

Coddington, J.A., P. Hammond, S. Olivieri, J. Robertson, V. Sololov, N. Stork, and E. Taylor. 1991. Monitoring and inventorying biodiversity from genes to ecosystems. Pp. 83-109. In Solbrig, O. (Ed.), *From Genes to Ecosystems: a Research Agenda for Biodiversity*. International Union of Biological Sciences, Paris.

D. Monitoring and Inventorying Biodiversity from Genes to Ecosystems⁵.

Introduction

Biologists recognize that it is not feasible to fully describe the world's biodiversity (di Castri & Younès 1990, Solbrig 1991). Yet an extensive program of inventorying and monitoring aimed at estimating diversity of species and changes in their numbers is essential for a fuller understanding of the role of biodiversity in ecosystem function. It is also necessary in order to set priorities for research. Furthermore, by giving a clearer view of the geographical distribution of biodiversity, such a program will inform conservation efforts.

The processes of inventorying and monitoring are essentially different and are dealt with separately in this section. Inventorying refers to the production of a list or inventory of biodiversity. Such an inventory can deal with genes, populations, communities or ecosystems, but the customary focus is on species diversity. Monitoring, on the other hand, refers to the recording of changes in biodiversity. Changes in diversity at all levels, from genes to ecosystems, can be monitored, but normally the species level and higher are monitored.

In this report we deal separately with inventorying and with monitoring. We first deal with some general issues, namely 1) the establishment of a central database/register of all described species; 2) the establishment of an international biosystematic network; and 3) the relative importance of the marine and terrestrial components of biodiversity. In the context of inventorying we examine 1) how, what and where to sample, and 2) how to analyze the resulting data in order to estimate species richness patterns. Under monitoring we discuss 1) the importance and use of geographic information

⁵Jonathan Coddington, Peter Hammond, Silvio Olivieri, Jane Robertson, Vladimir Sokolov, Nigel Stork, Elizabeth Taylor.

systems; 2) remote sensing techniques for monitoring of biodiversity as it changes through human activity; and 3) where on the globe monitoring should take place and how it might fit into existing and future international programs.

GENERAL CONSIDERATIONS

Taking Stock

The number of species with which we share the planet is very inexactly known and recent estimates vary from 1.84 to 30 million (Erwin 1982; Stork and Gaston 1990; Thomas 1990; Hodkinson and Casson 1991). We also lack a precise count of the number of species already described. Recent estimates vary from around 1.4 to around 1.7 million described species (Barnes 1989; Stork and Gaston 1990). Unfortunately, no centralized register, list, or count of described species exists. Creating such a list is clearly the first step in any inventorying effort.

Taking stock of progress made in inventorying the world's biota entails two separate steps. A first step is to prepare an accurate count of the known number of species per phylum, class, etc. down to family. It has been estimated that between 7000 and 8000 families of organisms have been described (Parker 1982). A subsequent, obviously much larger effort, should focus on a database of the known Linnaean Hierarchy from kingdoms to species, including taxonomic authority at the species level.

Current estimates of the number of described species vary widely because the lists from which they are derived are incomplete, inaccurate, and overlapping. Thus, a first effort to get an accurate count of the number of described species must be combined with the larger effort of making an accurate list.

Some lists already exist, e.g. the Dictionary of the Fungi, 1983 (generic names with species numbers/genus only); the Approved List of Bacterial Names 1980; as well as a miscellany

of catalogues and checklists focussed on smaller groups of organisms. However, for many groups including the largest, the insects, little progress has been made towards preparing comprehensive lists. Preliminary proposals for a complete inventory of described species have been drafted (Life list of Extant Organisms or LEO and the projected Species Plantarum project launched in 1990) at The Nature History Museum, London. Our first firm recommendation is the preparation of a list of all described species.

Recommendation D1. The SCOPE-IUBS-UNESCO program should encourage the preparation within five years of a count of all described species at the family level and above.

Practical problems concerning the distribution of taxonomic resources

A major practical problem, commonly known as the taxonomic impediment, needs to be addressed by the IUBS-SCOPE-UNESCO program if a global inventorying and monitoring effort is to be effective. This problem concerns 1) the lack of financial and human resources in the area of taxonomy, especially in developing countries where most biodiversity is located; 2) the lack of specialists in many important groups of organisms even in developed countries; 3) the disparity in the geographical distribution of collections and information, and 4) the inefficiency of current systematic methodology.

One of the factors limiting any program for inventorying and monitoring biodiversity is the availability of taxonomic expertise. Most systematists are located in the temperate latitudes, and in particular in Western Europe and North America. This is in stark contrast to the distribution of terrestrial species where the center of diversity is in the tropics, particularly in moist tropical forests. There is a need to strengthen national and regional facilities in those countries with the richest biodiversity.

Biological collections in developing countries vary in quality and quantity, but in general terms are poor and are unable to support the necessary local research effort to inventory biodiversity. This situation limits enormously the viability of an international program, limits local participation and creates unnecessary tensions between institutions. The cost of strengthening research institutions in less developed countries, and of developing and maintaining biological collections for this international effort will be high. One solution is to focus resources in regional centers specialized in inventorying particular taxa, with enough critical mass, local autonomy and financial stability to support locally based inventorying efforts. These centers would work in close relation with national research centers in developing countries.

There are several approaches that can serve as models. The U.S. Smithsonian Institution's BIOLAT-MAB program combines intensive research at important neotropical sites with a wide variety of training programs and in-country institutional support. Intensive training courses in taxonomy have been run in East Africa and Malaysia by the International Institute of Entomology of CAB International in Britain. Similar training courses have been offered for entomologists from the developing countries in the New World by the United States Department of Agriculture (USDA) Systematic Entomology Laboratory.

A possible model for organizing inventory efforts at the national level is provided by Costa Rica's Instituto Nacional de Biodiversidad (INBio), which commenced in 1990 (see box D1).

Regional centers to be effective must be linked to a global biosystematics network of regional and national centers, along the lines being developed by CABI for insects, fungi and nematodes. Such networks would be formed by trained taxonomists in centers with reference collections linked to international centers of expertise for different groups. To establish them will require the financial support of inter governmental organizations and national overseas aid agencies.

In the marine environment, an important challenge to network development is to identify long-term data sets available

in the marine laboratories all over the world. Examples of existing networks are the US National Association of Marine Laboratories (NAML), and the European Marine Research Stations (MARS) Network. These marine laboratories have a long history of taxonomic and ecological research on coastal ecosystems and are ideally placed in terms of their facilities, expertise and geographical location to make a major collaborative contribution to inventorying and monitoring biodiversity. Similar facilities exist in other regions of the world.

Box D1. The INBio Experience

The purpose of this organization is to undertake an inventory of the total biodiversity of Costa Rica, to examine its biological and commercial potential, and to provide a mechanism for fostering its utilization.

INBio has an ambitious target: to complete the inventory of Costa Rican species (approximately 500,000 species) within a decade. Much of the initial collection of specimens is being done by *parataxonomists*, a network of Costa Rican citizens who have been trained in proper collection and preparation techniques and who also do the initial sorting and identification of the prepared materials. Over 30 parataxonomists have already been trained by Costa Rican, US and UK scientists and they are rapidly amassing materials. The specimens are initially sorted by the parataxonomists but the identification and description of species is by Costarrican taxonomists and other specialists around the world. At present there are too few such native specialists and training of graduate taxonomists is urgently required if this exciting venture is to succeed. INBio also acts as a broker for studies on the utilization of the country's biodiversity. It has undertaken several contracts with institutions that are screening organisms for useful medical and agricultural materials, and has negotiated intellectual property agreements to provide recompense to Costa Rica from the commercialization of those materials.

An effort should be made to develop new and innovative ways of exchanging biological information so that local research is possible even without access to traditional collections. This should include the evaluation and use of video databases of biological collections, the use of computerized relational biological databases, and other technologies that would allow local researchers to have the necessary biological information at field level at less expense.

Consideration should also be given to improving the effectiveness of current systematic work by (a) streamlining species descriptive processes; (b) minimizing duplication between research workers; and (c) reducing the time systematists currently spend on non-taxonomic activities, notably nomenclatural procedures.

There is a great disparity in the numbers of systematists working on different groups of animals and plants and this is reflected, to some extent, in the number of papers on these organisms. May (1988), for example records that the number of papers per described species for each year (1978-1987) was one or more for birds and mammals compared to less than 0.1 for most non-vertebrate groups. Moreover, there are no specialized systematists for several plant and animal groups in major regions of the world. For example there is no recognized centipede specialist in North America, and the only expert on pseudoscorpions recently retired. Any international program of inventorying and monitoring will need to examine the distribution of taxonomic skills in developed as well as developing countries. The formation of a Global Network of Systematists will clarify the situation regarding the distribution of existing human resources and make co-ordination of future efforts easier.

RECOMMENDATION D1: A global network of systematists should be established under the auspices of the IUBS-SCOPE-UNESCO Program on biodiversity. This network: a) should include regional and national centers for biodiversity, and b) train parataxonomists and graduate taxonomists, c) help accelerate the inventorying of the world's biodiversity through improved systematic practices.

Relative importance of the marine and terrestrial components of biodiversity

Over two-thirds of the Earth's surface is ocean, and the biota of the oceans are essential to the structure and function of the global ecosystem. These considerations alone are sufficient to indicate the importance of both short- and long-term studies of marine biotic diversity. Going by the estimates of relevant systematists (Barnes 1989), one might have thought that most of the major marine groups were relatively well inventoried, excepting perhaps the biota of soft or abyssal sediments. But only fifteen years ago the new bacteria genus *Synechococcus* was discovered. They are now estimated to occur at about 1000-10000 cells per ml throughout the oceans. Molecular biologists believe that *Synechococcus* strains may be as distantly related to each other as orders and classes of organisms in other groups. In addition, during the past three years the free-living prochlorophytes have been discovered, and they too are abundant throughout the oceans. If these very abundant and highly diverse organisms were "missed" until just a few years ago, marine biodiversity could be several orders of magnitude higher than hitherto assumed.

Furthermore, patterns of species richness, especially in the open oceans, and more particularly the rate of turnover or replacement of species across spatial scales are poorly understood and should be a major focus of marine biodiversity research, just as on land. The rapid development of sampling methods and protocols appropriate to the marine arena is a priority. The same is true for microorganisms, terrestrial arthropods and other significant contributors to the terrestrial and freshwater species richness. Agreement on the use of common sampling methods, e.g. use of uniform mesh sizes when screening meiofauna, are vital.

The contribution of the marine realm to global biodiversity at the species level remains unclear, despite its exceptional contribution to diversity at higher taxonomic levels (e.g. phyla) and to different functional types. For example, if productivity and/or biomass correlates moderately well with numbers of species (see Table 4-1), then the total species

richness of the oceans may be low compared to terrestrial systems. Then again, the *Synechococcus* example shows that apparent biodiversity varies widely with taxonomic level. Perhaps the species level summarizes poorly the contribution of marine biotic diversity.

Table D-1: Productivity of terrestrial and Marine Systems^a.

	Marine total	Marine open ocean	Terrestrial
Area	361	332	149
Biomass	155	125	782 ^b
Net production	0.01	0.003	12.2 ^b

^a modified from Valiela, 1984.

^b per unit area

DOCUMENTING DIVERSITY PATTERNS

Sampling and Analytical Approaches

The development of sound measures and reliable estimates of biotic diversity, including patterns of species richness, is essential for the testing of hypotheses, such as those discussed in the previous sections, concerning the extent of global biodiversity and how it is distributed from ecosystem to ecosystem, from place to place and through time. In addition, rough estimates of biodiversity have a role to play in helping to identify testable hypotheses (see previous sections).

Much is already known about geographical patterns of species richness. For example, it is known that coral reefs and moist tropical forests are exceptionally rich in species, and it has recently been learned that deep sea sediments are also

extremely diverse. Deserts, tundra, and hot springs, on the other hand, generally exhibit low species diversity. Some taxonomic lineages, such as beetles are exceptionally rich in species, while others such as bryophytes, are comparatively poor in species. Local and global patterns of diversity are known in detail only for a very few groups of organisms, such as birds and butterflies. The geographical patterns of diversity are well understood in selected parts of the north temperate region, but essentially nowhere else. Nevertheless, our fragmentary knowledge base does provide a substantial list of species richness problems, such as for example the reason for the presence of a major center of endemism. For existing knowledge to be more generalizable it needs to be related to patterns of species richness exhibited by ultra-diverse communities as well as by ultra-diverse taxa.

A critical question is what methods should be used in sampling and estimating biodiversity. Ideally, methods should be fast, reliable, simple, and cheap. In the past, two scientific fields have been principally responsible for providing such methods: systematics and community ecology. Both their approaches have problems. To caricature them, samples collected by systematists represent well the species richness in an area but are statistically intractable, whereas the analysis of samples collected to answer ecological questions are statistically straightforward, but are unrepresentative of the total biota. The two approaches are complementary and some intermediate optimum is feasible and necessary.

Data analysis should also be considered in designing the sampling protocol. For example, the lognormal distribution (the classic way to estimate species richness; Magurran 1988) can be fit to a single, large sample of relative abundance data. Other estimation techniques however depend on a series of replicate samples (Heltsche & Forrester 1983; Lamas *et al.* 1991; Nee *et al.* 1991). Consequently, large samples formed by smaller, replicate samples allow a more thorough analysis.

Data should be collected so as to permit estimation of variability within and between samples and to place confidence intervals on estimates derived from them (Coddington *et al.*, in press). Yet, even if patterns of variance can be analyzed and

confidence limits set, the accuracy of the estimate remains unassessed. Accuracy can be assessed only by comparing methods (either sampling or analytical) to knowns (in effect, the parametric values of the quantities being estimated). The sampling protocol must therefore provide for complete enumeration of the richness of selected taxa so that estimates can be calibrated.

Data Collection

Biologists that are confined to the laboratory can contribute substantially to our understanding of species diversity if field collections are made available. Therefore, when inventorying the biota of a region, collections of living and dead organisms should be obtained for use by other scientific groups, especially molecular biologists. Molecular techniques examine biological diversity, including species diversity, in ways quite distinct from the methods used by many systematists, ecologists and evolutionary biologists. The results from molecular investigations complements the results of systematic and ecological investigations.

New data are needed to provide us with even the most general notion of the extent of the world's diversity in terms of species richness and how it is distributed. To reveal the general picture most economically and effectively three issues are central: what, how, and where to sample. To achieve a balanced view of global patterns of species richness, sampling effort should be allocated in proportion to expected species density or richness, both taxonomically and geographically. The former applies to what to sample, the latter to where. We address each in turn.

What to sample

A few lineages, such as terrestrial vertebrates have been investigated in great detail. However, from the point of view of understanding overall taxonomic diversity, as well as ecological

function, this knowledge is insufficient. We know very little about mega-diversity lineages such as arthropods, fungi, and nematodes. Unicellular and subcellular forms are so little studied that we can't even guess the extent of our ignorance. Biases, inaccuracies, and distortions in our knowledge of pattern may have resulted from our reliance on low-diversity vertebrate groups as model taxa.

Criteria for selecting taxonomic groups for species richness studies include their taxonomic diversity, abundance, and distribution, their functional role in ecosystems, and the ease and reliability with which species can be recognized. Also, groups chosen should encompass the major functional groups in ecosystems and the whole range of organism size. No one taxonomic group is optimal by all criteria. Scientists specializing in the study of the chosen groups must also be available and willing to undertake quantitative, comparative sampling. Yet, to devote the bulk of our resources to study only a few groups (especially the usual few: birds, mammals, butterflies, or tropical trees) would be a serious mistake for several reasons. First, it will discourage training of taxonomists in just those areas in which we are most ignorant and where the biota is most diverse. Second, it will further codify the narrow data base we already have by discouraging new sources of data. Third, these taxa are already studied by many specialists and attract much comparative work, precisely because they are easier to study and because much information is already available.

Therefore, decided preference should be given to high-diversity groups, that provide major ecosystem functions, and about which very little is known. However, information on almost any taxon is valuable at this point, especially in sites selected for intensive research.

How to sample

Methods used to collect data on species richness patterns vary from group to group. A variety of preservation methods for specimens should be used so that specimens can be

studied by a wide variety of scientists, especially molecular biologists. Variety at all levels of biological integration (gene to ecosystem) contribute to biodiversity, and thus the act of collecting a specimen or vouchering a population should serve scientists working at each of those levels. Molecular and cell biological techniques will examine biological diversity, including species diversity, in ways quite distinct from the methods used by many systematists, ecologists and evolutionary biologists.

Complete or as complete as possible inventories for a limited number of sites play an essential role in calibrating the results obtained by means of an individual sampling method. For inventory purposes intensive sampling with a range of methods is generally necessary with special attention directed towards covering patchiness and each layer where stratification occurs. A complete or near-complete inventory may provide data of direct value for species-richness estimations at various scales, but such inventories for speciose focal groups are costly. This expense is more justifiable if the inventory is coupled with quantitative sampling by a range of sampling methods. In so doing it is possible to evaluate and calibrate the more robust and reliable of the methods so that a restricted program of sampling can be designed to apply elsewhere.

Although the greatest diversity of plants and animals is in moist tropical forests, intensive sampling of organisms in the temperate latitudes still offer considerable benefits. Since most of ecological theory and classical taxonomy is based on temperate organisms and habitats we have a much greater understanding of how temperate biomes function. Furthermore such relatively species-poor systems are easier to deal with experimentally. Hypotheses for biodiversity in tropical biomes can be rooted in our understanding of temperate regions. Some estimates of how many species exist are based on known relationships within well-known temperate biotas extrapolated to less well-known tropical biotas. For example, of the 22,000 British insect species, 65 are butterflies. Butterflies are one of the best known insect groups and estimates of total species worldwide are confidently put at 15 to 20,000 (Robbins 1982). If the same ratio (butterfly:insect species) holds worldwide then total insect species richness would be 4.9 to 6.6 million. Testing such a relationship would

involve evaluating the variation in such a ratio at a number of tropical (and temperate) sites and examining differences in the distributions of butterflies and other insect species.

Another conceptually similar approach is that of rapid ecological assessments, for example the Rapid Assessment Program (RAP) recently launched by Conservation International. Many tropical areas (e.g. Amazonian foothills of the Andes in Ecuador and Peru, Madagascan rainforests) have been loosely identified as threatened 'hot spots' of diversity (Myers 1988) but the true significance of the fauna and flora, and in particular of endemics, in these areas is often poorly understood. The RAP team consists of experienced field biologists who in two or three weeks at a site assess the status of focal groups such as birds, large mammals, and trees. RAP provides very coarse, point estimates of the conservation value of prospective sites. As mentioned above, the approach assumes that total richness at a site correlates well with the richness of a few focal groups. Even if the latter is true, we do not know that birds, mammals, and trees are the best, or even acceptably accurate, focal groups to use. A RAP-style package for some mega-diversity groups (e.g. fungi, beetles, spiders, nematodes) is urgently required. Such a *sampling package* of sampling methods, extrapolative procedures of species estimation, and a list of suitable indicator groups is gradually being drawn together by a number of research groups (Hammond 1990; Coddington *et al.* in press). Extensive field trials in lowland rainforest in Sulawesi have provided some strong indications as to which are the best groups of insects to sample, how to sample them and what exactly these methods can tell us about diversity in general at particular sites (Hammond 1990). Others (Adis and Schubart 1986; Stork and Brendell in press) have also examined suitable sampling packages.

RECOMMENDATION D.3. A series of workshops is urgently required to examine and recommend basic sampling methods for various taxa, so that data collected on the same groups will be comparable. Each workshop should focus on a given taxon or discipline (e.g. arthropods, plankton, fungi, soil microorganisms, soils macro-organisms, trees, fishes, birds, mammals, etc.).

Where to sample

We feel that in order to obtain a preliminary notion of the planetary distribution of species richness on a useful scale, extensive sampling at as many points as possible should be combined with intensive sampling at a few sites, all located so as to maximize the utility of the data acquired. For example, intensively studied sites might be chosen to align along important, natural, environmental gradients (e.g. topography, rainfall, or seasonality). They might be chosen from those already selected for long-term study or preservation. Programs studying ecosystem function, community composition, and patterns in species richness would be synergistic.

In extensive sampling, the degree of resolution, that is, the scale at which species richness is mapped, is very important. The deciding factor here is the resources available for the sampling effort. The earth's surface is roughly $5.1 \times 10^8 \text{ km}^2$, comprising about $1.5 \times 10^8 \text{ km}^2$ of land and $3.6 \times 10^8 \text{ km}^2$ of ocean. Even at the relatively coarse scale of 10^6 km^2 (1000 km squares), 500 points would be required for an even coverage of the earth's surface. The more reasonable scale of 10^4 km^2 (100 km squares) would require 51,000 points. Although the latter seems impractical, the former is certainly possible.

It is not efficient to sample on a grid. Factors already known to explain much of the geographic variation in species richness (latitude, topography, climates) can be used to stratify the sampling and to allocate sampling effort efficiently. Even so, careful selection of sites for the extensive survey will not be simple.

An effort similar to that proposed to ameliorate taxonomic ignorance (see Taking Stock, above) might be quick and efficient. Systematists have detailed knowledge of the distribution of the taxa they study. Individually they can identify areas that may be candidates for a rapid assessment effort (e.g. centers of endemism). If the global network of systematists mentioned above is organized, it would be feasible to poll systematists representing all branches of systematics to compile a prioritized list of sites for rapid assessment. The poll should be geographically based, structured as a series of base maps gridded at 10000 km^2 resolution and on which scientists could propose candidate areas for inventory of taxa they knew well. Degree of taxonomic resolution is a factor: family categories are probably appropriate. Data resulting from the questionnaire would be 10000 km^2 pixels identified as key or critical areas for the earth's biota at the level of families. Such data would be machine readable and GIS analyzable.

Intensive sampling on a global basis is clearly impractical. High diversity areas ought to receive the bulk of the effort, but less diverse areas and particularly those that are simply unexplored cannot be ignored. In effect, sampling effort should be allocated according to expected species density or richness. Sites selected for intensive sampling as far as possible should be those already identified for long-term preservation (e.g. Biosphere Reserves) or for long-term monitoring and research (LTERS).

RECOMMENDATION D.4. A geographically and taxonomically based questionnaire requesting information from specialists about the best sites for monitoring should be developed and sent to all working systematists. The collective recommendations should be implemented through the proposed global network of systematists outlined above.

Data Analysis.

Data collection (sampling design) and data analysis interact. Different analytical techniques use data of different measurement scales (categorical [nominal], ranks [ordinal], or counts/measures [interval]). Interval quality data (e.g. enumeration or measurements of biomass) is expensive to obtain. More demanding techniques of estimation that require interval data may be appropriate at sites selected for intensive research but inappropriate for extensive rapid sampling at many points on the globe. Interval quality data can always be collapsed into less precise scales in order to compare intensive and extensive estimates. The reverse is not true.

Intensive research can calibrate extensive research. As outlined above, research to document global biodiversity should be two-pronged: estimates with fairly large confidence intervals at a large number of sites (extensive sampling), and precise estimates at a few selected sites (intensive sampling). The most reliable way to calibrate estimation procedures is against knowns. Intensive research to produce complete data on species richness can calibrate a method, but only extensive application of the method around the world will describe global patterns in species richness, and thus reveal as yet unknown new foci for intensive research. It is essential that methods be checked against knowns at regular intervals, either by intensive sampling of less diverse taxa chosen as exemplars of more diverse taxa, or intensive application of a single method.

Data quality

Both components of diversity (the relative abundance of taxa and their absolute number in a sample) can be measured with varying degrees of accuracy. The data required for an estimation of diversity can be collected in various ways.

Relative abundance of taxa within a site or a collection of samples can be scored as presence/absence, ordinal (e.g. rare, occasional, frequent, abundant), semi-quantitatively (e.g. a

log arithmetic scale such as 0-1, 1-2, 2-4, 4-8, etc.) or quantitatively (counts of individuals or measures of biomass).

Likewise, taxa can be discriminated with varying degrees of precision. It is much less time-consuming to sort a sample of organisms to (morpho)species than it is to identify the resulting list of species. Finding if a species has a name or what it is (see Taxonomic Impediment, above), is still very difficult for the vast majority of species on earth. Most biodiversity sampling, either intensive or extensive, will probably result in a list of codes documented by voucher specimens in museums, rather than in lists of Latin names. Thus, taxa can be resolved at different taxonomic scales (family, genus, species, subspecies, population) and if at the species level, at different geographic scales (species codes unique to a single sample, a set of samples at one site, cross-checked over several to many sites, or globally [Latin binomials]).

Finally, total sampling effort can be allocated among one to several subsamples or replicates. In general, many smaller replicate samples are preferable to a few larger samples because patterns of variation are more easily described in the former than the latter.

Exploratory Data Analysis.

Samples produce at least two kinds of data: relative biomass or number of individuals, and number of taxa or species. Variation in both these quantities can be analyzed independently of their use to estimate species richness or diversity, and such analyses can shed some light on the quality of the data (Coddington *et al.* in press). At least four factors are likely to contribute some variation to the above two statistics: site (plot, quadrat, hectare, community, region); collector (who did the work); method (collecting method or trap bias); and time (of day, local weather, seasonality, year). Because most analytical methods make assumptions about statistical normality, homogeneity of variances, and random sampling, data should be collected in such a way that these assumptions, or departures from them, can be assessed.

Box D2. Estimates of species richness.

All species richness estimators use various assumptions to extrapolate from the known to the unknown. They fall into two broad categories: statistical methods and calibration-multiplicative methods. In contrast, sampling until no new species are found is not estimation but exhaustive censusing of all the species accessible to the sampling method. Complete enumeration will frequently be appropriate in selected contexts in order to provide knowns against which sampling and estimation procedures can be calibrated.

Statistical methods make assumptions about the dispersion or distribution of species and their relative abundances. Use of parametric distributions such as the log-normal (Ugland and Gray 1982), poisson log-normal (Bulmer 1974), or negative binomial (Miller & Wiegert 1989) assume the data fit the distribution (Pielou 1975), and estimate total species richness based on that assumption. Non-parametric techniques (Burnham and Overton 1978; Chao 1984; Heltsche and Forrester, 1983; Lamas *et al.*, 1991) also make assumptions about the data, but may need less, or less precise, information. Methods using less precise data are not necessarily less effective estimators.

Calibration methods make the general assumption that ratios deduced from a known situation will hold in an unknown situation. For example, one may assume that a method that captures a fraction of a known biota in one place will do so in an unknown biota, or that the ranked richness of taxa shared between areas does not differ, or that richness is estimated by the ratio of the area being surveyed to the mean size of species ranges. Still other multipliers depend on assumptions about ecological interactions (number of herbivore specialists per tree species, parasite loads, or constant ratios of body sizes or number of species in trophic levels).

None of the analytical issues raised here are well-enough understood to recommend with confidence one method over another. Research on analytical methods requires at least: (1) compiling data from representative sites to evaluate analytical methods; (2) evaluating estimators through modelling and simulations under different conditions; (3) theoretical work on statistical issues.

RECOMMENDATION D.5. All samples taken should provide the following information: sample attributes (where, when, method, collector); a measure of sampling effort (area, volume, or time); a list of species in the sample (probably as morphospecies codes); and the abundance (no. of individuals or biomass) of each species in the sample.

RECOMMENDATION D.6. A workshop on techniques to estimate species richness is required. Both statistical and calibration-multiplication methods should be considered. Participants should include systematists, ecologists, and statisticians.

MONITORING BIODIVERSITY

Rationale for a Monitoring System for Biodiversity.

In order to rationally conserve and use biodiversity we need to understand how it changes through time, both now and in the past. Inventory work establishes a baseline distribution of biodiversity for particular places at particular times. Monitoring on the other hand, addresses the issue of change or lack of change of biodiversity through time at particular places. Changes in biodiversity occur through time in all communities and ecosystems. Some of these changes result from natural and others from human disturbances. The goal of a monitoring program is to document natural patterns of change or lack of change in order to establish a baseline for understanding the impact of natural disturbance on species composition and abundance in communities and ecosystems. Once this baseline is established it can be used to detect changes in biodiversity that result from human disturbance. Monitoring can also be used to test predicted change, the predictions derived from our theoretical understanding of the species dynamics of communities and ecosystems.

Our inventory of biodiversity will establish the distribution and abundance of biodiversity through space over relatively short spans of time. The monitoring program connects these observations over longer time periods and tracks changes in biodiversity. The monitoring program has three phases: (1) making baseline measurements for detecting change; (2) testing and refining hypotheses and empirical models outlined in the previous sections of this report; and (3) creating an early warning system for detection of deleterious changes in biodiversity through the establishment of a Global biodiversity assessment network.

The biodiversity monitoring program should combine remote sensing with field based monitoring. Remote sensing is the best tool available for the rapid survey of large areas for the detection of disturbance. It should be used to identify areas where rapid change is occurring and assess the causes of these changes (i.e., urbanization, forest clearance for agriculture, permafrost melt). This information can then be used to set priorities for field monitoring. Field monitoring can then be used to identify changes in biodiversity. Scale, intensity and extent of monitoring will depend on the nature of the disturbance and its predicted effects.

Global vs. Local Monitoring

Global monitoring efforts such as UNEP's GEMS are already attempting to identify changes in communities and ecosystems due to disturbance. These are normally based on remote sensing and thereby limited by the technique (e.g., resolution is coarse, spectral response is limited).

RECOMMENDATION D.7. The IUBS-SCOPE-UNESCO program should use existing remote sensing programs for detecting change and should not try to develop new initiatives for a global remote sensing program for biodiversity.

Comment. Too many technical problems exist and much research is needed to validate theoretical approaches. Remote sensing is also very expensive and available resources are needed for validation issues. It is probably better right now to work locally and validate approaches and methods at selected sites.

Geographic Information Systems (GIS) and Remote Sensing (RS) are technical tools that can be used within a research program for the inventorying and monitoring of biodiversity. Both have strengths and weaknesses depending on the particular application, and both have unresolved technical issues. Care must be taken to use the technologies appropriately. Use of RS due to its expense tends to concentrate resources and information. GIS is cheaper and more flexible and thus more amenable to local use. Since successful global inventory and monitoring effort relies upon regional and global cooperation and coordination of research effort, careful thought must be given to sharing the technology and data derived from its application.

Proposal for setting up a minimum core network of sites for monitoring changes in Biodiversity.

An ideal network would cover a selection of critical ecosystems. Examples are: areas that are being subjected to degradation through human activities (wetlands drained for agriculture, tropical forests, coral reefs, temperate forests under acid rain, etc.); transition zones (treeline in mountain areas, forest grassland borders, desert edges, areas that show shifts in biota due to climatic change); sites which have been intensively studied and have well established species lists, coupled with meteorological data sets and soil maps. Particularly interesting are sites which are aligned along gradients such as rainfall longitude, latitude and/or altitude. These could take the form of localized transects such as following the different altitudinal life zones up and down a mountain

Setting up such a network for the purpose of monitoring changes in the pattern of global biodiversity has, of necessity, to

be based on the opportunities offered by already existing sites and networking initiatives involving cooperative agreements among countries and scientific research institutions. In many ways, such a core network of sites could be built upon existing protected areas such as national parks. The international Biosphere reserve network offers a particularly good potential. Biosphere reserves encompass protected areas which are secure sites for setting up long term studies involving considerable financial and human investments; many of the research sites on all aspect of biodiversity are located within existing biosphere reserves (e.g. Manu, Tai, Moorhouse, Astrakansy) or are currently being planned as becoming or being incorporated into biosphere reserves (Waddensea, Jasper Ridge, Lamto). As biosphere reserves are proposed by the countries in which they are located for international recognition under MAB, they therefore benefit from the commitment of the institutions concerned to international cooperation on scientific questions of global magnitude and concern. Biosphere reserves are of interest to other international organizations involved in the conservation and understanding of biological diversity. For example UNEP, for *in situ* conservation of representative examples of the worlds major ecosystems; FAO, for the conservation of wild genetic resources and the maintenance traditional agriculture involving land races and ancient cultivars; IUCN, for combining conservation concerns with regional planning and management; WRI/IUCN/UNEP, for implementing the biodiversity strategy; Conservation International, for building up local support for conserving biological diversity, especially in "hot spots"; UNCED, for implementing the Agenda 21 on biodiversity; etc. The existence of the network, although far from being fully functional and effective, is attractive for future investments by the international scientific and donor community, for example under the recently started Global Environmental Initiative which specifically is designed for funding projects on halting the loss of biodiversity.

RECOMMENDATION D.8. Under the aegis of the IUBS/SCOPE/UNESCO program, a series of planning and coordination meeting should be organized to set up the core monitoring network. Sites selected should be those where the hypotheses outlined in the rest of this report can best be tested in the field.

Countries and institutions should be invited to propose sites and their associated scientific research institutions to set up an initial pilot core network of sites to test the hypotheses and elaborate a minimum monitoring program for the next 10 years. The network shall be open and can be supplemented as opportunities arise and as more countries wish to contribute to the global effort. In particular a major effort should be made to harmonize research, monitoring, inventorying, and data handling endeavors.

Choice of sites for major studies: Intensive and extensive studies

We suggest that inventorying of biodiversity should be both intensive and extensive. We recognize that the ecosystem function of many groups of organisms, particularly those of small size, is poorly understood, as is their taxonomy. Although the diversity and role of almost all groups of organisms has been investigated to some level at different sites around the world, a composite view of the function of these groups in single community is not possible. Studies such as those of Schaefer and others (Schaefer 1990) have provided a unique and informative view of the trophic structure and energy budget of the soil biota by compiling the results of a series of sampling and taxonomic programs of the components of the soil biota. We therefore recommend that similar and perhaps more comprehensive inventorying programs be carried out a few sites around the world (e.g. three tropical forest sites; one in each of the three major tropical forest regions of the world), with particular emphasis on the soil and on the usually less well studied micro-organisms such as fungi, nematodes, bacteria and protozoa.

Recognizing the long-term nature of studies on microorganism groups, especially seasonality and periodicity (repeated visits for more than 20 years are needed for the larger fungi), we see advantages in the sites chosen for intensive studies being ones for which a substantial body of information already exists.

Given that taxon richness and functional group richness at the community level are influenced by: 1) historical events, both natural and anthropogenic; 2) regional species pool; 3) local resource availability; and 4) local disturbance regime, and given that estimates of taxon richness and functional group richness depend on: 1) sampling scale; 2) sample size; 3) choice of taxon; and 4) availability of taxonomic expertise, it is recommended that we should: 1) select sampling sites along a natural gradient of a single major environmental variable, but within a single region that is homogeneous in species pool and history; 2) use transects in different regions, continents, and seas, as replicates to test hypotheses regarding the response of taxon and functional group richness to resource availability and disturbance; 3) select transects from areas with high and low numbers of species in the regional species pool; 4) select transects to encompass at least one existing long-term monitoring station, where manipulative experiments could be conducted and for which taxonomic and ecological reference data exist; 5) select resource variables that relate directly to major global change impacts, such as water and nutrients; 6) select different taxa to estimate richness at each site to avoid bias and group compensation problems ("ecological equivalents"). These recommendations apply widely to all biodiversity studies from genes to ecosystems.

Relations with International Monitoring Efforts.

Any monitoring program on biodiversity should take advantage of existing and planned efforts in related fields. Examples include: (1) The Global Change System for Analysis, Research and Training (START) of the International Geosphere Biosphere Program (IGBP) of ICSU. This program focuses on the establishment of regional research

centers which will coordinate and handle the data and train the personnel required by the IGBP core projects on global change. The first such center has been proposed in France, to serve essentially francophone Africa in which there would be selected research sites for the different core projects. IGBP mainly relates by its own definition to physical and chemical dimensions of global change but the core projects on ecological complexity appears to be most relevant to biological diversity and the IUBS/SCOPE/UNESCO program.

(2) The Global Ocean Observing System (GOOS) supported by IOC (International Ocean Commission) and WMO (World Meteorological Organization), also related to Global Change. GOOS represents a recent UN system initiative designed to reduce the level of uncertainty associated with predictions of global climate. Regional instruments of assessment and monitoring of marine and coastal areas are prepared to facilitate the collection, release and exchange of relevant data and information, and are included in the Agenda 21 for the 1991 United Nations Conference on Environment and Development (UNCED).

(3) UNEP (UN Environment Program, based in Nairobi) has a Global Environment Monitoring System (GEMS) which encourages regional and International cooperation on data collection and handling. A Scientific Advisory Committee on Terrestrial Environmental Monitoring and Assessment (SACTEMA) has been established in November 1990 with a view to setup a global system for monitoring selected environmental pollutants (e.g. heavy metals, DDT, etc.), on a suite of sites. The SACTEMA has set up three working groups looking into ongoing programs and initiatives.

(4) The Biodiversity Strategy and Program being currently established by World Resources Institute, the World Conservation Union (IUCN) and UNEP focuses more specifically on protection of biodiversity, for example through the setting up of national biodiversity institutes, cooperative management schemes for ecoregions such as large river basin regional seas, etc. In addition, an auditing system for biodiversity is envisaged, to be undertaken by the World

Conservation Monitoring Center (WCMC) based at Cambridge and Kew, U.K. This system will depend on the data accumulated for the *red data books* on rare, threatened and endangered animal and plant species, as well as the information on the conservation status of the 4,600 protected areas recognized by IUCN.

(5) An International Network of Biosphere Reserves has been established under UNESCO's Man and the Biosphere (MAB) Program in 1976. It is the only network of protected areas at the intergovernmental level which combines the *in situ* conservation of representative examples of natural and seminatural ecosystems with scientific research and monitoring, consideration of rural development and local resource use problems, as well as with environmental education and training. Governments, when proposing sites for international recognition as Biosphere Reserves, express their commitment to use these sites for cooperative research, exchanges of information and personnel. This network, although far from perfect, has the virtue of existing already and offers great potential for collaborative work with other research sites around the world for furthering the IUBS/SCOPE/UNESCO program on biodiversity.

(6) UNESCO'S Coastal Marine Project (COMAR) has resulted from demands by coastal states for scientific knowledge as a basis for the rational management of coastal zone ecosystems. The need for knowledge of continent-ocean interactions is greatest for the management of lagoons and estuaries, salt marshes, mangroves, sea-grass beds, coral-reefs and the intertidal zone. COMAR consists of a core program and regional activities. The core program is necessary to develop a background of theory, experience and coordination. The regional activities try to reinforce the capacities of countries to build coordinated research activities, monitoring, and training. Ongoing COMAR projects exist in North America, Europe, Asia, the Pacific, Latin America, the Caribbean, Africa, the Mediterranean and the Red Sea. COMAR provides a good basis for monitoring coastal ecosystems in a unique range of biogeographic coverage. Marine biodiversity is now considered as one priority for ongoing activities of COMAR.

Other initiatives which need to be taken into consideration for future work include the "Agenda 21", being developed on the topic of biodiversity in preparation for the 1992 United Nations Conference on Environment and Development (UNCED), and also the international extensions of the Sustainable Biosphere Initiative prepared by the Ecological Society of America (Lubchenko *et al.* 1990).

References Cited

- Adis, J. and Schubart, H.O.R. 1985. Ecological research on arthropods in central Amazonian forest ecosystems with recommendations for study procedures. In: Cooley, J.H., and Golley, F.B. (Eds.). *Trends in Ecological Research for the 1980's*. p. 111-144. NATO Conference Series, Series 1: Ecology. London: Plenum Press.
- Arber, W. 1990. *Genetic diversity is a prerequisite for a harmonious biological evolution*. Talk given at the Workshop on "Biological diversity and cultural diversity" organized by the European Academy and UNESCO, at UNESCO headquarters, Paris.
- Barbault, R. and S. Stearns. 1991. Towards an evolutionary ecology linking species interactions, life-history strategies and community dynamics: An introduction. *Acta Oecologica* 12: 3-10.
- Barnes, R.D. 1989. Diversity of organisms: how much do we know. *Amer. Zool.*, 29: 1075-1084.
- Brown, J. H., and Heske 1990. Control of a desert grassland transition by a keystone rodent guild. *Science* 250:1705-7.
- Brown, J. H., and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology* 58:445-449.
- Bormann, F. H. and G. E. Likens, 1979. *Pattern and Process in a Forested Ecosystem*. New York: Springer-Verlag.
- Bulmer, R.G. 1974. On fitting the Poisson lognormal distribution to species abundance data. *Biometrics* 30: 101-110.
- Burnham, K.P. and Overton, W.S. 1978. Estimation of the size of a closed population when capture probabilities vary among animals. *Biometrika* (65(3): 625-633.
- Carson, H. L. 1961. Heterosis and fitness in experimental populations of *Drosophila melanogaster*. *Evolution* 15: 496-509.
- Caswell, H. 1978. A general formula for the sensitivity of population growth to changes in life history parameters. *Theoret. Pop. Biol.* 14: 215-230.
- Chao, A. 1984. Nonparametric estimation of the number of classes in a population. *Scand. J. Statist.* 11: 265-270.
- Chesson, P. L., and T. J. Case. 1986. Overview: Nonequilibrium community theories: Chance, variability, history, and coexistence. In J. Diamond and T. J. Case, eds. *Community ecology*. Pp. 229-239. New York: Harper and Row.
- Coddington, J. A., Griswold, C. E., Silva, D., Pearanda, E., Larcher, S. F. (In Press.) Designing and testing sampling protocols to estimate biodiversity in tropical ecosystems. In: E. C. Dudley, ed., *The Unity of*

Acknowledgments

The organizers of the workshop wish to acknowledge the financial support from the National Science Foundation, The United States National Committee for the Man and the Biosphere Program, the International Union of Biological Sciences and MAB/UNESCO. Without their help this very successful gathering would not have been possible.

We also wish to recognize the selfless work and great effort of all that helped shape the present report. Their enthusiasm was boundless, their advice beneficial and wise, their knowledge and scholarship liberally offered. The discussions were stimulating and the interactions remarkable and noteworthy. To all we are very grateful. We hope that this workshop represents the beginning of a serious scientific effort to resolve some of the serious problems surrounding biodiversity loss.

Dr. David Foster, director, and all the staff of the Harvard Forest offered the use of the facilities and gave generously of their time. Thanks to all of them an agreeable living and working environment was created. Luca Cesari, William Hoffmann, Carlos Klink, and Adriana Moreira, helped with arrangements, transportation, and other organizational matters for which we are very grateful.

In closing the editor wishes to acknowledge very specially the advice and help received from old and new friends Don Stone and Bob Woodmansee. Their assistance made this workshop so much more important. Francesco di Castri and Hal Mooney as always provided inspired leadership. Bernd von Droste, James Edwards, Malcolm Hadley, Jane Robertson, Roger Soles, Patricia Werner, and Talal Younès, provided personal and institutional support which is gratefully acknowledged.

Evolutionary Biology: Proceedings of the International Congress of Systematic and Evolutionary Biology. College Park, MD: Dioscorides Press.

- Colwell, R. K. 1986. Community biology and sexual selection: Lessons from hummingbird flower mites. In T. J. Case and J. Diamond, eds. *Ecological communities*. Pp. 406-424. New York: Harper and Row.
- Connell, J. H. 1978. Diversity in tropical rainforests and coral reefs. *Science* 199: 1302-1309.
- Cooper, W. S. 1913. The climax forest of the Isle Royale, Lake Superior and its development. *Bot. Gaz.* 15: 1-44, 115-140, 189-235.
- Darwin, C. 1859. *The origin of species by means of natural selection*. Murray, London.
- DeAngelis, D.L. 1980. Energy flow, nutrient cycling, and ecosystem resilience. *Ecology* 61: 764-71.
- DeAngelis, D.L., W.M. Post, and C.C. Travis. 1986. *Positive Feedback in Natural Systems*. Springer-Verlag: Berlin.
- DeAngelis, D.L., P.J. Mulholland, A.V. Palumbo, A.D. Steinman, M.A. Huston, and J.W. Elwood. 1989. Nutrient dynamics and food-web stability. *Ann. Rev. Ecol. Syst.*, 20:71-95.
- DeBach, P. 1974. *Biological Control by Natural Enemies*. Cambridge, U. K.: Cambridge University Press.
- Diamond, J., and T. J. Case, ed. 1986. *Community ecology*. Harper and Row, New York.
- di Castri, F. 1991. Ecosystem evolution and global change. In O. T. Solbrig and G. Nicolis (eds.), *Perspectives in Biological Complexity*, pp. 189-218. Paris: IUBS.
- di Castri, F. and T. Youngs. 1990. Ecosystem Function of Biological Diversity. *Biology International*, Special Issue 22. Paris: IUBS.
- Drake, J. A., H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmánek, and M. Williamson. 1989. *Biological Invasions. A Global Perspective*. Scope 37. Chichester, U.K.: John Wiley & Sons.
- Ehrlich, P. R. and A. H.Ehrlich. 1981. *Extinction: The Causes and Consequences of the Disappearance of Species*. New York: Random House.
- Erwin, T. L. 1982. Tropical forests: their richness in Coleoptera and other arthropod species. *Coleopterists Bulletin* 36: 74-75.
- Falconer, D. S. 1981. *Introduction to Quantitative Genetics*. London: Longman.
- Fox, J. F. 1979. Intermediate disturbance hypothesis. *Science* 204: 1344-1345.
- Fuentes, E. R. 1976. Ecological convergence of lizard communities in Chile and California. *Ecology* 57:3-17.

- Gadgil, M. 1991. Conserving India's Biodiversity: the societal context. *Evolutionary Trends in Plants* 5:
- Gadgil, M. and O. T. Solbrig. 1972. The concept of *r*- and *K* selection: evidence from wildflowers and some theoretical considerations. *Amer. Nat.* 106: 14-31.
- Gautier-Hion, A. and G. Michaloud. 1989. Are figs always keystone resources for tropical frugivorous vertebrates? A test in Gabon. *Ecology* 70:1826-33
- Gilbert, L. E. 1980. Food web organization and the conservation of Neotropical diversity. In M. E. Soule and B. A. Wilcox, eds. *Conservation Biology*. Pp. 11-33. Sunderland, MA.: Sinauer Associates
- Grant, V. 1981. *Plant Speciation*. New York: Columbia University Press. 2nd edition.
- Grassle, J. F., P. Laserre, A. D. McIntyre and G. C. Ray. 1991. Marine Biodiversity and Ecosystem Function. *Biology International* Special Issue 23. 19 pp. Paris: IUBS.
- Gregorius, H.-R. 1990. A diversity-independent measure of evenness. 136:701-711.
- Grime, J.P. 1973. Competitive exclusion in herbaceous vegetation. *Nature* 242: 344-347.
- Grime, 1979. *Plant Strategies and Vegetation Processes*. Chichester: John Wiley.
- Hammond, P.M. 1990. Insect abundance and diversity in the Dumoga-Bone National Park, N. Sulawesi, with special reference to the beetle fauna of lowland rain forest in the Toraut region. In: Knight, W.J. and Holloway, J.D., (Eds.), *Insects and the Rain Forests of South East Asia (Wallacea)*, pp. 197-254. London: Royal Entomological Society, i-iv; 343 pp.
- Hawksworth, D.L. 1991. The fungal dimension of biodiversity: magnitude, significance, and conservation. *Mycol. Res.* 95(6): 641-655.
- Hedrick, P. W. 1984. *Population biology: the evolution and ecology of populations*. Boston: Jones and Bartlett publ.
- Heltshe, J.F. and Forrester, N.E. 1983. Estimating species richness using the jackknife procedure. *Biometrics* 39: 1-11.
- Hill, M. O. 1973. Diversity and evenness: A unifying notation and its consequences. *Ecology* 54:427-431.
- Hodkinson, I. D. and D. Casson. 1991. A lesser predilection for bugs: Hemiptera (Insecta) diversity in tropical rain forests. *Biol. J. of the Linnaean Society* 43: 101-109.
- Holling, C.S. 1973. Resilience and stability in ecological systems. *Ann. Rev. Ecol. Syst.*, 4:1-23.

- Holt, R. D. 1977. Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology* 12: 197-229.
- Holt, R. D. 1984. Spatial heterogeneity, indirect interactions, and the coexistence of prey species. *American Naturalist* 124: 377-406.
- Houghton, J. T., G. J. Jenkins, and J. J. Ephraums (eds.). 1990. *Climate Change*. Cambridge, U. K.: Cambridge University Press.
- Huffaker, C. B. 1958. Experimental studies on predation: dispersion factors and predator-prey oscillations. *Hilgardia* 27: 343-383.
- Hughes, R.G. 1986. Theories and models of species abundance. *Amer. Nat.* 128: 879-899.
- Huston, M.A. 1979. A general hypothesis of species diversity. *American Naturalist*, 113:81-101.
- Huston, M. A. 1985. Patterns of species diversity on coral reefs. *Ann. Rev. Ecol. Syst.* 16: 149-177.
- Huston, M.A. (in press). *The Ecological Regulation of Biodiversity*. Cambridge, U. K.: Cambridge University Press.
- Huston, M.A., D.L. DeAngelis, and W.M. Post, 1988. New computer models unify ecological theory. *BioScience*, 38:682-691.
- IGBP. 1990. *The International Geosphere-Biosphere Programme: A Study of Global Change (IGBP)*. The Initial Core Projects. Stockholm: IGBP.
- IUBS. 1989. *Proceedings of the 23rd General Assembly*, 16-21 October, 1988. Canberra, Australia. Paris: IUBS.
- Kidwell, M. G. 1990. Evolutionary aspects of hybrid dysgenesis in *Drosophila*. *Canadian Journal of Zoology* 68: 1716-1726.
- King, L. E. and B. A. Schaal. 1989. Ribosomal DNA variation among glade populations of *Rudbeckia missouriensis*. *Evolution* 43: 117-119.
- Kolasa, J., and S. T. A. Pickett, ed. 1991. *Ecological heterogeneity*. New York: Springer Verlag.
- Lamas, G., Robbins, R.K. and Harvey, D.J. 1991. A preliminary survey of the butterfly fauna of Pakitza, Parque Nacional del Manu, Peru, with an estimate of its species richness. *Publ. Mus. Hist. nat. UNMSM* 40(A): 1-19.
- Lewis, D. M. 1981. Determinants of reproductive success of the white-browed sparrow weaver, *Plocepasser mahali*. *Behav. Ecol. Sociobiol.* 9: 83-93.
- Lewis, D. M. 1982. Dispersal in a population of white-browed sparrow weavers. *Condor* 84: 306-312.
- Lewontin, R.C. 1969. The meaning of stability. *Brookhaven Symp. Biol.*, 22:13-24.
- Lubchenco, J. 1978. Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. *Am. Nat.* 112: 23-39.

- Lubchenco, J., A. M. Olson, L. R. Brubaker, S. R. Carpenter, M. M. Holland, S. P. Hubbell, S. A. Levin, J. A. MacMahon, P. A. Matson, J. M. McIlillo, H. A. Mooney, C. H. Peterson, H. R. Pulliam, L. A. Real, P. J. Regal, and P. G. Risser. 1991. The sustainable Biosphere Initiative: an ecological research agenda. *Ecology* 72: 371-412.
- MacArthur, R. H. 1960. On the relative abundance of species. *American Naturalist* 94:25-36.
- MacArthur, 1965. Patterns of species diversity. *Biol. Rev.* 40: 510-533.
- MacArthur, R. 1969. Patterns of communities in the tropics. *Biol. J. Linnaean Soc.* 1: 19-30.
- Magurran, A. E. 1988. *Ecological diversity and its measurement*. Princeton University Press, Princeton, N. J. 179 pp.
- May, R. M. 1975. Patterns of species abundance and diversity. In: M. L. Cody and J. M. Diamond (eds.), *Ecology and evolution of communities*, pp. 81-120. Harvard University Press, Cambridge, MA.
- May, R.M. 1988. How many species are there on Earth?. *Science* 241: 1441-1443.
- Miller, R.I. and Wiegert, R.G. 1989. Documenting completeness, species-area relations, and the species abundance distribution of a regional flora. *Ecology* 70(1): 16-22.
- Myers, N. 1988. Threatened biotas: "Hot Spots" in tropical forests. *The Environmentalist*, 8: 187-208.
- Naceem, S., and R. K. Colwell. 1991. Ecological consequences of heterogeneity of consumable resources. In J. Kolasa and S. T. A. Pickett, eds. *Ecological heterogeneity*. New York: Springer Verlag.
- Nee, S., P. H. Harvey, and R. M. May. 1991. Lifting the veil on abundance patterns. *Proc. Royal Society, London B.*, 243: 161-163.
- Nei, M. 1975. *Molecular Population Genetics and Evolution*. Amsterdam: North-Holland Publishing Co.
- O'Brien, S. J., M. E. Roelke, L. Marker, A. Newman, C.A. Winkler, D. Meltzer, L. Colly, J.F. Evermann, M. Bush, and D. E. Wildt . 1985. Genetic basis for species vulnerability in the cheetah. *Science* 227: 1428-1434.
- Paine, R. T. 1966. Food web complexity and species diversity. *American Naturalist* 100: 65-75.
- Paine, R. T. and S. A. Levin, 1981. Intertidal landscapes: disturbance and the dynamics of pattern. *Ecol. Monogr.* 51: 145-178.
- Parker, S.P., Ed. 1982. *Synopsis and Classification of Living Organisms*. New York: McGraw-Hill Book Company, 2 vols., 2398 pp.
- Patil, G.P., and C. Taillie. 1982. Diversity as a concept and its measurement. *Journal of the American Statistical Association* 77:548-567.

- Peet, R. K. 1975. Relative diversity indices. *Ecology* 56:496-498.
- Pianka, E. R. 1970. On r- and K- selection. *Amer. Nat.* 104: 592-597.
- Pielou, E. C. 1975. *Ecological Diversity*. New York: Wiley Interscience.
- Pielou, E. C. 1977. *Mathematical ecology*. Wiley, New York.
- Pimm, S.L. 1982. *Food Webs*. London: Chapman and Hall.
- Pimm, S.L. 1984. The complexity and stability of ecosystems. *Nature* (Lond.) 307:321-26.
- Pimm, S.L., Lawton, J.H. and Cohen, J.E. 1991. Food web patterns and their consequences. *Nature* (Lond.) 350: 669-674.
- Reid, W. V. and K. R. Miller. 1989. *Keeping Options Alive: The Scientific Basis for Conserving Biodiversity*. Washington, D.C.: World Resources Institute.
- Ricklefs, R. E. 1989. Speciation and diversity: The integration of local and regional processes. In D. Otte and J. A. Ender, (eds). *Speciation and its consequences*, pp. 599-622. Sunderland, MA.: Sinauer Associates.
- Robbins, R. K. 1982. How many species of butterflies? *News of the Lepidoptera Society* 1982: 40-41.
- Roughgarden, J. 1979. *Theory of population genetics and evolutionary ecology: An introduction*. Macmillan, New York.
- Sammarco, P. W., J. S. Levinton, and J. C. Ogden. 1974. Grazing and control of coral reef community structure by *Diadema antillarum* Philippi (Echinodermata: Echinoidea): a preliminary study. *J. Mar. Res.* 32: 47-53.
- Sayer, J.A. and Whitmore, T.C. 1991. Tropical moist forest: destruction and species extinction. *Biol. Conservation* 55: 199-213.
- Schaefer, M. 1990. The soil fauna of a beech forest on limestone: trophic structure and energy budget. *Oecologia* 82: 128-136.
- Schluter, D., and P. R. Grant. 1982. The distribution of *Geospiza difficilis* in relation to *G. fuliginosa* in the Galapagos Islands: Tests of three hypotheses. *Evolution* 36:1213-1226.
- Schoneveld-Cox, C. M. S. M. Chambers, B. MacBryde, and L. Thomas (eds.). 1983. *Genetics and Conservation*. Menlo Park, Ca.: Benjamin-Cummings Publishing Co.
- Schmida, A., and M. V. Wilson. 1985. Biological determinants of species diversity. *Journal of Biogeography* 12:1-20.
- Schwaegerle, K. and B. A. Schaal. 1980. Genetic variability and founder effect in the pitcher plant, *Sarracenia purpurea* L. *Evolution* 39: 53-65.
- Shugart, H. H. 1984. A theory of forest dynamics: the ecological implications of forest succession models. New York: Springer-Verlag.
- Simpson, B. B. 1988. Biological diversity in the context of ecosystem structure and function. *Biology International* 17: 15-17.

- Slatkin, M. 1985. Rare alleles as indicators of gene flow. *Evolution* 33: 1210-1218.
- Solbrig, O. T. 1991. *Biodiversity. Scientific Issues and Collaborative Research Proposals*. Mab Digest 9, 77 pp. Paris: Unesco.
- Solbrig, O. T. and B. B. Simpson, 1974. Components of regulation of a population of dandelions in Michigan. *J. Ecol.* 62: 473-486.
- Sousa, W. P. 1979. Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. *Ecology* 60: 1225-1239.
- Southwood, T.R.E. 1978. *Ecological Methods: With particular reference to the study of insect populations*, 2nd Ed.. New York: Chapman and Hall. xxiv + 524 pp.
- Steele, J. H. 1991 - Marine functional diversity. *BioScience* 41: 470-474.
- Stevens, G. C. 1989. The latitudinal gradient in geographical range: how so many species coexist in the tropics. *American Naturalist* 133:240-256.
- Stork, N.E. and Brendell, M.J.D. (In press). Arthropod diversity studies in lowland rain forest of Seram: Indonesia. In: Edwards, I. and Proctor, J. (eds.). *The Natural History of Seram*.
- Stork, N.E. and Gaston, K.J. 1990. Counting species one by one. *New Scientist* 11: 43-47.
- Strong, D. R., Jr., D. Simberloff, L. G. Abele, and A. B. Thistle. 1984. *Ecological communities: Conceptual issues and the evidence*. Princeton University Press, Princeton, N. J.
- Templeton, A. R. 1989. The meaning of species and speciation: a genetic perspective. In *Speciation and its Consequences*, pp. 3-27. Sunderland, Mass.: Sinauer Associates.
- Templeton, A. R., S. K. Davis, et al. 1987. Genetic variability in a captive herd of Speke's gazelle (*Gazella spekei*). *Zoo Biol.* 6: 305-313.
- Templeton, A. R., K. Shaw, et al. 1990. The genetic consequences of habitat fragmentation. *Ann. Mo. Bot. Garden* 77: 13-27.
- Terborgh, J. 1989. Where have all the birds gone?: essays on the biology and conservation of birds that migrate to the American tropics. Princeton: Princeton University Press.
- Thomas, C.D. 1990. Fewer species. *Nature* (Lond.), 347: 237.
- Tilman, D. 1982. *Resource Competition and Community Structure*. Princeton: Princeton University Press.
- Ugland, K.I. and Gray, J.S. 1982. Lognormal distributions and the concept of community equilibrium. *Oikos* 39: 171-178.
- Whittmore, A. T. and B. A. Schaal, 1991. Interspecific gene flow in sympatric oaks. *Proc. Nat. Acad. Sci., USA* 88: 2540-2544.
- Wilson, E. O. and F. M. Peter (Eds.). 1988. *Biodiversity*. Washington, D.C.: National Academy of Sciences Press.