomposition rates of litter in forests on infertile soils, and result in lower populations and richness of species of animals that depend on pollen, nectar and fruits.
6. A reduction in species-richness, vegetation layers, canopy height and leaf sizes (Brunig 1983).

9.2.3 Elevation

Associated with increasing elevation on the slopes of tropical mountains are increasing wind, rainfall and water logging of soils, and greater incidences of landslides (Leigh 1975; Lawton and Putz 1988). The following biological changes are correlated with these physical changes.

1. Decreasing productivity. Few data are available for tropical premontane forests, but litter production at montane sites in the Luquillo Experimental Forest in Puerto Rico is only half as great as in productive lowland forests (Odum 1970), and wood production is similar to that in lowland forests on highly infertile soils.

2. Decreased above-ground biomass but increased below-ground biomass. The root mass at El Verde, Puerto Rico, is greater than that of lowland forests on rich soils by about a factor of six, but above-ground biomass is lower by only a factor of two, in part because the leaf biomass of the premontane forests is similar to that of lowland forests.
3. Reduction in decomposition rates and an increase in litter accumulation. These changes increase nutrient retention in decomposing litter and decrease rates of nutrient transfer. Litter accumulation also dramatically alters the soil surface and the composition of the litter fauna.
4. Lower species richness in most taxa (Terborgh 1977; Janzen 1987).
5. A reduction in the diversity of plant life forms. Canopy height decreases, palms drop out with increasing elevation, and there is an overall reduction in leaf sizes (Leigh 1975; Tanner and Kapos 1982; Brown *et al.* 1983). In addition, there are shifts in the relative representation of life forms. Vine and lianas become less common and epiphytes increase in abundance and structural diversity (Brown *et al.* 1983), which increases nutrient capture, nutrient retention and nutrient transfers at the atmosphere-terrestrial interface (Silver *et al.* 1996).

9.3 STABILITY AND SPECIES RICHNESS

Discussions of the degree and causes of stability are frequently hampered by vagueness and inconsistency about what is meant by stability (Orians 1975). Stability may simply mean constancy, that is a low level of variation in some measurable property of the system. Stability may also refer to the resistance of the system to alteration by external perturbations (inertia), its speed of return to initial conditions following a perturbation (elasticity or resilience), the domain over which it returns to its initial state (global stability), and the tendency of the system to cycle in a predictable manner (cyclic stability). These varied properties, all of which are important components of overall stability, are often affected by different external factors, and these components of stability frequently respond differently to the same factors. In our analysis of the functioning of tropical forests, we attempt to address how all of these components of stability may be influenced by losses of biological diversity.

An important result of the past three decades of theoretical and empirical research on the *causes* of patterns in species richness is the demonstration that these patterns are the products of complex interacting forces that vary in relative importance in both time and space (Solbrig 1991). The *consequences* of biological diversity for system-level processes are also the products of many factors operating at variable spatial and temporal scales,

but these relationships have received much less attention than the causes of biological richness (Schulze and Mooney 1993).

In this discussion, we follow Lawton and Brown (1993) in treating "ecosystem processes", "behavior of ecological systems" and "ecosystem functioning" as equivalent terms. We do not use the term "ecosystem function" because we do not believe that ecosystems have goals or objectives. As a result of the activities of organisms living in them, ecosystems process materials and energy, and the efficiency and stability with which they do so is likely to be influenced by biodiversity. By "biodiversity" we mean not only the number of species (species richness), but also genetic variants within a species, evolutionary lineages, functional groups of organisms, and ecological communities. However, we concentrate here on species richness, in part because little is known about the genetic structure of populations of tropical species (but see Hamrick and Loveless 1989; Loveless and Hamrick 1987; Equiarte *et al.* 1993), but also because the task of erecting a classification of types of tropical forests and analyzing how biotic interactions differ among them remains to be accomplished.

In this chapter, we concentrate on relatively undisturbed lowland tropical moist forests, that is forests that receive more than 2000 mm year⁻¹ rainfall, but we briefly discuss the significance of moisture and elevational gradients for interactions between biodiversity and forest functioning. We also direct most of our attention to biotic interactions at local scales, realizing that landscape-level patchiness might modify the conclusions reached from a regional- versus local-scale analysis.

9.4 FUNCTIONAL GROUPS

The number of species in all ecological communities, especially tropical ones, greatly exceeds the number of key ecological processes. We refer to the species that participate in a particular process as a functional group (Vitousek and Hooper 1993). Functional groups are inevitably fuzzy assemblages, but they constitute a useful operational basis for identifying groups of species with potentially similar effects on ecosystem-level processes. If the loss of a species results in a large effect on some functional property of the ecosystem, that species may be called a keystone species (Gilbert 1980; Bond 1993).

Traditionally, ecologists have looked for and identified keystone species by their effects on the species richness and composition of the community in which they live. Here we explore keystone taxa that have major consequences for ecosystem processes, such as primary and secondary production and nutrient cycling. In this context, a keystone species may or may not significantly change the species composition of its community. The existence

of keystone species shows that not all members of a functional group are of equal significance for the process in which the group participates.

9.5 ENERGY FLOW AND MATERIAL PROCESSING INTERFACES

Analyzing the functional significance of biodiversity is a difficult task because there are no widely accepted schemes for classifying functional groups, and no single classification can aggregate organisms appropriately for more than one major ecosystem process. In our analysis of tropical forests we use two major ecosystem processes – energy flow and materials cycling – as the primary basis for establishing functional groups. We analyze these processes by examining interfaces at which most of the energy or materials are exchanged. At each of these interfaces there is a discontinuity of resource availability that is used by groups of species as an energy or nutrient source (Table 9.1).

Because energy is consumed and not recycled, flows along most energy pathways are unidirectional, and much energy is lost as heat at each transfer. Flow of materials at interfaces is typically bidirectional, but transfer rates are not necessarily equal. Indeed, because changes in relative rates of transfer of materials at interfaces may trigger major changes in ecosystem functioning, species that influence transfer rates are likely to be keystone species.

We emphasize that the amount of energy flow or material transfer at different interfaces may be a poor indicator of the significance of an interface for the ecosystem processes that are affected. For example, the transport of a small amount of energy and material by a pollinator may catalyze large investments by plants in fruit and seed production, with subsequent effects on population sizes and dynamics of frugivores, and, on longer time frames, on recruitment of plants (Terborgh 1986b). Similarly, the quantities of nutrients transferred may be an inadequate measure of the importance of an interface for ecosystem processes. Mobilization or immobilization of modest amounts of nutrients may also trigger large responses on the parts of organisms, with cascading effects in the ecosystem.

9.6 BIODIVERSITY AND FUNCTIONING OF TROPICAL FORESTS

The extent to which human activities are leading to the extinction of species in tropical forests is uncertain, but current rates of loss of tropical moist forests are extremely high (Whitmore and Sayer 1992; Wilson 1992; FAO

Table 9.1 Ecological interfaces where large amounts of energy or materials are exchanged

Energy flow		Materials processing		
Interface	Processes	Interface	Process	Organisms that live on the interface
Atmosphere-plant	Photosynthesis, transpiration	Atmosphere-organism	Capture and retention of nutrients, release of CO ₂ , CH ₄ , volatiles	Epiphytes
Within-plant	Carbon allocation to tissues, consumption of different plant tissues	Within-plant	Storage and translocation of nutrients, discard and uptake of nutrients	All plants
		Plant-soil		
Animal-animal	Predation, parasitism, mutualism	Litter-soil	Nitrification, denitrification	Soil biota
Detritus-detritivore	Decomposition	Soil-water table	Recapture of nutrients from ground water, loss of nutrients to ground water	Plant roots
Atmosphere-soil	Release of CO ₂ , NH ₄ , atmospheric deposition			Soil biota

1993). If continued, they are expected to result in extinctions of many species (Reid 1992), in part because of the small geographical ranges of many tropical species. For example, many species of cloud forest plants in Latin America are endemic to isolated sites smaller than 10 km² (Gentry 1992). Among the birds of South American tropical forests, 440 species (25% of the total) have ranges of less than 50 000 km². In contrast, only eight species (2% of the total) of birds in the United States and Canada have such restricted ranges (Terborgh and Winter 1980). However, researchers do not agree on the extent of probable losses and how they might be reduced by management practices in tropical forests (Lugo 1988b; Lugo *et al.* 1993). Whatever the extent of loss of species in tropical forests,

reductions in species richness can be expected to influence functional properties of tropical forest ecosystems in the following ways.

9.6.1 Energy flow

Energy captured by photosynthesis flows through ecosystems through many pathways, whose variety is correlated with the species richness of the system. Species richness could influence the rates and quantities of energy flowing through the system in a number of ways.

Primary productivity and biomass accumulation Primary productivity of tropical forests is apparently affected by plant species richness only at levels far below those that characterize most mainland tropical forests (Vitousek and Hooper 1993; Wright 1996). Even highly fragmented and highly disturbed tropical forests have many more species than the minimum number needed to yield full primary productivity. Moreover, because nearly all tropical forest woody plants are C_3 , loss of species is unlikely to affect the diversity of photosynthetic mechanisms except among herbaceous plants, which are minor components of undisturbed tropical moist forests. Therefore, to the best of our knowledge, biomass production in tropical forests under relatively constant conditions is insensitive to species richness.

However, the rate of biomass accumulation depends strongly on the nature and intensity of disturbance, and species differ in the speed with which they respond to disturbances. Therefore, although no data are available to test the hypothesis, species richness may influence the rate at which biomass accumulates after disturbance (Denslow 1996). In addition, variability in rates of photosynthesis per unit area may be inversely related to species richness if, as seems likely, some species perform better in wet years and others perform better in dry years. That is, richness may result in buffering of production under conditions of environmental variability (Tilman and Downing 1994). Variation in performance among tropical forest tree species is to be expected, but relevant data are yet to be gathered. Because tropical forest trees do not typically form annual growth rings, gathering data to measure the extent to which tree species richness buffers primary production under variable weather conditions may be difficult, but new methods to estimate the growth rates of tropical trees are being developed (Worbes and Junk 1989).

Forests that are naturally low in species richness grow on unusual tropical soils (Connell and Lowman 1989; Hart 1990). Examples include *Mora excelsa* stands adjacent to mangrove forests (Richards 1952) and *Eperua* forests of South America (Klinge and Herrera 1983; Cuevas and Medina 1988; Herrera *et al.* 1988). However, these forests have not yet been studied sufficiently to determine their productive capacity, the degree to which that

capacity is influenced by low species richness, or whether their interannual variation in total production is greater than in forests with greater species richness.

Within-plant carbon allocation and consumption Although secondary production has received less attention than primary production, its quantity, quality and temporal patterns are important components of ecosystem functioning. Secondary production, the summation of the growth of individuals and populations of all heterotrophic organisms, is completely dependent on primary production, nearly all of which in tropical forests results from photosynthesis by green plants. However, secondary production is not a simple function of primary production because plants have evolved a number of defensive structures and chemicals that deter consumption of their tissues by herbivores, parasites and pathogens. These defenses also lower the efficiency with which consumers are able to digest those tissues (McNaughton *et al.* 1989). Relationships between primary and secondary production are difficult to measure because many consumers are small or mobile, and because traces of their consumption of plant tissues may disappear rapidly.

The quantity of secondary production and its distribution among species are both potentially sensitive to species richness because different plants allocate their primary production in highly distinctive ways (Coley *et al.* 1985). Plant species differ strikingly in the proportion of primary production they allocate to defenses, which defensive compounds they synthesize, the quantities and composition of their tissues that function to attract mutualists (Coley and Aide 1991; Davidson *et al.* 1991), and the physical and chemical composition of their wood. Because tropical climatic conditions allow heavy herbivore pressure throughout the year, tropical woody plants allocate relatively large amounts of energy to the production of chemical defenses (Levin 1978; Levin and York 1978; McKey 1979; Coley and Aide 1991) and resources that attract predators and parasites of herbivores (Simms 1992).

Plants influence animal biodiversity and productivity via two primary mechanisms. They provide the energy that supports animal populations, and they provide physical, temporal and biochemical heterogeneity. Wood, roots sap, extrafloral nectar, leaves, flowers, fruits and seeds are useful categories of tissue and fluid because they differ strikingly in their physical and chemical structure and because there appears to be relatively little overlap in the species of animals using those different tissues and fluids (Table 9.2). Thus, consumers of those tissues are usefully considered functional groups.

Consumers may also increase primary productivity by maintaining individual plants and plant populations in rapid growth phases by reducing the accumulation of living plant biomass, by reducing respiratory losses, and

Table 9.2 Plant tissue and fluid types and their consumers

Tissue/fluid type	Representative consumers
Wood	Termites, larvae of wood-boring beetles, girdling beetles
Roots	Larvae of cicadas and beetles
Sap	Ants, aphids, membrascids, some hemiptera and diptera, some marsupials
Floral nectar	Lepidoptera, hymenoptera, birds, bats
Extrafloral nectar	Ants
Leaves	Larvae of many insects, orthopterans, adult beetles, leaf-eating monkeys, sloths, tree kangaroos, understory mammals, pathogenic fungi
Flowers	Larvae of moths, flies, wasps, birds, monkeys
Fruits	Sucking insects, frugivorous birds, fruit bats, frugivorous monkeys, other mammals
Seeds	Ants, bruchid beetles, rodents, granivorous birds

by recycling nutrients. These affects are important in algal communities and grasslands, but in tropical forests, where the amount of standing biomass is high in relation to net primary production, the relatively small amount of new primary production typically consumed by herbivores probably has little effect on total net primary production (Huston and Gilbert 1996).

“Mobile link” species (Gilbert 1980), such as pollinators, seed dispersal agents and plant defense mutualists, have little impact on fluxes of energy and materials in ecological time, but they may be critical to the maintenance of the species richness of tropical forests. Many plants depend upon a small suite of frugivores for dispersing their seeds; loss of those species is expected to have major influences on the long-term population dynamics of many tree species (Howe and Smallwood 1982; Terborgh 1986a). Also, most frugivores that are effective seed dispersers are relatively large organisms, active throughout the year. Because few tropical plants have ripe fruit at all seasons, frugivores tend to be dietary generalists. Maintenance of the frugivore functional groups may depend upon the presence of a small number of tree species, e.g. *Ficus* spp., that ripen their fruits at times of year when most species are not fruiting (Terborgh 1986a). Because those frugivores may be the primary dispersers of the seeds of many other species of plants, secondary production and recruitment of plant species may depend strongly on the presence of a small subset of the total tree species in the forests.

Animal–animal interactions The animal species that eat the tissues of tropical forest plants support a complex array of commensals, predators, parasites and parasitoids. Many of these animals, such as blood parasites of vertebrates, predatory mites and parasitoid wasps, are tiny and inconspicuous, but they are thought to be the principal agents reducing herbivory in both polyculture crop systems (Andow 1984) and natural vegetation (Gilbert 1977). Thus, these tiny organisms may act as rate regulators or “energy filters” (Hubbell 1973) by controlling herbivore populations, thereby reducing both the rate at which, and number of pathways by which, primary production becomes secondary production. For example, herbivorous insect larvae, which are major consumers of primary production, are attacked by both specialist and generalist invertebrate predators that typically maintain their populations well below outbreak levels (Huston and Gilbert 1996). Social wasps and ants, which are important predators of foliage-eating insects, are, in turn, attacked by army ants. Similarly, the intensity of grazing and browsing of tropical understory plants by vertebrates such as agoutis, peccaries, deer, rhinoceroses, wild cattle and tapirs may be greatly reduced by predators such as tigers and jaguars. In forest fragments lacking these predators, browsing vertebrates can dramatically alter the structure and species composition of understory vegetation (Dirzo and Miranda 1987, 1991).

Detritus–detritivores Energy flow in ecosystems would quickly be reduced if the activities of detritivores were depressed or eliminated. The extremely high rates of decomposition of fine detritus on the floors of tropical moist forests, combined with the fact that in many, but not all (Jordan 1985; Brown and Lugo 1990), tropical forests most nutrients in the system are found in the bodies of plants, not in the soil, indicates that changes in rates of energy processing by soil detritivores have major consequences for energy flows in those forests.

Microorganisms and fungi dominate many detritivore communities, but on some tropical islands and on low-lying mainland areas adjacent to the ocean, crabs are remarkably abundant and have major effects on ecosystem processes (Cushman 1996). On Christmas Island, for example, the native red land crab, *Gecarcoidea natalis*, reaches densities as high as 2.6 m^{-2} and a biomass of more than 1 t ha^{-1} (O’Dowd and Lake 1989). These crabs defoliate uncaged seedlings of tree and vine species within days, and they remove 39–86% of the annual leaf litter. The soil near burrow entrances has significantly higher concentrations of organic matter and mineral nutrients than soil elsewhere.

The taxonomy of tropical microbes is, unfortunately, extremely poorly known, and knowledge of the functional properties of microbial species is even poorer. Therefore, we do not know how many functional groups of

tropical forest microbes should be recognized, or how many species are able to cleave particular chemical bonds in detritus. Consequently, we do not know how sensitive ecosystem processes may be to deletions of microbial species; nor do we know which functional processes are likely to have the least functional redundancy (Lodge *et al.* 1996).

Tropical trees differ markedly in tissue chemistry (Rodin and Basilevich 1967; Golley 1983a,b), suggesting that they differ both in what they remove from the soil and in what they deposit on the soil surface. Soils under the legume *Pentaclethra macroloba* at La Selva, Costa Rica, have lower pH values than soils from areas away from individuals of this species, presumably because symbiotic microorganisms associated with *P. macroloba* trees fix nitrogen, which is then nitrified (Sollins, unpublished data). Soils under female *Trophis involucrata* individuals have higher phosphorus concentrations than soils under males (Cox 1981). The meager evidence so far available suggests that trees of different species may generate significant differences in the soils in the area affected by their roots and litterfall, but whether these differences are important for regeneration, growth and species richness in tropical forests remains to be determined (Parker 1994). Several studies have failed to detect significant differences in nutrient levels of soils between evergreen forests dominated by single species and mixed forests in India (Kadambi 1942), Zaire (Hart and Murphy 1989; Hart 1990) and Malaysia (Whitmore 1975).

9.6.2 Materials processing

The movement of materials in ecosystems is often strongly tied to movement of energy, but the two processes are often unconnected. Because uptake of mineral nutrients and their movement through plants is driven primarily by evaporation of water from surfaces of leaves, it is useful to consider materials processing separately from production for purposes of our analyses of the interfaces listed in Table 9.1.

Atmosphere-organism Plants, photosynthetic microorganisms and nitrogen-fixers are actively and massively involved with direct exchanges of materials with the atmosphere, but measurements of air quality above and within tropical rain forests are rare, and almost nothing is understood about atmosphere-canopy exchange of aerosols in tropical forests. Plants intercept airborne particles, either as dry or wet deposition, and release into the atmosphere carbon dioxide (especially at night), methane, a variety of volatile organic compounds and large quantities of water. Animals and microbes also release large quantities of carbon dioxide into the atmosphere. Exchanges of these materials by both groups appear to be directly proportional to the total biomass of organisms, irrespective of its distribution

among species, except that exchange of materials is lower in systems dominated by woody plants. However, epiphytes depend primarily upon direct nutrient exchange with the atmosphere for their nutrients and water. The species richness of epiphytes is high in most tropical forests (Gentry and Benzing 1990; Gentry and Dodson 1987), but because they tend to grow on different parts of the trees, nutrient exchange rates may depend upon the richness of species in addition to their total biomass (Silver *et al.* 1996). The best evidence for the role of epiphytes in nutrient cycling comes from tropical cloud forests, where nutrient availability is often low due to low soil concentrations and waterlogging. In those forests nearly half of the foliage nutrient pool may be stored in epiphyte biomass (Nadkarni 1984). Nitrogen-fixing epiphytes, especially cyanobacteria, fix substantial amounts of nitrogen relative to other sources in tropical forests (Lodge *et al.* 1996). Also, because the volatile organic compounds produced by plants are highly species-specific, the composition of airborne volatiles may carry a signature of the species richness of the forest canopy. However, the significance, if any, of such a correlation for ecosystem processes is unknown.

Unlike most other nutrients, the major sources of nitrogen to ecosystems are precipitation and biological nitrogen-fixation by free-living bacteria and cyanobacteria, by bacteria having mutualistic associations with plants, by fungi, and by gut-dwelling symbionts of termites (Prestwich *et al.* 1980; Prestwich and Bentley 1981). In species-poor systems, such as those growing on young tropical lava flows, invasion of a single tree species and lichenized fungi with nitrogen-fixing bacteria may dramatically increase nitrogen input to the system, productivity and ecosystem development (Vitousek *et al.* 1987; Vitousek and Walker 1989). However, whether the quantities of nitrogen entering and cycling with tree-species-rich tropical forests are influenced by the number of species of free-living or symbiotic nitrogen-fixing microorganisms is unknown.

Biotic interface In tropical forests, large quantities of nutrients are stored in live biomass (Jordan 1985). As we have already pointed out, the synthesis of defensive chemicals may result in conservation of nutrients by reducing losses to herbivores (McKey *et al.* 1978; Hobbie 1992), especially in forests where leaves are long-lived (Jordan 1991). Within-plant nutrient transfer, measured as the difference between nutrients stored in live tissues and nutrients deposited in litterfall, may be significant for the conservation of some nutrients, particularly phosphorus (Vitousek 1984). Plant species differ strikingly in the defensive compounds they synthesize (Coley and Aide 1991; Davidson *et al.* 1991) and the chemical composition of their wood. These differences, combined with differences in the degree to which plants recapture nutrients prior to discarding their leaves, could result in nutrient

dynamics being influenced by tree species richness. Unfortunately, however, few studies have compared the composition of live and senesced tissues in tropical forests. (For a more extensive discussion of this interface, see Silver *et al.* 1996.)

Plant-soil Nutrients are taken up from the soil and forest floor through fine roots and eventually returned again through decomposition of litterfall and below-ground litter inputs (Went and Stark 1968; Start 1971; Stark and Jordan 1978; Cuevas and Medina 1988). The decomposition of litter is carried out primarily by microbes whose diversity and functioning are still poorly known. The role of microorganisms in the nitrogen cycle appears to be especially important for productivity and biomass accumulation in tropical forests because different plant species require nitrogen in different inorganic forms (NH_4 , NO_2 , NO_3), and nitrogen often limits rates of photosynthesis in tropical forests. An important functional group of organisms in tropical forests are endomycorrhizal fungi that have mutualistic relationships with at least 80% of tropical plants (Janos 1983). The growth of tropical moist forest trees may be especially sensitive to losses in microbial diversity because, unlike temperate forests, which have relatively few tree species but many fungal species, tropical forests have many tree species but relatively few species of endomycorrhizal fungi (Malloch *et al.* 1980). Also, large-scale, long-term conversion of forests to grasslands or cropland results in major changes in soil nutrient pools and the soil biota (Olson 1963; Hamilton and King 1983; Macedo *et al.* 1993; Henrot and Robertson 1994), which affects nutrient cycling on those agro-ecosystems and the potential for regenerating forests on those lands.

The consequences of forest disturbances for ecosystem productivity and nutrient cycling depend on the scale and frequency of those disturbances. In the Atlantic lowlands of Costa Rica, intermediate-scale experimental clear-cutting of forests on residual soils resulted in rapid, short-term increases in nutrient concentrations in soil solutions, increased percolation of water through the soil, and increased losses of soil nutrients (Parker 1994). With no additional disturbance, the large pulse of nutrients lost in percolating water was transient. Concentrations returned to predisturbance levels in less than 2 years. Small-scale disturbances, such as natural or artificial treefall gaps, do not result in increased soil nutrient availability (Vitousek and Denslow 1986) or solution losses (Parker 1994) compared with intact forest. On the other hand, large-scale, long-term conversion of forests to grasslands or cropland results in major changes in nutrient pools and the soil biota (Olson *et al.* 1968; Hamilton and King 1963; Mazdeva *et al.* 1992; Macedo and Anderson 1993; Henrot and Robertson 1994). In combination with extraction of nutrients in harvested biomass, these changes cause the productivity of transformed tropical agroecosystems to decrease rapidly.

Atmosphere-soil Soil microorganisms, like the macroorganisms above ground, release to the atmosphere large quantities of carbon dioxide and methane (under anaerobic conditions), and the soil surface receives the atmospheric deposition that is not intercepted as well as throughfall and stem flow. Currently, tropical forests are a net source of atmospheric CO₂, but this is due to the reduction of the total area of forests and to extensive burning, not to loss of species *per se* (Hall and Uhlig 1991; Houghton 1991). Tropical forests release large quantities of methane to the atmosphere, much of it due to the activities of methanogenic bacteria in tropical wetlands (Bartlett and Harriss 1993). Gut symbionts of termites are also a significant source of methane (Wassmann *et al.* 1992; Martius *et al.* 1993). How emission rates of methane and other chemicals vary with biodiversity is unknown, and the lack of information on the identities and functional attributes of most soil microorganisms makes it impossible to identify the number of significant functional groups and the number of species found in most of those groups.

Soil-water table Most nutrients leave forested ecosystems through the soil. Because most tropical forests grow on deep, highly weathered soils with low nutrient-holding capacities (Sanchez 1976), the large volumes of water that move through the soil generate high potential losses of nutrients through leaching (Radulovich and Sollins 1991). Rates of movement of water on and within the soil are reduced by woody debris and fine litter, and by the extensive mats of fine roots that characterize tropical forests, especially those growing on nutrient-poor soils (Silver *et al.* 1996). Plant roots also recapture nutrients in the soil, and deep-rooted species may pump water from deep in the soil to the surface, where it may be transpired.

Empirical studies Only two studies that are useful for providing insights into the relationship between plant species richness and nutrient cycling in tropical forests have been carried out (see Silver *et al.* 1996, for more details). In Puerto Rico, Lugo (1992) compared nutrient-cycling processes between plantations with low species richness but of different ages with similar-aged secondary forests with higher species richness. The plantations had higher above-ground biomass and N and P pools than similar-aged secondary forests, but the secondary forests had greater root masses, deeper roots and higher root nutrient pools than the plantations. Plantations trees retranslocated more nutrients than secondary forest trees, so that the litterfall in secondary forests had greater nutrient concentrations, leading to faster rates of litter decomposition and nutrient mineralization. Both the greater root mass and depth of rooting, as well as the mix of

litter, were functions of species richness, but the long-term implications of these results for nutrient cycling are unclear.

Ewell *et al.* (1991) studied the influence of species richness over a period of 5 years on experimentally manipulated early forest successional plots in Costa Rica. Species richness at the end of the study ranged from zero (bare ground plots) to about 125 species in an enriched succession. Soil nutrient pools were positively correlated with species richness, which was attributed to more effective nutrient retention and maintenance of soil properties favorable for plant production. Whether such effects would persist through later years of succession is unknown.

9.6.3 Functional properties over longer temporal scales

Thus far, we have concentrated on processes occurring at a specific location and over short time-frames, i.e. on scales of a few days to a few years. However, the functioning of tropical forest ecosystems depends on the formation and maintenance of the structure of the forest, which is, in turn, the result of photosynthesis and biomass accumulation and biogeochemical cycling over many decades or centuries. The ways in which the forests respond to perturbations such as fire, drought, strong winds, unusually heavy rains, invasions of exotic species and losses of species typically found in the system are also important. These responses may be influenced by the richness of plant species in the forests that are not expressed under constant conditions.

Provision and maintenance of structure The many plant species that live in tropical moist forests can be grouped into a small number of life forms. Most species of canopy trees are similar enough in their growth forms that loss of particular species would not change the vegetation structure very much (Ewell and Bigelow 1996). However, certain life forms, particularly palms, lianas and epiphytic bromeliads, are both structurally highly distinctive and represented by a few sympatric species. Thus, these plants may function as "structural keystone species" whose removal would influence the degree to which the forests can be changed by perturbations, and the rate of recovery of the forests after perturbations (Denslow 1996).

Resistance to invasion Many exotic species have been introduced into tropical regions, as they have into temperate regions (Drake 1989). However, existing data suggest that exotic species have seldom invaded undisturbed mainland tropical forests (Ramakrishnan 1991). Weedy plants and animals are confined primarily to highly disturbed habitats. Why tropical forests are resistant to invasions by alien species is not understood (Rejmanek 1996).

9.6.4 Functional properties over larger spatial scales

Although we have not devoted much attention to processes on regional scales, the approach outlined in this paper may help us to understand how species richness influences large-scale processes. To think creatively about linkages across space, we need to have categories of materials that move across landscapes, the agents that drive their movements, the distances over which they move, and how those transfers are influenced by species richness (Table 9.3).

As indicated in Table 9.3, many linkages that connect local tropical forest ecosystems across space are probably strongly influenced by the total amount of vegetative cover, but they are probably little influenced by species richness *per se*. The variety of species present in the canopy may influence the composition of the airborne volatile organic compounds, but the significance of that relationship, if any, has not been determined. Moving animals spread diseases and plant propagules, and concentrate nutrients around their

Table 9.3 Landscape-scale linkages in tropical forests

Linkage	Process	Distance moved	Distance Effect	Influence of biodiversity
Atmosphere-organism	Release of CO ₂ , CH ₄ , volatiles, transpiration	Local→regional	Atmospheric deposition	Probably none
		Local→global	Increased precipitation	Probably none
Atmosphere-soil	Release of CO ₂ , CH ₄ , volatiles, evaporation	Local→regional	Atmospheric	Probably none
		Local→global	Increased precipitation	Probably none
Soil-water	Leaching	Local-watershed	Riparian deposition	Dependent on efficiency of root mat
	Movement of H ₂ O to watertable	Local→watershed	Recharge of ground water	Dependent on density of phreatophytes
Animal movement	Seasonal migration	Latitudinal→global	Spread of disease and propagules	Proportional to number of migrants
	Movement within tropics, breeding concentrations (birds, bats, ants, termites)	Local→regional	Nutrient concentration, local resource depletion, patchy deposition of seeds	Proportional to number of migrants

nests, roosts and resting places. Such nutrient "hot spots" may be important for the regeneration of trees and other processes. Termite mounds are an important example (Nye 1955; Cox and Gakahu 1985; Oliveira-Filho 1992).

Water distribution and quality Many tropical rivers and streams flowing through inhabited areas are polluted. Pollution alters the species richness and trophic dynamics of rivers, as found in lead- and mercury-polluted segments of the Orinoco River caused by gold mining (Pfeiffer and De Lacerda 1988), but there are no theoretical or empirical reasons to believe that resistance to degradation of water quality is related to loss of species. Similarly, the quantities of water flowing, and the temporal pattern of flows, is strongly influenced by vegetative cover, particularly the loss of forests, but the influence of plant species richness *per se* on patterns of water discharge from tropical forests is probably also small.

Atmospheric properties and feedbacks Tropical forests are currently a net source of atmospheric carbon dioxide, due to the reduction in the total acreage of forests and to subsequent burning. The sequestering of carbon by growing tropical forests is apparently poorly correlated with plant species richness. Tropical plantations can and do accumulate carbon at rates similar to, or greater than, those of natural species-rich forests of the same age (Cuevas *et al.* 1991; Ewel *et al.* 1991; Lugo 1992).

Landscape and waterscape structure Deforestation is dramatically altering tropical forest landscapes and waterscapes. Such fragmentation is evidently leading to loss of species, but how loss of species may, in turn, influence the structure of tropical landscapes or waterscapes is unclear. No existing theories predict such relationships.

Animal movements The transfer of most energy across tropical landscapes is the result of movement of animals. Tropical regions are invaded each year by many thousands of migrant birds that breed at high latitudes but winter in the tropics. Migrants may outnumber residents during part of the year in some tropical habitats. These migrants may compete with themselves and with residents for food (Keast and Morton 1980; Greenberg 1986), and they are potential agents of disease transmission, although little is known about the diseases of tropical birds or whether migrants are sources of infections in resident species.

Many species of birds, butterflies and moths migrate seasonally within the tropics, either elevationally (especially nectarivorous and frugivorous species) or from dry to wet forests during dry seasons (Stiles 1988; Loiselle 1991). These migrants are also potential movers of pathogens and they carry large numbers of propagules across the landscape. The importance of migration

corridors and suitable areas in which to live throughout the year are known to be important for the viability of populations of within-tropics migratory species, but the consequences of the potential loss of those species for the functioning of tropical forests are yet to be investigated.

In many ecosystems, bats and some species of birds assemble in large colonies during the breeding season. These colonies concentrate large quantities of nutrients in small areas, but colonies of birds in tropical forests are typically very small, and they probably have little effect on the concentration of nutrients. Notable exceptions are bat roosts in caves and the large colonies of oilbirds (*Steatornis caripensis*) that nest in caves along the Andean chain in South America. These birds carry large quantities of fruits, particularly of palms and lauraceous species, into their breeding caves, where the regurgitated seeds may accumulate to depths of several meters on the cave floors (Snow 1962), but these nutrients are, for the most part, unavailable to growing plants.

Animals may have a variety of effects on nutrient processing in tropical forests. Among these soil mixing and promotion of aggregate soil structure by earthworms and burrowing mammals, redistribution and concentration of canopy tissues in the soil, release of methane by wood-eating insects having methane-producing gut symbionts, and production of readily decomposed frass and feces. In Neotropical forests, leaf-cutting ants concentrate large quantities of nutrients in and around their large subterranean nests (Haines 1975). Most of these processes are influenced by many species of animals, but because typically one or a few species of leaf-cutting ants dominate a particular forest, nutrient-concentrating processes may be highly sensitive to the loss of a single species.

9.7 BIODIVERSITY AND RESPONSE TO DISTURBANCES

Human activities are causing a diverse array of disturbances in natural ecosystems, among which are increasing levels of atmospheric carbon dioxide, acid precipitation, changing global climates, increasing fragmentation of habitats and introduction of species into regions where they were previously absent. Given these and other large-scale changes to tropical and non-tropical systems, links between components of biodiversity and the ability of ecosystems to withstand and recover from such alterations are particularly important. As touched on by Silver *et al.* (1996) and Denslow (1996), such links may exist because redundancy within functional groups is only partial. Taxa within the same functional group are, by definition, similar in terms of the types of ecosystem-level effects they cause, but they may differ strikingly in terms of their responses to natural or human-caused perturbations. Combinations of similarities in ecosystems effects with differences in

responses to perturbations provide buffering of functional properties of ecosystems during present and future periods of alterations to ecological systems.

9.8 RESEARCH AGENDA

In this chapter we have explored the relationships between biological diversity and ecosystem functioning for moist forest, highlighting the shortage of information that is needed to assess biodiversity–ecosystem functional relationships. The shortage is even more dramatic for other types of tropical forests, which have not received the attention that has been directed toward wet forests. Dry forests, montane forests and wetlands are important types of tropical ecosystems. Because of their extension, the magnitude of anthropogenic alteration they are experiencing, and their crucial contribution to tropical biological diversity, losses of biodiversity in them may influence the functional properties of all types of tropical ecosystems. These ecosystem types require consideration if we are to document the range of variation of the relationships between biological diversity and ecosystem functioning. Interestingly, changes in forest structure and functioning are similar along gradients of temperature, fertility and moisture in spite of the dramatically different changes associated with each one. Thus, decreases in productivity, standing biomass, decomposition rates, life form diversity and species richness, and increases in below-ground allocation of plant resources accompany all three gradients. Determining the reasons for similar responses to different environmental conditions is a challenge for future tropical forest research.

Ecologists traditionally estimate primary production as the total amount of carbon fixed per unit area. Although such aggregated estimates are useful for some purposes, these data have a number of significant limitations. First, lumped values seriously underestimate above-ground primary production by ignoring carbon allocated to nectar, flowers and fruits – key resources for a range of influential consumer groups – and allocation downward into mycorrhizae. Second, lumping primary production tells us nothing about how carbon is allocated among different plant parts (roots, wood, leaves, nectar, flowers and fruits), and essentially treats primary producers as a single functional group. If we want to assess the contribution of different species, functional groups and life forms to ecosystem-level processes, we need more disaggregated estimates of primary production. Plant materials are packaged in fundamentally different ways, and these differences determine the identity of consumer groups and the rates of consumption and energy flow in ecosystems.

One of the most important areas of research on relationships between bio-

diversity and ecosystem functioning is determining the influence of the species composition of leaf litter on rates of decomposition and subsequent mineralization. Limited data suggest that decomposition rates can be mediated by litter diversity, with rates being higher for litter from richer species assemblages than from poorer species assemblages (Burghouts *et al.* 1994). Further testing of this relationship in tropical systems will shed light on the relationship between species richness and pivotal ecosystem processes such as decomposition.

Remarkably little is known about below-ground plant and microbial processes. Remedying this situation needs to be a major priority if we are to assess rigorously the links between biodiversity and ecosystem-level processes. Three areas are in particular need of attention. First, are there predictable structural patterns in the root systems of multispecies tropical assemblages? Second, how species-rich is the soil microbiota and into how many functional groups do those species fall? Third, when tropical forests are perturbed such that species or groups of species are deleted, do compensatory responses by other taxa result in reoccupation of the space?

Manipulative experiments need to be supplemented by research efforts focussed on comparative studies that contrast (a) naturally occurring mono-specific or low-diversity forests with neighboring high-diversity forests, (b) human-damaged systems with neighboring undisturbed systems, and (c) forest ecosystems along gradients of precipitation, soil fertility and elevation. Only with such studies can a comprehensive picture of the importance of biodiversity for ecosystem functioning be developed.

9.9 CONCLUDING REMARKS

Humanity needs to protect and nourish tropical forests for many reasons. Without implying that we think other reasons are less important than the ones we discuss here, we direct attention to those components that derive from the biological complexity of tropical forests. Because of their complexity, tropical forests have an extremely high information content. This information resides in the genomes of the individual species, the interactions among them, and the resulting ecosystem patterns and processes. Most of this information is not yet accessible to us because we have described only a modest fraction of the species living in tropical forests; we know almost nothing about ecological relationships among the species we have described, and we have only crude measures at just a few tropical sites of the rates and magnitudes of ecological processes.

Many benefits can be derived from preserving and studying the forests that are the repositories of that information. With improved knowledge of the players and the tropical forest theater we will gain a better under-

standing of how complex systems work. To live sustainably on Earth, humans need to understand the dynamics of many kinds of complex systems – physical, biological and social. Many degraded environments, both tropical and temperate, need to be restored. Knowledge of how tropical forests work is certain to be helpful in the design, development and execution of restoration efforts worldwide. Increasingly, humans are required to manage ecosystems more intensively in order to increase production of desired products, reduce losses of energy and materials through undesired channels, and establish integrated landscapes whose components interact in ways that improve the rates and stabilities of processes that maintain those systems. Management plans are more likely to achieve their objectives if they are based on solid understanding of the behavior of the systems being managed.

Throughout history, humankind has drawn upon tropical forests for products such as food, fiber, medicines, drugs and esthetic pleasure that enrich human life. All of these components are directly proportional to biological diversity. The woods and fibers of different species are useful for different purposes. The chemicals synthesized by living organisms that are the bases of medicines and drugs tend to be highly species-specific, or at least are produced by a small number of species, usually closely related ones. Future options to find and use new products are sacrificed as forests are lost and biological diversity is minimized. Also, as a result of our poor understanding of how tropical forests work we inadvertently cause losses of many species living in the forests we do preserve, further reduce options, and make the remaining forests vulnerable to perturbations they can currently withstand.

Perhaps the feature of tropical forests that most hinders our ability to understand their dynamics is the slow rate at which they change over time. The magnificent trees that dominate and give structure to tropical forests live, on average, more than a century. Some live much longer. Once a tree has gained its position in the forest canopy, it usually survives many years after the clues about the causes of its initial success have disappeared. Its current associates may be quite different from those it had when it was young, and the local climate may have changed as well. Only about 50 tree generations have elapsed since the final retreat of the last of the Pleistocene glaciers. During glacial advances, temperatures dropped on average about 6°C in tropical lowlands (Bush and Colinvaux 1990). Pollen profiles from tropical regions reveal that trees now restricted to middle elevations on mountainsides were intermingled with today's lowland trees close to sea level (Bush *et al.* 1990; Colinvaux *et al.* 1996). During glacial maxima, levels of atmospheric carbon dioxide were much lower than they were 100 years ago, and very much lower than today's levels, and the difference is steadily increasing (Intergovernmental Panel on Climate Change 1990). Tropical forests are probably still readjusting to post-glacial climatic changes. Some

types of disturbances, such as fires and hurricanes, produce immediate and sometimes catastrophic effects on tropical forests and their functional properties (Weaver 1989; Boucher *et al.* 1990; Walker *et al.* 1991). However, the longevity of trees causes long lags between the imposition of some types of disturbances and the completion of the functional responses of the forests. For example, loss of certain frugivores may not affect the composition and functioning of a forest for more than century, even if that loss will eventually result in the extirpation of a suite of forest tree species.

For these reasons, much attention will need to be given to understanding the rates at which different perturbations are likely to affect tropical forest processes, which processes they affect, how they exert their influences, and the time-frames over which their effects are likely to be realized. The processes that operate slowly are the ones most likely to be ignored and unappreciated, yet they may ultimately be among the most important determinants of the long-term functioning of tropical forests.

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