*INVITED PAPER*

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# Biodiversity and Ecosystem Processes in Tropical Ecosystems

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Living organisms on Earth are being subjected to major disruptions in the form of massive exchanges of species –pathogens, predators, and competitors– among biogeographic regions, overharvesting, habitat destruction, pollution, and climate change. Rates of habitat conversions, especially of forests, are higher in tropical regions than elsewhere on Earth (FAO 1993, Skole and Tucker 1993, Whitmore 1997). Until recently, biologists have directed most of their efforts toward estimating the extent and causes of species loss and developing ways to reduce the rate of extinctions. However, during the past decade much attention been paid to the consequences of the loss of species for the functioning of ecological processes (Chapin *et al.* 1998, Loreau 1998, Naeem 1996, 1997, Schulze and Mooney 1993, Tilman, 1997, Tilman and Downing 1994, Yachi & Loreau 1999). Most of this research has been conducted in temperate ecosystems or in the laboratory.

To assess the state of knowledge of the role of biodiversity in tropical forests in maintaining ecosystem processes, such as primary and secondary productivity, materials processing, provision and maintenance of structure, resistance to invasions and recovery from disturbances, a workshop was held at Oaxtepec, Morelos, Mexico, December 4-7, 1993 (Orians, Dirzo, and Cushman 1996). Here I summarize research conducted since the workshop and suggest some areas where research is urgently needed.

Tropical ecosystems are characterized by both high richness of species in many taxa and complex biotic interactions among component species. Most tropical plants are animal pollinated, are fed on by a wide variety of animals, and depend on animals for dispersal of their seeds. Tropical ecosystems exist in climates that vary in mean annual temperature, total annual rainfall and the length and severity of dry seasons, but have relatively minor seasonal changes in temperature. Seasonality of rainfall exerts a strong influence on temporal patterns of primary and secondary production and decomposition. Species richness in most taxa of macroorganisms is positively correlated with mean annual rainfall (Clinebell *et al.* 1995, Gentry 1992, Primack 1993) and inversely correlated with the length of the dry season. Both variables are strongly correlated in most tropical regions.

In this overview I focus on three central questions. Is productivity of tropical ecosystems positively correlated with biodiversity? Are more species-rich ecosystems more resistant to and better able to recover from disturbances? Does biodiversity enhance its own maintenance?

**Biodiversity and Ecosytem Productivity:** Four non-mutually exclusive hypotheses have been proposed to account for a positive relationship between biodiversity and productivity. The "sampling effect hypothesis" suggests that

species-rich plant communities are more productive because they have a higher probability of containing and being dominated by one or a few highly productive species. The "niche complementarity hypothesis" proposes that ecological differences among species result in more complete utilization of resources, and, hence, higher productivity, in more species-rich communities. The "positive mutualist interactions hypothesis" suggests that richer communities have more positive mutualistic interactions among component species than more depauperate communities. The "statistical effects" hypothesis suggests that stability and productivity increase with species richness because of the statistical averaging of fluctuations in the abundances of individual species (Doak et al. 1998).

Discriminating among the first and third of these hypotheses requires detailed local experiments. Distinguishing among the sampling effect and niche complementarity hypotheses is relatively straightforward because they make strikingly different predictions. The sampling effect hypothesis, but not the niche complementarity hypothesis, predicts that the dominance of some species in high-richness mixtures should be compensated by reductions in the productivity of subordinate species. Only the niche complementarity and mutualistic interactions hypotheses predict that the total productivity of a mixture of species should exceed the production achieved by the highest yielding of the component species, a phenomenon known as "overyielding." Recent theoretical results also suggest that more diverse communities may overyield so long as the environment varies (Yachi & Loreau 1999). The predictions of the "statistical effects" hypothesis are valid only if specific assumptions about relationships between the abundances and variability of populations of species are met. Under other plausible relationships between abundance and population variability, a variety of statistical outcomes are possible (Tilman et al. 1998).

Most current data have been gathered on plants because a major focus of studies of the ecological consequences of loss of biodiversity has been on relationships between primary productivity and species richness. Many stu-

dies have demonstrated a positive relationship between species richness and primary productivity, but interpretations of the results are controversial, in part because in some experiments species richness was manipulated by additions of nitrogen, thereby confounding causal relationships (Huston 1997).

The most extensive experiments to discriminate among competing hypotheses are being conducted in a variety of artificially established European grasslands, containing from one to 32 species of herbaceous plants, under a wide range of climatic conditions from Sweden to the southern Mediterranean (Hector et al. 1999). Preliminary results from these experiments, which were based on 2 m by 2 m plots, strongly support the niche complementarity hypothesis. Many of the high species richness plots had higher productivity than the most productive monoculture at the same site.

Some studies have been conducted with multitrophic level microbial communities (McGrady-Steed et al. 1997, Naeem and Li 1997). McGrady-Steed et al. (1997) used several species combinations to create alternative communities of identical species richness. They reported that $CO_2$ production increased as species richness increased, and that decomposition of particulate organic matter increased nonlinearly with species richness, achieving maximum values in communities of eight or more species.

Very few comparable experiments have been conducted with woody vegetation, nor have laboratory experiments been conducted with tropical plants or microorganisms. The only tropical field experiment to test relationships between species richness and ecosystem productivity of which I am aware is the pioneering study of Ewel et al. (1991) in Costa Rica. Useful results appear only slowly in experiments on communities dominated by woody plants, but experiments with tropical grasslands and savannas yield informative data more rapidly (McNaughton 1993, Sarankan and McNaughton 1999). Given the large areal extent of natural savannas and the vast areas that have been converted to artificial pastures in the tropics,

additional experiments are much needed to inform tropical management practices.

**Biodiversity and Resistance to Perturbations:** The proposition that species-rich communities should be more stable than species-poor communities is based primarily on the niche complementarity hypothesis. This hypothesis suggests that because species differ in their ecological requirements, the likelihood that ecosystems contain some species that can thrive in the face of a variety of perturbations is positively correlated with their species-richness. Loreau (1998) explored the role of plant species richness and ecosystem processes by modeling a situation in which plants compete locally for a limiting soil nutrient. She found that plant species richness did not necessarily enhance ecosystem productivity, but it did so if there was complementarity among species in the space they occupy below ground or if correlations between mean resource use intensity and diversity were positive. Species do, of course, differ in their requirements, but those differences may not be large enough to exert a significant effect on ecosystem performance under typically varying environmental conditions. More empirical data, especially from tropical ecosystems, are much needed.

A positive relationship between diversity and stability has been obtained with laboratory microcosms even under constant conditions. Naeem and Li (1997) established 318 replicated microbial microcosms with varying numbers of species per functional group (autotrophs, decomposers, herbivores, predators). Each microcosm was supplied with inorganic and organic nutrients, photoautotrophs, and decomposers. Most environmental conditions were constant, but the investigators varied nutrients, light, species per functional group - S/F, and number of unctional groups - F. Algal biomass declined with increasing F for all levels of S/F but bacterial densities showed no response to variations in F or S/F. The standard deviation of decomposer density among microcosms declined strongly as S/F increased, independently of light and nutrient levels. Autotroph biomass was lower and extinction higher in microcosms with higher F.

Experiments designed to test relationships between species richness and productivity can also reveal relationships between species richness and variability of primary production. The European grassland study, which has been running for only two years, is expected to yield such results over longer term time frames. The most convincing results in support of a positive relationship between diversity and stability have been obtained from an 11-year study of successional and native grasslands in Minnesota. The study period included the most severe drought during the past 50 years (1987-88). Species poor plots were more harmed by the drought and took longer to return to pre-drought conditions than species rich systems and native prairie (Tilman and Downing 1994).

In the experiments of McGrady et al. (1997) rates of ecosystem processes became increasingly predictable as species richness increased. To test the resistance of the experimental ecosystems to invasion, another measure of stability, 10 cells of *Euplotes* sp, a facultative heterotroph containing endosymbiotic algae, were introduced and population growth was measured after two weeks (10-15 generations of *Euplotes*). *Euplotes* invaded only communities containing fewer than six species, but *Euplotes* failed to invade some low diversity communities. Resistance to invasion was also stronger in species-rich than in species-poor experimental marine epifaunal communities established on small tiles in Connecticut (Stachowicz et al. 1999). Similar experiments should be conducted in tropical ecosystems.

Although investigations of woody vegetation yield results more slowly, trees leave a record of their production in growth rings. In most temperate ecosystems these rings represent annual growth increments, but the temporal signatures of growth rings in tropical woody plants often are difficult to interpret. Annual growth rings in tropical trees are clearly evident only in areas with well-marked dry seasons (Bass & Vetter 1989). If the time period signaled by growth rings of tropical woody plants can be determined, measurements of these growth rings, combined with

estimates of leaf fall, can be used to determine the degree to which plant species respond differently to climatic variability (Worbes and Junk 1989). If they do, the stability of overall ecosystem productivity should be positively correlated with plant species richness, at least at low to moderate species richness. Measurements of rates of increase in stem circumferences of trees are being used instead of growth rings to estimate ages of trees and rates of wood production (Terborgh et al. 1997c, Lieberman et al. 1995), but such data can be used to compare growth rates of individual species in relation to variable weather conditions only if individual trees are measured annually or at least every few years. Because gathering those data is technically easy and not particularly time intensive, such measurements should be pursued vigorously in tropical forests.

Ignorance of the potential role of species richness on ecosystem processes is greatest with respect to the role of invertebrates and soil microorganisms. For example, although ants are major components of ecosystems and participate in many ecosystem processes, little is known about how reductions in ant species richness affect ecosystem productivity and stability (Folgarait 1998). Some functional groups of microorganisms that play major roles in ecosystem processes are sensitive to environmental stresses, and low functional redundancy may exist in some groups of them (Lodge et al. 1996). The functional groups that merit the most future attention are those uniquely or predominantly mediated by microorganisms and on which other organisms ultimately depend. Thus, even though species of arbuscular mycorrhizal fungi (AMF) have traditionally been thought to colonize the roots of most vascular plants equally effectively, recent evidence strongly suggests that the species composition of AMF communities has the potential to determine plant community structure (van der Heijden et al. 1998). Investigations of the role of invertebrates and soil microbial species richness on ecosystem processes in tropical vegetation should receive very high priority.

**Biodiversity and the Maintenance of Species Richness:** Interactions among species can result in both losses of and increases in biodiversity. Competition can result in lowered biodiversity because, in the absence of disturbance, competitively dominant species may eliminate competitively weaker species. Mutualistic interactions increase biodiversity both because species richness creates opportunities for mutualistic interactions and because mutualistic interactions enable more species to survive (Huston and Gilbert 1996).

Predators influence community structure in two major ways. One way is by preferentially feeding on prey species that, in the absence of predation, are capable of competitively excluding other species (Paine 1966, Menge 1992, 1995). The other way predators influence community structure is via the "trophic cascade" effect, in which they trigger a series of interactions extending through successively lower trophic levels to autotrophs. Models suggest that autotrophs may be either enhanced by reduced herbivory or limited by increased herbivory, depending on whether the number of trophic levels is even or odd (Power 1992, Estes 1996). The best evidence for trophic cascades has been obtained from experiments with aquatic systems (Carpenter and Kitchell 1993).

In contrast to the dominance of temperate-zone studies on the influence of biodiversity on ecosystem productivity and stability, many investigations of the influence of biodiversity on maintenance of species richness are being carried out in tropical regions. Most of the investigations deal with the consequences of the loss of species. Because loss of species is typically accompanied by many other changes, it is generally difficult to distinguish the effects of loss of species from other influences. A useful comparison is provided by Barro Colorado Island (BCI) in Gatun Lake, Panama, which lost its top predators - jaguar, puma, harpy eagle - more than 50 years ago, and Cocha Cashu, Peru, where all top predators are present at normal abundances. On BCI densities of medium-sized mammals are much higher than they are at Cocha Cashu, whereas densities of rodents weighing less than one kilogram are similar at

the two sites. Terborgh (1992) believes that the differences are evidence of a top-down effect resulting from missing predators, but the issue is not yet resolved (Wright et al. 1994.)

To resolve the controversy, large scale, strictly controlled experiments that include censuses before and after predator exclusion are needed. To date, the best terrestrial experiment has been conducted in boreal forests of The Yukon, Canada (Krebs et al. 1995), but an extensive study is now underway in Venezuela at Lago Guri, a huge impoundment created in 1986. Flooding of the hilly forested landscape created hundreds of islands ranging in size from less than one hectare to more than 1 000 hectares. Many of the more remote islands lack vertebrate predators except for small raptors and snakes (Terborgh et al. 1997a, b). Within seven years of isolation, more than three-quarters of the species of terrestrial vertebrates that live in the same forest type on the mainland have become extinct on the islands. Most of the species that have persisted are found on only a few of the islands, but they maintain higher population densities on the islands than on the mainland. Island communities are deficient in pollinators and seed dispersers, but they have unusually high populations of seed predators (small rodents) and generalist herbivores (howler monkeys, iguanas, leaf-cutter ants). Ongoing research suggests that there is little recruitment of canopy trees, but the causes of the failed reproduction are not yet clear.

Many studies have been conducted in fragments that remain in formerly heavily forested regions (Laurance and Bierregaard 1997). Small forest fragments typically lose large predators and large frugivores much more rapidly than they lose species of woody plants. As a result, recolonization rates by tropical trees are often very slow because their major seed dispersers have become locally extinct (Harrington et al. 1997; Thebaud and Strasberg 1997).

The high deforestation rates in the tropics are creating many opportunities for carefully designed experiments, similar to those being carried out north of Manaus, Brazil. Fortunately, opportunities are now being created where pastures and fields and being abandoned and reforestation efforts are underway. Plantations that are being established as components of greenhouse gas mitigation projects should also be studied to determine rates of recolonization and how establishment of species differs in plantations with varying numbers of tree species. Comparisons between species-rich and species-poor agricultural systems and natural forests would also be valuable. As more information becomes available about the life history patterns and physiological characteristics of tropical trees, models of ecosystem performance that includes such information can and should be developed.

## ACKNOWLEDGMENT

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