DIVERSITY OF TROPICAL SPECIES

Questions That Elude Answers

Edited by

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By

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TABLE OF CONTENTS

Abstract

Information pertaining to six questions that have eluded answers is reviewed in order to stimulate research in tropical species diversity during the Decade of the Tropics program. The questions are: (1) How is species diversity measured? (2) Why is there such a high diversity of tropical species? (3) How is high species diversity maintained? (4) What ecological function, if any, does high species diversity serve? (5) How do humans benefit from a high diversity of species? (6) How is the diversity of species changing today? The importance of quantitative and geographically referenced species inventories is highlighted under the first question. It is suggested that evolutionary and ecophysiological approaches to questions 2 and 3 be clearly distinguished and that more attention is needed on the role of environmental factors, particularly stressors, and on the definition of parameters such as "resources." The evolution of a high number of species and the maintenance of high species diversity are two different subjects that routinely get confused in the literature. A general model for the maintenance of high species diversity is presented. It is proposed that the ecological funcion of high species diversity is related to the efficiency of resource use, particularly nutrients. Human interactions with, and dependency on, high species diversity has such a long history in the tropics that ecosystems formerly thought to be pristine are in fact human-derived. The resilient aspects of tropical forests vis-a-vis the current massive human intervention in the tropics are highlighted. Future protection of high species diversity will require improved management of tropical ecosystems, restoration and rehabilitation of damaged lands for production, sensible use of secondary forests and tree plantations, and greater attention to human needs.

Introduction

Describing, cataloging, and understanding the diversity (using diversity in its broadest sense) of living organisms is one of the fundamental tasks of biology. Nowhere else has this task been more complex and the skills of biologists so tested as in the tropics. With estimates of tropical organisms ranging anywhere from 3 to 8 million, and with less than 1 million of these having been described and catalogued, it is clear that the task is far from complete and may never be completed. In spite of the chronic shortage of information about tropical organisms, it is necessary to seek patterns in the distribution and abundance of species and to test hypotheses about the role of species diversity in the functioning of tropical ecosystems.

The paucity of information on the diversity of all organisms in any ecosystem prevents biologists from addressing issues concerning

species diversity using a community focus. Instead, biologists develop hypotheses for particular taxonomic groups of organisms and then extrapolate to other groups or to all tropical ecosystems. Generalizations based on particular taxa are flawed by the obvious fact that we do not know how representative one group of organisms is of other groups. The hazards of extrapolations based on taxonomic bias should not be ignored in discussions of species diversity. Baker (1970) discussed this problem by observing that most theories on species diversity are by zoologists and that theories developed with animals as models are not necessarily relevant to plants. However, Tilman (1982) demonstrated that resource competition theory (competition for nutrients, water, etc.) did apply to plants.

The high species richness in frost-free tropical regions has stimulated many comparisons between tropical and temperate ecosystems (e.g., MacArthur 1972). Often these comparisons are misleading. For example, a comparison between a lowland rain forest in Brazil and pine barrens in New Jersey may indicate more about edaphic differences than latitudinal effects. An often forgotten fact is that there are more differences in species richness within the tropics than between tropical and temperate regions. For example, Gentry (1982) found a three-fold difference in plant species richness between the dry and wet tropics but only a two-fold difference between tropical dry and temperate forests.

Other environmental factors are more fundamental in explaining ecological differences than latitude per se. Gradients of species diversity from coastal to montane regions, from dry to wet environments, from cold to warm climates, or from freshwater to saltwater can be described within tropical latitudes and compared to analogous gradients in temperate latitudes. Confining comparisons to similar types of conditions could improve understanding of the observed patterns in species diversity (Box 1).

BOX 1

Scientific observations have lead to the description of many patterns of species diversity in both spatial and temporal dimensions. Among the best known are the following:

1. The diversity of most groups of plants and animals increases towards the tropical latitudes, and within tropical latitudes species diversity increases towards the equator.

2. The number of species (plants and animals together) per unit area of land is usually greater in the tropical rain forests and lower in high latitudinal ecosystems.

3. Tropical forests have a higher diversity than high-latitudinal forests in all scales of measure: within habitat, between habitats, and landscapes.

4. Within a given altitudinal belt in the tropics, the number of tree species increases with increasing rainfall.

5. Across altitudinal belts, the number of tree species and bird species decreases with increasing altitude.

6. In islands, the number of animal species increases with the size of the island and with proximity to a continent. If the topography of the island is rugged, the number of species also increases.

7. Tropical mountainous areas (particularly high mountains) support a larger number of species (plant and animal) than equivalent temperate mountains because environments range from lowland tropical at the base to alpine conditions at the summit.

8. Ecosystems with severe limiting factors such as high salinity, flooding, or freezing temperatures have reduced species richness.

9. As rain forests recover from disturbance by acute events such as hurricanes or fire, species diversity increases in the disturbed area until a peak is reached after several decades.

10. High-yield systems under intensive human management are species-poor and increase in species diversity to values observed in less disturbed and more mature systems when management pressure is reduced.

11. The landscape is not uniform in terms of its species diversity. Often pockets with a large number of species can be interspersed within areas of low species diversity.

The scientific literature on species diversity is extensive, and it is not my objective to review it. The objective is to focus the discussion of tropical species diversity on a few questions whose answers continue to elude biologists. I hope to stimulate research during the "Decade of the Tropics" that would contribute to the unraveling of this fundamental mystery of biology. This overview presents a general model of the interaction of biotic and abiotic factors that maintains species diversity and addresses the following questions:

(1) How is species diversity measured?

(2) Why is there such a high diversity of tropical species?

(3) How is high species diversity maintained?

(4) What ecological function, if any, does high species diversity serve?

(5) How do humans benefit from a high diversity of species?

How is Species Diversity Measured?

There has been much controversy among ecologists about the assessment of species diversity. Numerous indices have been proposed, each with a different meaning and purpose (see the review by Peet 1974). I neither intend to review this broad field nor attempt to establish which is the best method. Instead I will call attention to the data available to assess species diversity. The nature of the data base focuses attention on the procedures used so far to measure species diversity and the need to increase the number of measurements.

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3

At the outset of this review I said that the size of the flora and fauna of the tropics is unknown. Taxonomists believe that only 20% of the tropical biota has been described (Raven 1977). However, this percentage may change if the estimates of large numbers of canopy insects in Panama and Peru prove to be applicable to all tropical ecosystems (Erwin 1983). Knowledge concerning the species richness in the world's tropics is meager because botanical and zoological explorations of the region are far from complete. Furthermore, surveys have not been systematic, and previously inaccessible habitats, such as the canopies of tall tropical forests, have not been fully explored (Erwin 1983, Perry 1986). For these reasons, traditional natural history surveys will continue to make significant contributions to the understanding of biological diversity and still remain the main source of information about the diversity of tropical biomes.

A recent innovation to botanical and zoological exploration has been introduced by the Smithsonian Institution in Washington, D.C. (Terry L. Erwin, personal communication, 1987). They are establishing a network of large plots (1-25 ha) where every tree is mapped as well as the topography of the terrain. Using computer-assisted technology, the three-dimensional architecture of the stand is also recorded. Insect and other animal collections are then geographically referenced and correlated with botanical data. This approach maximizes the usefulness of the survey because species diversity information can be related to area, environmental conditions, and other community features. This program couples traditional natural history surveys with quantitative vegetation and ecosystem analysis.

Data concerning species diversity is more limited on an area basis (e.g., species/ha) than information gathered from traditional natural history surveys. A global review of these kinds of data for plants revealed that the most common enumeration is for trees in plots of 0.1 ha (Rice and Westoby 1983). Recently, Peralta et al. (1987) and Hubbell and Foster (1987) reviewed information from permanent plots of various sizes in Malaysia, Costa Rica, and Panama. Similar plots are available in Puerto Rico (Brown et al. 1983) and Venezuela (Veillon 1983). These study areas provide unique opportunities to assess temporal changes in species diversity and to correlate these with episodic events such as hurricanes (Crow 1980, Weaver 1986).

An extensive data base normally ignored by ecologists is the information collected by foresters during forest inventories. These data have the advantage of being much more extensive than individual plot data, and unlike information from floras and other natural history-type studies, they are quantitative. Brown and Lugo (1984) used tree inventory data to make an independent analysis of the biomass of tropical forests, and they are now analyzing the species richness information from some of these surveys (Brown and Lugo, personal communication, 1988). The limitation of most plot information is that the focus is mainly on plants, especially trees of certain sizes. Animals, understory plants, epiphytes, and lower plant components are usually ignored. Quantitative animal surveys are more limited than plant surveys, and the data are biased to birds and mammals (e.g., Fleming et al. 1987).

Results of the most complete plant inventory in a tropical forest were recently published by Gentry and Dodson (1987) for three sites in Ecuador. This outstanding work demonstrated that when all plant groups are considered, species richness in the neotropics can be higher than that of the old world tropics, even if tree species are removed from the data set. Although the work of Gentry and Dodson sets a high standard for future inventories of tropical vegetation,

unfortunately this kind of work is extremely time consuming and requires strong institutional and scientific support.

Why is There Such a High Diversity of Tropical Species?

Much of the literature that addresses this question focuses on the evolutionary aspects of speciation and the mechanisms that explain biogeographical patterns of floras and faunas. These are long-term phenomena that contrast with the explanation of how different habitats maintain a relatively stable number of species per unit area. I believe that discussions of tropical species diversity should differentiate between theories that explain the evolution of species and those that explain their maintenance in a given habitat. Evolutionary and biogeographical arguments are more important for explaining patterns of speciation, while the ecosystem function theory is best suited for addressing the shorter-term phenomena (centuries) of maintenance of species in the environment. In this section I will address the evolution of tropical species and in the next section I address their maintenance in different ecosystems.

Biologists do not agree on explanations for the origin of the large number of species in the tropics. Arguments are usually circular or contradictory. Some of the competing hypotheses are listed below.

(1) High species diversity occurs in the tropics because conditions for evolution are optimal and extinctions · fewer (Dobzhansky 1950, Klopfer 1959, Terborgh 1980) or because the region appears to be a "center of diversity" for most taxa (e.g., Darlington 1957). Stebbins (1974) wrote a critical review of this hypothesis. The hypothesis is based on the concept of environmental stability in the tropical latitudes. Presumably the constancy of the environment favored evolution of species. Recent evidence suggests that environmental conditions in the tropics have not been as continuously favorable as previously assumed (c.f., Prance 1982). However, in disturbed habitats (by natural or human agents) evolutionary rates are also believed to increase in "bursts of creativity" through hybridization (Anderson 1948, Anderson and Stebbins 1954). Alternatively, disturbance may cause a relaxation in such biotic interactions as competition and thus lead to more speciation opportunities through species coexistance (discussed later).

(2) High species diversity was conserved over geologic time in the tropics because this is where low rates of extinction prevail (Stebbins 1974). Stebbins uses botanical evidence to argue that conditions for evolution are more favorable in climatically intermediate environments in terms of rainfall and low-frequency frost. He views tropical environments not as cradles of species diversity but as museums where primitive as well as advanced plant families survive because possibilities for extinction are few. Gentry (1986) challenged this view with observations of high endemism in the Andean foothills of western South America. According to Gentry, rapid evolution is occurring in these localities, and he considers the driving force to be: "...accidental and often suboptimal genetic transilience associated with founder-effect phenomena in a kaleidoscopically changing landscape."

(3) Instead of arguing for unique conditions in the tropics, Haffer (1982) argues that the mechanisms of evolution are the

5

same in tropical and other latitudes, e.g., mutation rates are similar. Species richness is the product of the simultaneous contribution of allopatric, parapatric, and sympatric speciation operating through three time periods (Quaternary, Tertiary, and Cretaceous). The allopatric mode is the most important contributor to species richness through long-distance dispersal and fragmentation of habitats. Habitat fragmentation in the tropics occurred through paleogeographic change in the distribution of land and sea, formation of river systems, and climatic-vegetation fluctuations that resulted in the formation of refugia. Species in these refugia either became extinct, survived without modification, or survived with differentiation into subspecies or species. Haffer's hypothesis focuses on the role of refugia as centers of evolution and survival. In these refugia, speciation + immigration of species >> extinction + emigration of species. The details and evidence for this hypothesis are discussed in Prance (1982) and by Simpson and Haffer (1978). Its weaknesses are summarized by Endler (1982), Benson (1982), and Gentry (1986).

(4) There are emerging paradigms of evolutionary theory caused by new developments in physics and chemistry (Ho et al. 1986) and by the potential impacts of catastrophic events on the biota (Sepkoski and Raup 1986). Periodic extraterrestrial factors (with return frequencies of millions of years) are now implicated in sudden (within days) mass species extinctions (Raup 1984, Sepkoski and Raup 1986), and the importance of competitive exclusion (den Boer 1986), competition, and other biotic interactions as the shaping forces of

evolution are under examination. Simultaneously the function of weather, climate, substrate, and other environmental factors external to the biota are becoming more prominent in the interpretation of evolutionary phenomena (Kruckeberg 1986, equation 1).

$$\text{Biological diversity} = f(cl, o, r, p, t, h) \quad \text{(equation 1)}$$
where
cl = climate
o = organisms
r = topography
p = parent materials (rocks)
t = time
h = heredity

These new perceptions of the biosphere apply to tropical environments and force tropical biologists to become more holistic in the formulation of hypotheses. Because disturbance is also becoming a paradigm for interpreting the current function of ecosystems (Pickett and White 1985), it is critical to maintain a time scale perspective so that short-term (maintenance) and long-term (origin) species phenomena can be segregated in the analysis.

The importance of the environment to the evolution of species has been challenged by Schopf (1984) who wrote (p 264): "This view of independence of the process of speciation vis-a-vis environment is not [his emphasis] to negate the obvious fact that every species is adapted to the particular habitat where you find it. Rather every species is specialized for its particular habitat to roughly the same degree, and the overall resultant of different diversities in different habitats is set by equilibrium matters in species/area relationships." Schopf plays down the environmental aspects per se, and instead emphasizes the continued change of the genome itself. Schopf dismissed the high diversity of species in the tropics as not unique due to the

presence of high species diversity in stable and uniform habitats such as deep sea continental slopes and continental rises. Yet, the highest species diversity values for such environments do not exceed 100 polychaete and bivalve species per thousand individuals (Sanders 1969). Arthropods in the litter layer of low diversity tropical forests such as those in Puerto Rico exceed 100 species/1000 individuals and the species diversity number increases considerably when other plant and animal groups living on the same space are added (Odum 1970). For species-rich rain forests in Thailand tree species alone exceed 300/1000 individuals (Odum 1970).

How is High Species Diversity Maintained?

A large number of hypotheses has been advanced to explain the maintenance of high species diversity in the tropics (Table 1). Some of these hypotheses contradict each other or confuse origin of species with maintenance of species diversity, some are circular, and others have been supported with questionable data. Giller (1984) discussed these hypotheses and claimed that each focuses on a different aspect of the problem and are therefore complementary rather than competitive theories. He proposed a model to integrate the various views (Fig. 1).

Table 1. Mechanisms for the determination of species richness and modes of action based on nonequilibrium (N) and equilibrium (E) hypotheses (Adapted from Giller 1984).

| Hypothesis and mechanism	Mode of action
(N) Evolutionary time	Degree of saturation with species
(N) Ecological time	Degree of saturation with species
(E) Environmental favorableness	Mean niche width and dimensionality of habitat
(E) Environmental stability	Mean niche width and resource diversity
(N) Environmental variability	Degree of allowable niche overlap
(N) Gradual change	Degree of allowable niche overlap
(E) Spatial heterogeneity	Mean niche width and resource diversity
(E) Area	Resource diversity and habitat dimensionality
(E) Productivity	Mean niche width and resource diversity
(E) Competition	Mean niche width
(N) Compensatory mortality	Degree of allowable niche overlap
(E) Circular network	Degree of allowable niche overlap
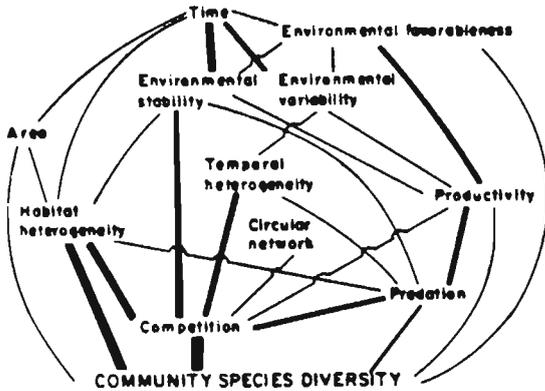
Figure 1. A casual network of factors that may influence the species diversity of a community. Thickened lines indicate the more important interactions. From Giller (1984).

MacArthur (1972) proposed an empirical formulation for explaining species richness (equation 2 below). His review of the literature led to the conclusion that the diversity of production or resource used by the entire community (Dr) was higher, and the diversity of utilization or niche width of each species (Du) was smaller, in tropical than in temperate environments. Therefore, regardless of evolutionary time or history of disturbance, the tropics would always have a higher species richness than temperate zones.

$$Ds = Dr/(Du\,[1/\alpha + C]) \qquad \text{(equation 2)}$$

where Ds = diversity of animal species using a common resource

Dr = diversity of production or resource used by the entire community

Du = diversity of utilization or niche width of each species (assumed identical)

C = number of potential competitors or neighbors in niche space (an expression of the dimensionality of the habitat)

α = the mean competitive coefficient or mean niche overlap.

A striking feature of the hypotheses proposed for maintenance of high species diversity in the tropics is that most of them (7 out of 12 in Table 1) highlight the role of abiotic factors (Table 2), but the prevailing view among biologists is centered in biotic mechanisms (c.f.,

Table 2. Major causal factors determining species richness and diversity

Causal factor or factor complexes	Outcome
Genetic changes	Creation of genotypes
Symbiotic relationships, including competition	Selection and extinction
Geomorphological changes	Change in rate of speciation

Table 2. (cont'd)

Causal factor or factor complexes	Outcome
Climate change	Extinction and selection of species
Extreme episodic climatic events	Change in habitat structure and species diversity
Fire and other stressors	Change in species diversity
Dispersers (wind, water, biotic agents)	Species distribution
Biotic agents	Change in and regulation of species richness and diversity
Causal factor or factor complexes	Outcome
Human interference	Habitat change, species extinction, genetic changes, change in species richness and diversity

Pianka 1966, Terborgh 1973, Giller 1984). Abiotic factors are included in all formulations, but always as an auxiliary component of the explanation. For example, Dobzhansky (1950) mentions the environmental challenge to which organisms respond and adds that, in the tropics, environments provide more challenges than all the others outside the tropics. But Dobzhansky quickly qualified the challenge of the tropical environment as stemming chiefly from "... the intricate mutual relationships among the inhabitants."

The following quote from Kruckeberg (1986, p. 461) best illustrates the point I am making. "The elaboration of plant species diversity should be viewed as a two-way street: environmental challenges are met, then responded to, by biological invention—read, evolution [his emphasis]... Self-evident, perhaps, but there is a tendency for the evolutionary biologist to become preoccupied with the living component of the duality—to look for biological mechanisms and outcomes, rather than those non-living agents of selection and isolation fashioned out of geological processes."

MacArthur (1972) attributed a dominant role to species competition in his discussion of geographic patterns of species diversity even though his mathematical formulation (equation 2) shows the abiotic environment (Dr) to be important in the determination of species diversity. Giller (1984) concluded in a similar manner that "... it is so widely accepted that competition is the major organizing principle in ecology, that it has almost achieved the status of paradigm." This paradigm is being challenged

by views on the role of disturbance in communities.

Ideas on how species can be added to communities are generally based on resource availability in a habitat and the partitioning of available resources among species (Fig. 2). In this example the "forcing function" is resource availability, and through biotic interactions more or fewer species can occupy the habitat. I will discuss later the definition of what constitutes a "resource." Ways of measuring these resources are critical to making further progress in the understanding of species richness in the tropics.
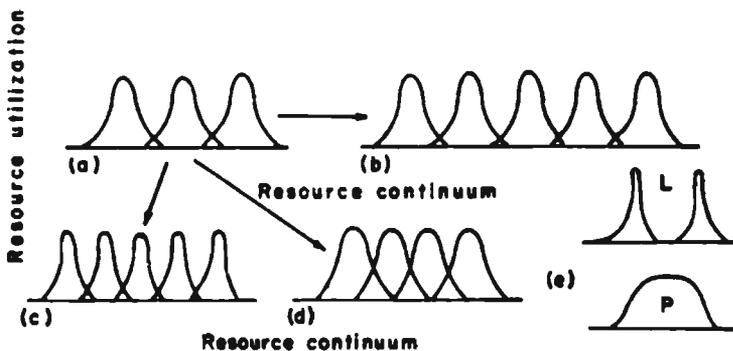

Figure 2. Species can be added to a community (a) by several mechanisms: increasing the resource base (b); increasing in species specialization (c); increase in species overlap (d); changing niche shape from platykurtic, P, to leptokurtic, L (e). From Giller (1984).

The lack of attention given to abiotic factors is clear from the model in Fig. 1. Yet ecologists studying ecosystem function (of which species diversity is a part) emphasize the role of abiotic factors as regulators or determinants of ecosystem dynamics. Could scientific understanding of the maintenance of species diversity increase if more attention were paid to the role of abiotic factors? In a review of the role of disturbance in natural communities, Sousa

(1984, p. 383) concluded: "There is a growing realization that disturbance may play as great a role in community dynamics as do biological interactions such as competition and predation, which have received far more empirical and theoretical attention from ecologists. The interplay between disturbance and these biological processes seems to account for a major portion of the organization and spatial patterning of natural communities."

Consideration of abiotic factors in the question of maintenance of high species diversity has not been successful because these factors have not been holistically focused. For example:

- The idea of stable environments as necessary for high species diversity originated in benthic oceanic environments (Sanders 1969) with little consideration to other abiotic factors, such as the balance between and intensity of subsidies and stressors acting on the biota;

- Huston's (1979, 1980) hypothesis that nutrient-rich environments support fewer species than nutrient-poor ones was flawed in four important ways: (1) the inclusion of forests with saturated soils in the analysis, (2) the use of nutrient concentrations as the index of fertility (as opposed to total nutrient inventory and nutrient turnover), (3) the narrow range of soil fertility reflected in the Costa Rica example, and (4) by implicitly assuming that more order and ecosystem complexity is possible with fewer resources, a view that violates the

second law of thermodynamics; and

- Terborgh (1973) addressed and discarded the notion of "favorableness" in plant ecology on the basis that it was circular. He concluded instead that species diversity is determined by the balance of speciation, competition, immigration, adaptation, and extinction. All of these biotic characteristics are, of course, driven in part by abiotic factors, but the discussion of abiotic factors in Terborgh's paper was minimal (Table 3).

Tilman (1982) wrote the most comprehensive analysis on the relationship among abiotic resources, plant community structure, and species diversity (using the term in the same general context as used in this paper). He showed that plant species diversity can be related to resource requirements and that the ratio of resource supply rate determines species dominance. According to Tilman, species coexist in spatially heterogeneous habitats by differing in the proportion of nutrients they require. Spatial heterogeneity was defined as the amount of variance among randomly sampled microhabitats in the

Table 3. Alternative views on the interactions between biotic and abiotic factors in the context of plant species diversity in the tropics.

Terbog 1973	Alternative view
A species that occupies a rich habitat adjacent to an impoverished one may evolve improved competitive ability within the habitat, thus increasing in density and causing extinction in other species, or it may acquire genes that will enable it to invade the other habitat and take advantage of reduced competition.	A species that occupies a rich habitat adjacent to an impoverished one may maintain fitness to its habitat because there is no compelling reason to invade other habitats. A stressed environment with a lower number of species may present more difficulties to invading species because overcoming the stressor requires increased and coverging specialization, and there is less opportunity for diversification.
Both biological and geological successions lead to a common end point embodied in the concept of a mesic environment. Thus environmental evolution at once accounts of peripheral habitats and for the commonness and comparative stability of mesichabitats.	Periodic disturbances maintain peripheral habitats (ridges, swamps, bogs, marshes, sand dunes) in a steady state rather than in transition to a common end point. Mesic refers to intermediate water availability, and such environments are rare. For example, most tropical forests are in dry and wet environments as opposed to moist environments.
Both reduced invasion rates and a high likelihood of extinction would act to limit the number of species in peripheral habitats.	The number of species in peripheral habitats are limited by the number of alternative physiological solutions to the environmental challenges in these habitats.

1 1

Table 3. (cont'd)

Terbog 1973	Alternative view
All species have the same amount of niche space.	Differences in species richness among habitats suggest that not all habitats have the same amount of niche space.
Speciation is area-dependent, extinctions are negatively area-dependent, and species richness is the net balance.	Speciation and extinction are important processes for explaining the origin of species diversity, but they are less important for maintaining species.
Communities offer an increasing resistance to invasion as they grow in richness.	Communities may offer increasing resistance to invasion over a successional sere, but in space, highly stressed communities with few species are not usually invaded.

supply of resources averaged over the reproductive period of the individual. The analysis of Tilman led him to propose a "humped" curve for the relation between species diversity and resource richness. Increased resource richness initially causes a steep increase in species diversity with a maximum of diversity at intermediate levels of resource richness. Species diversity then decreases gradually as resource richness reaches high levels.

Although Tilman summarizes many observations that support his suggestion, I suggest a modification to his analysis that would make it more general. Tilman's analysis excluded abiotic factors that could not be construed as resources (e.g., temperature and salinity) as well as the cost of obtaining, concentrating, and using a given resource and the total availability of a resource (for example, nutrients in soil are only a fraction of all the nutrients available to plants). Using these ecological considerations, it may be possible to demonstrate that the species diversity curve is a humped curve, not along a resource richness gradient alone, but perhaps along a gradient of resource richness and environmental stress (discussed later).

The extensive 1984 review by Giller led him to conclude: "In the analysis of species diversity and diversity patterns, one cannot look for a single explanation involving only one causal factor. There is a multitude of ways in which the mechanisms discussed ... can interact and have interacted over evolutionary time to produce the assemblages we see today. Conceptually, species diversity may be studied as the relationship of physical environmental factors and diversity, or through the role of biotic processes. The physical environment, including present conditions and past history, determines the pattern of biotic interactions, and ultimately an understanding of diversity patterns requires an autecological approach (species tolerances, etc.).

This will provide knowledge of the action of mechanisms operating through the physical environment. Biotic interactions, in turn, produce patterns in resource partitioning, which are the proximate cause of coexistence and hence observed species diversity" (Giller 1984, p. 111).

Giller's conclusion is sound and provides both a conceptual focus to the study of species diversity and a justification for the emphasis on biotic interactions (see also Kruckeberg 1986). His focus is clearly evolutionary and long-term. It is also clear that understanding of the species diversity question will require a comprehensive approach and an indepth understanding of ecosystem dynamics. The lack of agreement among ecologists in terms of what constitutes the proper focus (e.g., evolutionary vs. ecophysiological) or in terminology definitions

may be a major obstacle to a comprehensive study of the species diversity question. For example, the evaluation of the productivity hypothesis for explaining species diversity (Connell and Orians 1964) has been affected by the confusion over the concept of productivity (c.f., Baker 1970, Pianka 1966) or by equating productivity to food availability (c.f. Giller 1984). Also, terms such as "resource" require a more rigorous definition because in the absence of precise definitions they are being defined without due regard to their availability to organisms. The costs of concentration, uptake, transport, and assimilation, as well as total inventories in ecosystems, are the most common omissions in the literature dealing with resource availability ideas. Furthermore, resource-availability is strongly influenced by abiotic factors (Box 2).

BOX 2

Temperature, Earthworm—Microorganism
Mutualism, and Species Richness

Nutrients from decaying plant material are partly accumulated as stable organic reserves that are not accessible to plants or microbial decomposers. However, if labile carbohydrates are added to the soil, a "priming effect" occurs, and microbial populations are able to metabolize the organic material and release the nutrients. Root exudates and earthworm intestinal mucus are examples of natural carbohydrates that serve this priming function. An interesting and significant mutualism develops between the microbial flora and roots or earthworms. Studies show that in the case of the earthworms this mutualistic relationship is driven by temperature and may be a critical element in the regulation of plant species diversity (Lavelle 1983). The same may also be true of plants and their rhizosphere.

Such a system is very efficient in the tropics because of enhanced metabolism due to high temperatures. Earthworms in the tropics can digest low-quality soil organic matter, while those in cold climates cannot and are limited to surface soil organic matter of high quality. It is too cold in the temperate region for earthworms in temperate communities to exploit the deeper, low-quality soil organic matter that is within reach of the tropical earthworms. Therefore, a range of resources not available to cold climate communities becomes available in warm ones, and new niches are added to the community (Fig. 3).

13

A holistic focus to the study of the complex species diversity patterns of tropical landscapes requires more emphasis on the role of abiotic factors. An ecophysiological ap-
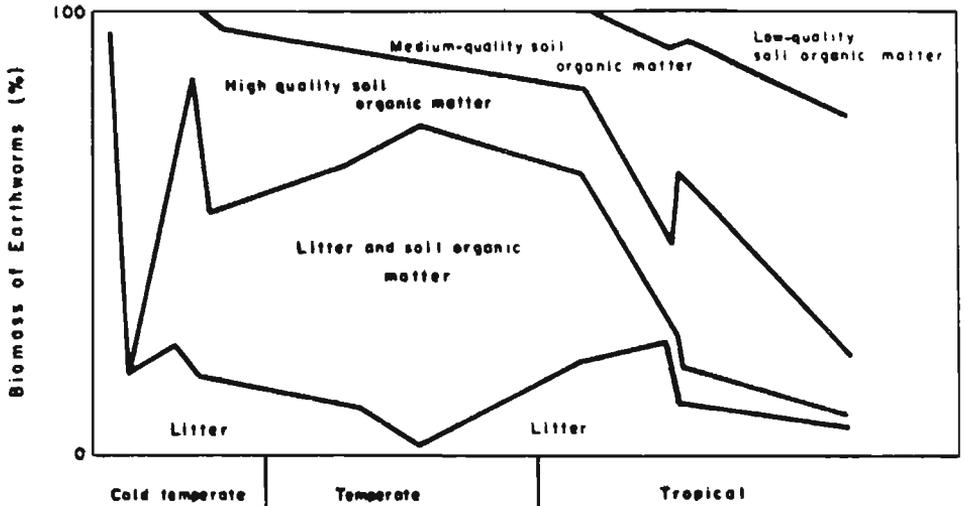

Figure 3. Changes in the feeding structure of earthworm communities along a thermo-latitudinal gradient. From Lavelle (1983). Implications of these data are explained in Box 2.

proach focused on the ecosystem level of biotic organization will be required to achieve this level of understanding. Indices of environmental action over the biota will have to be developed to test patterns and hypotheses. At the most general level, I offer a model (Fig. 4) where abiotic factors are grouped into two categories: those that subsidize the system and those that stress it. The model and its explanation (Box 3) summarize interactions and assumptions believed to be involved in maintaining species diversity.

The first assumption of the model is that the development and maintenance of species diversity involves the expenditure of energy and other resources. These expenditures occur through the energy and resource budgets of organisms. Odum (1970) proposed a relationship (equation 3) to illustrate the rapid rise in the cost of ecosystem organization with an increasing number of species.

The terms on the left side of the equation represent the number of possible combinations between two species if organization, defined as connection, interaction, or insulation of food chains, is
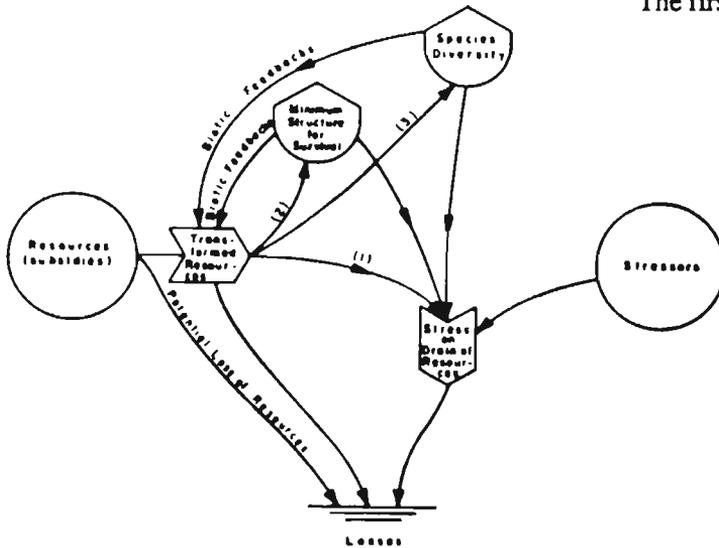

Figure 4. A model of species diversity with emphasis on the abiotic factors that maintain species diversity and the ecological role of species diversity. Box 3 explains the model; the assumptions of the model are discussed in the text (adapted from Lugo 1978).

BOX 3

Explanation of the Model

The model in Fig. 4 (from Lugo 1978) illustrates the major factors involved in the maintenance of species diversity. The circles represent factors external to any biotic assemblage or ecosystem. The tank symbol represents the minimum biotic structure required for the function of an ecosystem and the species diversity of the system. The arrow-shaped symbols illustrate interactions among biotic and abiotic factors. Lines represent the flow of matter, energy, or information that makes ecosystem function possible. The heat sink symbol illustrates the laws of energy and matter that require all systems of nature to have energy degrading into entropy.

The model illustrates the following observed phenomena. Biotic systems (ecosystems) are subjected to environmental factors that may either stress or subsidize their function (a push-pull phenomenon). If stressors are much higher than subsidies (resources) in a given site, it is possible that life itself may not occur at that locality (all resources flow through pathway 1). As more subsidies become available (better conditions and activation of pathway 2) biotic structures develop (illustrated by the tank symbol on the left), and feedbacks between the biota and the environment are immediately established. These feedbacks facilitate the use of resources and contribute to an increase in the resources available to the biota in an area. More favorable conditions allow for the development and support of greater complexity in the biota, and therefore more diversity is possible when pathway 3 is activated. This diversity probably has the role of furthering the feedback mechanisms both with the environment and within the system so that more efficient resource use is possible (c.f. Box 2 on temperature, earthworm—microorganism mutualism, and species richness). When diversity is at a maximum, the potential loss of resources is minimized. This model generates a "humped" curve between species diversity and intensity of stress.

As described, the model can be used to generate hypotheses about the effects of environmental factors on species diversity, the role of diversity within an ecosystem, and the role of biotic interactions in regulating species diversity. For example, the model proposes a system of priorities for resource use in an ecosystem. Energy and other resources are first used to overcome stressors, then to maintain a minimum biotic structure, and last to increase and maintain species diversity.

$$(N^2-N)/2 = (fE_aA)/k \qquad \text{(equation 3)}$$

where N = number of species

   f = fraction of the energy and resource budget allocated to organization

  E_a = energy and resource input per unit area

  A = total area of the system

  k = daily cost of maintaining species interactions

complete. Organization is complete when all possible combinations among species occur. The terms on the right of equation 3 represent the amount of energy and resources available for supporting organization. The potential number of combinations among species increases geometrically with the number of species, but the input of energy and resources to the ecosystem is limited on an area basis. Odum (1970) argues that energy and resource input limits the number of species that can be supported on a unit area as well as the degree of organization possible in a given ecosystem. Only a fraction of the total resources can be allocated to organization because resources have to also be allocated to many other functions, including reproduction, evolutionary progress, intra-species maintenance, and overcoming environmental stressors.

If the number of species (N), is plotted against the number of combinations among species (left term in equation 3) one obtains a plot of a species-area curve. The abscissa (area) is numerically equal to the value of the permutation when fE_t/k is taken as unity in equation 3. This suggests that the pattern of number of species per unit area, a well-documented community attribute, can be explained in part by the amount of energy and resources converging on an area of landscape. The ultimate explanation of the species-area curve is embodied in the fraction of the total energy and resource budget of the biota that is allocated to maintenance of organization.

Odum (1970) suggested that systems with a low number of species allocate a small fraction of their resource budget to organization and a large fraction of the resource budget to other functions. Thus, more energy is needed to eliminate a species from such ecosystems and more energy is available to organisms in the system to compensate for stress. In complex ecosystems, the opposite pattern would occur, i.e., a larger fraction of the energy and resource budget would be dedicated to organization, and complexity would be disrupted more readily with reductions in energy or resource inputs. Odum also suggested that species in complex systems are tightly organized over short distances where there is a higher probability of interaction, but they are loosely organized over long distances were the probability of an interaction is lower. This explains breakaways from species-area relations when larger areas are included in the sampling.

A second assumption of the model in Fig. 4 is that species diversity pays off by allowing a higher efficiency in the use of those resources (energy, water, nutrients) required to sustain biotic activity in a site. In the model, this function is illustrated with feedback from the diversity symbol to the input of resources to the system. The intensity of this feedback is postulated to be inversely proportional to the flow representing the loss of resources from the system. This assumption is based on the observation that species-rich tropical forests have more complex biogeochemistry and appear to have greater nutrient cycling capacity than monospecific forests (Golley 1983, Jordan 1985, Lugo, in press). The ecological function of species diversity is addressed in another section in this paper.

The third assumption of the model is that there is a ranking of priority in the allocation of resources through the development of an ecosystem structure. When abiotic conditions are extreme, few if any organisms can survive. Those that do are able to accumulate very small amounts of biomass. Examples are lichens on rock outcrops, bacteria in hot springs, and the presence of organisms in permanent ice fields, substrates near active volcanoes, deep ocean bottoms, rocks exposed to extreme wave and tide action, and shifting sands in deserts. With abatement of extreme abiotic conditions, a minimal amount of structure necessary for survival will develop. Monospecific ecosystems of higher productivity result. These include many stressed environments such as mangroves, marshes, the tundra, coastal sand dunes, and herbaceous communities in granite outcrops. A high degree of ecosystem complexity and species diversity develop if the resources available in a site compensate for the resource drains associated with site stressors.

There are many field observations and empirical data to support the notion that resource availability (subsidies) and stressors, both abiotic factors, influence ecosystem species diversity. For example, Holdridge (1967) demonstrated that forest complexity (measured as the product of basal area, height, stem, density, and number of tree species in 0.1-ha plots) increased with the availability of water (ratio of

potential evapotranspiration to precipitation). But water availability must be matched with high nutrient availability if the water is to be used by the system. High nutrient availability does not require high nutrients in the soil because nutrients can be recycled rapidly or stored in vegetation. Thus a nutrient-rich system might appear from its soil to be nutrient-poor much like a rich person who invests income might appear to be cash-poor by the amount of money in that person's wallet.

The positive effects of high water availability could be modified by edaphic or atmospheric factors. Poor soil aeration, flooding, high nighttime temperatures, low saturation deficits in the atmosphere, excessive winds, and low nutrient availability are examples of abiotic factors that stress forests and reduce the capacity of sites to support high levels of complexity and species diversity. What these modifying factors do is reduce resource availability to organisms by increasing the cost of obtaining resources or by increasing the cost of survival such that less energy is available for growth and complexity.

For example, high nighttime temperatures increase leaf respiration and reduce photosynthate storages that could be used for other plant or ecosystem functions. Wind has a similar effect by removing structure (e.g., branches, leaves, etc). Factors such as poor soil aeration or low atmospheric saturation deficits reduce the capacity of plants to obtain and transport nutrients, thus slowing ecosystem productivity and diverting resources to sustain complex adaptations of nutrient conservation and recycling. Thus it is possible to visualize why a plot of species richness against resources results in a humped-shaped curve (Tilman 1982), when in reality a stress factor may be responsible for the decline in the number of species (as discussed below). Research is needed to quantitatively determine the nature and intensity of environmental subsidies and stressors and their effects on ecosystem complexity.

Slobodkin and Sanders (1969) asked the question: "Why don't more species adapt to stress?" An answer derived from the discussion above would address the high energy cost of certain adaptations vs. the energy or resource limitations to which populations are exposed. In highly stressed environments there would be strong selective pressure for the most energy-efficient solution to the stress because those species that are efficient in resolving the environmental problem of a site would have more resources left to invest in growth. For certain stressors such as salinity, frost, or fire, the number of solutions available are few. Thus, once developed through natural selection, such an adaptation is likely to be narrow and competitively superior over alternative solutions to the stressor. But solving the problem of stress does not imply that the successful species can survive in a stressful environment without paying a price. Metabolic resources must continuously be allocated to overcome the extreme condition. The costs and benefits of plant adaptation to extreme conditions are discussed in detail by Givnish (1986).

A relaxation of environmental stress frees more energy for alternative uses. If such relaxation is accompanied by an increase in the resources available to organisms (energy subsidies), a greater species richness should be supported by these sites. Usually when this happens, a new component of species invades the site because in the absence of the stress, species adapted to stressful environments spend too much energy in adaptations that are no longer needed and are not competitive when the stress is removed. Examples are the inability of slow growing CAM-metabolism species to compete with faster growing C-3 or C-4 metabolism plants when water resources increase, or the invasion of mangroves and saltmarshes by hydrophytes when salinity decreases.

Currie and Paquin (1987) presented evidence of the abiotic explanation of species diversity. They constructed isoplets of tree species richness for the North American continent and found that 86 percent of the species richness could be explained by climate (realized evapotranspiration accounted for 76 percent of the variation) and topography regardless of historical factors. Their logistic equation of climate and species richness explained species richness in Europe and led them to conclude that contemporary available energy limits species richness in ecosystems.

What Ecological Function does High Species Diversity Serve?

Species were first distinguished by morphological characteristics, and it soon became obvious that a species function in the ecosystem could also be categorized. The trophic function is one of the ways to categorize and evaluate the ecological role of a species. Symbiotic interactions among species is another important ecological role when there is a richness of species because the survival of some species is dependent upon services provided by others. The importance of some species to other species is fairly well established in ecology. Where questions persist is on the function of high species diversity in the ecosystem. If the assumption that there is a cost associated with the maintenance of complexity is correct (previously discussed), why are there complex systems? Or is the subsistance of many species in certain environments simply an accident or byproduct of conditions there?

Early work on this topic centered on the contribution of species diversity to ecosystem stability (c.f., van Dobben and Lowe-McConnell 1975). If species diversity could be related to ecosystem stability, a clear ecological function could be assigned to species richness. Interest in this question ebbed when it was realized that ecosystem stability was related to the stability of abiotic forces. For example, complex cities that lose their monetary inputs, coral reefs subjected to reduced light intensity, or tropical forests whose nutrient pool leaches out suffer a loss in complexity and species diversity in proportion to the loss of the main resource. Thus, no matter how species-complex an ecosystem might be, its structure could collapse with a reduction of input subsidies or an increase of stressful energies. However, it is not yet known if high species diversity facilitates the recovery of ecosystems after collapses such as those just described.

Understanding of the ecological role of high species diversity may be approached by analyzing those ecosystems with the highest species inventories. In terrestrial environments, these ecosystems occur in the highest rainfall areas of the lowland tropics, which are characterized by the absence of frost and relatively constant temperature (Holdridge 1967, Holdridge et al. 1971, Gentry 1982, Gentry and Dodson 1987; this is also discussed in the section Diversity of Forest Types in the Tropics). In marine ecosystems high numbers of species occur in coral reefs exposed to constant water motion as well as a high amount of light energy and stable temperature and salinity conditions. However, in both environments the potential for the loss of nutrients is high because of leaching. In rain forests, the leaching agent is rainfall while in reefs it is the constant flow of nutrient-poor waters through the corals. Vareschi's (1986) assertion that cloud forests are the world's most complex ecosystems is consistent with the suggestion that high rates of water-leaching are associated with high species diversity because cloud forests are leached by rain and cloud water, which together increase leaching stress. Because species represent alternative ways of dealing with abiotic conditions, it could be hypothesized that a high number of species acting within the framework of an organized

community improves the efficiency of resource use.

It is necessary to clarify what is meant by the efficiency of resource use. Resources include water, light, and nutrients. The efficiency of their use is a ratio of output to input at any sector of the ecosystem. Table 4 gives examples of use-efficiency ratios for nutrient cycling in forests. These ratios are grouped in two categories: those under biotic control and those under abiotic control. It is extremely important to understand that there are multiple locations, both in ecological space and in different sectors of a nutrient cycle, where organisms can exert control on the efficiency of use of a resource. Thus, the meaning of efficiency of nutrient or resource use only makes sense when a particular flow or process is specified. A plant can be efficient in nutrient uptake but inefficient in retranslocation. Viewed in this context, the potential usefulness of a diversity of resource-use strategies is obvious, particularly when environmental forces induce resource loss.

Single species can produce very high use-efficiency ratios depending upon the conditions under which they grow. My hypothesis of the

Table 4.   Nutrient cycling use-efficiency ratios. Units have a t time and area basis on both numerator and denominator (e.g. $g.m^{-2}.yr^{-1}$). Nutrient mass is always in the numerator for consistency, but the inverse could be used as well.

Process	Use-efficiency ratios	Comments
Biotic control		
Nutrient uptake	Uptake : transpiration	Chapin (1980)
	Uptake : root respiration respiration	Difficult to measure root
	Uptake : (transpiration) (root respiration)	Would measure total cost of nutrient uptake
Nutrient fixation	Need* : photosynthesis	Chapin (1980)
Liberation by respiration	Mobilization : leaf respiration	Difficult to measure Mobilization in leaves
Retranslocation	Retranslocation : leaf respiration	
Litterfall	Nutrient mass : mass fall posed by Vitousek (1982; 1984)	Inverse of the number pro-
Decomposition	Uptake plus inmobilization : inputs to soil and litter	

Table 4. (cont'd)

Process	Use-efficiency ratios	Comments
Use of fixed nutrients	Nutrient turnover in vegetation	
Abiotic control		
Leaching	Leaching : rainfall	Parker (1983)
Susceptibility to stressors	Loss : intensity of forcing function[§] any compartment	Many environmental factors could cause loss from
Cycle "tightness"	Sum of inputs : sum of losses	This ratio is commonly used in the literature

* Refers to the nutrient requirement necessary to maintain the normal rate of productivity.
§ Refers to nutrient lost to the system as a function of an environmental factor acting as a stressor (e.g., an unusual flood, a fire, etc.).

role of species diversity, however, focuses on the synchronized effect of many species vis-a-vis a potentially stressful abiotic environment. In the wet tropics, high species diversity may be instrumental in cycling and recycling nutrients in spite of enormous abiotic forces that would leach out all chemical nutrients if the synchronized counterforce of the biota were not there.

To test the ecological function of high species numbers in very wet environments, experiments with species removals would have to be conducted in rain forest life zones (*sensu* Holdridge 1967). What would happen in such environments if all species were removed? I predict: (1) site degradation due to high rates of leaching and erosion, (2) a slow rate of ecosystem recovery, and (3) eventual restoration of high species diversity. Once disturbed, the succession in these ecosystems is like that of stressed ecosystems.

The apparent paradox of the occurrence of high-diversity systems in environments that appear to be stressful can be explained with three arguments:

(1) The same factor (water leaching) that causes stress is instrumental in making resources (nutrients) available because multiplying large volumes of water by their low nutrient concentrations results in a large nutrient pool. Thus, a resource opportunity exists, but the mechanisms for capturing nutrients (e.g., the richness of species with its richness of capturing and recycling mechanisms) are missing.

(2) When succession in high-rainfall areas (*sensu* Holdridge 1967) begins with absolutely no biota, it takes an enormous amount of time to fully stock the system with species; once achieved, the system maintains homeostasis but is always vulnerable to disturbance.

(3) Other abiotic factors must be optimal for high-species establishment in these high-rainfall environments because if these other factors are also stressful, high species richness will not materialize. Systems of lower stature and species diversity will develop instead.

The hypothesis that species diversity enhances the capacity of an ecosystem to conserve and circulate nutrients and other resources is supported by advances in the understanding of nutrient cycling in complex tropical forests (c.f., Golley 1983, Jordan 1985). Species richness will result in more efficient cycling of nutrients in high-rainfall areas because:

(1) The chemical composition of tropical plant tissue varies with species and allows many alternative pools of species to store limiting nutrients.

(2) There is an increased probability for different strategies of nutrient retention to be present in the community; these strategies have been documented in northern ecosystems (e.g., Thomas 1969, Muller 1978).

(3) Symbiotic associations with many species of mychorrizal fungi improve uptake and retention of nutrients in spite of low storage of these nutrients in soils.

(4) Diversity of root systems may contribute to specialized uptake and conservation

of nutrients from different soil environments before they are leached (Caldwell and Richards 1986).

(5) Many species of epiphytes and animals (e.g., ants, termites, earthworms, and stream fauna) recover nutrients from clouds and rain water, deep soil horizons (Lee and Wood 1971), soil organic matter (Box 2, Lee 1983), nutrient-poor decomposing wood (Frankland et al. 1982), or stream water before these nutrients are lost to the system.

(6) Many species are needed to recover and concentrate organic matter of low nutritional quality (e.g., detritus food chains in marine and freshwater wetlands; earthworms, Box 2; Swift et al. 1979, Swift 1984).

(7) Experiments show that high diversity of species is associated with greater homeostasis with respect to leaf area (Brown and Ewel 1988) and more root mass available for nutrient uptake (Berish and Ewel 1988; Lugo, in press).

In short, the richness of the biota may represent multiple mechanisms to conserve and recycle nutrients in ecosystems. If so, the concerted activity of many species may counteract the high potential for nutrient loss in high-rainfall environments where species richness is known to peak. However, it is not known if the combined activity of many species in a community is synergistic and related to an increase in nutrient-use efficiency that would not occur if the number of species were lower. Research needs to address this question.

Observations on the convergence of high numbers of sclerophyllous plant species in nutrient-poor environments (e.g., dry forests and

21

communities in ultramaphic soils) and of deciduous plants in nutrient-rich environments support the hypothesis that there is a nutritional role for high species diversity because in both instances the whole community responded to an unusual environmental situation with an unusual nutrient cycling strategy. In the wet tropics the diversification of nutrient strategies may be an analogous ecosystem response. Another set of observations that supports the hypothesis was contributed by Gentry and Emmons (1987). They observed a close relation between the species diversity of understory plants, rainfall, and soil fertility and proposed that the level of understory fertility provides an indicator of overall ecosystem fertility.

If the activities of species are indeed synchronized so that a greater resource-use efficiency occurs within the system, this would lead to an increasingly altruistic or symbiotic concept of population interactions in ecosystems (Alexander and Borgia 1978). Such a view would be in sharp contrast to a view of population interactions as being mostly competitive (MacArthur 1972). While competition obviously has an important role in community function and organization, cooperation may be equally important, particularly under extreme environmental conditions where the nutritional and substrate resources of the system could easily be lost by the action of abiotic forces unchecked by synchronized biotic activity.

How do Humans Depend on a High Diversity of Species?

The need to conserve species diversity is usually justified on the direct use of species by people (Box 4). Are there other compelling

BOX 4

Importance and contributions of species and genetic diversity to humankind	
Contribution	General examples
Renewable natural resources	
New food sources or improvement of existing sources	Grain and seeds (wing bean) Fruits (cuposcu; eggplant) Leaves and stems Roots and tubers (potato) Mammal protein (beef) Fish protein (pirarucu; tilapia) Avian and reptile protein (jacamin) Invertebrate protein (shrimp)
New fiber sources or improvement of existing fibers	Plant stems (rami) Olant reproductive parts (cotton) Animal fibers (silk)

Contribution	General examples
New fuel sources	Plant oils (palms)
	Plant fermentation (sugar cane)
	Animal fats and oils
New chemicals	Curatives for diseases
	Anticancer drugs and immunity enhancers
	Hypotensives and cardiotonics
	Reproductive regulators
	Perfumes and condiments
	Chemical intermediates for synthesis
Construction materials	Timber for trusses and flat board (hardwoods, poles)
	Roofing and siding (palms)
Other raw materials for artesan work or tools	Fine-grained wood for working
	Hard organic polymers (keratin, chitin)
	Bone and ivory (inorganic structural)
	Dried inflorescences or leaves
	Skins and animal parts
	Decorative or ritual items
Environmental health and life support systems	
Buffering of disturbance	Ground cover against erosion
	Maintenance of vegetation cover for climatic regulation
	Pollution absorption
	Natural control of crop pests
	Natural control of disease vectors
Maintenance of balanced food chains and their products	Soil structure, fertility, and activity
	Carbon and nitrogen fixation
	Nutrient cycles and availability
	Watershed and water quality control
	Timber quality control and growth rates
	Cross-pollination of economic plants
	Natural fruit dispersal
	Seed germination capacity

23

Contribution	General examples
Socio-cultural and spiritual values	
Sources of new knowledge, theories, and understanding	Information in the accumulated genetic heritage: variation through space, interactions, adaptive patterns, and life histories Systems characters: nutrient cycling, energy flow, structure and function, and patterns of diversity and complexity
Sources of integration and re-creation	Analysis of complex environmental signals: perception, interpretation, and adaptive response Dynamics of systems: water flow, plant growth, and animal societies Integration with origins and universal perspectives

reasons for conserving species diversity? A recent book (Norton 1986) addressed the economic, sociologic, ecological, and philosophical issues in the human-species diversity relationship. Chapters in Norton's book described anthropocentric (utilitarian arguments) and intrinsic (non-utilitarian arguments) values of species and advocated inclusion of values that are altruistic or aesthetic, rather than purely prudential.

Another important aspect of the human factor in the species diversity debate is the historical adjustments of species diversity to human needs. Accumulating evidence suggests that over millennia, humans have so modified ecosystems that it is almost impossible to identify pristine or human-influence-free tropical forests (Lugo and Brown 1986). For example, Rambo (1979) listed direct selection, dispersal, habitat modification, and domestication as the main modes of interaction between humans and other plant and animal species. An analysis of the situation in Malaysia led him to conclude that: (1) humans are not a new factor in the functioning of Malaysian ecosystems and (2) nearly all Malaysian forests show evidence of human impact, including those believed to be pristine. Mayan cultures are believed to have caused similar impacts in Mexican forests (Barrera et al. 1977, Rico-Gray et al. 1985); examples from other parts of Central and South America (Sanford et al. 1985) and from Africa (Hamilton et al. 1986) are also available. In the Mayan example, human-made forests, silvicultural systems, and close interdependence between forest composition and human use were documented (Gómez-Pompa et al. 1977, Gómez-Pompa 1988).

The implications of these studies is that human survival and ecosystem diversity are

closely related, with dynamic interplays among them. Clearly, research that addresses this kind of symbiosis, as opposed to research aimed at showing negative human impacts, is also needed.

How is the Diversity of Species Changing Today?

To assess the current change in tropical species diversity it is necessary to understand the patterns of land-use change, the diversity of forest types, and the relationship between land-use change and species richness.

Rate of change in the area covered by tropical forests

The rate of change in tropical forest area has been discussed in depth only by Lanly (1982), who made an effort to document the rate of forest loss as well as the rate of increase in the area of secondary forests (by reforestation, afforestation, and natural regeneration; Fig. 5). Other attempts usually emphasize "conversion" or "modification" of mature forests with little or no analysis of "recovery" (Myers 1980). Lanly's data show that of the 11.3 million ha of mature forest lands deforested annually, 5.1 million ha are converted to secondary forest fallow. He estimated the total area of this forest type to over 400 million ha and that almost 1 million ha of secondary forest is created annually from non-forested land through natural regeneration or human intervention. Such large forest areas cannot be dismissed as irrelevant to the conservation of species diversity because they support a significant biota (discussed later), and under certain conditions they are capable of supporting more complexity than the mature system they replace (Ewel 1983, Brown and Lugo, in press).

Lanly's 1982 data also show that deforestation rates are higher in closed than in open forests (Fig. 5). Within the closed forest category
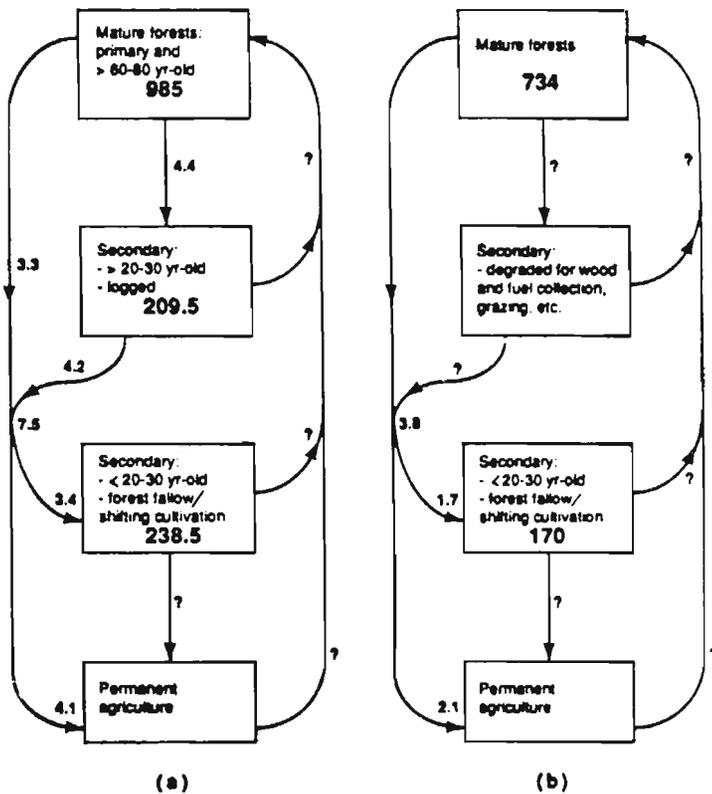
Figure 5. Pathways of land conversion in tropical forest lands. Data are in million hectares (Food and Agriculture Organization 1981; Lanly 1982); values inside the boxes represent total area in 1980 and those on directional lines represent the annual rate of conversion. Closed forests (a) have a complete canopy cover, open forests (b) do not and support a grass understory.

(forests with a complete canopy cover without a grass understory), a large fraction of the conversion involves logged forests that have previously been modified by human activity. Because the dynamics of change in land use and change in forest species richness depend upon the country, region, and economic condition, it behooves scientists to be extremely careful when projecting local experiences to global scales.

The diversity of forest types in the tropics

The Holdridge Life Zone Classification System identifies some 120 ecological life zones in the world, 68 of which are tropical or subtropical (Holdridge 1967). Thirty-two of the tropical and subtropical life zones are capable of supporting forests. About 19 million km² of mature forests exist in the tropics, and they are distributed as follows: 42% in the dry forest life zones, 25% in the wet and rain forest life zones, and 33% in the moist forest life zones (Brown and Lugo 1982). Statistically significant relationships suggest that life zone conditions are related to a characteristic number of tree species (Holdridge et al. 1971), biomass and rate of primary productivity (Brown and Lugo 1982), and the ability to resist and recover from disturbance (Ewel 1977).

Quantitative studies of the relationship between tree species richness and environmental factors show that the total number of tree species increases linearly with rainfall (Gentry 1982) and correlates positively with the ratio of potential evapotranspiration to rainfall (Holdridge et al. 1971; Lugo and Brown 1981) or with actual evapotranspiration (Currie and Paquin 1987). Gentry found a 3.5-fold difference (from 40-140 species per 0.1-ha plot) in the number of tree species (dbh > 2.5 cm) along a rainfall gradient of 1,000 to 3,000 mm. For every 1,000 mm of rainfall, the community gained about 50 tree species. Gentry indicated that species richness

doubles from dry to moist forests and triples from dry to wet forests. Quantitative studies such as these are extremely important for obtaining accurate estimates of potential species extinctions resulting from forest loss. Gentry (1977) discusses such a phytogeographical approach to demonstrate that the number of species lost when forests are destroyed depends on the type of life zone environment being destroyed. Recognizing that tropical forests are diverse in terms of their environmental, and species richness is critical for global estimates of species extinctions, generalizations to all the tropics based on fragmented, qualitative studies are at best of limited usefulness.

An additional complicating factor is that different life zones are subjected to different deforestation rates (Tosi 1980, Sader and Joyce 1988). In tropical America, for example, most human populations are clustered in dry and moist forest life zones, which consequently suffer the heaviest from human impacts (Tosi 1980, Tosi and Voertman 1964, Sader and Joyce 1988). The very wet life zones support the highest number of plant species and are subjected to the lowest rate of deforestation (particularly those in inaccessible locations; c.f., Lugo et al. 1981, Sader and Joyce 1988). The fact that intensities and consequent impacts of human activity vary among life zones has significant implications on the reliability of species extinction estimates.

Relationship between deforestation rate and loss of species

The empirical relationship between deforestation rates and loss of species is not known. However, any calculation of the reduction of diversity as a result of deforestation must use this relationship. Myers (1983) suggested that islands whose forests are grossly disrupted over 90% of the area, but whose inhabitants have protected the remaining 10% of the forests,

stand to lose 50% of the forest species. Lovejoy (1980) discussed five possible functions that the relationship between forest area loss and loss of species could assume, and he used a gradually increasing rate function to arrive at the extinction estimates in the Global 2000 Report. Ehrlich and Ehrlich (1981, p. 280) assumed that the diversity of species would be lost more rapidly than the forest itself and used an exponential function (equation 4) to estimate depletion of species.

$$D = Q_0/r \, (e^{rt-1}) \qquad \text{(equation 4)}$$
where D = depletion of species diversity
Q_0 = rate of depletion as a fraction of remaining diversity
r = rate of increase of Q_0
e = constant
t = time

This exponential function assigns a constant rate of increase (r) to the rate of depletion based on human population growth (1.5%/yr), human impacts in overdeveloped countries (1%/yr), and rate of species depletion due to forest loss (1%/yr). The total rate of increase (3.5%/yr) plus an assumed current rate of species extinctions ($Q_0 = 1\%$/yr, but 2%/yr in a second calculation) were substituted in the exponential function to obtain the estimate of species depletion (D).

The rates of deforestation used in both estimates (Lovejoy 1980, Ehrlich and Ehrlich 1981) are 3.8 to 5.5 times higher than the rates obtained by Lanly (1982). If Lanly's values are substituted in Lovejoy's analysis, the estimate of species extinctions by the year 2000 would be 9% of the total biota instead of 33 to 50% (Table 5). The high estimate of Ehrlich and Ehrlich would be halved by simply using a different

Table 5. Extinction of species in tropical forests implied by deforestation rates reported in Lanly (1982), extinction-deforestation relations used in Lovejoy (1980), and the exponential function of Ehrlich and Ehrlich (1981).

Region	Species present* (x10³)	Projected deforestation[1] 1980-2000 (%)	Loss of species (%)	Extinctions (x10³)
Latin America*	300 - 1,000	17.1	10	30 - 100
Africa*	150 - 500	8.9	4	6 - 20
Asia*	300 - 1,000	15.1	10	30 - 100
Total*	759 - 2,500	12.3	8.8	66 - 220
Total ($Q_0 = 0.0062$, $r = 0.035$)≠		25†		

* From Lovejoy (1980)
† By 2010
§ From Lanly (1982)
≠ From Enrlich and Ehrlich (1980)

value for the assumed fraction of the biota presently undergoing depletion (Q_o). The function used by Ehrlich and Ehrlich is very sensitive to changes in assumptions because of its exponential nature and the absence of any negative feedback to stabilize its response. Therefore, any change in the value of any of the factors contributing to r or Q_o would change the prediction significantly (Table 5).

Correcting for differences in forest species richness, forest recovery rates, and differential human impact by forest type will certainly lower any of the estimates that do not now consider mitigating factors. Furthermore, the functions used to relate forest loss to species loss are still to be established experimentally. When and if this comes about, the results may be more or less conservative than those assumed by either Lovejoy or Ehrlich and Ehrlich.

Seeking a better estimate

To estimate the reduction in the number of species in the tropics it is necessary to consider: (1) the effect of forest types on species abundance, (2) the spatially selective (life zone) intensity of human activity, (3) the role of secondary forests as species refugia, and (4) the role of natural disturbances in maintaining regional species richness. At a regional level one also has to consider the importance of exotic species in the maintenance of species richness, particularly in human-impacted ecosystems. This approach seeks balance by considering factors that maintain species richness as well as those that decrease it. Considerable research is required to provide sound estimates based on this approach because critical data concerning ecosystem functions are not available in enough breadth to support enlightened management or policy making. Kangas (1987) proposed the use of species-area curves to predict extinctions. This method needs to be tested but offers the advantage of using a concept (species-area) that

has wide acceptance in the field and for which a large data base exists.

Calling attention to the positive terms in the species extinction equation

Most calculations of species extinction rates emphasize the negative aspects of the species-loss equation, and this can have beneficial effects in terms of public awareness of environmental problems. I will call attention to the positive aspects of this calculation by using examples from the Caribbean. These examples are used with trepidation because natural conditions in the Caribbean (particularly the frequency of hurricanes) select for resilient ecosystems, and it could be argued that this selective force invalidates the examples given. However, human impacts have been so intense in the Caribbean that the region remains a test case for theories that emphasize island fragility. In addition, the essence of my argument is that in the development of any prediction involving biotic phenomena (whether it is species extinctions, global carbon cycle, or acid rain effects) it is necessary to include the plethora of checks and balances that typify ecosystem function. In the Caribbean, ecosystems must cope with hurricanes and intensive human-induced disturbances while elsewhere periodic fire, earthquakes, frost, or landslides may play the natural role of ecosystem stressors.

In Puerto Rico, human activity reduced the area of primary forests by 99%, but, because of coffee shade and secondary forests, forest cover was never below 10 to 15%. This massive forest conversion did not lead to a correspondingly massive species extinction, certainly nowhere near the 50% alluded to by Myers (1983). An analysis of the bird fauna (Brash 1984) concluded that: (1) seven bird species (four endemic) became extinct after 500 years of human pressure (equivalent to 11.6% of the bird fauna), and (2) exotic species enlarged the species pool.

More land birds have been present on the Island in the 1980's (97 species) than were present in pre-Colombian time (60 species). The resiliency of the bird fauna was attributed to its generalist survival strategy (a characteristic of island fauna) and to the location of secondary forests and coffee plantations (on mountain tops along the east-west axis of the Island), which acted as refugia.

A caveat to these calculations is that prehistoric extinctions caused by humans could dramatically change the results of the analysis. In Hawaii, for example, prehistoric people caused the extinction of 40 endemic bird species, or about half of the birds species in the Hawaiian islands (Olson and James 1982a, b). In the Caribbean islands the fossil record also shows large number of mammal and bird species extinctions some due to prehistoric people and others due to climatic change (Pregill and Olson 1981).

Secondary forests in Puerto Rico have served as refugia for primary forest tree species as well (Woodbury, personal communication; Wadsworth and Birdsey 1982). After 20 to 30 yr of growth, the understory of these ecosystems is supporting species associations characteristic of mature forests. A random survey of 4,500 trees in secondary forests of two life zones (moist and wet forests) resulted in a tally of 189 tree species (Birdsey and Weaver 1982). This survey excluded four of the six forested life zones in the Island and the species-rich mature public forests. Yet it is significant that 25% of the tree species found on the Island (Puerto Rico has 750 tree species, 203 of which are naturalized; Little et al. 1974) were recorded in Birdsey and Weaver's survey of secondary forests. Dominant species in these secondary forests reflect human activity, and although many of the native species typical of mature forests are rare in the forest canopy (142 tree species accounted for 16% of the total basal area of secondary forests),

they are now beginning to appear as pole-size individuals on these forest sites. Obviously secondary forests in highly impacted regions require time to fulfill their role as foster ecosystems for endangered species. But if time is available, a wide variety of tree species will reappear on forest lands.

In the United States, where extensive human-caused deforestation and subsequent forest recovery has occurred, remnant secondary forest "islands" account for a significant portion of landscape species diversity (Burgess and Sharpe 1981). As a group, these secondary forest islands constitute a landscape of greater species richness than found in a landscape dominated only by climax forests. Clearly, secondary forests require more scientific attention before their role and value in human-impacted landscapes may be properly assessed (see Brown and Lugo, in press).

Catastrophic natural events may also be deleterious to the maintenance of species diversity, particularly to those species already at the edge of extinction. However, these catastrophic events are natural phenomena with predictable rates of recurrence to which the biota as a whole is adapted. Evidence is mounting to show that tropical forest ecosystems have endured catastrophic events for millenia (e.g., periodic fires in the moist forests of the Amazon [Sanford et al. 1985] and Borneo). In the Caribbean, hurricanes appear to be important in the maintenance of species diversity. Long-term study areas in the Luquillo Experimental Forest show progressive reductions in tree species between hurricane events (Crow 1980; Weaver 1986). Periodic hurricanes appear to maintain a diverse mix of successional and climax species on a given site. Without hurricanes, successional species would be more restricted. Sanford et al. (1985) suggest that fire performs the same function for Amazonian moist forests.

Studies of regeneration strategies of mature forest species have indicated that disturbance is usually associated with the early phases of seedling germination and establishment in most forest types, including tropical forests (Pickett and White 1985). This has led Pickett and White to propose the concept of "patch dynamics" as a focus of scientific inquiry aimed at understanding ecosystem dynamics. The relevance of this to the maintenance of species diversity is that environmental change and disturbance may be required to maintain a species-rich tropical landscape.

Because humans have facilitated immigration and created new environments, exotic species have successfully become established in the Caribbean islands. This has resulted in a general increase in the total inventories of bird and tree species. Some of these exotic species are pests and termed "biological pollution" (Council on Environmental Quality 1980). However, many exotic species have become so well integrated into the natural landscape that most islanders consider them native.

While there is a clear aversion to exotic species by preservationists and biologists (in cases such as predatory mammals and pests, with good reason!), this may not be fully justified if the full inventory of exotic fauna and flora and certain ecological arguments are taken into consideration. For example, growth of exotic plant species usually indicates disturbed environments, and under these conditions, exotic species compete successfully (Vermeij 1986). They may accumulate and process carbon and nutrients more efficiently than the native organisms they replace. In so doing, many exotic species improve soil and site quality and either pave the way for the succession of native species or form stable communities themselves. There is no biological criterion to judge a priori the smaller or greater value of one species vs. that of another, and if exotic species are occupying environments that are unavailable to native species, it would probably be too costly or impossible to pursue their local extinction. Conversely, because of the trouble and cost involved in the eradication of exotic species, extreme caution is needed before advocating any introduction of species to an environment.

The need for better land and resource management in the tropics

In summary, strong evidence can be assembled to document the resiliency of the functional attributes of tropical ecosystems (including their ability to maintain species richness) when they are subjected to intensive human use. Initial human intervention results in the loss of a few highly vulnerable species. Massive forest destruction would probably be necessary to remove better distributed species. Massive extinctions may only be the result of complete removal of residual forests. Because massive species extinctions may be impossible to stop if human destruction of forests continues unabated, the evidence for ecosystem resiliency is not to be construed as an excuse for continued abuse of tropical environments. Rather, ecosystem resiliency is an additional tool available to tropical resources managers (Holling 1973).

Experience in the Luquillo Experimental Forest Biosphere Reserve in Puerto Rico has demonstrated that species richness can be restored to lands that have been used heavily for agriculture, that growing timber commercially need not eliminate all natural species richness on a site, and that tropical lands respond to sensible care and management. I know of no technical reason why sensible land management in tropical areas cannot lead to the success usually associated with temperate zones. The obstacles to progress are social and are rooted in poor training and education programs, lack of facilities and infrastructure, weak resource manage-

ment institutions, misguided foreign aid programs, world economic policies, lack of commitment to forestry research and enforcement of regulations, and the absence of a land conservation ethic (Mares 1986, Schmidt 1987).

A strategy for forest and species conservation in tropical regions should focus on the restoration to forest production of forest lands where food production is not sustainable. This, and sensible use of secondary forests and tree plantations, will reduce the pressure on forest lands with mature forests or with unique ecological characteristics, and set us on a course to meet the needs of the needy while protecting species diversity.

Acknowledgements

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NATIONAL ADHERING ORGANIZATIONS

ARGENTINA - Consejo Nacional de Investigaciones Cientificas y Technicas
AUSTRALIA - Australian Academy of Science
AUSTRIA - Osterreichische Akademie der Wissenschaften
BELGIUM - Académie Royale de Belgique
BRAZIL - Conselho Nacional de Pesquisas
BULGARIA - Bulgarian Academy of Sciences
CANADA - National Research Council
CHILE - Sociedad de Biologia de Chile
CHINA - Association for Science and Technology, Beijing
CHINA - Academia Sinica, Taipei
CUBA - Academia de Ciencias
CZECHOSLOVAKIA - Czechoslovak Acadmy of Sciences
DENMARK - Det Kongelige Danske Videnskabernes Selskab
EGYPT - Academy of Scientific Research and Technology
FINLAND - Societas Scientarum Fennica
FRANCE - Académie des Sciences
GERMAN DEMOCRATIC REPUBLIC - Deutsche Akademie der Wissenschaften
GERMANY (FEDERAL REPUBLIC) - Deutsche Forschungsgemeinschaft
GHANA - Ghana Science Association
HUNGARY - Academy of Sciences
INDIA - Indian National Science Academy
IRAQ - Scientific Research Foundation
IRELAND - Royal Irish Academy
ISRAEL - Academy of Sciences and Humanities
ITALY - Consiglio Nazionale delle Ricerche

JAPAN - Science Council of Japan
JORDAN - Yarmouk University, Amman
LEBANON - Conseil National de la Recherche Scientifique
MEXICO - Consejo Nacional de Ciencia y Technologia
MONACO - Centre Scientifique de Monaco
NETHERLANDS - Koninklijke Nederlandse Academie van Wetenschappen
NEW ZEALAND - The Royal Society of New Zealand
NORWAY - Det Norske Videnskaps-Academi
PHILIPPINES - National Research Council of the Philippines
POLAND - Academy of Sciences
ROMANIA - Academy of the Socialist Republic of Romania
SAUDI ARABIA - King Abdulaziz City for Science and Technology
SOUTH AFRICA - Council for Scientific and Industrial Research
SPAIN - Consejo Superior de Investigaciones Cientificas
SUDAN - National Council for Research
SWEDEN - Kunglige Vetenskapsakademien
SWITZERLAND - Société Helvétique des Sciences Naturelles
UNITED KINGDOM - The Royal Society
U.S.A. - National Research Council, National Academy of Sciences
U.S.S.R. - Academy of Sciences
VENEZUELA - Consejo Nacional de Investigaciones Cientificas y Technicas
YUGOSLAVIA - Union of Biological Sciences